THE DISTRIBUTIONS OF THE CARIBBEAN FRUIT FLY, *ANASTREPHA SUSPENSA* (TEPHRITIDAE) AND ITS PARASITOIDS (HYMENOPTERA: BRACONIDAE) WITHIN THE CANOPIES OF HOST TREES

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ABSTRACT

In the area of LaBelle, Florida (Hendry County), the Caribbean fruit fly, *Anastrepha suspensa* (Loew), is commonly attacked by three braconid parasitoids, *Doryctobracon areolatus* (Szepligeti), *Diachasmimorpha longicaudata* (Ashmead), and *Utetes anastrephae* (Viereck). Fruits from fifteen individual trees of four species, Surinam Cherry (*Eugenia uniflora* L.), Cattley guava (*Psidium cattleianum* Sabine), guava (*P. guajava* L.), and loquat (*Eriobotrya japonica* [Thunb.]), were systematically sampled in order to determine the distribution of *A. suspensa* and its parasitoids within the tree's canopies. Fruits infested by *A. suspensa* were lighter than infested ones in *P. guajava*. This may be due to the presence of the larvae. There was no evidence that *A. suspensa* preferred to oviposit in fruits at particular heights above ground or distances from canopy edges. Fruits containing larvae parasitized by *U. anastrephae* were significantly lighter than those containing larvae parasitized by either *D. areolatus* or *D. longicaudata,* and it was not present in *P. guajava*, the species with the heaviest fruits. There were no differences, either overall or within host tree species, among the heights above ground or distances from canopy edges of fruits containing larvae parasitized by any of the three braconids. Niche similarity in *D. areolatus* and *D. longicaudata* may be due to the absence of a shared evolutionary history. Both are recent introductions to Florida, but while *D. areolatus* is a neotropical species, *D. longicaudata* is from the Indo-Philippine region. Thus, there has been little opportunity for divergence. Knowledge of the distributions within tree canopies of the pest-fly, and of its natural enemies, may lead to improvements in its biological control.

Key words: *Diachasmimorpha longicaudata, Doryctobracon areolatus*, *Utetes anastrephae,* biological control, parasitoids, fruit flies

RESUMEN

En el área de LaBelle, Florida (condado de Hendry), la mosca del Caribe, *Anastrepha suspensa* (Loew), es atacada comúnmente por tres parasitoides bracónidos, *Doryctobracon areolatus* (Szepligeti), *Diachasmimorpha longicaudata* (Ashmead), y *Utetes anastrephae* (Viereck). Para determinar la distribución de *A. suspensa y sus* parasitoides dentro de las copas de los árboles se colectaron sistemáticamente frutas de quince árboles individuales de cuatro especies, *Eugenia uniflora* L., *Psidium cattleianum* Sabine, P. *guajava L., y Eriobotrya japonica* [Thunb.]. Se documentó que las guayabas infestadas por *A. suspensa* eran más ligeras que las que no estaban infestadas. Esto puede ser debido a la presencia de las larvas. No hubo evidencia de que A. *suspensa* prefiriera ovipositar en frutas en particulares alturas o distancias de los bordes de las copas dentro de los árboles. Se notó que las frutas con larvas parasitadas por *U. anastrephae* eran significativamente más ligeras que aquellas con larvas parasitadas ya sea por *D. areolatus o D. longicaudata; U. anastrephae* no estuvo presente en P. *guajava,* la especie con los frutos más pesados. No se detectaron diferencias, ya sea en forma general o entre especies de hospederos, entre las alturas y las distancias de los bordes de las copas dentro de los árboles, y entre las frutas con larvas parasitadas por cualquiera de los tres bracónidos. Es posible que la similitud de los nichos ecológicos de *D. areolatus y* de *D. longicaudata* sea debida a la ausencia de una historia compartida de evolución. Las dos especies fueron introducidas recientemente a Florida, y mientras que *D. areolatus* es una especie neotropical, *D. iongicaudata* es de la región Indo-Filipina, así que la oportunidad para una divergencia no ha sido mayor. El conocimiento sobre la distribución dentro de las copas de los árboles de esta mosca plaga, y también la de sus enemigos naturales, nos puede ser útil para mejorar su control biológico.

