

Spatial and Temporal Distributions of Parasitoids of Mexican *Anastrepha* Species (Diptera: Tephritidae) within the Canopies of Fruit Trees

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ABSTRACT In Veracruz State, Mexico, the temporal and spatial distributions of 5 species of parasitic Hymenoptera attacking larvae of 5 *Anastrepha* species in 7 species of fruit tree canopies were examined. Parasitism by *Doryctobracon areolatus* (Szepligeti) (Braconidae), *Diachasmimorpha longicaudata* (Ashmead) (Braconidae), and *Utetes anastrephae* (Viereck) (Braconidae) was higher in 3 of 4 significant cases in the lower portions of the canopies. *U. anastrephae* was more abundant in the interior of canopies (2 cases), whereas *D. areolatus* was more common in the margins (1 case). In 6 of 7 instances the mean sizes of fruits containing parasitoids were smaller than those of infested fruits without parasitoids. *U. anastrephae* attacked larvae in a narrow range of smaller host-fruit species relative to other parasitoids. The efficiency (proportion of larvae attacked in a fruit) of *D. longicaudata* compared to that of other parasitoids increased with fruit size. *D. longicaudata* may be better able to locate or attack hosts in larger fruits. In all of 17 instances there were on average more host larvae in fruits containing parasitoids than in fruits without parasitoids. In all of 18 significant instances the larval density (larvae per gram weight of fruit) was higher in fruits that contained parasitoids than in fruits that did not. Parasitism by *D. areolatus*, *Doryctobracon crawfordi* (Viereck), *D. longicaudata*, and *U. anastrephae* often changed over time during the fruiting period, but was as likely to decrease as increase. *D. areolatus* had a pattern of decreasing parasitism during the fruiting periods of individual trees as the season changed from rainy to dry. There were only a few instances of significant relationships between parasitism and local differences in the canopy with respect to fruit numbers, host numbers, and host density. In 2 instances there were significant negative relationships between parasitism caused by the commonly cooccurring *D. areolatus* and *U. anastrephae*. In 2 other cases, parasitism by *D. crawfordi* and *D. longicaudata* was positively correlated. *D. longicaudata* is a recent introduction to Mexico and the positive relationships may indicate a niche overlap not present between the 2 native species, *D. areolatus* and *U. anastrephae*. Fewer than expected numbers of fruits containing both *D. areolatus* and *U. anastrephae* together was further evidence of niche differences. This pattern did not occur in fruits containing *D. crawfordi* and *D. longicaudata*. Information on the distribution of parasitoids at levels ranging from within canopies to across regions may guide biological control efforts, allowing the match of candidate species to locations.

KEY WORDS *Diachasmimorpha*, *Doryctobracon*, *Utetes*, *Aganaspis*, microhabitat, foraging ecology

TROPICAL AND SUBTROPICAL tephritid fruit flies, such as *Anastrepha* spp., attack scores of species of fruits and vegetables (Norrbon and Kim 1988). Because of quarantines, they are major barriers to agricultural exports and economic development (Aluja 1994). These flies confront an array of natural enemies over their lifetimes (Sivinski 1996). Relatively little is known of the dangers that face the adults and eggs of *Anastrepha* species. In southern Mexico, ants, rove beetles, and chickens consume large numbers of larvae, exposed as they seek pupation sites, and the shallowly buried pupae (Crawford 1927). Within fruits, larvae are embedded in both food and shelter. However, braconid, chal-

cidoid, and cynipoid parasitoids have overcome the obstacles of rind and pulp to attack developing tephritids.

Mexico has a native guild of fruit fly parasitoids (Aluja et al. 1990, Hernandez-Ortiz et al. 1994). In addition, there have been repeated attempts to import exotic Hymenoptera into tropical and subtropical America to control both the introduced Mediterranean fruit fly, *Ceratitidis capitata* (Wiedemann), and economically important species of native *Anastrepha* (e.g., Wharton et al. 1981, Wharton 1989, Aluja 1994). Only the opiine braconid *Diachasmimorpha longicaudata* (Ashmead) has become widely established. This parasitoid was recovered originally from *Bactrocera* (= *Dacus*) species in Malaysia and other Indo-Pacific countries (Clausen

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Table 1. *Anastrepha* species collected in various fruits in the study sites

<i>Anastrepha</i> spp.	<i>P. guajava</i>	<i>S. mombin</i>	<i>S. purpurea</i>	<i>M. indica</i>	<i>C. sinensis</i>	<i>T. mexicana</i>	<i>X. americana</i>
<i>A. alveata</i>	—	—	—	—	—	—	X
<i>A. fraterculus</i>	X	—	—	—	—	—	—
<i>A. ludens</i>	—	—	—	X	X	—	—
<i>A. obliqua</i>	—	X	X	X	—	X	—
<i>A. striata</i>	X	—	—	—	—	—	—

1978). Released in Hawaii, *D. longicaudata* attacked Mediterranean fruit fly and the oriental fruit fly, *Bactrocera dorsalis* (Hendel). Although it eventually was overshadowed in Hawaii by related species, it proved easy to rear on many pest tephritids and was widely distributed (Clausen 1978). In Costa Rica, *D. longicaudata* is the most common parasitoid of *C. capitata* (Salas 1958, Guitierrez 1976, Wharton et al. 1981, Fischel 1989, Jiron and Mexon 1989). It is also the leading parasitoid of *Anastrepha* spp in Chiapas, Mexico (Aluja et al. 1990). *D. longicaudata* is a solitary, endoparasitic koinobiont that locates fruit trees through volatiles produced by ripe and decaying fruits (Greany et al. 1977, Messing and Jang 1992), and late instar fly larvae within fruits by the vibrations produced as maggots feed and move (Lawrence 1981). Generally, eggs hatch before host pupation, with the molt to 2nd instar occurring inside the puparium. Development is completed within the puparium of the fly (Lawrence 1982, Ibrahim et al. 1994).

Native parasitoids in the Mexican fauna are far less well known. *Doryctobracon areolatus* (Szepligeti), another opiine, has a life history similar to that of *D. longicaudata*. It is a larval-pupal parasitoid and females oviposit in late instars. *D. areolatus* ranges from Mexico to Argentina (Wharton and Marsh 1978, Yepes and Velez 1989, Katiyar et al. 1995). It appears to be a specialized parasitoid of *Anastrepha* spp. (Clausen et al. 1965) and has been introduced into Florida [as *Parachasma cereus* (Szepligeti)] to combat the Caribbean fruit fly, *Anastrepha suspensa* (Loew) (Baranowski and Swanson 1970, 1971). *D. areolatus* has been recovered from pupae of *A. ludens* infesting yellow chapote, *Sargentia greggii* Watts, an important native host plant and reservoir for pest populations that afflict commercial fruit (Gonzales-Hernandez and Tejada 1979; see also the native host plants described in Piedra et al. 1993 and Hernandez-Ortiz et al. 1994). In one of the few published accounts of its behavior, Aluja and Birke (1993) noted that ovipositing female *D. areolatus* were most abundant in fruit trees in the early morning and late afternoon, and that this periodicity paralleled that of the *Anastrepha obliqua* (Macquart) females whose larvae they were attacking. Brief notes have been published on the behavior, rearing, and collection of *D. areolatus* in Brazil (Cacador 1976, 1977; Saia and da Silva 1978).

