

Phenological Comparison of Two Braconid Parasitoids of the Caribbean Fruit Fly (Diptera: Tephritidae)

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Environ. Entomol. 27(2): 360-365 (1998)

ABSTRACT Two species of Braconidae, *Diachasmimorpha longicaudata* (Ashmead) and *Doryctobracon areolatus* (Szepligeti), commonly attack the Caribbean fruit fly, *Anastrepha suspensa* (Loew), in central Florida. There are temporal changes in the relative abundance of the 2 parasitoids, with a tendency for *D. longicaudata* to become more common as the fruiting periods of various host trees progress. An exception occurs when *D. longicaudata* declines relative to *D. areolatus* during the late-autumn and winter fruiting of the citrus fruit calamundin, χ *Citrofortunella mitis* J. Ingram & H. E. Moore. During the year there is a spring rise and then an autumn decline in the relative abundance of *D. longicaudata*. This pattern is not explained by any within-tree changes in fruit size or host larval densities. Many changes in relative abundance are consistent with *D. areolatus* being superior to *D. longicaudata* in finding host patches, but inferior at exploiting hosts (counter-balanced competition). Seasonal changes in maximum temperatures are also correlated to changes in the relative abundance of *D. longicaudata* to *D. areolatus*. It appears that the outcome of the competition between the 2 species is influenced by climatic conditions.

KEY WORDS fruit flies, Braconidae, *Diachasmimorpha*, *Doryctobracon*, population dynamics, biological control

IN 1965, THE Caribbean fruit fly, *Anastrepha suspensa* (Loew), was introduced accidentally into southern Florida. It subsequently spread until it occupied the southern $\approx 2/3$ of the state's peninsular region (Baranowski et al. 1993). Caribbean fruit fly larvae consume over 90 species of fruits, including several species of citrus (Norrbon and Kim 1989). Because of quarantine restrictions, much of Florida's exported grapefruit (*Citrus χ paradisi*) is grown in fly-free zones monitored by the state's Department of Agriculture and Consumer Services (Simpson 1993).

In 1969, an opiine braconid, *Doryctobracon areolatus* (Szepligeti) (= *Parachasma cereus*), was released in Dade County, Florida, to attack *A. suspensa* (Baranowski and Swanson 1970). *D. areolatus* is one of the most widespread native parasitoids of *Anastrepha* spp. in the New World (Wharton et al. 1981, Aluja et al. 1990). It was initially abundant in extreme southern Florida where the releases occurred, but declined drastically after the 1972 establishment of another opiine braconid, *Diachasmimorpha* (= *Biosteres*) *longicaudata* (Ashmead), in the same area (Baranowski and Swanson 1971, Baranowski et al. 1993).

Diachasmimorpha longicaudata was originally recovered from *Bactrocera* spp. in Malaysia, but proved easy to rear on a number of tephritid species. It was

later established throughout Latin America (Clausen 1978, Sivinski 1996) and brought to Florida via Mexico (Baranowski et al. 1993). After systematic releases across the peninsular portion of the state, it reduced Caribbean fruit fly populations by 40% (Baranowski et al. 1993). Currently, it is used in augmented releases to protect fly-free-citrus zones along the mid-Atlantic Florida coast (Sivinski 1996, Sivinski et al. 1996).

Doryctobracon areolatus was believed to have become rare in Florida until it was discovered to have spread to, and flourished in, the midpeninsular region of the state, the northern portion of the Caribbean fruit fly's range (A.E. and J.S., unpublished data). Thus, *D. areolatus* appears to have been displaced by *D. longicaudata* in their extreme southern site of mutual introduction, but it manages to compete under other, as yet undefined, conditions elsewhere.

