

Natural establishment of a parasitoid complex on *Bactrocera latifrons* (Diptera: Tephritidae) in Hawaii

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Abstract

Bactrocera latifrons (Hendel) (Diptera: Tephritidae) is the most recent of four tephritid fruit fly species accidentally introduced into Hawaii. Although parasitoids have been released against other tephritid fruit fly species and have shown partial success in Hawaii, no parasitoids were released until 2004 to suppress populations of *B. latifrons*. The present study was conducted to document the parasitoid complex that has naturally established against *B. latifrons* in Hawaii and to assess whether there is a need for improving the biological control of this species. Based on ripe turkeyberry (*Solanum torvum* Sw) fruit collections over three consecutive years *B. latifrons* was the dominant tephritid fruit fly infesting turkeyberry at all four sites surveyed, across three major islands in Hawaii. The overall percentage parasitism of *B. latifrons* ranged from a low of 0.8% (Hana, Maui) to a high of 8.8% (Kahaluu, Oahu). Five primary parasitoid species were recovered from individually held *B. latifrons* puparia: *Fopius arisanus* (Sonan), *Psytalia incisi* (Silvestri), *Diachasmimorpha longicaudata* (Ashmead), *D. tryoni* (Cameron), and *Tetrastichus giffardianus* Silvestri. *F. arisanus* was the predominant parasitoid at three of the four sites. Low levels of parasitism suggest that there is a need to improve biological control of *B. latifrons*, to minimize chances of this species causing economic impacts on crop production in Hawaii. We discuss the possibility of improving biological control of *B. latifrons* through augmentative releases of *F. arisanus* or introduction and release of specific and efficient new parasitoid species.

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Keywords: *Bactrocera latifrons*; *Fopius arisanus*; *Psytalia incisi*; *Diachasmimorpha longicaudata*; *Diachasmimorpha tryoni*; *Tetrastichus giffardianus*; Biological control

1. Introduction

Bactrocera latifrons (Hendel) (Diptera: Tephritidae) is a tephritid fruit fly of primarily Asian distribution (e.g., Pakistan, India, Sri Lanka, Burma, China, Thailand, Laos, Vietnam, Malaysia, Singapore, Brunei and Taiwan) (Carroll et al., 2005; White and Elson-Harris, 1992). It is the most recent (and 4th) invasive tephritid fruit fly species to become established in Hawaii. The fly was first detected on the island of Oahu in 1983 (Vargas and Nishida,

1985a,b) and has since spread throughout the island chain (Peck and McQuate, 2004; Harris et al., 2001; Liquido et al., 1994; Vargas and Nishida, 1985a,b). It has been found to have a host range in Hawaii of at least 15 plant species in the families Solanaceae and Cucurbitaceae (Liquido et al., 1994). Although, at present, little economic damage has been attributed to this species in Hawaii, it has the potential to impact production of solanaceous crops such as peppers (*Capsicum annuum* L. and *C. frutescens* L.), eggplant (*Solanum melongena* L.) and tomatoes (*Lycopersicon esculentum* Mill.) and some cucurbitaceous crops (Liquido et al., 1994). Infestation beyond these two plant families has been reported, but those records have been considered to be either aberrant host associations (e.g., Euphorbiaceae

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and Rosaceae) or doubtful records (e.g., Anacardiaceae, Euphorbiaceae, Musaceae, Myrtaceae, Oxalidaceae, Rosaceae, Rubiaceae, Rutaceae, and Sapindaceae) (White and Elson-Harris, 1992).

The three other tephritid fruit fly species which had invaded Hawaii in earlier years are the melon fly, *Bactrocera cucurbitae* (Coquillett), in 1895 (Back and Pemberton, 1917); the Mediterranean fruit fly, *Ceratitidis capitata* (Wiedemann), in 1907 (Back and Pemberton, 1918); and the oriental fruit fly, *B. dorsalis* (Hendel) first reported in 1945 (van Zwaluvenburg, 1947). An area-wide integrated pest management strategy was recently implemented in Hawaii to control the four introduced fruit fly species, with initial attention focusing on Mediterranean fruit fly, melon fly and oriental fruit fly. Management techniques included bait-spray applications, sanitation, cultural practices, use of the sterile insect technique (SIT), and releases of hymenopteran parasitoids (Klungness et al., 2005; Vargas et al., 2004, 2003). Because population densities of *B. latifrons* are typically low, and have caused minimal economic damage to date, there was little incentive for suppression efforts to be directed against this species.

In earlier years, releases of introduced parasitoids in Hawaii resulted in some of the most successful examples of classical biological control of fruit flies in the world (Clausen et al., 1965; Wharton, 1989). Although some research has been conducted on the biology and ecology of *B. latifrons*, no parasitoids have been released as of 2004 to suppress populations of this pest. The discovery of different sites in Hawaii with relatively high populations of *B. latifrons* (McQuate et al., in press) suggests that further studies are needed on the present status, and potential means of suppression, of this tephritid fruit fly pest, more than 20 years after its introduction to Hawaii. The objective of the present study is to document the parasitoid complex that has naturally established against *B. latifrons* in Hawaii and to assess whether there is a need for improving the biological control of this species. Information on extant parasitoids of the fruit fly is also important to avoid the possible displacement of established biological control agents in future biological control attempts (see Samways, 1997).