The Caribbean fruit fly, *Anastrepha suspensa* (Loew), was sporadically captured in Florida throughout the first half of the century (Baranowski et al. 1993). These immigrants from the Greater Antilles failed to establish until 1965, when a population introduced into the Miami area expanded over the peninsular portion of the state (Weems 1966). *Anastrepha suspensa* attacks over 90 species of fruits in Florida (Norrbom & Kim 1988) and has restricted the movement of citrus fruits into California, Texas, and Japan. To protect citrus exports, the Florida Department of Agriculture has organized a system of fly-free zones based on negative-trapping (Simpson 1993).

Shortly after the establishment of *A. suspensa*, parasitoids were introduced for its control. The first of these was the opiine braconid *Doryctobracon areolatus* (Szepligeti) (= *Parachasma cereus*) (Baranowski & Swanson 1970, 1971). *Doryctobracon areolatus* is a widespread species, ranging from Mexico to Argentina (Wharton & Marsh 1978). It is a parasitoid of several pestiferous *Anastrepha* species, including the Mexican fruit fly, *A. ludens* (Loew), and finds its hosts in both native and commercial, exotic fruits (e.g., Aluja et al. 1990, Hernandez-Ortiz et al. 1994). While initially abundant in south Florida, it was soon replaced at the original site of introduction by a second opiine braconid, *Diachasmimorpha longicaudata* (Ashmead) (Baranowski et al. 1993). This Indo-Philippine species was originally recovered from *Bactrocera* spp. but proved to attack a number of tephritids and was widely disseminated (Clausen 1978). At present, *D. areolatus* is common only in the northern portion of the Caribbean fruit fly's range, while *D. longicaudata* predominates in the south (Eitam 1998). There is a relatively narrow region, just south-west of Lake Okechobee, where both species are abundant. A third opiine species, *Utetes anastrephae* (Viereck), is native to Florida, where it historically parasitized *Anastrepha* spp. present in the extreme southern portion of the state and the Florida Keys (Baranowski et al. 1993). The spread of *A. suspensa* has allowed it to increase its own range into the middle of the peninsula (Eitam 1998). In addition to Florida, *U. anastrephae* occurs throughout Latin America, reaching as far south as Argentina (Wharton and Marsh 1978). It has a noticeably shorter ovipositor than either *D. areolatus* or *D. longicaudata*.

Augmented releases of *D. longicaudata* have been employed to help maintain Florida's fly-free zones (see Sivinski et al. 1996). It would be useful if the environments favored by *D. areolatus, D. longicadata* and *U. anastrephae* were better understood. In this way, augmentative releases of one or all species could be tailored to particular conditions. Should there be "gaps" in the foraging behaviors of the three species, new natural enemies that flourish in these specific microhabitats might be identified and imported. One context in which the species might differ is their distributions within host tree canopies.

Characteristics of the canopy structure affect, or are suspected to affect, the foraging of a number of parasitic Hymenoptera species (see Godfray 1994 and cit.). Differences within the canopy in light, heat, humidity, and risk of predation are among the factors that could select for both nonrandom distributions of hosts and specialized foraging tactics by natural enemies. For example, the red scale, *Aonidiella aurantii* (Mask.), is 27 fold more vulnerable to attack by aphelinid parasitoids when feeding on the periphery of citrus trees rather than in their interior (Murdoch et al. 1989). Closer to the present topic, the opiine braconid *Psyttalia (= Opius) concolor* (Szepligeti) appears to parasitize a greater proportion of tephritids in the upper halves of large Greek olive trees (Kapatos et al. 1977). Darby (1933) suggested that the opiine *Doryctobracon crawfordi* (Viereck) is more apt to attack *A. ludens* larvae in mangos than in sweet limes because the relatively open foliage of the lime provides less refuge from heat and low humidities. In southern Mexico, *D. areolatus* is more likely than, *U. anastrephae* to parasitize *Anastrepha obliqua* (Macquart) in fruits near the margins of certain tree canopies (Sivinski et al. 1997).

In this study, we examined the spatial distributions of *A. suspensa* and its three local parasitoids in the canopies of four species of host trees. We also examined the size, as estimated by weights, of fruits that escaped infestation by *A. suspensa*, that contained *A. suspensa* but not parasitoids, and those that contained both *A. suspensa* and its various parasitoids. Information on the temporal distribution of *D. areolatus* and *D. longicaudata* in Florida can be found in Sivinski et al. (1998).