Doryctobracon crawfordi (Viereck) has been collected from Mexico through northern South Amer-

ica. Like *D. areolatus*, it seems to be restricted to *Anastrepha* spp. hosts (Wharton and Gilstrap 1983). In Mexico it is a common parasitoid of *A. ludens*, a major agricultural pest of citrus and mangos (e.g., Crawford 1927) and, like *D. areolatus*, has been recovered from yellow chapote (Plummer and McPhail 1941, Gonzales-Hernandez and Tejada 1979). *D. crawfordi* appears to be sensitive to extreme heat and fails to develop at temperatures tolerated by its hosts (Darby 1933, Darby and Knapp 1934). It also appears to be limited by low humidities, is rarely seen in the field during the dry season, and in some locations will go into an estivation that may be broken by increasing moisture levels (Darby and Knapp 1934).

Utetes (= *Brachanastrepha*) *anastrephae* (Viereck) is yet another broadly distributed, but seldom studied, opiine braconid. It is a solitary larval-pupal parasitoid that ranges from Florida, where it is relatively uncommon, to Argentina (Wharton and Gilstrap 1983, Hernandez-Ortiz et al. 1994).

The eucoilid *Aganaspis* (= *Ganaspis*) *pelleranoi* (Brethes) seeks out tephritid larvae by entering previously existing holes in fruits such as coffee, guava, and orange (Ovruski 1994). In addition to parasitizing *Anastrepha* spp. (Aluja et al. 1990), it has been reared from Mediterranean fruit fly in Costa Rica (Wharton et al. 1981).

The environment of these parasitoids is complex. Their host flies are often polyphagous, developing in fruit trees that are widely separated and bear asynchronously. The foliage of a tree is divided into various microhabitats characterized by differences in temperature, light, humidity, height, distance from the canopy edge, local host numbers, competitors and fruit abundance, and morphology, all of which are subject to changes over time.

These characteristics affect, or are suspected to affect, the foraging of other parasitic Hymenoptera (see Godfray 1994). For example, the red scale, *Aonidiella aurantii* (Maskell), is much more vulnerable to attack by aphelinid parasitoids when feeding on the periphery of citrus trees than in their interior (Murdoch et al. 1989). The opiine braconid *Psytalia* (= *Opius*) *concolor* (Szepligeti) appears to parasitize a greater proportion of its tephritid hosts in the upper half of large Greek olive trees (Kapatos et al. 1977). Darby (1933) suggested that *D. crawfordi* is more apt to attack *Anastrepha* larvae in mangos than in sweet limes because the relatively open foliage of the latter provides less refuge from heat and low humidities.

Table 2. Parasitoids attacking the various *Anastrepha* species in the study sites

<i>Anastrepha</i> spp	Da	Dc	Dl	Ua	Ap
<i>A. alveata</i>	X	—	—	—	—
<i>A. fraterculus</i>	X	X	X	—	X
<i>A. ludens</i>	X	X	X	—	X
<i>A. obliqua</i>	X	X	X	X	—
<i>A. striata</i>	X	X	X	—	X

Da, *Doryctobracon areolatus*; Dc, *D. crawfordi*; Dl, *Diachasmimorpha longicaudata*; Ua, *Utetes anastrephae*; Ap, *Aganaspis pelleranoi*.

In this article, we address the relationships of these various spatial and temporal factors to parasitism of *Anastrepha* species in Veracruz State, Mexico. Within-tree *Anastrepha* spp. distribution in the same field sites considered here is examined elsewhere (M.A., unpublished data).

Materials and Methods

Parasitoid Specimens. The occurrence of various *Anastrepha* species with the various fruit and parasitoid species is summarized in Tables 1 and 2. For more details see Lopez et al. (unpublished data). Parasitoids were identified with the aid of Robert Wharton, Texas A&M University. Voucher specimens are in the collections of J.S. and M.A., and are in the permanent collections of the Instituto de Ecología, A. C., Xalapa, Veracruz, Mexico.

Study Sites and Trees. All sites were in central Veracruz State, Mexico, and collections were made during 1993 and 1994. The trees sampled included 2 *Spondias purpurea* L. (tropical plum), referred to as Sp93 and Sp94; 3 *Spondias mombin* L., referred to as Sm93, Sm94a and Sm94b; 1 *Ximenia americana* L., referred to as Xa93; 2 *Mangifera indica* L. (mango) referred to as Mi93 and Mi94; 1 *Tapirira mexicana* Marchand, referred to as Tm93; 3 *Psidium guajava* L. (guava), referred to as Pg93a, Pg93b and Pg94; 4 *Citrus sinensis* Osbeck (orange), referred to as Cs93a, Cs93b, Cs94a, and Cs94b. Pg93a, Pg93b, Pg94 and Tm93 were near the village of Tejeria, at 19 22' N latitude, 96 56' W longitude and an altitude of 1,000 m. The climate is characterized as semiwarm and humid (Garcia 1973), with a mean annual temperature of 19°C and a mean annual rainfall of 1,750 mm. Sm93, Sm94a, Sm94b, Mi93, Mi94, Cs93a, Cs93b, and Xa93 were in the vicinity of the village of Llano Grande, at 19 22' N latitude and 96 53' W longitude and an elevation of 950 m. The climate is characterized as semiwarm and humid with a mean annual temperature of 19°C and a mean annual rainfall of 2,250 mm. Sp93 and Sp94 were near the village of Apazapan, located at 19 19' N latitude and 96 21' W longitude and an elevation of 347 m. The climate is characterized as intermediate warm-sub-humid with a mean annual temperature of 25°C and a mean annual rainfall of 1,250 mm. Cs94a and Cs94b were in the vicinity of the village of Monte Blanco, located at 19 23' N latitude and 96 56' W

longitude and an altitude of 1,000 m. The climate is characterized as semiwarm and humid with a mean annual temperature of 19°C and a mean annual rainfall of 1,750 mm.

Fruit and Insect Collection. All fruits were collected when their time upon the branch was judged complete. This was accomplished by gently shaking the branch near the fruit. If the fruit fell it was assumed to have been nearly ready to drop of its own accord. When a fruit is picked, the larvae within it are no longer vulnerable to parasitism. Thus, it is critical that the fruit and its occupants be exposed for the typical period in situ to determine the activity of parasitoids in the tree canopy. Fruits were assigned a location by means of a grid system, typically based on 5 equal divisions of the 2 horizontal axes and 3 equal divisions of height. The resulting 3-dimensional quadrants differed in size among trees. Another estimate of location was whether the fruit grew on the edge of the tree canopy (<5 cm from the end of a branch) or in its interior (>5 cm from the tip of the branch).