We chose to base our assessment of natural parasitization of *B. latifrons* on flies and parasitoids recovered from ripe turkeyberry (*Solanum torvum* Sw) fruits. Turkeyberry is a solanaceous plant native to the Antilles, but is now a pantropical weed. In Hawaii, it was first collected on Maui in 1954, where it was naturalized along Iao stream. It has also naturalized in Kaneohe and Palolo Valley on Oahu (Wagner et al., 1990), as well as in Waimanalo, Kahului, and Laie on Oahu, Haiku and Hana on Maui and Pepeekeo on Hawaii Island (A.H.B-G. and G.T.M., personal observation). Turkeyberry is a good host for the study of *B. latifrons* because it produces abundant, small fruits from which *B. latifrons* can be readily recovered. Recently, the basic population biology of *B. latifrons* has been documented on this host (McQuate et al., in press). Additionally, because turkeyberry fruits are available throughout

most of the year at multiple sites spread over several Hawaiian Islands, we were able to compare the parasitoid assemblages among a number of different sites. Because *B. latifrons* maintains relatively low populations, even when host biomass is abundant (Liquidó et al., 1994), pupal recovery can be a rather slow process, necessitating collection over several years for adequate recovery for assessment of the established parasitoid fauna, especially when parasitism levels are also low.

2. Materials and methods

2.1. Study sites

Ripe (yellow) turkeyberry fruits were collected from four sites in Hawaii, U.S.A. The coordinates of these sites were recorded in Universal Transverse Mercator (UTM) projection using a Garmin GPS 12 (Garmin, Olathe, KS) and plotted using ArcGIS9 (ESRI, Redlands, CA) to show the location of collection sites (Fig. 1): (1) Haiku, adjacent to Haiku Road, on the island of Maui (UTM Easting, Northing 778393, 2315918m Zone 04 Q), (2) Hana, adjacent to Maia Road on the island of Maui (810035, 2301293m Zone 04 Q), (3) Kahaluu, adjacent to Waihee Road on the island of Oahu (619799, 2373163m Zone 04 Q), and (4) Pepeekeo, adjacent to Kaupakuea Homestead Road, on the Hamakua Coast on the island of Hawaii (279225, 2195044 m Zone 05 Q). Turkeyberry plants at all but the Kahaluu site were in cattle and/or horse pastures. The Kahaluu site was an abandoned field, but had previously been used as a horse pasture. All are low elevation sites (under 400 m) and all are on the windward sides of their respective islands, with annual rainfall at the Pepeekeo site estimated to average 380 cm, and annual rainfall at the other sites averaging near 190 cm (Armstrong, 1983). All fruits collected in the field were processed in our Hilo (island of Hawaii) or Honolulu (island of Oahu) rearing laboratories.

2.2. Parasitoid collection and processing

From 6 October 2003 to 10 August 2006, ripe turkeyberry fruits were collected from plants at each site, as available, and transported to the laboratory. No ground fruits were collected because turkeyberry fruits, unless physically knocked off, typically do not fall off, but dry on the plant. Consequently, ground fruits were typically not found. Our goal was to recover at least 1000 *B. latifrons* puparia from each site. The number of fruit collections to achieve this goal varied among sites depending on fruit availability and infestation levels. Sampling started in Haiku in 2003, in Hana and Pepeekeo in 2004 and in Kahaluu in 2005. A total of 29 collections, across all sites, were made from 2003 to 2006: three in 2003, 12 in 2004, 11 in 2005 and three in 2006 (Table 1).

Fruits were counted, weighed and then placed in screened containers to which sand or vermiculite had been

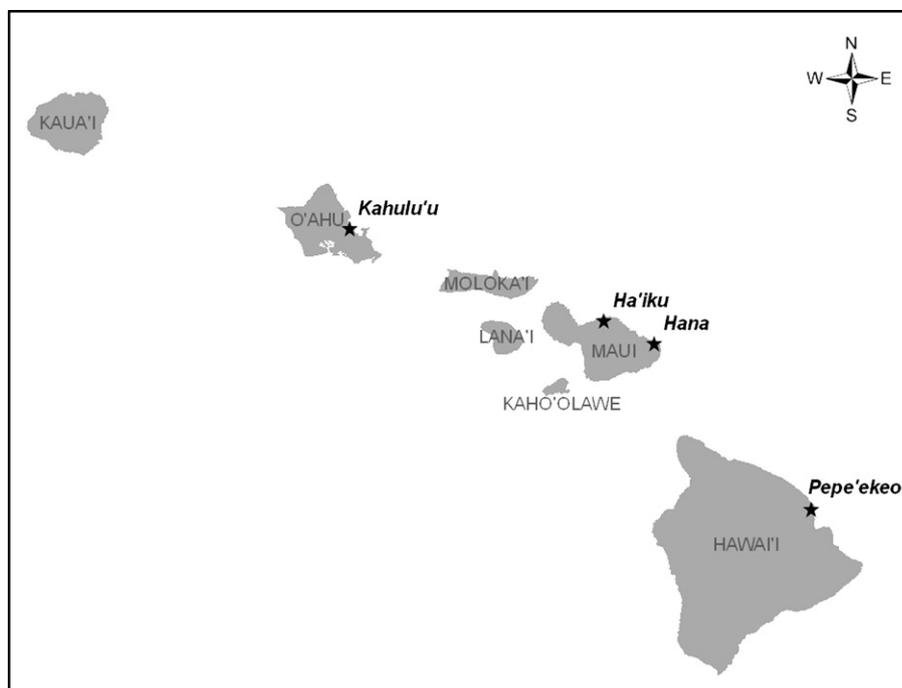


Fig. 1. Location of sites in Hawaii where ripe (yellow) turkeyberry fruits were collected for assessment of natural parasitism of *B. latifrons*.

added to serve as a pupation medium. The sand or vermiculite was sieved through a strainer weekly for four successive weeks in order to recover pupating larvae and puparia. Although turkeyberry fruits are primarily infested by *B. latifrons*, they are also occasionally infested by *B. dorsalis* in Hawaii. Therefore, all puparia were identified to species, before emergence of adult fruit flies or parasitoids, based on the numbers of tubules and form of the prothoracic spiracles. (White and Elson-Harris, 1992). Each puparium, once identified, was placed in a separate 22-ml plastic cup for recovery of emerging flies and parasitoids.