METHODS

Fruits were collected from preferred host tree species in the LaBelle area, Hendry Co., Florida from 1992 to1994. These included six Surinam cherry trees (*Eugenia uniflora* L.), three loquat (*Eriobotrya japonica* (Thunb.), one guava (*Psidium guajava* L.), and five Cattley guava (*Psidium cattleianum* Sabine) (Table 1). Fruit sampling was done systematically, i.e., fruits from every part of the trees were collected every week. Fruits were obtained by gently shaking the branch next to their petioles. If they fell, they were assumed to have nearly completed their tenure on the tree. Thus, the fly larvae inside the fruits had been exposed to attack by parasitoids for a "typical" period in that location. Prior to shaking fruits, distance from the ground and distance from the edge of the foliage was determined, as was compass direction measured in degrees. After removal, fruits were weighed and then kept individually for one week on damp vermiculite at ca. 27°C. and ambient humidity. Fruit weight provides a useful estimate of fruit size (Sivinski 1991). Pupae were held for an additional four weeks, after which the emerging adults were identified. Voucher specimens are in the collection of J. Sivinski at USDA-CMAVE, Gainesville, FL.

Statistical comparisons of the weights and canopy-locations of fruits containing *A. suspensa* and its various parasitoids were made by multivariate ANOVA, with the various means distinguished through the Waller-Duncan k-ratio t-test ("proc GLM", SAS Inst. Raleigh, N.C. 27605). In the initial analysis of all fruits from all trees of all species, the error term used to derive the F value was taken from the interaction of all trees of all species and the species of insect present in the fruits. The relationships among compass direction, infestation, and parasitism were examined by dividing the canopy into six sections, each encompassing 60 degrees. Comparisons of the distributions of *A. suspensa* and its various parasitoids among these sections were by two-way crosstabulation chi-square tests (SAS Inst. Raleigh, N.C. 27605).

TABLE 1. THE NUMBERS OF THE VARIOUS SPECIES OF HOST TREES AND THE NUMBERS OF FRUITS SAMPLED. ALSO INCLUDED ARE THE LEVELS OF INFESTATION (*A. SUSPENSA* PUPAE RECOVERED / G OF PICKED FRUIT HELD IN THE LABORATORY) AND THE MEAN PERCENT PARASITISM (PARASITOIDS / PARASITOIDS + ADULT *A. SUSPENSA*) BY THE DIFFERENT PARASITOIDS IN THE VARIOUS HOST TREES (*UTETES ANASTREPHAE* = *UA*; *DORYCTOBRACON AREOLATUS* = *DA*; *DIACHASMIMORPHA LONGICAUDATA* = *DL*). FRUITS OF THE VARIOUS HOST TREE SPECIES ARE CHARACTERIZED BY MEAN SIZE (WEIGHT IN GRAMS) AND LOCATION WITHIN THE CANOPIES (MEAN HEIGHT FROM THE GROUND [CM] AND DISTANCE FROM THE EDGE OF THE CANOPY [CM]). IN ALL APPROPRIATE INSTANCES STANDARD ERRORS ARE ENCLOSED IN PARENTHESES FOLLOWING THE MEANS.

	Surinam cherry	loquat	Cattley guava	guava
N of trees	6	3	5	1
N of fruits	1336	336	656	315
pupae / gram	0.49 (0.01)	0.08 (0.005)	0.96 (0.02)	0.061 (0.006)
Ua parasitism	2 (0.4)	0.3 (0.3)	0.4 (0.001)	0
Da parasitism	26 (1.0)	16 (3.0)	18 (1.0)	0.5 (0.3)
Dl parasitism	14 (1.0)	0	13 (1.0)	0.4 (0.3)
weight (grams)	3.68 (0.04)	15.3 (0.21)	7.41 (0.12)	47.17 (0.10)
height (cm)	195.9 (2.68)	289.9 (6.44)	185.0 (3.01)	213.7 (4.35)
distance (cm)	12.10 (0.45)	24.05 (3.11)	8.75 (0.28)	10.51 (0.54)