After collection, fruits were placed on sand in plastic containers with screened lids. These were held at ambient temperatures and humidities at the Instituto de Ecología, Xalapa, Veracruz. Mexican populations of *D. longicaudata*, *D. areolatus*, *U. anastrephae*, and *A. pelleranoi* commonly estivated. To obtain accurate estimates of parasitism, pupae were examined for emergence 1 mo after collection, and then weekly for 1 yr. All fruits from the study trees, over the entire fruiting periods, were collected daily. The only exceptions were those that fell of their own accord or were removed by animals.

Data Analysis. Statistical tests were performed with the use of SAS (SAS Institute 1994). The 7 forms of analyses are as follows: (1) height (analysis of variance [ANOVA] of the 3 divisions of the canopy followed by comparison of means using the Waller-Duncan *k* ratio *t*-test); (2) parasitism on the margins of the canopies (<5 cm from branch tips) relative to their interiors (>5 cm, *t*-test); (3) the mean weights, numbers of hosts and mean host densities (pupae per gram of weight) of fruits containing parasitoids, and infested fruits without a particular parasitoid (*t*-tests); (4) changes in parasitism in the entire tree over time (multiple stepwise regression of time and the quadratic of time); (5) comparison of parasitism in areas of the trees with various fruit densities, host numbers, and host densities (i.e., these characteristics as they occurred daily in the quadrants defined by the grid and the height divisions) (multiple stepwise regression of fruit density, host number, and host density); (6) the spatial relationships of 2 parasitoids in a single tree (pairs of Kolmogorov-Smirnov tests determined whether the 2-dimensional [length and width of the sample grid] distributions differed [i.e., the shapes of the distributions were compared twice, once along the axis of length, and once along the axis of width]); (7) the effects of

continuous variables and their interaction factors on parasitism (multiple stepwise regression of fruit weight, pupae per fruit, pupae per gram of fruit, time, time * time, fruit weight * time, fruit weight [time * time], pupae per fruit * time, pupae per fruit [time * time], pupae per gram of fruit * time, pupae per gram of fruit [time * time], fruit weight * number of pupae per fruit); the species distribution of parasitoids within fruits (chi-square test). When appropriate, data were arcsine transformed.

Not all trees or species of parasitoids within a tree were included in every analysis. For example, a certain tree might have few fruits in the interior of its canopy, and a comparison between parasitism on the margin and in the interior was not possible. Temporal data were organized generally and analyzed on a daily basis (i.e., comparisons of the means, sums, and variances of the fruits and insects collected on different days). Parasitism in oranges was treated on a weekly basis because of the relatively small numbers of fruits ripening over a longer period.

Results

Because of the large number and variety of data we begin with an overview to help orient the reader. Parasitism was compared at various heights within canopies (Tables 3 and 4) and at the margins and interiors of the canopies (Table 5). Infested fruits that did and did not contain parasitoids are compared on the basis of characteristics that could influence their value as foraging sites to parasitoids (i.e., size [as estimated by weight; Table 6; Figs. 1-3], the number of hosts present [Table 7], and the density of hosts [pupae per gram of weight; Table 8]). The effect of time during fruiting period on percent of parasitism was examined (Table 9), as were patterns of seasonal change (Fig. 4). Characteristics that could vary locally within a canopy were then considered for their influence on parasitism (i.e., the numbers of fruits, the numbers of hosts, and the mean density of hosts [pupae per gram] in subsets of the canopy [Table 10]). Finally, we address the influence of competition between parasitoid species on their distribution (Tables 11 and 12; Fig. 5). Findings are summarized in Tables 13 and 14. Details follow.

Height. There was little indication that parasitoids are more likely to forage in any of the 3 different vertical regions of the canopy (Table 4). In the 5 trees with *U. anastrephae*, 2 had significantly higher parasitism in one level or another, but this greater abundance was in the top of a canopy in one instance and the bottom in the other (although the actual height was similar in both instances; Sm93 and Sm94b). *D. areolatus* was relatively more abundant in the lower level of Cs93a as was *D. longicaudata* in Pg94. In 3 of the 4 significant cases, parasitism was higher at the bottom of the canopy.

Canopy Margin Versus Interior. Only 7 trees had sufficient infested fruits in both regions to compare (>10 fruits in the interior; Table 5). Of these, 3 had different percentages of parasitism. *D. areolatus* was relatively more abundant on the margin of G93a and *U. anastrephae* was more common in the interiors of Sm93 and Sm94b.

Fruit Size (Weight). There were 7 instances of significant differences between infested fruits with and without parasitoids (Table 6). In the 6 cases of braconid parasitism, the mean weights of fruits with parasitoids were smaller. However, this was not true of *A. pelleranoi* in G93a. *A. pelleranoi* enters wounds in fruits to search for hosts within the pulp, and may not be as affected in its foraging by fruit size as the braconid species, which remain on fruit surfaces and reach hosts with their ovipositors (see Sivinski 1991).

In general, larger fruits have lower percentages of parasitism (Fig. 1). This appears to be a result of the protection larvae receive by being sheltered under greater amounts of pulp and rind. There was no significant effect of the ease of locating larvae within fruits (as estimated by larval density) on the values for parasitism in Fig. 1. Because large fruits could contain more larvae, a negative relationship between parasitism and size could also result from these larger cohorts being beyond the capacity of a parasitoid to exploit. The result of this "swamping" effect could be lower parasitism in larger fruits. In a somewhat similar situation, Chua (1993) found a negative correlation between parasitism of *Bactrocera* spp. by the opiine *Biosteres vandenboschi* (Fullaway) and the number of larvae in mangos. He interpreted this as an effect of female parasitoids dispersing their progeny (i.e., "not putting all their eggs in one basket"). However, the relationship between the parasitism values in Fig. 1 and the mean numbers of larvae in the fruits is insignificant, suggesting that it is not parasitoid swamping that accounts for the correlation between fruit size and percentage of parasitism.

The difficulties to parasitoids posed by large fruit size could account for the consistently greater presence of parasitoids in the smaller of the infested fruits within any particular tree. Size could also determine the species of fruits that various parasitoids forage upon. *U. anastrephae*, which has a short ovipositor, was found only in a narrow range of smaller fruits (Fig. 2). *D. longicaudata* appeared to become relatively more efficient than other cooccurring parasitoids as the size of fruits increased (Fig. 3). That is, the proportion of larvae parasitized by *D. longicaudata* became progressively greater in larger fruits than did the proportions parasitized by other species. This suggests that it is better able to locate or reach, or both, deep-feeding larvae.

