The Distributions of Parasitoids (Hymenoptera) of *Anastrepha* Fruit Flies (Diptera: Tephritidae) along an Altitudinal Gradient in Veracruz, Mexico

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In the state of Veracruz, Mexico, fruits from 38 sites at various altitudes were collected monthly over a period of 2 years, and the tephritid fruit flies of the genus *Anastrepha* and associated parasitoids that emerged from these fruits were identified and counted. Of the 26 species of fruits that contained *Anastrepha* larvae, 18 species also contained a total of 10 species of *Anastrepha* parasitoids. These consisted of 4 native and 1 exotic species of opiine braconid larval–pupal parasitoids, 2 native species of eucoilid larval–pupal parasitoids, 1 exotic species of eulophid larval–pupal parasitoid, 1 exotic species of pteromalid pupal parasitoid, and 1 native species of diapriid pupal parasitoid. Overall parasitism (including flies from fruit species that bore no parasitoids) was 6% and was greatest, 16%, at 600–800 m in altitude. The relative contributions of individual parasitoid species to overall parasitism were frequently influenced by both the altitude (and correlated changes in temperature and precipitation) and the species of plant in which the *Anastrepha* larvae were found. This was particularly the case among the more abundant and widespread Braconidae. To distinguish the role of altitude from that of the distributions of the host plants, these braconids were examined in 4 individual species of fruit that grew over a broad range of altitudes. In guava (*Psidium guajava* L.) and "jobo" (*Spondias mombin* L.) the parasitoid *Doryctobracon areolatus* (Szepligeti) was relatively more common at low altitudes. Its congener, *Doryctobracon crawfordi* (Viereck), was relatively more abundant at high altitudes in sour orange (*Citrus aurantium* L.). *Utetes anastrephae* (Viereck) became relatively more common at higher altitudes in *S. mombin,* whereas *Diachasmimorpha longicaudata* (Ashmead) tended to become relatively rare at the highest altitudes in *C. aurantium,* but increased at high altitudes in *P. guajava* compared to other braconids. Different altitudinal patterns of abundance in different fruits suggests the importance of both biotic and abiotic factors in parasitoid distributions. We discuss the effect of an expanding agricultural frontier on parasitoid abundance and relate our findings to the design of a fruit fly biological control program that tailors mass releases to parasitoid climate preferences.

Key Words: biogeography; biological control; Braconidae; Diapriidae; Eucoilidae; Eulophidae; Pteromalidae.

INTRODUCTION

The distributions of insect parasitoids are affected by biotic and abiotic factors. These include temperature and humidity, abundance of hosts, and presence of competitors. Among parasitoids of the tephritid fruit flies, it is believed that low winter temperatures limit the distribution of the braconid *Fopius arisanus* (Sonan) in Australia (Snowball and Lukins, 1964). In Latin America, another braconid, *Doryctobracon crawfordi* (Viereck), is more sensitive to high temperatures than its host, *Anastrepha ludens* (Loew) (Darby, 1933; Darby and Knapp, 1934), and thus does not occur throughout the range of the fruit fly host species.

Moreover, there may be complex interactions among abiotic factors, hosts, and competitors that influence parasitoid distributions. Biogeographical studies of Braconidae introduced into Florida to attack the Caribbean fruit fly, *Anastrepha suspensa* (Loew), have revealed largely disjunct distributions of the two most abundant species, *Doryctobracon areolatus* (Szepligeti) and *Diachasmimorpha longicaudata* (Ashmead) (Eitam, 1998). Both species were originally common in the southern portion of the peninsula, but now only *D. longicaudata* occurs in the southern third of the state, whereas *D. areolatus* is the sole species present in the region north of Lake Okeechobee. There is only a relatively narrow band to the west and south of the lake where they coexist. These latitudinal differences in
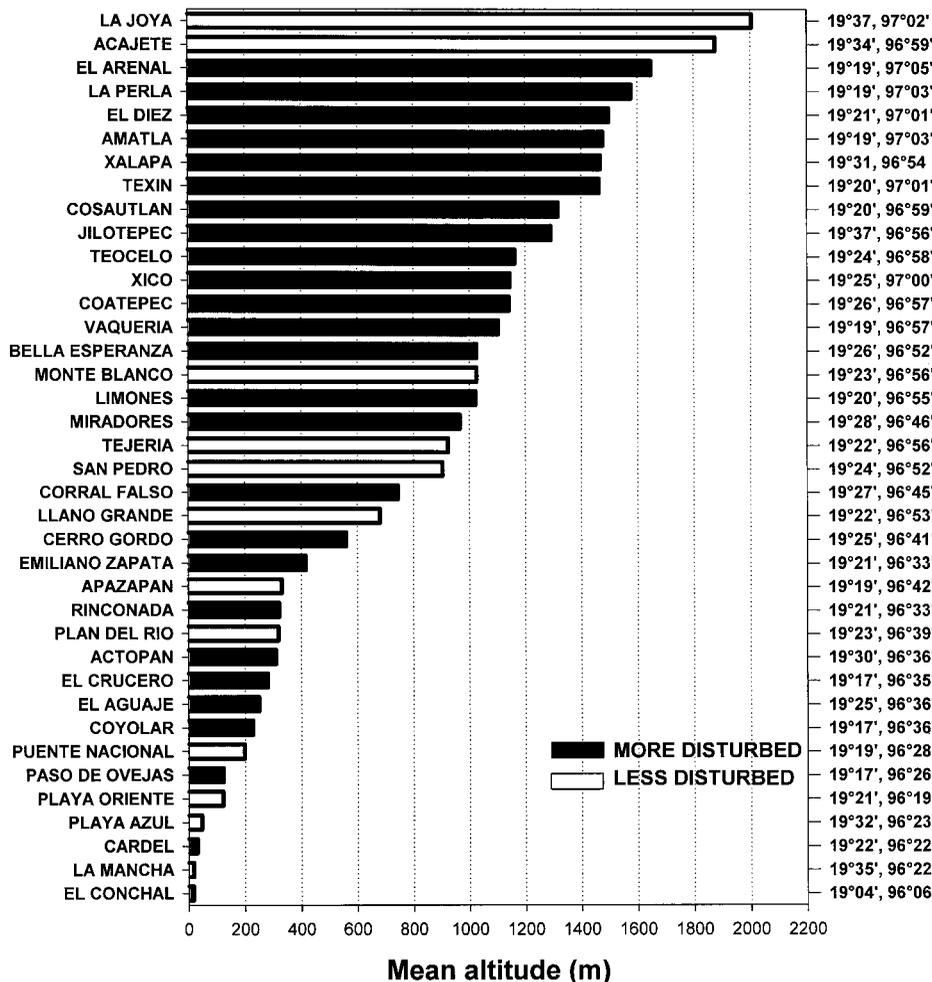
FIG. 1. The altitudes of sample sites in southern Veracruz, Mexico. Latitude and longitude are located to the right of the bar representing each site, and the color of the bar represents the nature of the habitat at the site.

distribution are thought to be due to the interaction of temperature and fruit fly host plant continuity.