RESULTS

Anastrepha suspensa was the only tephritid reared from the samples, and *D. areolatus* and *D. longicaudata* were the predominate parasitoids. *U. anastrephae* was present in relatively small numbers and was not recovered at all from guava, the species with the largest fruits. In Table 1 the various species of trees are described in terms of numbers of trees sampled, numbers of fruits sampled, mean infestations (*A. suspensa* larvae / g), mean percent parasitism (parasitoids / parasitoids + *A. suspensa*) by the three species of parasitoids, mean fruit weights, mean heights of fruits above ground, and the mean distances of fruits from the edge of the canopies. There were significant differences among the mean heights and weights of the various species of host fruits, however, there were no differences in the mean distances fruits hung from the various canopy edges (Table 2).

Overall, fruits that contained *A. suspensa* larvae and uninfested fruits did not differ in locations within the canopies; i.e., they were similar in terms of heights above ground and distances from canopy edges (Table 2). There were significant differences in the weights of infested and uninfested fruits, and there was a significant interaction between species of host fruit and the pattern of weight difference in infested and uninfested fruits (Table 2). When host species were examined individually, only guava, whose infested fruits were lighter, displayed any significant weight difference (Table 3).

Fruits from all trees of all species of hosts that contained unparasitized larvae and those containing larvae parasitized by *U. anastrephae, D. areolatus,* and *D. longicaudata* did not differ in heights above ground or distances from the edges of canopies (Table 4). However, fruits with unparasitized larvae were significantly heavier than those containing parasitized larvae, and those fruits containing larvae parasitized by

TABLE 2. ABOVE—THE WEIGHTS (G) AND WITHIN CANOPY LOCATIONS (HEIGHTS ABOVE GROUND [CM] AND DISTANCES FROM CANOPY MARGINS [CM]) OF FRUITS FROM ALL TREES OF ALL HOST SPECIES THAT WERE EITHER INFESTED WITH *A. SUSPENSA* OR WERE UNINFESTED. STANDARD ERRORS ARE IN PARENTHESES FOLLOWING MEANS. BELOW—THE RESULT OF A MULIVARIATE ANOVA THAT COMPARES THE MEAN WEIGHTS, HEIGHTS ABOVE GROUND, AND DISTANCES FROM CANOPY MARGINS OF A) FRUITS THAT WERE EITHER INFESTED WITH *A. SUSPENSA* OR UNINFESTED, B) WEIGHTS, HEIGHTS, AND DISTANCES OF FRUITS OF DIFFERENT SPECIES, AND C) THE INTERACTION BETWEEN PATTERNS OF INFESTATION REGARDING FRUIT WEIGHT, HEIGHT, AND DISTANCE AND HOST SPECIES.

	Uninfested n = 516	Infested n = 2152
Weight	21.96 (1.04)	8.61 (0.24)
Height	217.23 (4.37)	204.74 (2.15)
Distance	15.15 (1.42)	12.03 (0.48)

		df	F	p
Infestation	Weight	1	14.12	0.0037*
	Height	1	.026	0.62
	Distance	1	0.06	0.81
Host Species	Weight	3	1329.8	0.0001*
	Height	3	6.3	0.0009*
	Distance	3	0.69	0.58
Infest* Host	Weight	3	27.17	0.0001*
	Height	3	1.06	0.41
	Distance	3	3.03	0.08

TABLE 3. A COMPARISON OF THE WEIGHTS (G) OF FRUITS THAT DO AND DO NOT CONTAIN LARVAE OF *A. SUSPENSA* IN ALL OF THE VARIOUS HOST TREE SPECIES. STANDARD ERRORS ARE IN PARENTHESES FOLLOWING THE MEANS, AND SAMPLE SIZES FOLLOW STANDARD ERRORS.