The 2 species of parasitoids occur in similar numbers in a narrow band across central Florida, south of Lake Okeechobee (A.E. and J.S., unpublished data). Surveys of insects in this area found that *D. longicaudata* and *D. areolatus* differed in relative abundance among various, often nearby, fruit trees and in particular fruit trees over time (Sivinski et al. 1996). In this article we further document temporal variation in the relative numbers of the 2 parasitoids. We then correlate these changes in their abundances to 3 types of environmental variables: (1) climatic conditions, (2) fruit tree characteristics (i.e., fruit size and host larval density), and (3) the presence of the other species in particular trees.

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Materials And Methods

Fruits were obtained in the town of LaBelle, Hendry County, Florida, and its immediate surroundings from 1992 to 1994. These included Surinam cherry, *Eugenia uniflora* L. (3,641 fruits from 14 trees); loquat, *Eriobotrya japonica* (Thunb.) (986 fruits from 11 trees); calamundin, *Citrofortunella mitis* J. Ingram & H. E. Moore (2,275 fruits from 8 trees); Cattley guava, *Psidium cattleianum* Sabine (689 fruits from 5 trees); common guava, *Psidium guajava* L. (657 fruits from 12 trees); and grapefruit, *Citrus paradisi* Macf. (269 fruits from 8 trees). All are common hosts throughout the Caribbean fruit fly's Florida range (see Norrbom and Kim 1988). Data taken from a limited area, such as LaBelle, minimizes any spatial differences in environment that might effect the various host plants and the insects they contained. The fly population in LaBelle, in terms of the infestation levels in various fruit species and adult numbers throughout the year, is described in Sivinski et al. (1996).

We chose to examine in the greatest detail a single, "focal", host tree, one that from experience we expected to be infested heavily with Caribbean fruit fly larvae parasitized by both species of parasitoids. Patterns of parasitism discovered in this focal tree were then compared with those found in other trees. The focal tree was a Surinam cherry. Surinam cherry #1 was 4.75 m in height and bore fruit from 15 March to 10 May 1994. Sampling in this and all other trees was done systematically (i.e., never more than 10% of ripe fruits from every part of the tree were collected every week). By restricting fruit collections the effect of sampling on insect populations within a tree canopy was minimized. A total of 437 fruits was taken from Surinam cherry #1 during the 8-wk fruiting period. These fruits were obtained in this and other trees by gently shaking a branch. Fruits that fell were assumed to be ready to drop of their own accord and, hence, had completed their time of exposure to parasitoids foraging in that portion of the tree. Fruits were weighed to estimate size (see Sivinski 1991) and placed individually on vermiculite in 450-ml plastic containers covered with fine-mesh screen. They were held in the laboratory at ambient temperatures and humidities for 4 wk. After that time, insects were removed from containers and identified.

Diachasmimorpha longicaudata is known to forage extensively over fallen fruits (Purcell et al. 1994). To determine if samples taken solely from tree branches might misrepresent the relative proportions of the 2 parasitoids, samples of ripe fruits on the tree and fallen fruits without insect exit holes were taken from 16 Surinam cherry trees. The samples from each tree were divided in half, and one portion (the control) was taken immediately to the laboratory. Control fruits that had been picked from the tree and those that had fallen from the tree and were gathered from the ground under the canopy were kept separately. This was done to determine if the presumably longer exposure of fallen fruits to parasitoids resulted in greater parasitism. The other (exposed) was left ex-

posed for 1 wk on the ground under the tree from which the sample was taken in plastic 450-ml containers. Fruits rested on vermiculite that filled the bottom portion of the containers. The containers were placed in northern, southern, eastern and western points underneath tree canopies and in locations where fallen fruits had been located. After exposure, fruits were held as described above.

Data were analyzed by the following tests and with the aid of SAS (SAS Institute 1988). Comparisons of the mean proportions of larvae parasitized (parasitoids/[parasitoids + *A. suspensa*]) in fruits collected directly from trees and those from the ground under trees, and of fruits taken from trees and fruits exposed for 1 wk under trees, were made with Students 2-sample *t*-test (1-tailed) using arcsine transformed data. Relationships among proportion parasitisms and fruit size, host larval density, abiotic environmental factors, and the proportion parasitisms of the other species were examined through parametric correlations and multiple and single factor regressions. A number of correlation coefficients were compared during an examination of the effects of different degrees of competition on the relative abundance of the 2 parasitoids (see *Results, Interspecific Competition*). This set of correlations contained only those cases where the linear relationships had a greater *r*-square value than did the quadratic relationships. This simplified approach was undertaken to avoid the complications of attempting to compare parabolic relationships.