For solitary parasitoids (i.e., all braconids), percent parasitism was calculated by dividing the total number of adult parasitoids emerging from the puparia of a given fly species (i.e., *B. latifrons* or *B. dorsalis*) by the total number of puparia obtained from a fruit sample and multiplying by 100. For gregarious parasitoids (i.e., *Tetrastichus*), the number of parasitoids recovered was first divided by the average number of parasitoids recovered per parasitized puparium and then that number was divided by the total number of puparia obtained from a fruit sample and multiplied by 100. Unclosed puparia were examined for determination of parasitism based on the position and architecture of emergence holes (Ramadan and Wong, 1990; Pemberton and Willard, 1918). A subsample of these unclosed puparia was dissected to document the cause of mortality and presence and species of parasitoids.

Parasitoid species were identified using the taxonomic keys of Wharton and Gilstrap (1983) and confirmed by Bernarr Kumashiro in comparison with type specimens housed at the Hawaiian Department of Agriculture (HDOA). Nomenclature follows Wharton (1997). Voucher parasitoid and fly specimens are saved in the entomological

collections of the University of Hawaii at Manoa and HDOA.

3. Results

3.1. Pupal recovery from turkeyberry fruits

Numbers of turkeyberry fruits collected, weight of fruits, number of *B. latifrons* and *B. dorsalis* puparia recovered, and total percentage parasitism for each site are presented in Table 1. The goal of recovery of 1000 *B. latifrons* puparia per site was exceeded at 3 of the 4 sites. At the 4th site (Pepeekeo), only 897 *B. latifrons* puparia were recovered because turkeyberry plants were bulldozed before the targeted 1000 puparia could be recovered. Turkeyberry infestation by tephritid fruit flies ranged from a low of 44.3 puparia/kg at Pepeekeo to a high of 252.5 puparia/kg at Kahaluu. Of the tephritid infestation, over 96% at each site was *B. latifrons*. Recovery of *B. dorsalis* varied among sites from a low of 0.34% (Hana) to a high of 3.71% (Haiku).

Percentage parasitism of *B. latifrons* ranged from a low of 0.8% (Hana) to a high of 8.8% (Kahaluu). Percentage parasitism of *B. dorsalis* ranged from a low of 0% (Hana and Pepeekeo) to a high of 15.4% (Kahaluu). The site with the highest parasitism for *B. latifrons* was also the site for the highest parasitism of *B. dorsalis* (Kahaluu).

3.2. Parasitoid species diversity and abundance

The number of parasitoids of each species recovered from fruit fly puparia is presented in Table 2. Five parasitoid species were identified from *B. latifrons* puparia; three

Table 1
Recovery of tephritid fruit flies and total tephritid fruit fly parasitoids from ripe (yellow) turkeyberry fruits at four sites in Hawaii

Site	No. of fruit collections ^a	No. of fruits	Fruit weight (kg)	Total no. puparia	Fruit fly species	No. puparia by species	Puparia per kg fruit	Adult flies	Unemerged puparia	Parasitized puparia	Parasitism (%)
Haiku	9	13,333	20.497	1671	<i>B. latifrons</i>	1609	78.5	1317	182	110	6.8
					<i>B. dorsalis</i>	62	3.0	42	11	9	14.5
Hana	5	13,542	24.252	2378	<i>B. latifrons</i>	2370	97.7	2140	211	19	0.8
					<i>B. dorsalis</i>	8	0.33	8	0	0	0
Kahului	3	3624	6.626	1673	<i>B. latifrons</i>	1634	246.6	1434	57	143	8.8
					<i>B. dorsalis</i>	39	5.9	25	8	6	15.4
Pepeekeo	12	9899	20.755	919	<i>B. latifrons</i>	897	43.2	756	123	18	2.0
					<i>B. dorsalis</i>	22	1.1	18	4	0	0

^a Number of collections by year: Haiku : 2003 (3), 2004 (5), 2005 (1); Hana: 2004 (4), 2005 (1); Kahului: 2005 (3); Pepeekeo: 2004 (3), 2005 (6), 2006 (3).

of these species also parasitized *B. dorsalis* puparia. The relative proportions, across all samples, of recovered parasitoids is presented in Table 3 and described further below.

3.2.1. Braconidae

Braconids were the most common parasitoids. Four species of braconids in three genera were recovered. *Fopius arisanus* (Sonan) was the most abundant braconid and was the dominant parasitoid at three of the four sites, accounting for 70.3% of parasitoid adults and 80.3% of the braconids. *Psytalia incisi* (Silvestri), was the second most abundant braconid, accounting for 11.7% of parasitoid adults and 13.4% of the braconids. *Diachasmimorpha tryoni* (Cameron) was the third most abundant braconid. It accounted for only 3.1% of adult parasitoids and 3.5% of the braconids and was recovered only from the Haiku site, accounting for 8.0% of all adult parasitoids at that site. *Diachasmimorpha longicaudata* (Ashmead) was the fourth most abundant braconid. The highest percentage of *D. longicaudata* was recorded at the Pepeekeo site, where the wasp accounted for 5.6% of the parasitoids.