	Uninfested	Infested	df	F	p
Surinam	3.7 (0.11)	3.7 (0.04)	1	0.61	0.47
Cherry	n = 195	n = 1168			
Loquat	15.3 (0.32)	15.3 (0.28)	1	0.06	0.83
	n = 130	n = 205			
Cattley	7.3 (0.87)	7.4 (0.12)	1	4.47	0.13
Guava	n = 24	n = 631			
Guava	50.5 (1.61)	43.4 (1.12)	1	12.61	0.0004*
	n = 167	n = 148			

TABLE 4. ABOVE- THE WEIGHTS (G) AND WITHIN CANOPY LOCATIONS (HEIGHTS ABOVE GROUND [CM] AND DISTANCES FROM CANOPY MARGINS [CM]) OF FRUITS FROM ALL TREES OF ALL HOST SPECIES THAT EITHER CONTAINED UNPARASITIZED LARVAE OF *A. SUSPENSA* (= *AS*), OR CONTAINED LARVAE PARASITIZED BY THE VARIOUS PARASITOIDS (*UTETES ANASTREPHAE* = *UA*, *DORYCTOBRACON AREOLATUS* = *DA*, *DIACHASMIMORPHA LONGICAUDATA* = *DL*). STANDARD ERRORS IN PARENTHESES FOLLOW MEANS, AND MEANS SHARING THE LETTER FOLLOWING THE STANDARD ERROR ARE NOT SIGNIFICANTLY DIFFERENT. BELOW—THE RESULT OF A MULIVARIATE ANOVA THAT COMPARES THE MEAN WEIGHTS, HEIGHTS, AND DISTANCES FROM CANOPY MARGINS OF A) FRUITS THAT CONTAIN UNPARASITIZED *A. SUSPENSA* LARVAE AND THOSE THAT CONTAIN LARVAE PARASITIZED BY THE VARIOUS PARASITOIDS, B) WEIGHTS, HEIGHTS, AND DISTANCES OF FRUITS OF THE VARIOUS HOST SPECIES THAT CONTAIN *A. SUSPENSA* LARVAE, AND C) THE INTERACTION BETWEEN THE PATTERNS OF PARASITISM REGARDING FRUIT WEIGHT, HEIGHT, AND DISTANCE AND HOST TREE SPECIES.

	As	Ua	Da	Dl
Weight	11.14 (0.45) a	4.78 (0.50) c	6.0 (0.19) b	6.3 (0.2) b
Height	211.3 (3.3) a	218.4 (19.4) a	204.2 (4.1) a	181.9 (4.0) a
Distance	11.78 (0.71) a	16.76 (6.62) a	11.62 (0.86) a	11.40 (0.71) a

		df	F	p
Parasitoid	Weight	3	2.56	0.09[1]
	Height	3	0.55	0.66
	Distance	3	2.59	0.08
Host Species	Weight	3	58.0	0.0001*
	Height	3	0.40	0.76
	Distance	3	0.01	0.99
Parasitoid* Host	Weight	7	2.37	0.07
	Height	7	0.53	0.80
	Distance	7	2.35	0.07

[1]A Waller-Duncan K-ratio t-test found some means to be significantly different.

U. anastrephae were significantly lighter than those containing larvae parasitized by *D. areolatus* or *D. longicaudata* (Table 4). In the later two parasitoid species, there were significant negative correlations between the mean weights of fruits from the various host species and the mean percent parasitism of the fruit fly larvae they contained (Fig. 1). However, within species there were no relationships between fruit weights and percent parasitism (Table 5).

There were no significant differences between the compass locations of infested and uninfested fruits, either overall or in any of the individual host fruit species. Neither were there any differences among the compass location distributions of the various parasitoid species.

DISCUSSION

Anastrepha suspensa larvae were evenly distributed within the canopies of host trees. Guava fruits containing fly larvae were lighter in weight than those that did