Results

Comparison of Parasitism of Caribbean Fruit Flies in Fallen Fruits and Those Still in Trees. There was no significant difference in the relative numbers of *D. areolatus* and *D. longicaudata* in fruits that were either picked from the tree or had already fallen to the ground. There was no significant difference in the proportions of the 2 parasitoids emerging from fruits exposed for 1 wk on the ground under host trees and fruits that had been taken directly to the laboratory after picking from the tree (Table 1). There were no differences between unexposed and exposed fruits in the overall rate of parasitism (Table 1). Biases that might misrepresent the abundance of one parasitoid species or the other because fruit samples were only picked directly from host trees were assumed to be unimportant to the further interpretation of the data.

Influence of Climate on Relative Abundance of *D. areolatus* and *D. longicaudata*. In the focal tree (Surinam cherry #1), overall percent parasitism increased over time (Fig. 1a). Parasitism by *D. areolatus* did not change significantly over time ($F = 4.28$, $df = 7$, $P = 0.09$), although there was a tendency for it to become greater as the fruiting period progresses ($y = 9.88 + 3.44x$, $SE[b] = 1.67$). Parasitism by *D. longicaudata* significantly increased over time ($y = -12.5 + 5.83x$, $SE = 1.07$, $F = 26.7$, $df = 7$, $P < 0.002$). The relative abundance of *D. longicaudata* increased linearly over time (Fig. 1b). It was the disproportionate increase in the numbers of *D. longicaudata* that is responsible for

Table 1. The mean \pm SE parasitism rates and proportions of Da and D1 in the parasitoid guild attacking Caribbean fruit flies infecting Surinam cherries in central Florida

Aspects of Parasitism	Fruit exposed on ground	Control (tree)	Control (ground)
Parasitism	0.66 (0.11)	0.63 (0.11)	0.62 (0.13)
Proportion flies	0.34 (0.11)	0.37 (0.11)	0.38 (0.13)
Proportion D1	0.04 (0.03)	0.03 (0.02)	0.06 (0.03)
Proportion Da	0.56 (0.10)	0.53 (0.10)	0.50 (0.11)
Differences between exposed and control fruits			
	t	df	p
Parasitism	0.02	15	0.99
Proportion flies	0.02	15	0.99
Proportion D1	0.82	15	0.42
Proportion Da	-0.13	15	0.90
Differences between control fruits collected from trees and the ground			
	t	df	p
Parasitism	-0.32	15	0.75
Proportion flies	0.19	15	0.85
Proportion D1	0.13	15	0.90
Proportion Da	-0.37	15	0.72

Fruits exposed on the ground were from samples of picked and freshly fallen fruits. Controls are divided into those that were taken from the ground and those collected from the trees. Thus, data reflect insects present in fruits over a span of time ranging from their ripening on the tree to >7 d on the ground.

the increasing percent parasitism in the later weeks of the fruiting period.

Through the year, the proportion of *D. longicaudata* in all species of fly-host trees in LaBelle rises through late winter and spring (January–April) and then falls in the autumn (September–December) (Fig. 2a). Generally, this pattern appears to also occur within the various species of fly-host trees (Fig. 2b). Surinam cherries, such as Surinam cherry #1, bear relatively more *D. longicaudata* parasitized pupae as the fruiting season progresses from February through April. Calamundin, the host tree with the longest and latest fruiting period in the area, supports relatively fewer *D. longicaudata* on average as autumn progresses (Fig. 2b; September–December, $r = -0.99$, $n = 5$, $P = 0.01$). However, *D. longicaudata* in guava appears to show little evidence of a similar decline in autumn (Fig. 2b; July–October; $r = 0.92$, $n = 4$, $P = 0.08$).