3.2.2. Eulophidae

The only Eulophid species recovered in the present study was the gregarious endoparasitoid, *Tetrastichus giffardianus* Silvestri. The number of progeny per host puparium and sex ratio recorded from the different collection sites are presented in Table 4. Haiku and Kahului had the highest numbers of puparia parasitized by *T. giffardianus*, accounting for 47.2% and 27.8% of the total number of *T. giffardianus*—parasitized-puparia, respectively. Based on a total of 36 *B. latifrons* puparia parasitized by *T. giffardianus*, the mean (\pm SEM) number of wasps to emerge per puparium was 8.89 (\pm 0.9). Twenty-five percent of all puparia contained five or less and fifty percent contained eight or less *T. giffardianus*. The maximum total progeny from a single puparium was 20, which was recorded twice from Haiku.

4. Discussion

This study reports the results of three consecutive years of survey on an Asian fruit fly pest, *Bactrocera latifrons*, and parasitoids, with important behavioral and ecological differences: (1) An egg-larval, solitary endoparasitoid, *F. arisanus* from Asia, the origin of the insect pest; (2) Two larval, solitary endoparasitoids, *D. longicaudata* and *P. incisi* from Asia, the origin of the insect pest; (3) A larval, solitary endoparasitoid, *D. tryoni* from Australia; and (4) A larval gregarious endoparasitoid, *T. giffardianus* from Africa. These parasitoids have fortuitously adapted to *B. latifrons* first detected in Hawaii more than 30 years after the last major biological control program against fruit flies in the State. *F. arisanus*, *D. longicaudata* and *P. incisi*, have potentially co-evolved with *B. latifrons*. *Diachasmimorpha tryoni*, and *T. giffardianus*, have also adapted to *B. latifrons*. *F. arisanus* and *D. longicaudata* were recovered in higher numbers than were the parasitoids of Australian

Table 2
Recovery of parasitoids, by species, from each species of fruit fly recovered from ripe (yellow) turkeyberry fruits at four sites in Hawaii

Sites	Fruit fly species	<i>F. arisanus</i>		<i>P. incisi</i>		<i>D. tryoni</i>		<i>D. longicaudata</i>		<i>T. giffardianus</i>	
		Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
Haiku	<i>B. latifrons</i>	34	31	2	13	4	5	2	2	82	88
	<i>B. dorsalis</i>	2	3	0	1	2	1	0	0	0	0
Hana	<i>B. latifrons</i>	3	3	3	6	0	0	0	0	14	12
	<i>B. dorsalis</i>	0	0	0	0	0	0	0	0	0	0
Kahuluu	<i>B. latifrons</i>	61	65	2	3	0	0	1	1	46	48
	<i>B. dorsalis</i>	3	3	1	1	0	0	1	1	0	0
Pepeekeo	<i>B. latifrons</i>	3	4	1	4	0	0	0	1	11	19
	<i>B. dorsalis</i>	0	0	0	0	0	0	0	0	0	0

Table 3
Relative abundance of parasitoids (percentage of total collected) reared from *B. latifrons* puparia recovered from ripe (yellow) turkeyberry fruits from four study sites on three major islands in Hawaii (6 October, 2003 to 10 August, 2006)

Parasitoid species	Total number parasitoids recovered	Braconids (%)	Total parasitoids (%)
Braconids			
<i>Fopius arisanus</i>	204	80.3	70.3
<i>Psytalia incisi</i>	34	13.4	11.7
<i>Diachasmimorpha tryoni</i>	9	3.5	3.1
<i>Diachasmimorpha longicaudata</i>	7	2.8	2.4
Total Braconids	254		
Eulophids			
<i>Tetrastichus giffardianus</i>	320 ^a	12.4	
Total parasitoids	574		

^a This number actually represents a total number of 36 puparia collected that yielded an average number of 8.89 *T. giffardianus* emerged per parasitized *B. latifrons* puparium.

Table 4
Progeny (mean \pm SEM) per host puparium and sex ratio (\pm SEM) of *Tetrastichus giffardianus* Silvestri (Hymenoptera: Eulophidae) parasitizing *Bactrocera latifrons* (Hendel) (Diptera: Tephritidae) in different localities in Hawaii

Sites	Number of parasitized puparia	Progeny per puparium	Sex ratio (% females)
Maui			
Haiku	17	10.0 \pm 1.3	51.1 \pm 1.9
Hana	4	6.5 \pm 1.9	43.9 \pm 6.4
Hawaii			
Pepeekeo	5	6.0 \pm 3.4	58.3 \pm 2.8
Oahu			
Kahuluu	10	9.4 \pm 1.2	53.6 \pm 1.4
All sites	36	8.0 \pm 1.0	51.7 \pm 3.0

and African origin (*D. tryoni* and *T. giffardianus*), perhaps because of the known long evolutionary history they have with *B. latifrons*.

Although infestation of turkeyberry by *B. dorsalis* was limited, with few recovered parasitoids, *F. arisanus* was the predominant parasitoid of *B. dorsalis* as was true also for *B. latifrons*. Biological control of *B. dorsalis* started two years after its introduction to Hawaii in 1945. From 1947 to 1952, 24 natural enemy species were imported and released into Hawaii (Clausen et al., 1965), with no further introductions of parasitoids of tephritid fruit flies from 1953 to 2002.