Number of Larvae in Fruits. The number of hosts in a fruit could influence the likelihood of larvae being discovered by a parasitoid or of at least one larvae being reached and attacked. There were

Table 3. Mean \pm SE parasitism by various species of parasitoids at various height levels in the study trees

Height	<i>P. guajana</i> 93a	<i>P. guajana</i> 93b	<i>P. guajana</i> 94	<i>S. mombin</i> 93	<i>S. mombin</i> 94a	<i>S. mombin</i> 94b	<i>M. indica</i> 93	<i>M. indica</i> 94
100	—	—	—	—	—	—	—	—
200	—	—	—	—	—	—	—	—
300	DI a0.14 \pm 0.3 82	—	DI a0.03 \pm 0.03 44	—	—	—	—	—
	De a0.05 \pm 0.01 82	—	Ap a0.01 \pm 0.01 44	—	—	—	—	—
	Da a0.02 \pm 0.005 82	—	—	—	—	—	—	—
400	Ap a0.01 \pm 0.006 82	—	—	—	—	—	—	DI a0.01 \pm 0.01 19
	DI a0.12 \pm 0.02 228	DI a0.008 \pm 0.004 334	DI a0.04 \pm 0.01 165	—	—	—	—	—
	De a0.04 \pm 0.007 228	De a0.001 \pm 0.004 334	De a0.002 \pm 0.002 165	—	—	—	—	—
	Da a0.03 \pm 0.007 228	Da a0.009 \pm 0.007 165	Da a0.009 \pm 0.007 165	—	—	—	—	—
500	Ap a0.01 \pm 0.005 228	—	Ap a0.01 \pm 0.007 165	—	—	—	—	—
	DI a0.12 \pm 0.03 121	DI a0.02 \pm 0.005 421	DI b0.003 \pm 0.002 392	—	—	Da a0.16 \pm 0.08 13	—	—
	De a0.05 \pm 0.01 121	De a0.006 \pm 0.003 421	De a0.009 \pm 0.009 392	—	—	Ua a0.69 \pm 0.10 13	—	—
	Da a0.05 \pm 0.01 121	—	Da a0.006 \pm 0.0006 392	—	—	—	—	—
600	Ap a0.02 \pm 0.01 121	—	—	—	—	Da a0.36 \pm 0.05 67	—	DI a0.05 \pm 0.04 13
	—	—	—	—	—	Ua ab0.47 \pm 0.05 67	—	—
700	—	—	—	—	—	—	Da a0.003 \pm 0.003 39	—
800	—	—	—	DI a0.007 \pm 0.0007 201	—	Da a0.40 \pm 0.01 864	—	DI a0.05 \pm 0.02 17
	—	—	—	Da a0.68 \pm 0.03 201	—	Ua b0.43 \pm 0.02 864	—	Ap a0.002 \pm 0.002 17
	—	—	—	Ua b0.06 \pm 0.02 201	—	—	—	—
900	—	—	—	—	Da a0.40 \pm 0.12 13	—	—	—
	—	—	—	—	Ua a0.50 \pm 0.12 13	—	—	—
1,000	—	—	—	Da a0.63 \pm 0.02 571	—	—	—	—
1,100	—	—	—	Ua a0.12 \pm 0.1 571	—	—	—	—
1,200	—	—	—	—	Da a0.37 \pm 0.03 227	—	—	—
	—	—	—	—	Ua a0.38 \pm 0.03 227	—	—	—

Actual median height of a level falls within 1 of the 100-cm broad ranges. The number of infested fruits sampled follows mean \pm SE. Means that share a letter prefix are not significantly different. (Data analyzed by ANOVA and means separated by Waller-Duncan *k* ratio *t*-test.) See Table 2 for abbreviations of parasitoids.

Table 4. Mean \pm SE parasitism by various species of parasitoids at various height levels in the study trees

Height	<i>C. sinensis</i> 93a	<i>C. sinensis</i> 93b	<i>C. sinensis</i> 94a	<i>C. sinensis</i> 94b	<i>S. purpurea</i> 93	<i>S. purpurea</i> 94	<i>T. mexicana</i> 94	<i>X. americana</i> 93
100	—	—	—	—	—	—	—	—
200	Da a0.14 \pm 0.09 16 Dc a0.06 \pm 0.02 16 Dl a0.07 \pm 0.04 16	Dc a0.03 \pm 0.03 6	Dl a0.10 \pm 0.04 43 Dc a0.25 \pm 0.05 43 Da a0.02 \pm 0.009 43 Ap a0.001 \pm 0.001 43	Dc a0.50 \pm 0.5 2	—	Da a0.41 \pm 0.06 68	—	Da a0.33 \pm 0.33 3
300	Da b0.01 \pm 0.005 43 Dc a0.07 \pm 0.02 43 Dl a0.09 \pm 0.03 43	Dc a0.01 \pm 0.01 37 Dl a0.003 \pm 0.003 37	Dl a0.06 \pm 0.01 127 Dc a0.28 \pm 0.03 127 Da a0.008 \pm 0.003 127 Ap a0.003 \pm 0.003 127	Dl a0.04 \pm 0.04 14 Dc a0.06 \pm 0.03 14	Da a0.009 \pm 0.004 390 Ua a0.001 \pm 0.005 390	Da a0.35 \pm 0.04 162	—	Da a0.30 \pm 0.15 10
400	Da b0.04 \pm 0.02 62 Dc a0.08 \pm 0.02 62 Dl a0.11 \pm 0.02 62 Ap a0.006 \pm 0.004 62	Dc a0.002 \pm 0.002 59 Dl a0.002 \pm 0.002 59	Dl a0.05 \pm 0.02 79 Dc a0.24 \pm 0.03 79 Da a0.006 \pm 0.003 79 Ap a0.01 \pm 0.01 79	Dc a0.14 \pm 0.07 10	Da a0.02 \pm 0.01 183	Da a0.42 \pm 0.02 310 Ua a0.02 \pm 0.006 310	—	Da a10.0 \pm 0 2
500	—	—	—	—	—	—	Da a0.39 \pm 0.05 82 Dc a0.01 \pm 0.01 82 Dl a0.08 \pm 0.03 82 Ua a0.19 \pm 0.04 82	—
600	—	—	—	—	—	—	—	—
700	—	—	—	—	—	—	Da a0.26 \pm 0.08 28 Dc a0.04 \pm 0.04 28 Dl a0.05 \pm 0.04 28 Ua a0.30 \pm 0.09 28	—
800	—	—	—	—	—	—	—	—
900	—	—	—	—	—	—	Da a0.35 \pm 0.13 12 Dl a0.22 \pm 0.12 12 Ua a0.17 \pm 0.09 12	—
1,000	—	—	—	—	—	—	—	—
1,100	—	—	—	—	—	—	—	—
1,200	—	—	—	—	—	—	—	—

Actual median height of a level falls within 1 of the 100 cm broad ranges. The number of infested fruits sampled follows mean \pm SE. Means that share a letter prefix are not significantly different. (Data analyzed by ANOVA and means separated by Waller-Duncan k ratio t-test.) See Table 2 for abbreviations of parasitoids.