The following survey was carried out in the state of Veracruz, Mexico to determine the distributions of the hymenopterous parasitoids of the tephritid genus *Anastrepha* along an altitudinal gradient. Since a number of biotic and abiotic environmental factors, such as temperature and precipitation, vary predictably with altitude, this information may suggest whether these factors influence the ranges and abundances of the various species and may guide future research. Ultimately, such knowledge might be useful to biological control programs that seek to introduce or augmentatively release native *Anastrepha* parasitoids into favorable habitats and to those that wish to import additional parasitoids into Mexico to fill niches that may not be occupied by native species.

The *Anastrepha*–parasitoid guild of Veracruz has recently been described in detail by Lopez *et al.* (1999). Ten species were recovered in samples in the present survey.

Doryctobracon areolatus, an opiine braconid, is a specialized, solitary, koinobiont endoparasitoid of *Anastrepha* larvae, which are attacked inside host fruits. As in other opiines, development is completed in the host pupa and the adult emerges from the host puparium. It is a widespread species that occurs from Mexico to Argentina (Wharton and Marsh, 1978; Yépes and Vélez, 1989; Katiyar *et al.,* 1995) and has been established in Florida (as *Parachasma cereus;* Baranowski *et al.,* 1993). Throughout its range it is often the dominant member of *Anastrepha*–parasitoid guilds and is particularly common in native, as opposed to introduced commercial, fruits (López *et al.,* 1999 and citations therein). It readily enters diapause as a 3rd instar larva, principally during the dry season (Aluja *et al.,* 1998).

Doryctobracon crawfordi is another widespread opiine braconid specializing in *Anastrepha* larvae. However, it has a longer ovipositor than *D. areolatus* (Sivinski *et al.,* 1997) and is more likely to be recovered from large, commercially grown fruits, such as citrus

TABLE 1

The Species of Fruits Sampled, the Families to Which They Belong, and Their Local Common Names

Species	Family common name	Altitude (m)															
		0		200		400		600		800		1000		1200		1400		1600	
		kg	No.	kg	No.	kg	No.	kg	No.	kg	No.	kg	No.	kg	No.	kg	No.	kg	No.
Calocarpum mammosum	Sapotaceae "mamey"									12.2	4	111.6	10	7.0	1				
Casimiroa edulis	Rutaceae "zapote blanco"											9.0	4	4.4	3				
Chrysophylium mexicanum	Sapotaceae "zapote niño"			3.2	2							10.2	3						
Citrus aurantium	Rutaceae "naranja cucha"	96.0	28	154.1	49	91.5	25	7.2	2	106.7	22	172.4	29	2.2	2	18.3	6	18.7	12
Citrus maxima	Rutaceae "pomelo"			59.1	14	14.4	6												
Citrus paradisi	Rutaceae "toronja"	29.8	5			27.7	3			50.1	9	3.9	2			63.2	9		
Citrus sinensis	Rutaceae "naranja dulce"	13.6	6	1.6	1			27.5	8	34.1	10	154.6	27	28.7	12			2.0	2
Inga jinicuil	Leguminoseae "jinicuil"											1.2	1						
Inga spuria	Leguminoseae "chalahuite peludo"							0.1	1	0.2	1	0.3	1						
Mangifera indica	Anacardiaceae "mango"	87.3	17	121.8	25	18.5	4	29.7	8	4.4	2	10.9	3						
Manikara zapote	Sapotaceae "chicozapote"			87.8	21	9.4	3												
Passiflora edulis	Passifloraceae "granada amarilla"											0.6	2						
Passiflora foetida	Passifloraceae "granada roja"											0.5	3						
Pouteria hypoglauca	Sapotaceae "zapote calentura"	16.1	5																
Prunus persica	Rosaceae "durazno"											1.3	2			5.0	3		
Psidium guajava	Myrtaceae "guayaba"	68.5	22	56.4	25	16.2	7	10.2	5	2.9	12	79.0	29	38.0	9	45.3	14	1.8	1
Psidium guineense	Myrtaceae "guayaba acida"									8.3	3								
Psidium sartorianum	Myrtaceae "guayaba tejon"	1.5	2					0.7	1	5.9	2								
Spondias sp.	Anacardiaceae "cundoria"	15.5	3							8.0	4	2.6	3						
Spondias mombin	Anacardiaceae "jobo"	22.1	11	3.9	2	1.7	1	13.9	3	12.0	7	4.4	2						
Spondias purpuria	Anacardiaceae "ciruela"	41.5	17	56.0	17	8.7	9	0.4	1	2.4	2	15.4	4						
Spondias radkolferi	Anacardiaceae "jobo cimarron"									5.8	4	0.5	2						
Syzygium jambos	Myrtaceae "pomarrosa"									1.3	1	18.4	17	0.5	1	0.1	1		
Taperia mexicana	Anacardiaceae "cacao silvestre"											1.7	5						
Terminalia catappa	Combretaceae "almendro"	3.9	4	4.2	5														
Ximenia americana	Olacaceae "ciruela acida"			2.6	4			2.0	2										

Note. Under each altitude category are listed the number of samples obtained and their summed weights.

and mango (Crawford, 1927; López *et al.,* 1999). As noted earlier, it appears to be sensitive to high temperatures and low humidities, and while rarely seen in the field during the dry season, it does not enter diapause in the manner of *D. areolatus* (Aluja *et al.,* 1998; see, however, Darby and Knapp, 1934).