Fopius arisanus, naturally occurring from southern India to Taiwan, was introduced to Hawaii in the late 1940s against *B. dorsalis* (Fullaway, 1951; Wharton and Gilstrap, 1983; Wharton, 2005). Following its introduction, *F. arisanus* was found to successfully parasitize and complete development in *C. capitata* (Bess et al., 1961; Vargas et al., 2001). *F. arisanus* was shown to be the dominant parasitoid reared from fruits in Kula, Maui (Wong et al., 1984) as well as in Makaha and Waianae Valley (both on Oahu) (Harris and Lee, 1986). The dominance of *F. arisanus* was explained by its superior dispersal ability (Bess et al., 1950) and ability to efficiently utilize resident fruit fly hosts (Harris and Lee, 1989; Harris et al., 1991). Under laboratory conditions, *F. arisanus* also oviposits in eggs of the melon fly (Nishida and Haramoto, 1953). Although it appears that *F. arisanus* is not able to develop in the melon fly egg, it has a negative effect on the fitness of the egg (Bautista et al., 2004). *F. arisanus* is a polyphagous egg-larval parasitoid, attacking at least 18 host species (Rousse et al., 2005). It was deliberately introduced in several countries, including Australia, Fiji, Mauritius, Mexico, Costa Rica, Peru, Argentina, Guatemala and the USA Mainland (Rendon et al., 2006; Wharton, 2005; Ovruski et al., 2000). It is only known to have become established in Costa Rica on the Mediterranean fruit fly (Wharton et al., 1981). The occurrence of *F. arisanus* in turkeyberry is consistent with its relatively large success over opiine parasitoids in most environments where the parasitoid has established (Wharton, 2005; Wang and Messing, 2002, 2003).

Psytalia incisi has an Indo-Pacific origin (Wharton, 2005). The wasp was introduced to Hawaii in the late 1940s against the oriental fruit fly, *B. dorsalis* (van den Bosch et al., 1951). Following its introduction in Hawaii, *P. incisi* was found to successfully parasitize and complete

development in *C. capitata* as well (Wharton and Gilstrap, 1983). *P. incisi* is known to successfully develop in various *Bactrocera* spp. in Thailand and Malaysia (Chinajariya-wong et al., 2000). The parasitoid has been successfully introduced and established in other countries, including Argentina, Australia, Costa Rica, Fiji, Mauritius, Mexico, The Philippines and the mainland USA. (Wharton, 2005).

Diachasmimorpha tryoni originated from Australia and was introduced in Hawaii between 1912 and 1913. It successfully established against *C. capitata* (Silvestri, 1914; Pemberton and Willard, 1918) and since then has been consistently reported as one of the important biological control agents of this fly (Wharton, 2005; Wong et al., 1991; Wong and Ramadan, 1987). *D. tryoni* has also been introduced and successfully established against fruit-infesting tephritids in other genera such as *Anastrepha* (Wharton, 2005). Although *D. tryoni* has been successfully reared in the laboratory on *B. latifrons*, this is the first record of *D. tryoni* successfully attacking *B. latifrons* in the field in Hawaii. The recovery of *D. tryoni* has been reported from *B. dorsalis* only when the host fly has been previously attacked by other primary parasitoids (see Ramadan et al., 1994).

Diachasmimorpha longicaudata originated from the Indo-Pacific region (Wharton, 2005) and was introduced to Hawaii between 1948 and 1952 to suppress the oriental fruit fly (Bess et al., 1961). Following its introduction, *D. longicaudata* was found to successfully parasitize and complete development in *C. capitata* and is reported to successfully develop in several other *Bactrocera* and *Anastrepha* spp. (Clausen et al., 1965; Wharton et al., 1981). It is the most widely employed parasitoid for augmentative bio-control programs against fruit flies in Latin America and the southern United States, primarily because it can be easily mass-reared and adapts readily to different fruit fly species of economic importance (see Wharton, 2005).

Tetrastichus giffardianus is a gregarious larval endoparasitoid that was successfully introduced from West Africa to Hawaii against *C. capitata* in 1914 and was also subsequently released against *B. dorsalis* in 1950 to 1951 (Willard, 1937; Clausen et al., 1965). Female *T. giffardianus* oviposit in late instar larvae, with adults subsequently emerging from the host puparium (Silvestri, 1914; Clausen, 1978; Ramadan and Wong, 1990; Purcell et al., 1997). This species has been studied in association with Mediterranean fruit fly and oriental fruit fly in Hawaii and was mass-reared and released against Mediterranean fruit fly and native tephritid pests in Brazil (see Wharton, 2005). Average parasitoid progeny per *B. latifrons* puparium reported here (8.0) is greater than that reported by Ramadan and Wong (1990) for *B. dorsalis* and *C. capitata* puparia (6.4). This is probably due to the larger size of *B. latifrons* puparia in comparison to laboratory reared *B. dorsalis* and *C. capitata*. In most cases, the slightly female biased sex ratio found in our study was reported in previous studies (Pemberton and Willard, 1918; Ramadan and Wong, 1990; Purcell et al., 1996) and also in a recent study on

the closely related species, *Tetrastichus giffardii* Silvestri (Hymenoptera: Eulophidae) (Mohamed et al., 2006).