Table 5. Mean parasitism \pm SE on the margins (top numeric value) and interiors (bottom numeric values) of tree canopies

Parasitoid	<i>P. guajava</i> 93a	<i>P. guajava</i> 93b	<i>S. mombin</i> 93	<i>S. mombin</i> 94b	<i>C. sinensis</i> 93b	<i>T. mexicana</i> 93	<i>X. americana</i> 93
Da	0.33 \pm 0.11 0.007 \pm 0.03	—	NS	NS	—	NS	NS
Dc	NS	NS	—	—	NS	NS	—
Dl	NS	NS	NS	—	NS	NS	—
Ua	—	—	0.09 \pm 0.01 0.22 \pm 0.05	0.42 \pm 0.02 0.49 \pm 0.03	—	NS	—
Ap	NS	—	—	—	—	—	—

NS, nonsignificant comparisons. An empty block indicates no comparison was made, either because of the lack of fruit in one region or the absence of a particular parasitoid. Data analyzed by *t*-test. See Table 2 for abbreviations of parasitoids.

17 instances of fruits yielding parasitoids containing more larvae than infested fruits without parasitoids, 9 nonsignificant cases, and 0 of fruits without parasitoids containing more pupae (Table 7).

Larval Density (Pupae per Gram of Fruit). As above, larval density could effect the probability of a parasitoid locating and exploiting hosts. In addition, high density might force larvae closer to the surface, where they could be more vulnerable to parasitoids. Weevils and caterpillars feeding in hawthorns (*Crataegus* spp.) may thus force *Rhagoletis pomonella* (Walsh). Parasitism of the fly doubles when these other insects are also present in fruits (Feder 1995). There were 19 instances of fruits with parasitoids having higher mean larval densities than fruits without parasitoids, 8 nonsignificant cases, and 0 of fruits without parasitoids having larger mean densities (Table 8).

Time During the Fruiting Period. There were 15 instances of significant changes in mean parasitism over the fruiting periods (Table 9). Eight of these relationships were positive and 7 negative. Every parasitoid species and nearly every tree species was represented in these cases. There were 15 examples of no significant change over time.

Seasonal Changes. Changes in parasitism over time were common, but equally likely to be positive or negative. One explanation is that seasonal differences in the times of the various fruiting periods either favored or discouraged the growth of parasitoid populations. Wet and dry seasons are pronounced in the study areas (precipitation peaks in June–July; M.A., unpublished data). However, there is no general pattern in the direction of temporal change in parasitism during the year. There were a number of instances of significant temporal changes in parasitism by *D. areolatus* over the progression from wet to dry season (Fig. 4). As conditions became drier there was a tendency for parasitism by *D. areolatus* to decline over the fruiting periods of particular trees.

Environments in Different Parts of the Canopy (Microhabitats). Local differences in the density of fruits, the numbers of hosts, and the mean densities of hosts within fruits could influence the foraging of parasitoids. Presumably parasitoids would be able to locate hosts more easily when the values of these characteristics are relatively high and forag-

ing might be concentrated by the higher rate of contact with fruits or hosts (see discussion of parasitoid learning and foraging in Godfray [1994]). The variety of microhabitats within the canopy was sampled by subdividing the canopy into quadrants (typically, 3 levels of 25 cubes forming 75 quadrants) and obtaining average daily values of fruit number, host number, and host density within these quadrants. Relatively few significant relationships between parasitism and microhabitat characteristics were discovered (Table 10). This could be caused by the unimportance of the above factors or too coarse sampling (i.e., quadrants were so large that both favorable and unfavorable sites were likely to be included within them). Eight of the 10 significant relationships were positive, the predicted direction.

Competition Among Parasitoids. With multiple species of parasitoids in the same tree, (*D. areolatus*, *D. crawfordi*, and *D. longicaudata* were sometimes recovered from a single piece of guava fruit), there is the potential for competition to influence spatial and temporal distributions. For example, in the 3 *S. mombin* trees there were high levels of parasitism by both *D. areolatus* and *U. anastrephae*. In 2 of the trees, when daily mean parasitism by *D. areolatus* was low, that of *U. anastrephae* was high (Table 11). This could reflect a situation where conditions favorable to *U. anastrephae* were less so for *D. areolatus* and vice versa. However, of 4 relationships between *D. longicaudata* and *D. crawfordi*, 2 were insignificant and 2 significantly positive (Table 12). That is, conditions favoring one species appeared to favor the other as well. Recall that *D. longicaudata* is a recent introduction to the area. It and *D. crawfordi*, having no history of competition or opportunity to evolve separate niches, might have retained a substantial overlap in their environmental preferences. *D. areolatus* and *U. anastrephae* are both native to the area and presumably have had the opportunity to escape competition through diverging specializations.

Differences in ovipositor length, such as occur between *D. areolatus* and *U. anastrephae*, result from divergence to avoid competition in other parasitoid guilds (e.g., those attacking saw flies [Price 1972]). The shorter ovipositor of *U. anastrephae* might indicate a specialization for foraging

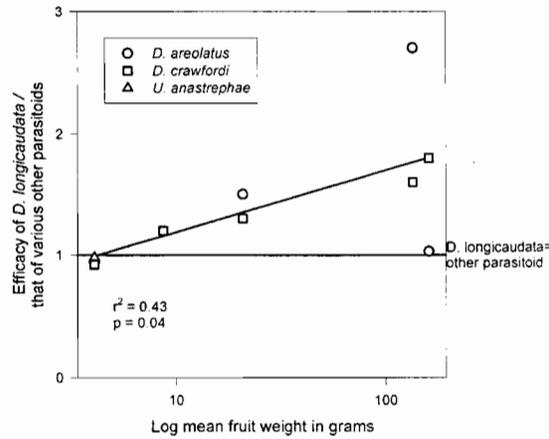


Fig. 3. The relationship between the ratio of parasitism by *D. longicaudata* relative to other species of parasitoids and the mean size of the fruits from which the parasitism values are derived. There is an alternative explanation for this relationship. If *D. longicaudata* was more abundant than other species in the canopies of the trees with larger fruits, then it would be more likely for there to be multiple *D. longicaudata* females visiting any particular fruit. This could result in greater proportions of larvae in these fruits being parasitized *D. longicaudata*. However, there is no significant relationship between the percent parasitism by *D. longicaudata* (an estimate of its abundance) and the mean proportion of larvae in fruits parasitized by *D. longicaudata* ($r = 0.31, P = 0.44$).

on smaller fruits, on which it may be better able to compete with *D. areolatus*. In Sm93 and Sm94b, fruits yielding only *U. anastrephae* were significantly smaller than those containing only *D. areolatus*. In all 3 *S. mombin* trees, *U. anastrephae* was found in fruits with significantly fewer larvae than *D. areolatus*. Perhaps *U. anastrephae* is particularly effective at foraging for hosts when they occur at low densities inside fruits.

Further support for the hypothesis that different species forage on different subsets of fruits within tree canopies, and that this divergence is the result of a history of competition, was found in the frequency of fruits in particular trees that yielded 2 species of parasitoids. In 4 of 5 samples from *S. mombin* trees there are fewer than randomly expected fruits containing both *D. areolatus* and *U. anastrephae* (Table 12). In 3 orange trees containing *D. crawfordi* and *D. longicaudata*, the only significant departure from a random distribution was an instance of there being more fruits containing both parasitoids than expected (Table 12). Again, the 2 native species, *D. areolatus* and *U. anastrephae*, displayed a possible divergence in niche.