Utetes anastrephae (Viereck) is still another native opiine which occurs naturally from Florida to Argentina. *U. anastrephae* has the shortest ovipositor of any of the braconids sampled and is typically recovered from a narrow range of the smaller host fruits (e.g., Sivinski *et al.,* 1997). Individual 3rd instar larvae may enter a dry season diapause (Aluja *et al.,* 1998).

Opius hirtus (Fischer) is an opiine with a relatively short ovipositor, and one that is apparently more specialized than other members of the Veracruz guild. Most Mexican specimens have been reared from *Anastrepha cordata* Aldrich; although it has been recovered from *Anastrepha alveata* Stone (López *et al.,* 1999) and even from the papaya fruit fly *Toxotrypana curvicauda* Gerstaecker (Wharton, 1983).

Diachasmimorpha longicaudata is an exotic opiine, originally from the Malaysia–Philippine region, where it attacks species of the tephritid genus *Bactrocera* (Clausen, 1978). It has proved easy to rear on several pest fruit flies and has been widely disseminated. In Veracruz it is a common parasitoid, particularly in exotic commercial fruits (López *et al.,* 1999). Like *D. areolatus,* individuals may enter a dry season diapause (Aluja *et al.,* 1998).

Aganaspis pellenaroi (Brethes) and *Odontosema anastrephae* Borgmeier are eucoilid parasitoids of larvae, which reach their hosts by entering wounds in fruit. The species differ in host preferences. *A. pellenaroi* is associated with various fruits, while *O. anastrephae* is most commonly found attacking larvae in guavas (*Psidium* spp.) (Wharton *et al.,* 1998). Individual 3rd instar larvae of both species may enter diapause (Aluja *et al.,* 1998).

Aceratoneuromyia indica (Silvestri) is a gregarious eulophid parasitoid of late instar larvae that was originally collected in India and has since been widely disseminated (Silvestri, 1914; Clausen, 1978). Like the previously mentioned eucoilids, *A. indica* enters fruits through breaks in their skins and pushes through the pulp searching for hosts (see a graphic account in Silvestri, 1914). It does not exhibit diapause (Aluja *et al.,* 1998).

Coptera haywardi (Ogloblin) is a diapriid endoparasitoid of fruit fly pupae (Sivinski *et al.,* 1998). It is apparently specialized on species of Tephritidae, although it develops in the laboratory on a wide range of genera within the family. It does not enter diapause (Aluja *et al.,* 1998).

Pachycrepoideus vindemiae (Rondani) is a pteromalid pupal parasitoid of Diptera with a broad host range (Krombein *et al.,* 1979) and a nearly cosmopolitan dis-
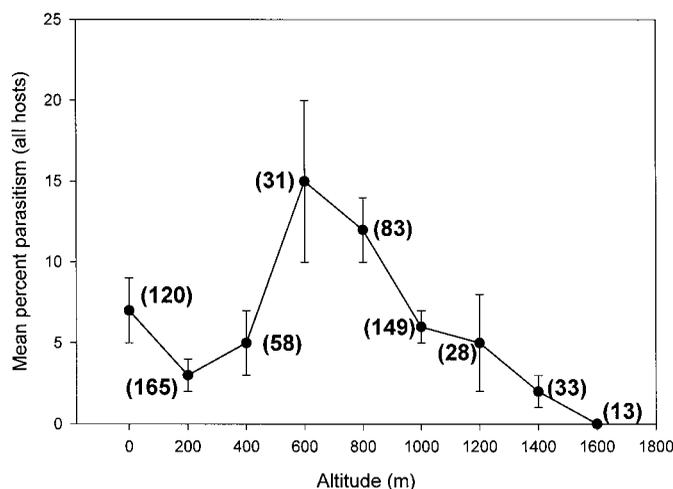

FIG. 2. Means and standard errors of parasitism (summed parasitoids/summed parasitoids + *Anastrepha* spp. adults) in all species of fruits from sample sites at various altitudes in southern Veracruz, Mexico. Numbers in parentheses represent numbers of samples taken at a particular altitude.

tribution (Clausen, 1978). It does not exhibit diapause (Aluja *et al.,* 1998).

METHODS

Fruits were systematically searched for and collected monthly in 38 sites in central Veracruz, Mexico during a period of 2 years. The sites and their latitudes, longitudes, and altitudes are presented in Fig. 1. Sites were subjectively characterized as either more or less disturbed by agricultural activity (Fig. 1). For example, a coffee plantation containing fruiting shade trees was deemed "more disturbed," whereas dispersed fruit orchards surrounded by native vegetation were characterized as "less disturbed." Only one site, Acajete, consisted solely of native vegetation. However, it and La Joya, the highest site, were excluded from analysis since no *Anastrepha* were recovered from either. To minimize variance, sites at similar altitudes were considered together, and all sites were characterized as occurring in one of the following categories: 0–199, 200–399, 400–599, 600–799, 800–999, 1000–1199, 1200–1399, or 1400–1599 m. These categories are referred to in the text as 0, 200, 400, 600, 800, 1000, 1200, and 1400 m, respectively.

Twenty-six species of fruits were found to contain *Anastrepha* larvae. These are listed in Table 1, along with the altitudes at which they occurred, the numbers of samples obtained at each altitude, and the summed weight of the samples taken at each altitude. These data reflect the range of the fruit species along the gradient, i.e., fruits were always sampled where they occurred and not just at certain altitudes.

Mature fruits were picked from trees or vines or were taken from the ground beneath host plants. Fruits from a particular time and place were weighed and

TABLE 2

The *Anastrepha* Species and Species of Parasitoids Obtained from the Various Fruit Species Sampled