Of the climatic variables, mean monthly minimum temperature, mean monthly maximum temperature, mean monthly overall temperature, monthly minimum and maximum temperature, and total monthly precipitation, the best single fit to the change in the ratio of *D. areolatus* to *D. longicaudata* was maximum temperature (r -square = 0.60, $y = -2.8 + 0.03x$, $SE(b) = 0.008$, $F = 14.7$, $df = 11$, $P < 0.003$; environmental data from NOAA, Climatological Data, Asheville, North Carolina; due to interrupted recordings in LaBelle, data include measurements from 1990, 1991, and 1992). The best 2-factor model included the mean minimum temperature and the polynomial of minimum temperature and accounted for 68% of the variance in the *D. areolatus* to *D. longicaudata* ratio ($y = -0.07 + 0.000001x$, $SE(b) = 0.0000004$, $F = 11.6$, $df = 11$, $P < 0.007$).

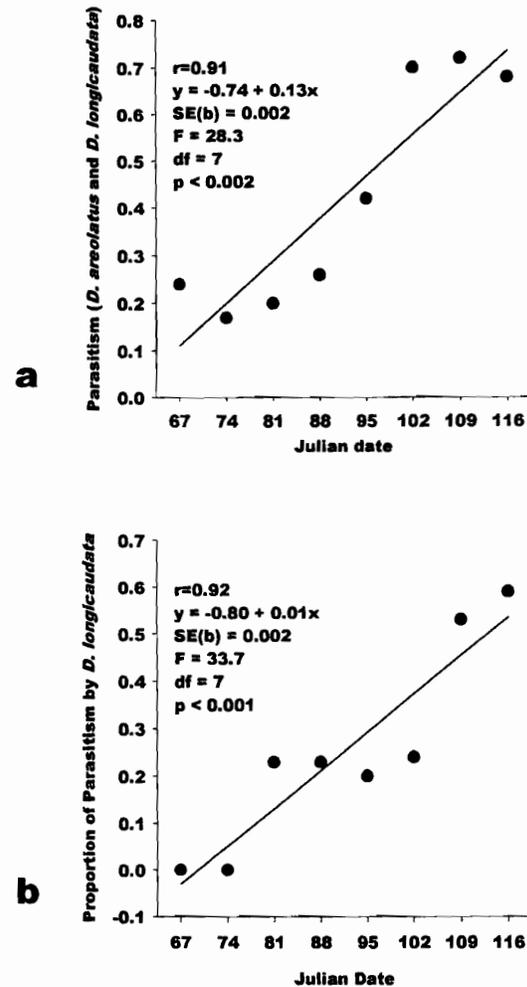


Fig. 1. (a) Parasitism of *Anastrepha suspensa* larvae by Da and D1 combined over the fruiting period of the focal Surinam cherry tree (Surinam cherry #1). (b) The proportion of D1 in the parasitoids attacking Caribbean fruit fly larvae over the fruiting period of the focal Surinam cherry tree (Surinam cherry #1).

Interspecific Competition. In the focal tree parasitism by *D. areolatus* increased along with that by *D. longicaudata*, until their combined parasitism was high and suitable hosts presumably became rarer (Fig. 3a). At this point the percent parasitism by *D. areolatus* began to drop. Among other trees, when total percent parasitism (and presumably competition) over the entire fruiting period was high there was a tendency for negative relationships to occur between the percent parasitisms of *D. areolatus* and *D. longicaudata* (Fig. 3b). The data did not support an alternative explanation that a correlation between time of year and total percent parasitism could spuriously generate the relationship between *D. areolatus* and *D. longicaudata* (Fig. 3b). In a stepwise regression, median date of the fruiting period explained only 4% of the variation, whereas percent parasitism accounted for