Parasitism of *B. latifrons* in turkeyberry was very low. It may be possible that these parasitoids do not prefer searching turkeyberry even if suitable fruit fly hosts are abundant. However, the levels of parasitism reported here could be underestimating the real parasitism for several reasons. First, fruit sampling may cause a considerable reduction in the site density of fly larvae that could have been available for the parasitoids and resulted in low estimates of parasitism (Sivinski et al., 1996; Wong et al., 1991). Second, the impact of some parasitoids may have been underestimated by not sampling freshly fallen fruit on the ground. For example, *D. longicaudata* has been found to attack larvae in fallen fruit on the ground (Purcell et al., 1994). In that study, *D. longicaudata* increased in abundance, and parasitism levels were highest, in guavas that remained on the ground for 6–10 days. Furthermore, the eulophid parasitoid, *Tetrastichus giffardianus* (Silvestri), was more abundant in 4- to 9-day-old ground fruit. Both parasitoids were recorded in our study, but fruits fallen on the ground (which were very few) were not sampled. Turkeyberry fruits typically stay on plants and do not readily fall. Third, parasitism rates reported here were based on parasitoid emergence only. First instar larvae or parasitoids that died from probing activities of parasitoids on earlier stages of the hosts were not taken into account. However, the possibility of parasitism of uneclosed puparia was taken into consideration through the dissection of a subset of 144 unemerged puparia. From this subset it was found that, based on the presence of melanized and encapsulated eggs, 9% of all dissected puparia contained parasitoids while scars, indicative of parasitoid probing, were present in an additional 86.8%.

It is possible that we failed to detect some of the parasitoid species established on *B. latifrons* that may more readily parasitize *B. latifrons* in plant hosts other than turkeyberry. Additionally, because in our study, no soil sample was analyzed we may have missed pupal parasitoids such as *Dirhinus giffardii* (Chalcididae) and *Pachycrepoideus vindemmiae* (Pteromalidae) (two ectoparasitoids of tephritid fruit flies) that were found to develop well on *B. latifrons* in recent laboratory studies (Wang and Messing, 2004a,b).

Although we reared *P. incisi*, *D. tryoni* and *D. longicaudata* from our field samples, the parasitism levels were low. This is possibly due to the competitive interaction of these larval parasitoids with the early acting egg-larval parasitoid, *F. arisanus*. Eggs of larval parasitoids die in the presence of *F. arisanus* larvae in multiparasitized hosts of both *C. capitata* and *B. dorsalis* through physiological suppression of development, a mechanism consistent with what has been found for other larval fruit fly parasitoids tested in Hawaii (Wang and Messing, 2002, 2003; Wang et al., 2003; Haramoto, 1953; van den Bosch and Haramoto, 1953). Host species does not appear to be a factor that influences the competitive outcome between *F. arisanus*

and larval parasitoids suggesting that these parasitoids may have suffered from the competitive superiority of *F. arisanus* in *B. latifrons*.

The pattern of parasitism among the parasitoid species recovered in our study is consistent with result of interspecific competition as recently demonstrated by Wang and Messing (2002, 2003; and Hawkins, 2000). In addition to this pattern of parasitism, we note that parasitism of *B. latifrons* was higher at sites with higher *B. dorsalis* infestation of turkeyberry fruits. It would be ecologically worthwhile to investigate factors determining parasitism of *B. latifrons* in conditions of coexistence with *B. dorsalis* and various parasitoids in different environments.

The observed overall low level of parasitism suggests a need to improve biological control of *B. latifrons*, to minimize chances of this species to develop an economic impact on crop production in Hawaii. Improvement of biological control could be achieved either through augmentative releases of parasitoids that are already established in Hawaii or through introduction and release of specific and efficient new parasitoids.

Augmentative release of parasitoids has been proposed for fruit fly suppression (Knipling, 1992), and Ovruski et al. (2000) has provided a review of augmentative biological control programs. *F. arisanus* appears to be a good candidate for augmentative biological control of *B. latifrons* because it has been consistently reared from the fly in both lab and field conditions and methods for its mass production have been developed (Bautista et al., 1999). This parasitoid has been recently mass-reared and used in augmentative releases against *B. cucurbitae* (R. Bautista, unpub. res.) so could be augmentatively released for control of *B. latifrons*. This potentially could help to increase parasitism rates by *F. arisanus*, especially at sites where there is limited or no co-infestation of fruits by *B. latifrons* and *B. dorsalis*, so little opportunity for *F. arisanus* individuals to switch over to *B. latifrons* from *B. dorsalis*.

For the alternative option of releasing new parasitoid species against *B. latifrons*, careful consideration would need to be made of which species might have the best potential for biological control of *B. latifrons*. We anticipate that any parasitoid, to be effective against *B. latifrons*, should have a well known microhabitat preference with the fruit fly pest, and a well known evolutionary history or a high searching capacity and demonstrated host specificity. We suggest two parasitoids that could be considered as potential candidates for biological control of *B. latifrons*: (1) *Diachasmimorpha kraussii* (Fullaway) (Hymenoptera: Braconidae), a parasitoid known from Australia. It was previously introduced into Hawaii in 1949 for biological control of *B. dorsalis*, with over 25,000 individuals released between 1950 and 1954 but failed to become established. Subsequent laboratory studies in Hawaii showed that *D. kraussii* successfully parasitized both *B. latifrons* and *C. capitata* but not *B. dorsalis* (Messing and Ramadan, 2000). Therefore, it could, if successfully colonized in the field, contribute to the suppression of *B. latifrons* as part