Plant species	No. of parasitoids	Parasitoid species	Anastrepha species
Psidium guajava	8	*D. areolatus*	*A. striata*
		D. crawfordi	*A. fraterculus*
		D. longicaudata	
		A. pelleranoi	
		O. anastrephae	
		A. indica	
		C. haywardi	
		P. vindemiae	
Psidium guineense	7	*D. areolatus*	*A. striata*
		D. crawfordi	*A. fraterculus*
		D. longicaudata	
		U. anastrephae	
		A. pelleranoi	
		O. anastrephae	
		A. indica	
Psidium sartorianum	5	*D. areolatus*	*A. striata*
		D. crawfordi	*A. fraterculus*
		D. longicaudata	
		U. anastrephae	
		A. pelleranoi	
Calocarpum mammosum	5	*D. areolatus*	*A. serpentina*
		D. longicaudata	
		A. pelleranoi	
		A. indica	
		P. vindemiae	
Syzygium jambo	4	*D. areolatus*	*A. fraterculus*
		D. crawfordi	
		D. longicaudata	
		U. anastrephae	
Cundoria sp.	4	*D. areolatus*	*A. obliqua*
		D. longicaudata	
		U. anastrephae	
		A. indica	
Citrus sinensis	5	*D. areolatus*	*A. ludens*
		D. crawfordi	
		D. longicaudata	
		A. indica	
		P. vindemiae	
Citrus paradisi	3	*D. crawfordi*	*A. ludens*
		D. longicaudata	
		A. indica	
Citrus aurantium	4	*D. areolautus*	*A. ludens*
		D. crawfordi	
		D. longicaudata	
		A. indica	
Citrus maxima	1	**P. vindemiae**	*A. ludens*
Citrus reticulata	0	—	*A. ludens*
Spondias mombin	3	*D. areolatus*	*A. obliqua*
		D. longicaudata	
		U. anastrephae	
Spondias purpurea	6	*D. areolatus*	*A. obliqua*
		D. longicaudata	
		U. anastrephae	
		A. indica	
		C. haywardi	
		P. vindemiae	
Spondias radkolferi	3	*D. areolatus*	*A. obliqua*
		D. longicaudata	
		U. anastrephae	
Mangifera indica	3	*D. areolatus*	*A. obliqua*
		D. longicaudata	
		P. vindemiae	

TABLE 2—*Continued*

Plant species	No. of parasitoids	Parasitoid species	Anastrepha species
Manilkara zapota	5	*D. areolatus* *D. crawfordi* *U. anastrephae* **A. indica** **P. vindemiae**	*A. serpentina*
Casimiroa edulis	4	**D. longicaudata** *A. pelleranoi* **A. indica** **P. vindemiae**	*A. serpentina*
Ximenia americana	3	*D. areolatus* *U. anastrephae* *O. hirtus*	*A. alveata*
Prunus persica	2	*D. crawfordi* **D. longicaudata**	*A. fraterculus* *A. ludens*
Tapirira mexicana	1	**D. longicaudata**	*A. obliqua*
Terminalia cattapa	0	—	*A. fraterculus*
Inga jinicuil	0	—	*A. distincta*
Inga spuria	0	—	*A. distincta*
Inga vera	0	—	*A. distincta*
Passiflora edulis	0	—	*A. chiclayae*
Passiflora foetida	0	—	*A. chiclayae*
Pouteria hypoglauca	0	—	*A. aphelocentema*
Chrysophyllum mexicanum	0	—	*A. hamata*

Note. Exotic fruits and parasitoids are printed in boldface lettering.

placed together in 500-ml plastic containers that contained a pupation medium either of vermiculite or of a combination of sand and soil. To provide ventilation, holes were cut in the middle of the container lids and then covered with organdy cloth. All fruits were transported to the laboratory at the Instituto de Ecología, Xalapa, Veracruz, where they were held under cover at ambient temperature and humidity. Every 2nd day, fruit containers were inspected to ascertain whether the pupation medium required moistening or whether the fruit had rotted. If the fruit had disintegrated or was covered with mold, it was dissected and any larvae or pupae were removed. The pupation medium was also shifted every 2nd day and the number of puparia recorded. Pupae were kept in their pupation medium until they died or adults emerged. Since a number of parasitoid species enter diapause, unemerged pupae that were not clearly dead were held for a period of 12 months.

Parasitoids were identified through comparisons with specimens previously identified by Robert Wharton (Texas A and M University, College Station, TX) and Lubomir Masner (Canadian Bureau of Land Resources, Ontario, Canada). Flies were identified by Vicente Hernández-Ortíz of the Instituto de Ecología, A. C. (Xalapa, Veracruz, Mexico). Voucher specimens

TABLE 3

The Relationships of Parasitism by Individual Species (Parasitoid a/Summed Parasitoids + *Anastrepha*) to the Variables Altitude, Host Plant, and Habitat and to Their Various Interactions as Determined by Multiple Regression

Species	Altitude			Host plant			Habitat			Altitude × host			Altitude × habitat			Host × habitat		
	df	F	P	df	F	P	df	F	P	df	F	P	df	F	P	df	F	P
D. areolatus	1	6.3	**<0.01**	25	19.7	**<0.0001**	1	0.4	0.52	17	9.2	**<0.0001**	1	0.2	0.69	13	0.6	0.88
D. crawfordi	1	10.2	**<0.002**	25	3.8	**<0.0001**	1	0.1	0.73	17	1.7	**<0.04**	1	0.2	0.69	13	0.1	0.99
D. longicaudata	1	0.1	0.99	25	1.5	0.06	1	2.1	0.15	17	0.5	0.94	1	5.3	**<0.02**	13	0.6	0.86
U. anastrephae	1	0.01	0.94	25	13.7	**<0.0001**	1	4.4	**<0.04**	17	6.9	**<0.0001**	1	0.1	0.74	13	3.4	**<0.0001**
A. pelleranoi	1	1.1	0.06	25	1.1	0.32	1	0.4	0.52	17	0.4	0.98	1	0.2	0.68	13	0.1	0.99
O. anastrephae	1	2.1	0.14	25	0.6	0.94	1	6.5	**<0.01**	17	0.6	0.90	1	10.7	**<0.001**	13	3.5	**<0.0001**
A. indica	1	5.4	**<0.02**	25	0.33	0.99	1	0.1	0.83	17	0.65	0.85	1	0.4	0.55	13	0.4	0.97
P. vindemiae	1	1.3	0.25	25	1.9	**<0.006**	1	0.1	0.99	17	1.3	0.21	1	0.2	0.63	13	0.1	0.99
C. haywardi	1	2.7	0.10	25	0.5	0.99	1	0.1	0.77	17	0.3	0.99	1	0.1	0.76	13	0.8	0.69