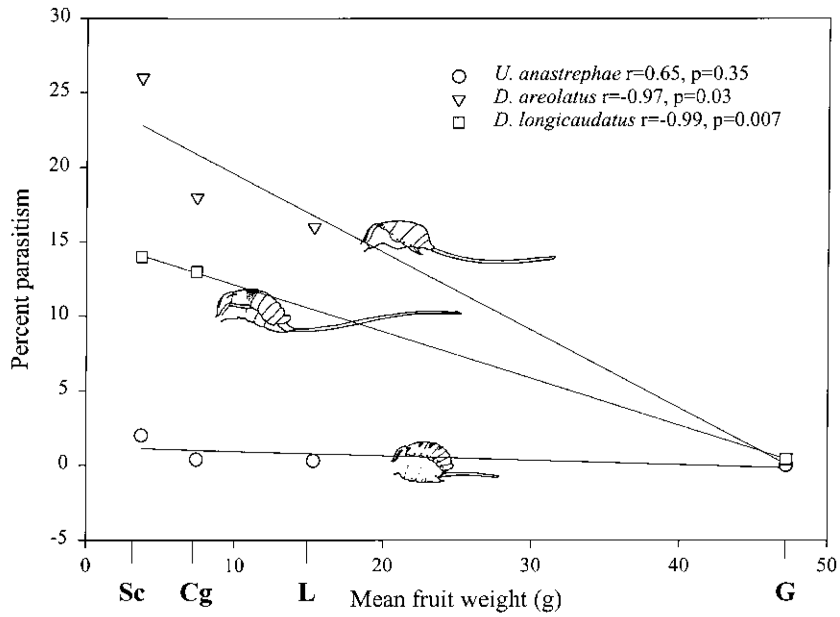

Fig. 1. The relationships between the mean fruit weights of the various host trees (Sc = Surinam cherry, L = loquat, Cg = Cattley guava, G = guava) and the percent parasitism of *A. suspensa* larvae by the various parasitoids (*Utetes anastrephae*, *Doryctobracon areolatus*, and *Diachasmimorpha longicaudata*). The drawings of abdomens near the different lines illustrate the relative lengths of the ovipositor in the various parasitoid species. The data point for *D. longicaudata* on loquat was omitted from the analysis because this parasitoid is rarely abundant during the winter months when loquat is fruiting.

not, and similarly, various fruits in southern Mexico, containing different *Anastrepha* species, are often lighter than uninfested fruits (Sivinski et al. 1997). Some tephritids oviposit in small, green fruits and increase the rate of maturation and, by unknown means, decrease the size of the fruits they occupy, e.g., the papaya fruit fly, *Toxotrypana curvicauda* Gerstaeker (Landolt 1985). Since female *A. suspensa* often oviposit in immature guava fruits (e.g. Burk 1983), lighter infested fruits may be due to the action of the larvae. Alternative explanations are that females prefer to lay eggs, or larvae are better able to survive, in smaller fruits.

Doryctobracon areolatus parasitized *A. suspensa* larvae in all the fruit species sampled, while *D. longicadata* was obtained from larvae in all but loquat fruits. *Utetes anastrephae* was absent in the large fruits of guava, and common only in the smallest fruits, those of Surinam cherry. In southern Mexico, *U. anastrephae* is also restricted to smaller fruits, and its limited foraging range is presumably reflected in its shorter ovipositor (Sivinski et al. 1997). In general, and in *D. areolatus* and *D. longicaudata* in the present study, mean percent parasitism is significantly higher in host tree species with smaller fruits (e.g., Sivinski et al 1997). This may be due to a preference for smaller fruits (Sivinski 1991), or the greater access parasitoids have to fly larvae liv-

Table 5. Comparisons of the weights (g) of fruits that contained unparasitized *A. suspensa* larvae and those that contained larvae parasitized by the various parasitoids (*Utetes anastrephae* = *Ua*, *Doryctobracon areolatus* = *Da*, and *Diachasmimorpha longicaudata* = *Da*). Standard errors are in parentheses following means and sample sizes follow standard errors. Means sharing a letter are not significantly different. the single specimen of *Ua* recovered from loquat was discarded from the calculations.

	As	Ua	Da	Dl	F	p
Surinam	3.67 (0.07)	4.24 (0.38)	3.62 (0.09)	4.04 (0.09)	0.41	0.75
Cherry	538 a	18 a	316 a	189 a		
Loquat	15.6 (0.33)		15.2 (0.63)		41.86	0.11
	141 a		33 a			
Cattley	6.75 (0.20)	9.6 (0.20)	7.46 (0.19)	8.08 (0.23)	2.05	0.19
Guava	196 a	2 a	219 a	201 a		
Guava	43.3 (1.22)		38.8 (1.56)	41.0 (1.45)	0.24	0.79
	132 a		4 a	2 a		

ing in the shallow pulp of smaller fruits. The absence of *D. longicaudata* from loquats may be due to the tree's late winter fruiting season. *Diachasmimorpha longicaudata* is relatively rare throughout the winter months in the LaBelle area of Florida, regardless of the host tree (Sivinski et al. 1998).