Parasitoid species sometimes have significantly different overall spatial distributions within a tree canopy (Fig. 5). However, these differences provide no evidence for a history of competition and eventual niche divergence. Over entire fruiting periods *D. areolatus* and *U. anastrephae*, and *D. longicaudata* and *D. crawfordi*, had significant differ-

Table 7. Mean \pm SE numbers of fruits fly pupae collected from infested fruits with parasitoids (bottom value) and without (top value)

Parasitoid	<i>P. gajajava</i> 93a	<i>P. gajajava</i> 93b	<i>S. mombin</i> 93	<i>S. mombin</i> 94a	<i>S. mombin</i> 94b	<i>M. indica</i> 94	<i>C. sinensis</i> 93a	<i>C. sinensis</i> 94a	<i>S. purpurea</i> 93	<i>S. purpurea</i> 94	<i>T. mexicana</i> 93	<i>X. americana</i> 93
Da	7.3 \pm 0.28	—	3.0 \pm 0.14	3.1 \pm 0.16	1.8 \pm 0.05	—	NS	7.9 \pm 0.39	1.4 \pm 0.03	1.6 \pm 0.06	NS	NS
Dc	9.6 \pm 0.79	NS	3.7 \pm 0.08	3.9 \pm 0.20	2.4 \pm 0.07	—	10.2 \pm 0.87	10.7 \pm 1.6	2.6 \pm 0.50	2.1 \pm 0.07	—	—
Dl	7.3 \pm 0.29	NS	—	—	—	—	5.6 \pm 0.42	5.6 \pm 0.42	—	—	—	—
Ua	9.0 \pm 0.63	NS	—	—	—	14.4 \pm 1.6	14.8 \pm 1.4	9.5 \pm 0.52	—	—	NS	—
Ap	6.4 \pm 0.29	—	—	—	—	31.5 \pm 7.8	10.6 \pm 0.86	14.8 \pm 1.5	—	—	NS	—
	10.0 \pm 0.49	—	NS	2.7 \pm 0.17	1.6 \pm 0.05	—	—	—	—	1.8 \pm 0.05	NS	—
	—	—	—	4.1 \pm 0.17	2.4 \pm 0.07	—	—	—	—	2.9 \pm 0.35	—	—

NS, not significant, see Table 2 for abbreviations of parasitoids. Format of the table corresponds to that of Table 5. Data analyzed by t-test.

Table 8. Mean ± SE host densities (pupae per gram of weight) in infected fruits with parasitoids (bottom value) and without (top value)

Parasitoid	<i>P. guajava</i> 93a	<i>P. guajava</i> 93b	<i>P. guajava</i> 94	<i>S. mombin</i> 93	<i>S. mombin</i> 94a	<i>S. mombin</i> 94b	<i>M. indica</i> 94	<i>C. sinensis</i> 93a	<i>C. sinensis</i> 94a	<i>S. purpurea</i> 93	<i>S. purpurea</i> 94	<i>T. mexicana</i> 93	<i>X. americana</i> 93
Da	0.34 ± 0.01	—	—	0.77 ± 0.14	0.68 ± 0.03	0.23 ± 0.007	—	0.07 ± 0.005	0.06 ± 0.04	0.08 ± 0.05	0.11 ± 0.005	NS	NS
Dc	0.46 ± 0.04	—	—	0.93 ± 0.08	0.80 ± 0.04	0.30 ± 0.009	—	0.08 ± 0.01	0.08 ± 0.05	0.14 ± 0.08	0.16 ± 0.008	—	—
DI	0.34 ± 0.01	0.10 ± 0.002	—	—	—	—	—	0.06 ± 0.005	0.04 ± 0.03	—	—	—	—
Ua	0.41 ± 0.02	0.15 ± 0.02	—	—	—	—	NS	0.09 ± 0.009	0.07 ± 0.05	—	—	NS	—
Ap	0.29 ± 0.009	NS	0.14 ± 0.004	—	—	—	—	0.07 ± 0.005	—	—	—	NS	—
	0.46 ± 0.02	—	0.19 ± 0.02	NS	0.59 ± 0.03	0.21 ± 0.007	—	0.09 ± 0.01	—	—	0.13 ± 0.005	NS	—
	—	—	—	—	0.85 ± 0.03	0.31 ± 0.008	—	—	—	—	0.26 ± 0.03	—	—
	0.34 ± 0.01	—	—	—	—	—	—	—	—	—	—	—	—
	0.44 ± 0.02	—	—	—	—	—	—	—	—	—	—	—	—

NS, not significant. See Table 2 for abbreviations of parasitoids. Format of the table corresponds to that of Table 5. Data analyzed by *t*-test.

Table 9. Model *R*² values derived from the multiple regressions of parasitism against time and the quadratic value of time

Parasitoid	<i>P. guajava</i> 93a	<i>P. guajava</i> 93b	<i>P. guajava</i> 94	<i>S. mombin</i> 93	<i>S. mombin</i> 94a	<i>S. mombin</i> 94b	<i>M. indica</i> 94	<i>C. sinensis</i> 93a	<i>C. sinensis</i> 94a	<i>S. purpurea</i> 93	<i>S. purpurea</i> 94	<i>T. mexicana</i> 93	<i>X. americana</i> 93
Da	0.41 (+)	—	0.11 (-)	0.24 (+)	0.75 (+)	0.62 (-)	—	NS	0.85 (-)	0.49 (+)	NS	0.97 (-)	NS
Dc	0.47 (+)	NS	0.26 (-)	—	—	—	—	NS	NS	—	—	NS	—
DI	0.41 (+)	NS	0.34 (-)	—	—	—	0.17 (+)	NS	NS	—	—	NS	—
Ua	—	—	—	0.33 (-)	NS	NS	—	—	—	—	0.56 (+)	NS	—
Ap	NS	—	0.35 (-)	—	—	—	—	—	—	—	—	—	—

NS, not significant. See Table 2 for abbreviations for parasitoids. Direction of the relationship is indicated in parentheses. Format of the table corresponds to that of Table 5.

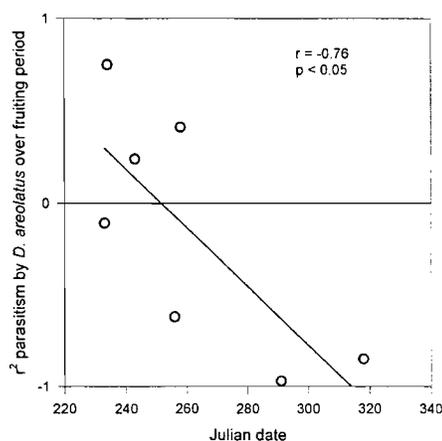


Fig. 4. Relationship between model R^2 values of changes in parasitism by *D. areolatus* over fruiting periods and the time of year at which the fruiting periods occurred (Julian date of the median day of the fruiting period). Negative R^2 values refer to inverse correlations.

ences in overall spatial distributions approximately half the time (2 out of 5 cases in *D. areolatus* versus *U. anastrephae*, 2 out of 4 cases in *D. longicaudata* versus *D. crawfordi*). That is, overall spatial distributions in the 2 native species differed about as often as did those between a native and the introduced species.