Note. Listed under each variable are the degrees of freedom (df), the *F* value, and the probability value. Statistically significant values are in boldface lettering.
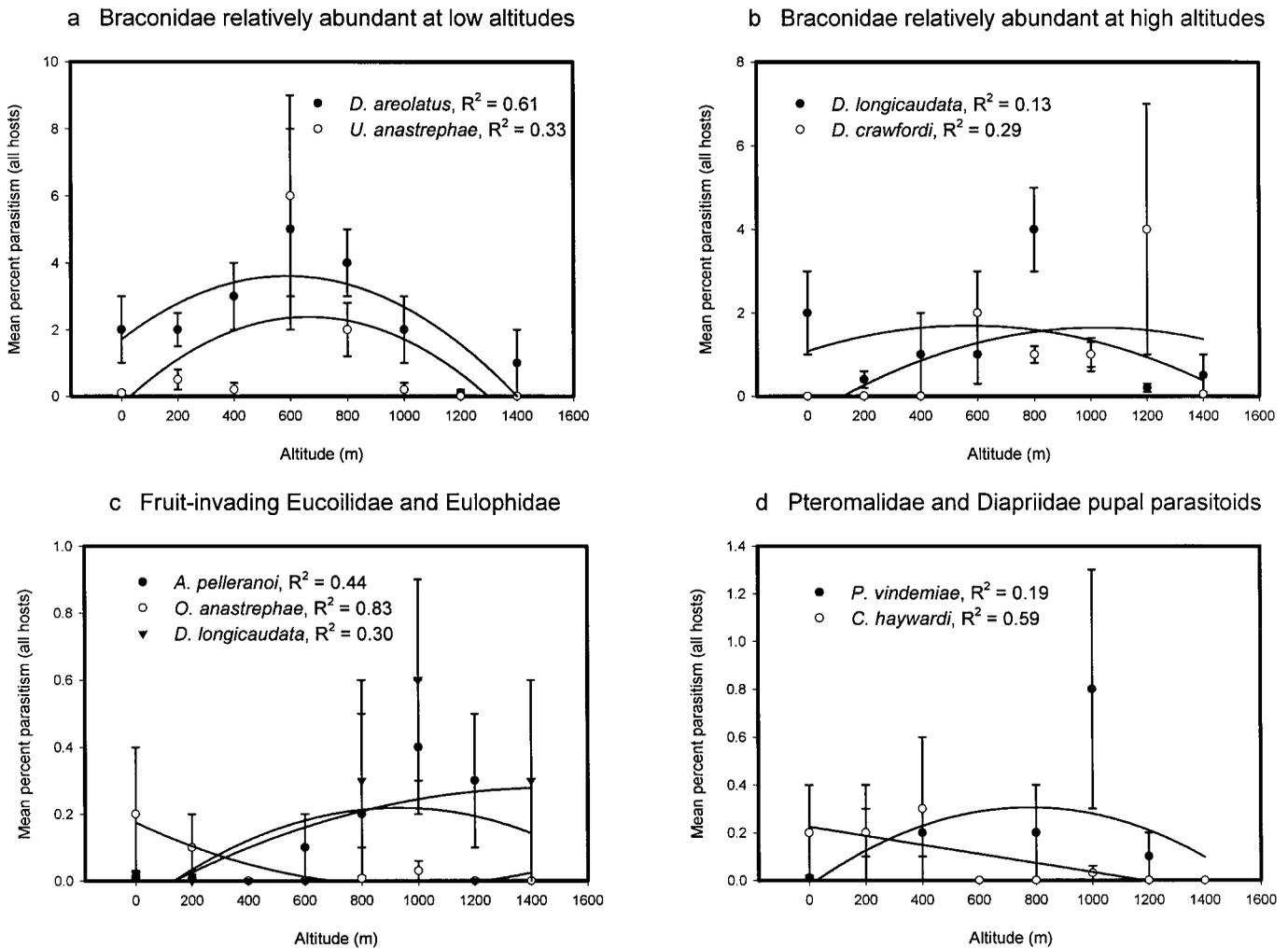
a   Braconidae relatively abundant at low altitudes

b   Braconidae relatively abundant at high altitudes

c   Fruit-invading Eucoilidae and Eulophidae

d   Pteromalidae and Diapriidae pupal parasitoids

FIG. 3.   Means and standard errors of parasitism by individual species of parasitoids at various altitudes.

were placed in the permanent collection of the Instituto de Ecologia only in those cases in which a particular species had not been previously preserved.

Parasitism was calculated as the number of parasitoids divided by the summed number of parasitoids and host flies emerging from a particular sample. An exception was parasitism due to the gregarious eulophid *A. indica;* in this instance, the number of parasitized pupae was divided by the summed number of parasitized pupae and host flies.

Data were analyzed through regressions and multiple regressions performed by the General Linear Models Procedure of the statistical analysis system SAS (SAS Institute, 1989). After consultation with Victor Chew (Department of Statistics, University of Florida, Gainesville, FL), error values were chosen from Type I "sum of squares." Dependent variables examined were percentage parasitism by particular species (absolute abundance) and the proportion of parasitism due to particular species (relative abundance). The latter was included because, regardless of the level of naturally occurring parasitism under a particular set

of circumstances, the designers of an augmentative biological control program would wish to know which of the available parasitoids performs the best. Independent variables consisted of altitude, host plant, and the degree of anthropogenic disturbance. Significant interactions between host plants and altitude on the distribution of parasitoids led to examinations of the effects of altitude on parasitoids within certain individual plant species. This eliminated, in these particular cases, the host plant variable and so made the effect of altitude more apparent.