of an Integrated Pest Management program of the fruit fly pest in Hawaii. We have pursued this option by making inoculative releases of *Diachasmimorpha kraussii* beginning in March 2004, at a site with well established turkeyberry plants and known to also have a well established *B. latifrons* population. The recovery and establishment of this wasp will be presented elsewhere; (2) *Aganaspis daci* (Weld) (Hymenoptera: Eucolidae), a parasitoid which originated from Asia. It was first detected parasitizing fruit flies of the genus *Dacus* in Malaysia (Weld, 1951). *Aganaspis daci* is reported as a solitary larval parasitoid of several fruit fly species in South-East Asia and Australia (Clausen et al., 1965). Different aspects of the basic biology of *A. daci* were studied in the laboratory associated with programs directed against *Bactrocera dorsalis* (Hendel) in Hawaii (Clausen et al., 1965) and *Anastrepha suspensa* (Loew) in Florida (Nunez-Bueno, 1982). This species has also been introduced to Mexico (Jimenez-Jimenez, 1956) and Costa Rica (Wharton et al., 1981; Jiron and Mexzon, 1989). More recently, the establishment of the wasp was confirmed in *Ceratitidis capitata*-infested figs in Greece (Papadopoulos and Katsoyannos, 2003). Based on preliminary reports on its host range and biological performance, *A. daci* is a potential candidate for biological control of *B. latifrons* (Mohsen Ramadan, unpubl. results).

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References

- Armstrong, W.R., 1983. Atlas of Hawaii, second ed. University of Hawaii Press, Honolulu, HI.
- Back, E.A., Pemberton, C.E., 1917. The melon fly in Hawaii. U.S. Dept. Agric. Bull. No. 491, Washington, DC.
- Back, E.A., Pemberton, C.E., 1918. The Mediterranean fruit fly in Hawaii. U.S. Dept. Agric. Bull. No. 536, Washington, DC.
- Bautista, R.C., Harris, E.J., Vargas, R.I., Jang, E.B., 2004. Parasitization of melon fly (Diptera: Tephritidae) by *Fopius arisanus* and *Psytalia fletcheri* (Hymenoptera: Braconidae) and the effect of fruit substrates on host preference by parasitoids. Biol. Control 30, 156–164.
- Bautista, R.C., Mochizuki, N., Spencer, J.P., Harris, E.J., Ichimura, D.M., 1999. Mass-rearing of the tephritid fruit fly parasitoid *Fopius arisanus* (Hymenoptera: Braconidae). Biol. Control 15, 137–144.
- Bess, H.A., van den Bosch, R., Haramoto, F.H., 1950. Progress and status of two recently introduced parasites of the oriental fruit fly, *Dacus dorsalis* (Hendel) in Hawaii. Proc. Hawaii. Entomol. Soc. 14, 29–33.
- Bess, H.A., van den Bosch, R., Haramoto, F.H., 1961. Fruit fly parasites and their activities in Hawaii. Proc. Hawaii. Entomol. Soc. 17, 367–578.