Summary. The height of an infested fruit in a canopy had little effect on the parasitism of the larvae it contained. In the few instances of significant differences, there was weak evidence that some parasitoids may be more active or effective in the lower portions of tree canopies (Table 13). Parasitism by *U. anastrephae* was greater in the interiors of some canopies. There was a consistent pattern of higher parasitism by the braconid species in smaller infested fruits and in those containing larger numbers of hosts. Overall, time plays an important role in changes in percentage of parasitism, although the direction of that change is highly variable. Increasing seasonal drying may limit the increase of *D. areolatus* populations within individual trees. There are only sporadic relationships between fruit density, host density, and the densities of hosts within fruits in different parts of the canopy and the percentage of parasitism in those locations. The relative lack of overlap in the distributions and abundances of 2 native species, *D. areolatus* and *U. anastrephae*, may reflect evolved divergences in their foraging. Such divergences are not apparent between cooccurring native and introduced species, *D. crawfordi* and *D. longicaudata*.

The characteristics of trees and fruits and host distribution that influence parasitism also influence each other. For example, *U. anastrephae* foraged more on the smaller infested fruits in the interior canopies of Sm93 and Sm94b. On average, the fruits of Sm93 are smaller in the interior. Is *U. anastrephae* searching for small fruits in the interior or is it

Table 10. Model R^2 values derived from multiple regressions of parasitism in tree canopy quadrants to fruit numbers in the quadrants (fn), pupal numbers in the quadrants (pn), and mean host density (hd [i.e., pupae per gram of weight])

Parasitoid	<i>P. guajava</i> 93a	<i>P. guajava</i> 93b	<i>P. guajava</i> 94	<i>S. mombin</i> 93	<i>S. mombin</i> 94a	<i>S. mombin</i> 94b	<i>M. indica</i> 94	<i>C. sinensis</i> 93a	<i>C. sinensis</i> 94a	<i>C. sinensis</i> 94b	<i>S. purpurea</i> 93	<i>S. purpurea</i> 94	<i>T. mexicana</i> 93	<i>X. americana</i> 93
D _a	NS	—	—	NS	fn 0.03 (+)	NS	—	NS	—	—	inf 0.03 (+)	pn 0.02 (+)	NS	NS
D _c	NS	—	—	—	—	—	—	NS	hd 0.02	NS	—	—	pn 0.13 (+)	—
D _l	pn 0.02 (-)	NS	NS	—	—	—	NS	NS	NS	NS	—	—	NS	—
U _a	—	—	—	NS	NS	—	—	—	—	—	—	hd 0.04 (+)	NS	—
A _p	fn 0.01 (-)	—	—	—	—	—	—	—	—	—	—	—	—	—

NS, not significant. See Table 2 for abbreviations for parasitoids. + and - signs in parentheses refer to the direction of the relationship. Format of the table corresponds to Table 5.

Table 11. Model R^2 values of the relationship between parasitisms by the 2 most abundant parasitoids in various trees

Parasitoid/species	<i>S. mombin</i> 93	<i>S. mombin</i> 94a	<i>S. mombin</i> 94b	<i>P. guajava</i> 93a	<i>C. sinensis</i> 93a	<i>C. sinensis</i> 94a	<i>C. sinensis</i> 94b
Da vs Ua	0.56 (-)	NS	0.27 (-)	—	—	—	—
Dl vs Dc	—	—	—	NS	0.64 (+)	0.47 (+)	NS
Parasitism	75	76	83	19	21	33	15

Directions of the relationships are in parentheses. Percentage of parasitism is given at the bottom of the table. Format corresponds to that of Table 5.

present in small fruits because of a preference for the interior of the canopy? In this particular case the other tree, Sm94b, did not have the same fruit-size distribution, leaving open the possibility that *U. anastrephae* prefers both small fruits and canopy interiors. However, the general problem of correlations among spatial and temporal characteristics of the canopies remains. Interaction factors between parasitism and the continuous variables of fruit weight, numbers of pupae in fruits, host density (pupae per gram of fruit), and time revealed no particular pattern (Table 14).

Discussion

We are aware that field surveys such as this can weave a bewildering pattern of correlation and speculation. We have attempted to be conservative in our analyses, and are the first to appreciate that a principle accomplishment of this work is to provide direction for further studies with greater control of their variables. That caveat aside, we believe that as information on the distributions of fruit fly parasitoids accumulates it will be prove useful in agriculture and in the study of insect ecology. There is increasing interest in exploration for new natural enemies for the biological control of Tephritidae (Sivinski 1996). Knowledge of candidates could guide establishment and augmentation programs, helping to determine which species would

be best suited to particular climates, floras, seasons, and preexisting parasitoid guilds.

The potential for tailoring releases and introductions rests on the differences among the candidates. When species have distinct ranges, host preferences, or foraging patterns within canopies then designing biological control programs would be simplified. For example, both *D. areolatus* and *D. longicaudata* have been introduced into Florida to suppress the Caribbean fruit fly. *D. areolatus* flourished when first established, but has been largely replaced by *D. longicaudata* in the southern part of the peninsula (Baranowski et al. 1993). In the northern portion of the range of this fly only *D. areolatus* occurs. The zone of overlap is relatively narrow. Clearly, there are factors on the regional scale, presumably environmental, that influence the competitiveness and distributions of the 2 species (J.S. and Ari Eaton, unpublished data). There are also patterns

Table 12. Expected and observed numbers of fruits containing both of 2 parasitoid species in various trees

Fruits	Expected	Observed	Significance
Fruits with Da and Ua			
<i>S. mombin</i> 93 (2)	19	11	<*
<i>S. mombin</i> 93 (3)	30.6	12	<*
<i>S. mombin</i> 94b (1)	112	69	<*
<i>S. mombin</i> 94b (2)	14	5	<*
<i>S. mombin</i> 94a (1)	62.4	53	NS
Fruits with Dc and Dl			
<i>C. sinensis</i> 93a	4.8	15	>*
<i>C. sinensis</i> 94b	26	26	NS
<i>C. sinensis</i> 94a	24	21	NS

Abbreviations of parasitoid species and trees are explained in the text. Numbers in parentheses refer to the week of the fruiting period during which the sample was taken. *Refers to statistical significance; < refers to an observed number of fruits being lower than expected; > refers to an observed number of fruits being higher than expected; NS, absence of significance. Data analyzed