RESULTS

It is assumed that changes in insect abundance along an altitudinal gradient are not the result of differences in altitude *per se,* but are due to changes in environmental factors predictably affected by altitude. In the region where the present study took place, mean annual temperatures and mean annual precipitations had been previously obtained for 12 sites that occurred at altitudes ranging from 35 to >1400 m (Aluja *et al.,*

TABLE 4

The Relationships of Relative Parasitism by Individual Species (Parasitoid a/Summed Parasitoids) to the Variables Altitude, Host Plant, and Habitat and to Their Various Interactions as Determined by Multiple Regression

Species	Altitude			Host plant			Habitat			Altitude × host			Altitude × habitat			Host × habitat		
	df	*F*	*P*	*df*	*F*	*P*	*df*	*F*	*P*	*df*	*F*	*P*	*df*	*F*	*P*	*df*	*F*	*P*
D. areolatus	1	86.2	**<0.000 1**	19	9.4	**<0.000 1**	1	3.0	0.08	15	2.6	**<0.001**	1	0.0	0.85	10	1.2	0.29
D. crawfordi	1	69.9	**<0.000 1**	19	10.9	**<0.000 1**	1	1.2	0.27	15	2.9	**<0.000 4**	1	1.4	0.24	10	1.7	0.09
D. longicaudata	1	4.7	**<0.03**	19	3.6	**<0.000 1**	1	2.6	0.11	15	1.9	**<0.03**	1	1.6	0.21	10	1.2	0.32
U. anastrephae	1	1.0	0.33	19	9.3	**<0.000 1**	1	1.0	0.32	15	6.4	**<0.000 1**	1	0.0	0.99	10	1.4	0.18
A. pelleranoi	1	4.3	**<0.04**	19	3.3	**<0.000 1**	1	0.0	0.97	15	0.1	0.93	1	0.1	0.83	10	0.0	0.99
O. anastrephae	1	3.1	0.08	19	1.0	0.46	1	5.5	**0.02**	15	0.7	0.79	1	6.5	**<0.0 1**	10	2.2	**<0.0 2**
A. indica	1	4.0	**<0.05**	19	1.0	0.44	1	0.3	0.59	15	1.8	**<0.05**	1	1.2	0.29	10	1.4	0.18
P. vindemiae	1	1.3	0.25	19	6.8	**<0.000 1**	1	0.0	0.98	15	1.8	**<0.05**	1	0.6	0.44	10	1.8	0.06
C. haywardi	1	4.0	**<0.05**	19	0.6	0.94	1	0.6	0.48	15	0.4	0.98	1	0.1	0.77	10	1.1	0.34

Note. Listed under each variable are the degrees of freedom (*df*), the *F* value, and the probability value. Statistically significant values are in boldface lettering.

1998). These environmental factors could potentially effect parasitoid distributions, and they were significantly correlated to altitude (r[temperature] $= -0.88$, $P < 0.0003$; r[precipitation] $= 0.73$, $P < 0.007$); i.e., as might be expected, with greater altitude mean temperature decreased and rainfall increased.

A total of 698 samples of the various fruits from the different collecting sites yielded 78,876 *Anastrepha* spp. pupae. Of these, 629 samples contained parasitoids. The mean overall parasitism was 6% (SE = 0.6), with the highest parasitism occurring at 600–800 m (Fig. 2). Various host fruits supported different parasitoid guilds (Table 2), with the greatest diversity found in the native *Psidium, Spondias,* and *Manilkara* spp. and in the exotic *Citrus* spp. Of the 28 species of fruit that contained *Anastrepha* larvae, 8 did not yield parasitoids. The braconid *O. hirtus* was recovered in small numbers from only 2 samples (one from *A. obliqua* in *Spondias mombin* and another from *A. alveata* in *Ximenia americana*) and was not included in subsequent analyses. The presence of the pupal parasitoids *P. vindemiae* and *C. haywardi* in the samples was unexpected because *Anastrepha* typically pupate in the soil, and only fruits were taken from the field. There are several possible explanations for this occurrence, ranging from parasitoids infiltrating the sample-holding facility at the Instituto de Ecología to their emergence from the relatively uncommon pupae that remain within the host fruits. Because of this ambiguity, these two species were excluded from the calculation of total parasitism, but their individual altitudinal distributions were determined.

Altitude was a significant factor affecting the proportion of larvae parasitized by *D. areolatus* (greatest at low altitudes), *D. crawfordi* (greatest at high altitudes), and the eulophid *A. indica* (greatest at high altitudes) (Table 3; Fig. 3). However, larval host plants contributed more often to the distribution of parasitism than did altitude. Disturbance of the habitat by agricultural activities was a significant factor in the distributions of two parasitoids (Table 3).

The relative contributions of the various parasitoids to parasitism were influenced often, but not invariably, by altitude (Table 4). For example, the relative contribution of *D. areolatus* became less with increasing altitude (Fig. 4a), whereas its congener *D. crawfordi* was relatively more common at higher altitudes (Fig. 4b). At the same time the species of host fruit had a substantial effect on proportion of parasitism by the various parasitoid species, and there were several highly significant interactions between altitude and host fruit, i.e., the relationships of parasitism with altitude were different in different host fruits (Table 4). Whether the habitat had been greatly disturbed by agriculture was important only in the relative abundance of the rare eucoilid *O. anastrephae*.