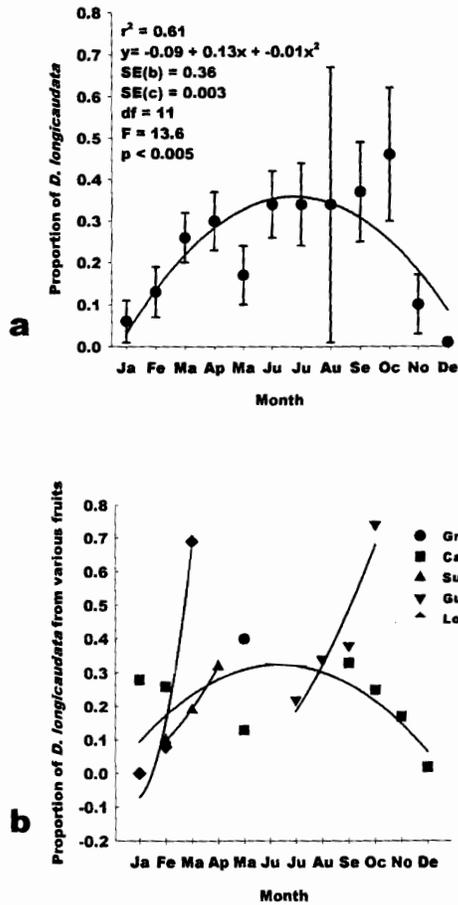


Fig. 2. (a) The proportion (standard error) of D_l in the parasitoid fauna collected from all fruit fly host plants over the years 1992, 1993, 1994. (b) The proportions of the parasitoid faunas from various host plants over time; circle = grapefruit, square = calamundin, upright triangle = Surinam cherry, upside down triangle = guava, diamond = loquat.

60% of the variation. Among the different fruit species *D. longicaudata* declined relative to *D. areolatus* only in calamundin during the winter fruiting period (Fig. 2b).

Changes within Host Plants. Parasitism by either *D. areolatus* and *D. longicaudata* might be favored by changes in fruit morphology or mean-fly infestation levels over the fruiting period of the tree. In general, parasitism by *D. longicaudata* decreases with increasing fruit size (Sivinski 1991) and there is a similar trend in parasitism by *D. areolatus* (Sivinski et al. 1997). The mean size of fruits on the LaBelle host plants generally decreased over the fruiting season of the species (Surinam cherry #1, $r = -0.67$, $n = 3641$, $P = 0.0001$; guava, $r = -0.60$, $n = 657$, $P = 0.0006$; loquat, $r = -0.89$, $n = 986$, $P = 0.001$; Cattley guava, $r = -0.22$, $n = 689$, $P = 0.46$). There is no significant correlation between the mean weights of fruits sampled on any given day in the LaBelle area and the mean ratio of *D. longicaudata*/*D. areolatus* reared from those fruits (Surinam cherry #1,