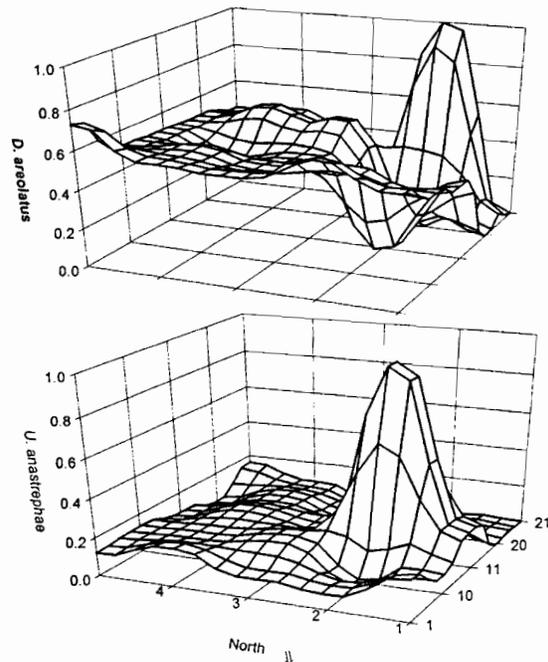


Fig. 5. Distribution of parasitism by *D. areolatus* (top) and *U. anastrephae* (bottom). The tree is Sm93. As in another of the 3 *S. mombines* examined, *U. anastrephae* was significantly more abundant in the interior of the

Table 13. A summary of tables listing the significant relationships of the various parasitoids to spatial and temporal characters of fruit tree canopies

Canopy characteristics	Da	Dc	Dl	Ua	Ap
Ht	Higher in lower level (1)	—	Higher in lower level (1)	Higher in lower level (1) Higher in upper level (1)	—
Margin	Higher on margin (1)	—	—	Higher in interior (2)	—
frt wt	Higher in smaller (1)	Higher in smaller (1)	Higher in smaller (2)	Higher in smaller (1)	Higher in smaller (1) Higher in larger (1)
pn	Higher with more pupae (7)	Higher with more pupae (3)	Higher with more pupae (3)	Higher with more pupae (3)	Higher with more pupae (1)
hd	Higher in more infested (8)	Higher in more infested (4)	Higher in more infested (3)	Higher in more infested (3)	Higher in more infested (1)
Time	4+ 4-	1+ 1-	2+ 1-	1+ 1-	1-
Microhab					
fn	1+	—	—	—	1-
hd	1+	1+	1+	1+	—
pn	1+	1+	1-	1+	—

Ht refers to height; margin to canopy margin; frt wt to size of fruits; pn to number of pupae; hd to host density (pupae per gram of fruit); time to changes in parasitism over fruiting period; microhab fn, hd, and pn to changes in parasitism related to the numbers of fruits, host densities, and numbers of pupae in the canopy quadrants. Statements within the blocks refer to parasitism (e.g., higher in lower level means that parasitism is greater in the lower level of the canopy). Numbers of significant differences in a category is given in parentheses, + and - signs refer to the direction of a relationship. Abbreviations are as those used in previous tables. Blocks were filled where no statistical significance had been discovered.

of distribution among Mexican parasitoids in terms of hosts and host trees (M.L., unpublished data). The native *D. areolatus* and *U. anastrephae* were more common in native plants; *D. crawfordi* was limited to guavas and citrus (see additional host in Katiyar et al. [1995]); parasitoids recovered from mangos were nearly all *D. longicaudata* (see Table 3; also Gonzales-Hernandez and Tejada 1979, Messing and Jang 1992, Hernandez-Ortiz et al. 1994).

When species occurred together, distributions on the scale of within-tree canopies did not appear

to be so pronounced as those on the levels of region or host tree; recall that a single guava fruit can contain *D. areolatus*, *D. crawfordi*, and *D. longicaudata*. However, there was some evidence of differences in the foraging patterns of *D. areolatus* and *U. anastrephae* within tree canopies. These differences may have occurred through divergence because of a history of competition, a notion that finds support from the apparent absence of within-canopy distribution differences between the native *D. crawfordi* and the introduced *D. longicaudata*.

Table 14. Partial R^2 values for the effects of continuous variables of fruit wt (rt wt), number of pupae in fruit (pn), host density in fruits (hd), and time during fruiting period (time) and their interaction factors on parasitism in focal trees

Parasitoid species	frt wt	pn	hd	Time	Time 2	frt wt° time	pn° time	hd° time	frt wt° time 2	pn° time 2	hd° time 2	frt wt° pn
Da (<i>S. mombin</i> 93)	0.30	—	—	—	—	—	—	—	—	—	—	—
Da (<i>S. mombin</i> 94b)	—	—	—	—	—	—	—	—	—	—	0.74	—
Da (<i>S. purpurea</i> 94)	—	—	—	—	—	—	—	—	—	—	—	—
Da (<i>P. guajava</i> 93a)	—	—	—	—	—	—	—	—	—	—	0.50	—
Dc (<i>C. sinensis</i> 94b)	—	—	—	—	—	0.08	0.20	—	—	—	0.59	—
Dc (<i>C. sinensis</i> 94a)	—	—	—	—	—	—	—	—	—	—	—	—
Dc (<i>C. sinensis</i> 93a)	0.27	—	0.69	—	—	—	—	—	—	0.04	—	—
Dl (<i>C. sinensis</i> 94b)	—	—	—	—	—	—	—	—	—	—	—	—
Dl (<i>C. sinensis</i> 94a)	—	0.21	—	—	—	—	—	0.22	—	—	—	—
Dl (<i>C. sinensis</i> 93a)	—	—	—	—	—	—	—	—	—	—	—	—
Dl (<i>P. guajava</i> 93a)	—	—	—	0.41	—	0.21	—	—	—	—	—	—
Ua (<i>S. mombin</i> 93)	0.33	—	—	—	—	—	—	—	—	—	—	—
Ua (<i>S. mombin</i> 94b)	—	—	—	—	—	—	—	0.15	—	0.18	—	—
Ua (<i>S. purpurea</i> 94)	—	—	—	—	—	—	0.29	—	—	—	0.65	—

Focal trees were chosen for their relatively high levels of parasitism (see Table 3). Format is that of Table 11.

Because the degree of specialization and the resulting diversity in patterns of foraging is an interesting feature of fruit fly parasitoid guilds, it would be useful to have a better understanding of its generation. We have hypothesized that competition is responsible, in part, for the different behaviors and, ultimately, the different ovipositor lengths of *D. areolatus* and *U. anastrephae*. Another source of evolutionary change in parasitoids is defensive adaptations in hosts that in turn select for countermeasures in their enemies (see Godfray 1994 and references therein). These countermeasures in the parasitoid may eventually limit its ability to attack other insects (or the same insect on different host plants) and could accelerate the process of specialization and speciation (e.g., Tschirntke 1992).

Such arms races between fruit flies and wasps may be relatively uncommon in tephritid parasitoids whose hosts appear to have relatively little control over their defenses. The influence of fruit size on parasitism emphasizes the importance of the plant tissue surrounding the fly to the success of the parasitoid. The form and amount of this fruit tissue appears to be under the control of the plant. Fruit fly larvae are not, at present, known to radically change the morphology of the fruits they inhabit, except sometimes to decrease fruit size and cause premature maturation (e.g., the papaya fruit fly, *Toxotrypana curvicauda* Gerstaecker [Landolt 1985]). The evolutionary options for fruit flies to escape their parasitoids physically may be limited mostly to female choice of oviposition site.

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