To minimize the effect of different host fruits on parasitism and isolate the effects of altitude, the relative contributions of the four common braconid species to overall parasitism were individually examined in four species of host fruits that occurred at a large number of altitudes (Table 5; Fig. 5). The Braconidae are particularly interesting because they
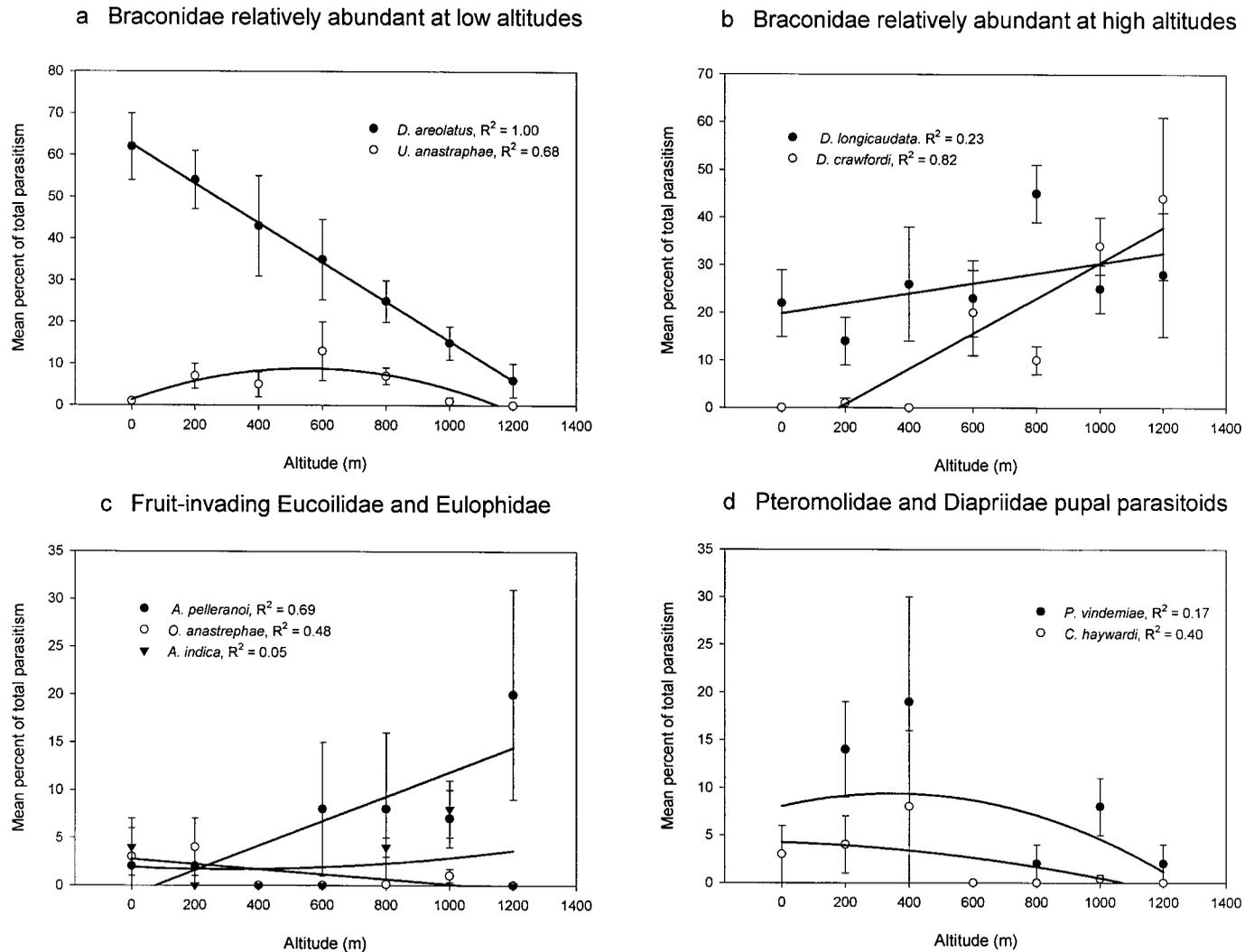
a   Braconidae relatively abundant at low altitudes

b   Braconidae relatively abundant at high altitudes

c   Fruit-invading Eucoilidae and Eulophidae

d   Pteromolidae and Diapriidae pupal parasitoids

FIG. 4. Means and standard errors of relative parasitism by individual parasitoid species at various altitudes. Relative parasitism refers to the contribution of an individual species to overall parasitism, i.e. (parasitoid sp. a/summed parasitoids).

were responsible for most of the parasitism and displayed suggestive altitudinal patterns in their contributions to overall parasitism (Fig. 4). Parasitism only by *D. areolatus* was consistently influenced by altitude regardless of host plant. Parasitism by *D.* *crawfordi* was related to altitude in only one of the three hosts in which it was found, and in *D. longicaudata* in two of its four hosts. Parasitism by *U. anastrephae* was significantly related to altitude in one of its two hosts.

TABLE 5

The Relationships of Relative Parasitism by Individual Braconid Species (Braconid a/Summed Braconidae)
to Altitude in Four Species of Host Fruits as Determined by Regression

	D. areolatus			*D. crawfordi*			*D. longicaudata*			*U. anastrephae*		
	df	F	P	df	F	P	df	F	P	df	F	P
C. aurantium				22	7.7	**<0.004**	22	12.0	**<0.004**			
C. sinensis				30	2.8	0.12	30	3.8	0.10			
P. guajava	39	5.6	**<0.05**	39	0.5	0.56	39	3.6	0.17	39	0.5	0.45
S. mombin	24	20.0	**<0.0001**				24	4.4	**<0.05**	24	12.9	**<0.0002**

Note. Listed in each instance are the degrees of freedom (*df*), the *F* value, and the probability value (in boldface lettering when significant).
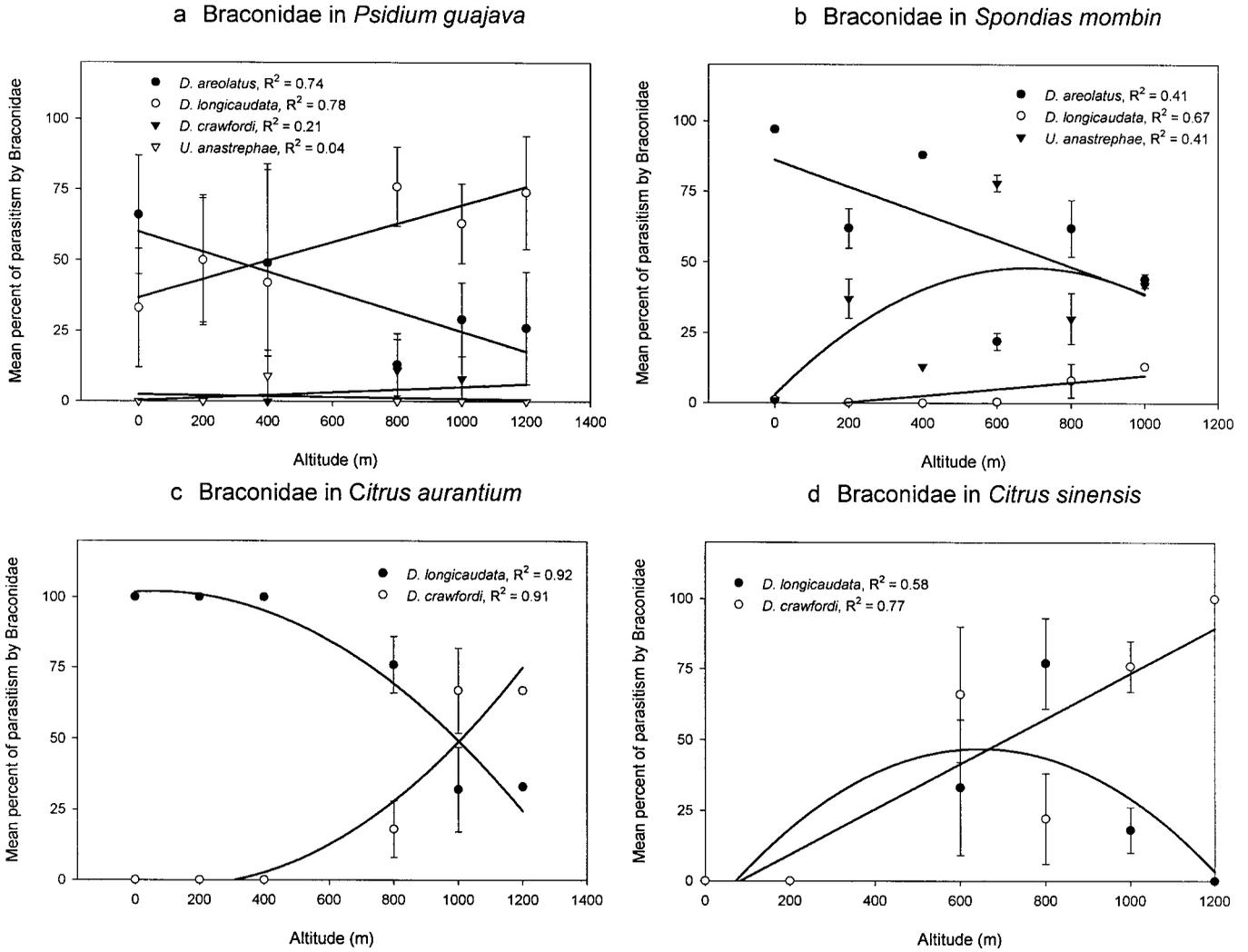
FIG. 5. Means and standard errors of relative parasitism by individual braconid species at various altitudes and in particular species of fruit.