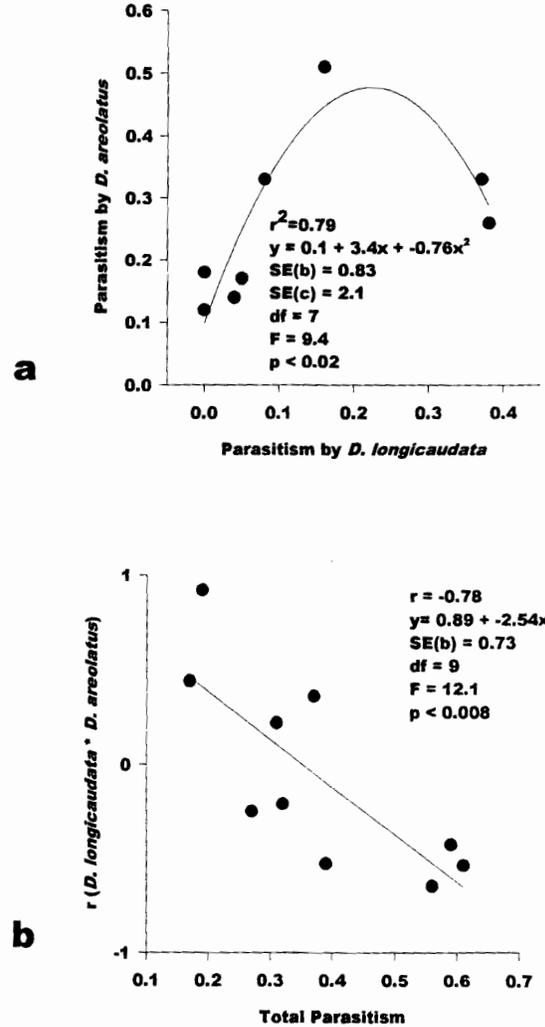


Fig. 3 (a) The relationship between mean weekly parasitisms by D_l and D_a in the focal Surinam cherry tree. (b) The relationship between total percent parasitisms and the correlation coefficients (r) of relationships between percent parasitisms by *D. areolatus* and *D. longicaudata*.

$r = -0.01$, $n = 16$, $P = 0.96$; guava, $r = -0.20$, $n = 12$, $P = 0.77$; Cattley guava, $r = -0.13$, $n = 12$, $P = 0.65$).

Another feature of the biotic environment that sometimes changed with time in LaBelle is the density of fruit fly larvae (larvae per gram of fruit; Surinam cherry #1, $r = 0.70$, $n = 3641$, $P = 0.0001$; guava, $r = 0.15$, $n = 657$, $P = 0.43$; loquat, $r = 0.50$, $n = 986$, $P = 0.17$; Cattley guava $r = -0.89$, $n = 689$, $P = 0.0001$). The ability of various parasitoids to exploit hosts is known to change with host density (Godfray 1994 and citations therein). If the capacities of *D. areolatus* and *D. longicaudata* to forage at different densities vary, their abundance might be correlated to temporal changes in host abundance. However, there is no evidence that the ratio of *D. longicaudata*/*D. areolatus* changed with the infestation levels in the focal tree or in the various

other host trees in the LaBelle area that harbored both *D. areolatus* and *D. longicaudata* (daily means; Surinam cherry #1, $r = 0.02$, $n = 8$, $P = 0.90$; Surinam cherry #1, $r = -0.005$, $n = 34$, $P = 0.98$; guava, $r = 0.55$, $n = 38$, $P = 0.20$; Cattley guava, $r = -0.11$, $n = 28$, $P = 0.72$).

Discussion

Both *Diachasmimorpha longicaudata* and *D. areolatus* are specialized parasitoids of late instar frugivorous tephritid larvae. In Florida, both are imported parasitoids of a non-native host, the Caribbean fruit fly, and both attack its larvae in all of its major fruit hosts. Because coexistence is possible in areas such as LaBelle, niche overlap between the 2 is unlikely to be complete.

Patterns of relative abundance within trees and over time also suggest differences in the niches of *D. areolatus* and *D. longicaudata*. When parasitism by *D. longicaudata* in the focal tree was at its highest, parasitism by *D. areolatus* was low (i.e., conditions appeared to favor one species over the other at that point). Also, in various trees where fly larvae-hosts were heavily exploited, and competition was presumably high as well, larger numbers of one parasitoid tended to occur along with smaller numbers of the other (i.e., correlations between percent parasitisms of the 2 species were negative). However, among trees where overall parasitism was low, and competition for hosts presumably low as well, both species generally displayed similar patterns of percent parasitisms (i.e., correlations between the percent parasitism of the 2 species over the fruiting season were most often positive). One explanation for this pattern is that an inferior competitor is being suppressed when competition is intense.