There were no distinct microhabitat preferences among the three parasitoid species, either in terms of heights within the canopies or distances from the canopy edges. Fruits containing larvae parasitized by *U. anastrephae* were farther from the edges of the host tree canopies than those containing larvae parasitized by *D. areolatus* or *D. longicaudata*, albeit not significantly so. However, in southern Mexico *U. anastrephae* often parasitized larvae in fruits that were deeper, on average, in the canopies of host trees than those attacked by *D. areolatus* (Sivinski et al. 1997)

One difference in the foraging of *D. areolatus* and *D. longicaudata,* not addressed in the present study, is the latter species' propensity to forage over fallen fruits (e.g., Purrcell et al., 1996, see however, Sivinski et al. 1998). In a Mexican study, *D. areolatus* attacked larvae in fruits on the ground under tree canopies, but to a lesser extant than *D. longicaudata* (Sivinski et al. 1997).

It is possible that the substantial overlap in the spatial niches of *D. areolatus* and *D. longicaudata* in tree canopies is due to a lack of shared history over evolutionary time. Competition between the two long-ovipositor species may not yet have led to selection for divergence in morphology and behavior. There is similar overlap between the within-canopy distributions of *D. longicaudata* introduced into Mexico and yet another neotropical *Doryctobracon* species, *D. crawfordi* (Veireck) (Sivinski et al 1997).

Competition between *D. areolatus* and *D. longicaudata* is also the most likely reason for their generally distinct geographical distributions in Florida. It appears that only the ability of *D. areolatus* to forage in habitats with relatively low host diversity and /or survive in climates characterized by low winter temperatures has allowed it to resist displacement by *D. longicaudata* (Eitam 1998; Sivinski et al. 1998). Interestingly, *U. anastrephae* with its short ovipositor and specialization on only smaller fruits, is present in the Florida ranges of both long ovipositor species.

There are other examples of the coexistence of native and introduced parasitoid species with different ovipositor lengths, and the displacement of native species by introduced species with similar ovipositor lengths; e.g., both occurred among the Ichneumonidae attacking the Swaine jack pine sawfly, *Neodiprion swainei* Middleton (Price 1972). In this instance, ovipositor length is correlated to the host stage attacked. Short ovipositor species lay eggs in exposed larvae while long ovipositor species reach down to pupae buried in leaf litter. The significance of ovipositor length in braconid fruit fly parasitoids, and how it influences interspecific competition, is less obvious. As far as is known all three of the braconids examined in Florida attack fruit fly larvae, not eggs or pupae, inside fruits (Eitam 1998; J. Sivinski and M. Aluja, personal observation). Since longer ovipositors appear to be able to reach both shallow and deeply placed hosts, i.e., long ovipositor species are present in the entire size range of host fruits, the adaptive significance of *U. anastrephae*'s short ovipositor remains to be determined.

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REFERENCES CITED

ALUJA, M., J. GUILLEN, P. LIEDO, M. CABRERA, E. RIOS, G. DE LA ROSA, H. CELEDONIO, AND D. MOTA. 1990. Fruit infesting tephritids (Dipt.: Tephritidae) and associated parasites in Chiapis, Mexico. Entomophaga 35: 39-38.

BARANOWSKI, R., AND R. W. SWANSON. 1970. Introduction of *Parachasma (= Opius) cereus* (Hymenoptera: Braconidae) into Florida as a parasite of *Anastrepha suspensa* (Diptera: Tephritidae). Florida Entomol. 53: 161-162.

BARANOWSKI, R., AND R. W. SWANSON. 1971. The utilization of *Parachasma cereus* (Hymenoptera: Braconidae) as a means of suppressing *Anastrepha suspensa* populations. Proc. Tall Timbers Conf. Biol. Cont. by Habit. Manag. No. 3: 249-252.

BARANOWSKI, R., H. GLENN, AND J. SIVINSKI. 1993. Biological control of the Caribbean fruit fly, *Anastrepha suspensa* (Loew). Florida Entomol. 76: 245-250.