DISCUSSION

Altitude influences the relative abundances of a number of tephritid parasitoids, but the relationships are generally not simple and are related to the species of fruit in which the host fly larvae develop. Relationships between host plant and parasitism have been previously determined or suspected. A simple example is the well-documented negative correlation between fruit size and braconid parasitism, presumably because host larvae in larger fruit are able to feed at greater depths and are more difficult for parasitoids to reach with their ovipositors (e.g., Sivinski *et al.,* 1997). Although all parasitoids become less effective in increasingly larger fruits, the decline is steeper in some parasitoid species (e.g., *U. anastrephae* with its short ovipositor) than in others (e.g., *D. longicaudata* with its very long ovipositor). As a result, a parasitoid such as *U. anastrephae* will be numerous only in habitats that

contain small-fruit hosts, regardless of the altitudes at which the fruits occur.

U. anastrephae is an example of how complicating factors, such as host plants, obscure altitudinal relationships. There was no altitudinal component to its relative contribution to overall parasitism. Yet, when host plants were considered individually, there was a highly significant altitudinal relationship in the host plant *S. mombin,* a small fruit in which *U. anastrephae* was particularly abundant.

With the host plant caveat aside, there are some patterns of altitudinal relative abundance that may help explain how the species of the Veracruz *Anastrepha*–parasitoid guild coexist through partitioning their shared resource. For example, the two species of *Doryctobracon* are both capable of attacking late instar larvae, but competition may be minimized by *D. crawfordi's* preference for cooler, high-altitude environments and by *D. areolatus'* adaptations, including a

pronounced propensity to enter dry season diapause, to relatively warm, low-altitude habitats (see Aluja *et al.,* 1998).

However, simple differences in temperature tolerance are unlikely to be the sole determinants of parasitoid distributions. As noted earlier, both *D. areolatus* and *D. longicaudata* were introduced into south Florida for the biological control of *A. suspensa.* After ~25 years, only *D. longicaudata* is now found in the southern portion of the fly's range where the original introductions of both occurred, whereas only *D. areolatus* occurs in the northern portion (Eitam, 1998). Thus, in Florida and in the presence of fellow opiines *D. longicaudata* and *U. anastrephae, D. areolatus* has come to predominate at higher latitudes, whereas in Mexico and in the presence of *D. crawfordi, U. anastrephae,* and the exotic *D. longicaudata,* it is most abundant at lower altitudes. Because higher altitudes and latitudes would be expected to share certain abiotic characteristics, such as lower average and minimum temperatures, the opposing Mexican and Floridian abundance patterns suggest the importance of biotic factors, including competitors, in parasitoid distributions. In this instance, the Mexican altitudinal distribution of *D. areolatus* predicts that had it alone been introduced into Florida, it might have been even more common in the southern portion of *A. suspensa's* range than it is now in the northern portion.

As altitudinal and other data on host preferences and the regional, temporal, and microhabitat distributions of fruit flies and their natural enemies accumulate, potential strategies for tephritid biological control emerge (see Sivinski *et al.,* 1997; Aluja *et al.,* 1998; Lopez *et al.,* 1999). While parasitism can be substantial, sometimes over 90%, such high mortalities often do not occur at the appropriate times and places to suppress the growth of pest populations. Management of native and established parasitoids, through either augmentation or conservation, may be able to concentrate parasitism where and when it will exert the most control (e.g., Wong *et al.,* 1992). One such target location is the native vegetation in the vicinity of orchards. Fruit fly reservoirs in native vegetation threaten nearby agriculture, and flies in smaller native fruits appear to be particularly vulnerable to parasitism. Thus, augmentative releases and/or conservation efforts directed at fly populations before their spread into crops may be both more effective and timely than treating the crops themselves (e.g., Sivinski *et al.,* 1996).

Altitude and other components of the environment should influence the choice of parasitoids to be mass-released. For example, the native *D. crawfordi* and the exotic *D. longicaudata* have similarly long ovipositors and similar spatial distributions within tree canopies and they may commonly compete for larvae in the same host fruits (Sivinski *et al.,* 1997). Both are candidates for mass-rearing and augmentative releases against pest *Anastrepha* (M.A., pers. commun.). In sour

orange (*Citrus aurantium*), an important reservoir of *A. ludens,* the Mexican fruit fly or orange worm, altitude influences the relative abundances of the two species, with *D. crawfordi* more common at higher altitudes and *D. longicaudata* most abundant at low. *D. longicaudata* (and the native *D. areolatus* as well) would be suited to low, dry environments with a diversity of pest species and host trees, while *D. crawfordi* would forage better in moist, occasionally cool habitats that might contain feral trees of cultivated citrus fruits.

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