What might be the nature of the competition between *D. longicaudata* and *D. areolatus*? Many of the changes in relative abundance were consistent with "counter-balanced competition" (see Zwölfer 1971). In counter-balanced competition, 2 species are able to coexist because one is better able to locate host patches (infested trees; i.e., it is a superior *extrinsic competitor*), whereas the other better exploits the hosts once it arrives at the patch (i.e., it is a better *intrinsic competitor*; see also Schröder 1974). In most fruit host species and throughout most of the year, *D. longicaudata* became relatively more abundant as the fruiting seasons of the various tree species progressed. This could be due to *D. longicaudata* being a better intrinsic competitor. Only the autumn-winter decline of *D. longicaudata* in calamundin is inconsistent with the hypothesis.

Intrinsic competition appears to influence the community structure of introduced opiine braconid fruit fly parasitoids in Hawaii (Bess and Haramoto 1958, Clausen et al. 1965). Historically, *D. longicaudata* was eclipsed as the dominant parasitoid of pest tephritids by *Biosteres vandenboschi* (Fullaway), which in turn was largely replaced by *B. arisanus* (= *oophilus*) (Sonan). It has been proposed that each successive spe-

cies had the advantage of attacking an earlier stage of host development; *D. longicaudata*, late instar larvae, *B. vandenboschi*, early-instar larvae, and *B. arisanus*, fruit fly eggs. However, the relative vulnerability of *D. longicaudata* to encapsulation by oriental fruit fly larvae may also have contributed to its replacement (Palacio et al. 1991). Should *D. longicaudata* be a superior intrinsic competitor compared with *D. areolatus* in Florida, it is not because of its earlier presence in larvae. *D. areolatus* oviposites in the same late instar larvae attacked by *D. longicaudata* (A.E., personal communication). Nor was there evidence that changes in host fruit size or the density of larvae inhabiting fruits favored one species over the other.

If *D. longicaudata* and *D. areolatus* are in a state of counter balanced competition in LaBelle, the fulcrum of that balance changes in other locations. In the southern portion of their mutual range, *D. areolatus* nearly disappeared after the introduction of *D. longicaudata*. Such a pattern suggests that the competition between the 2 parasitoids can be influenced by environmental factors. In LaBelle, temperature is the abiotic factor best correlated to the yearly rise and fall of parasitism by *D. longicaudata* relative to that of *D. areolatus*. From the available evidence it is possible that higher temperatures favor *D. longicaudata* or that *D. areolatus* can better tolerate lower temperatures. Climatic fluctuations over the span of the year appear to effect the outcome of competition between the 2 parasitoids and perhaps ultimately allow them both to be common and widespread within the LaBelle area. Biogeographic studies of parasitoid distributions at different altitudes and latitudes underway in Florida and Mexico will provide further information about the relationship between *D. areolatus* and *D. longicaudata* and temperature.

There are agricultural benefits to be derived from determining the conditions that favor different species of fruit fly parasitoids. As of 1997, *D. longicaudata* is being reared and augmented in Florida to protect Caribbean fruit fly-free zones from high densities of pests in nearby urban areas (see Sivinski et al. 1996). However, *D. longicaudata* may not be the natural enemy best adapted to a particular site, perhaps including the Indian River County area where mass releases are presently occurring. If alternative parasitoids are available, releases could be tailored to specific times and places. It is also possible that introductions of natural enemies into Florida and elsewhere could be guided by understanding the limitations of parasitoids already present.

Acknowledgments

Pablo Liedo, Russell Messing, and Mary Purcell suggested numerous improvements to an earlier draft of the manuscript. Debbie Smith and Janet Voelker sought, collected, and watched over an enormous amount of fruit. Nothing could have been done without their careful and dedicated labors. Tim Holler helped in numerous ways, both in organization and in the field. The figures were professionally produced by

Gina Posey. The manuscript was prepared, with her usual speed and competence, by Valerie Malcolm. Victor Chew provided valuable statistical advice. This study was performed in part with funds from a USDA-OICD International Collaborative Research Project, 60-43YK-0016.

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Received for publication 13 February 1997; accepted 5 August 1997