BURK, T. 1983. Behavioral ecology of mating in Caribbean fruit flies, *Anastrepha suspensa* (Loew). Florida Entomol. 66: 330-344.

CLAUSEN, C. P. 1978. Introduced Parasites and Predators of Arthropod Pests and Weeds: a World Review. USDA-ARS Agr. Handbook No. 480.

DARBY, H. H. 1933. Insects and microclimate. Nature. 131: 839.

EITAM, A. 1998. Biogeography of Braconid Parasitoids of the Caribbean Fruit Fly, *Anastrepha suspensa* (Loew) (Diptera: Tephritidae), in Florida. Dissertation, University of Florida.

GODFRAY, H. C. J. 1994. Parasitoids Behavioral Ecology and Evolutionary Ecology. Princeton Univ. Press, Princeton N. J.

HERNANDEZ-ORTIZ, V., R. PERE-ALONSO, AND R. WHARTON. 1994. Native parasitoids associated with the genus *Anastrepha* (Diptera: Tephritidae) in Los Tuxtlas, Veracruz, Mexico. Entomophaga 39: 171-178.

KAPATOS, E., B. S. FLETCHER, S. PAPPAS, AND Y. LAUDEHO. 1977. The release of *Opius concolor* and *O. concolor* var. *siculus* (Hym.: Braconidae) against the spring generation of *Dacus oleae* (Diptera: Tephritidae) on Corfu. Entomophaga 22: 265-270.

LANDOLT, P. 1985. Papaya fruit fly eggs and larvae (Diptera: Tephritidae) in field-collected papaya fruit. Florida Entomol. 68: 354-356.

MURDOCH, W. W., R. F. LUCK, S. J. WALDE, J. D. REEVE, AND D. S. YU. 1989. A refuge for red scale under control by *Aphytis*: structural aspects. Ecology 70:1707-1714.

NORRBOM, A. L., AND K. C. KIM. 1988. A list of the reported host plants of the species of *Anastrepha* (Diptera: Tephritidae). USDA-APHIS-PPQ Pub No. 81-52.

PRICE, P. W. 1972. Parasitoids utilizing the same host: adaptive nature of differences in size and form. Ecology 53: 190-195.

PURCELL, M., C. JACKSON, J. LONG, AND M. BATCHELOR. 1994. Influence of guava ripening on parasitism of the oriental fruit fly, *Bactrocera dorsalis* (Hendel) (Diptera: Tephritidae), by *Diachasmimorpha longicaudata* (Ashmead) (Hymenoptera: Braconidae) and other parasitoids. Biol. Cont. 4: 396-403.

SIMPSON, S. E. 1993. Caribbean fruit fly-free zone certification protocol in Florida (Diptera: Tephritidae). Florida Entomol. 76: 228-232.

SIVINSKI, J. 1991. The influence of host fruit morphology on parasitism rates in the Caribbean fruit fly (*Anastrepha suspensa* [Loew]). Entomophaga 36: 447-455.

SIVINSKI, J., C. O. CALKINS, R. BARANOWSKI, D. HARRIS, J. BROMBILA, J. DIAZ, R. BURNS, T. HOLLER, AND G. DODSON. 1996. Suppression of a Caribbean fruit fly (*Anastrepha suspensa* (Loew): Tephritidae) population through augmented releases of the parasitoid *Diachasmimorpha longicaudata* (Ashmead) (Braconidae). Biol. Cont. 6: 177-185.

SIVINSKI, J., M. ALUJA, AND M. LOPEZ. 1997. The spatial and temporal distributions of parasitoids (Hymenoptera) of Mexican *Anastrepha* species in the canopies of host trees. An. Entomol. Soc. America 90: 604-618.

SIVINSKI, J. M. ALUJA, T. HOLLER, AND A. EITAM. 1998. Phenological comparison of two braconid parasitoids of the Caribbean fruit fly (Diptera: Tephritidae). Environ. Entomol. 27: 360-365.

WEEMS, H. 1966. The Caribbean fruit fly in Florida. Proc. Florida Sta. Hort. Soc. 79: 401-405.

WHARTON, R., AND P. M. MARSH. 1978. New World opiine (Hymenoptera: Braconidae) parasitic on Tephritidae (Diptera). J. Washington Acad. Sci. 68: 147-167.