- Carroll, L.E., Norrbom, A.L., Dallwitz, M.J., Thompson, F.C., 2005 onwards. Pest fruit flies of the world-Larvae. Version: 13th April 2005. <http://delta-intkey.com>.
- Chinajariyawong, A., Clarke, A.R., Jirasurat, M., Kritsaneepiboon, S., Lahey, H.A., Vijaysegaran, S., Walter, G.H., 2000. Survey of opiine parasitoids of fruit flies (Diptera: Tephritidae) in Thailand and Malaysia. *Raffles Bull. Zool.* 48, 71–101.
- Clausen, C.P., 1978. In: *Introduced Parasites and Predators of Arthropod Pests and Weeds: A World Review*, Agriculture Handbook No. 480, Clausen, C.P. (Ed.), Agricultural Research Service, United States Department of Agriculture. pp. 313–335.
- Clausen, C.P., Clancy, D.W., Chock, Q.C., 1965. Biological control of the oriental fruit fly (*Dacus dorsalis* Hendel) and other fruit flies in Hawaii. *USDA Tech. Bull. No. 1322*, pp. 1–102.
- Fullaway, D.T., 1951. Review of the Indo-Australasian parasites of the fruit flies (Tephritidae). *Proc. Hawaii Entomol. Soc.* 14, 243–250.
- Haramoto, F.H., 1953. The Biology of *Opius oophilus* Fullaway (Hymenoptera: Braconidae). Master Thesis, University of Hawaii, USA.
- Harris, E.J., Lee, C.Y.L., 1986. Seasonal and annual occurrence of Mediterranean fruit flies in Makaha and Wainae Valleys, Oahu, Hawaii. *Environ. Entomol.* 15, 507–512.
- Harris, E.J., Lee, C.Y.L., 1989. Development of *Ceratitidis capitata* (Diptera: Tephritidae) in Coffee in wet and dry habitats. *Environ. Entomol.* 18, 1042–1049.
- Harris, E.J., Okamoto, R.Y., Lee, C.Y.L., Nishida, T., 1991. Suitability of *Dacus dorsalis* and *Ceratitidis capitata* (Diptera: Tephritidae) as hosts of the parasitoid, *Biosteres arisanus* (Hymenoptera: Braconidae). *Entomophaga* 36, 425–430.
- Harris, E.J., Liquido, N.J., Spencer, J.P., 2001. Distribution and host utilization of *Bactrocera latifrons* (Diptera: Tephritidae) on the island of Kauai, Hawaii. *Proc. Hawaii Entomol. Soc.* 35, 55–66.
- Hawkins, B.A., 2000. Species coexistence in parasitoid communities: does competition matter? In: Hochberg, M.E., Ives, A.R. (Eds.), *Parasitoid Population Biology*. Princeton University Press, Princeton, pp. 198–213.
- Jimenez-Jimenez, E., 1956. Las moscas de la fruta y sus enemigos naturales. *Fitofilo* 16, 4–11.
- Jiron, L.F., Mexzon, R.G., 1989. Parasitoid hymenopterans of Costa Rica: geographical distribution of the species associated with fruit flies (Diptera: Tephritidae). *Entomophaga* 34, 53–60.
- Klungness, L.M., Jang, E.B., Mau, R.F., Vargas, R.I., Sugano, J.S., Fujitani, E., 2005. New approaches to sanitation in a cropping system susceptible to tephritid fruit flies (diptera: tephritidae) in Hawaii. *J. Appl. Sci. Environ. Manage.* 9, 5–15.
- Knipling, E.F., 1992. Principles of Insect Parasitism Analyzed from New Perspectives. *USDA-ARS Agriculture Handbook*, p. 693.
- Liquido, N.J., Harris, E.J., Dekker, A., 1994. Ecology of *Bactrocera latifrons* (Diptera: Tephritidae) populations: host plants, natural enemies, distribution, and abundance. *Ann. Entomol. Soc. Am.* 87, 71–84.
- McQuate, G.T., Bokonon-Ganta, A.H., Peck, S.L., in press. Background population biology and prospects for suppression of the solanaceous fruit fly, *Bactrocera latifrons* (Diptera: Tephritidae). *Proc. Hawaii Entomol. Soc.*, in press.
- Messing, R.H., Ramadan, M.M., 2000. Host range and reproductive output of *Diachasmimorpha kraussii* (Hymenoptera: Braconidae), a parasitoid of Tephritid fruit flies newly imported to Hawaii. In: Tan, K.H. (Ed.), *Area-wide Control of Fruit Flies and Other Insect Pests*. Penerbit Universiti Sains Malaysia, Penang, Malaysia, pp. 713–718.
- Mohamed, S.A., Wharton, R.A., von Mérey, G., Schulthess, F., 2006. Acceptance and suitability of different host stages of *Ceratitidis capitata* (Wiedemann) (Diptera: Tephritidae) and seven other tephritid fruit fly species to *Tetrastichus giffardii* Silvestri (Hymenoptera: Eulophidae). *Biol. Control* 39, 262–271.
- Nishida, T., Haramoto, F., 1953. Immunity of *Dacus cucurbitae* to attack by certain parasites of *Dacus dorsalis*. *J. Econ. Entomol.* 46, 61–64.
- Nunez-Bueno, L., 1982. *Trybliographa daci* Weld (Hymenoptera: Cynipidae): Biology and aspects of the relationship with its host *Anastrepha suspensa* (Loew) (Diptera: Tephritidae). Ph.D. Thesis, Department of Entomology and Nematology, University of Florida, pp. 153.
- Ovruski, S.S.S., Aluja, M., Sivinski, J., Wharton, R., 2000. Hymenopteran parasitoids on fruit-infesting Tephritidae (Diptera) in Latin America and the southern United States: diversity, distribution, taxonomic status and their use in fruit fly biological control. *Int. Pest Manage. Rev.* 5, 81–107.
- Papadopoulos, N.T., Katsoyannos, B.I., 2003. Field parasitism of *Ceratitidis capitata* larvae by *Aganaspis daci* in Chios, Greece. *BioControl* 48, 191–195.
- Peck, S.L., McQuate, G.T., 2004. Ecological Aspects of *Bactrocera latifrons* (Diptera: Tephritidae) on Maui, Hawaii: movement and host preference. *Environ. Entomol.* 33, 1722–1731.
- Pemberton, C.E., Willard, H.F., 1918. A contribution to the biology of fruit-fly parasites in Hawaii. *J. Agricult. Res.* 15, 419–467.
- Purcell, M.F., Duan, J.J., Messing, R.H., 1997. Response of three hymenopteran parasitoids introduced for fruit fly control to a gall-forming tephritid, *Procecidochares alani* (Diptera: Tephritidae). *Biol. Control* 9, 193–200.
- Purcell, M.F., Van Nieuwenhoven, A., Batchelor, M.A., 1996. Bionomics of *Tetrastichus giffardianus* (Hymenoptera: Eulophidae) an endoparasitoid of Tephritid fruit flies. *Environ. Entomol.* 25, 198–206.
- Purcell, M.F., Jackson, C.G., Long, J.P., Batchelor, M.A., 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. Control* 4, 396–403.
- Ramadan, M.M., Wong, T.T., 1990. Biological observations on *Tetrastichus giffardianus* (Hymenoptera: Eulophidae), a gregarious endoparasitoid of the Mediterranean fruit fly and the Oriental fruit fly (Diptera: Tephritidae). *Proc. Hawaii Entomol. Soc.* 30, 59–62.
- Ramadan, M.M., Wong, T.T.Y., Herr, J.C., 1994. Is the oriental fruit fly (Diptera: Tephritidae) a natural host for the opiine parasitoid *Diachasmimorpha tryoni* (Hymenoptera: Braconidae)? *Environ. Entomol.* 23, 761–769.
- Rendon, P., Sivinski, J., Holler, T., Bloem, K., Lopez, M., Martinez, A., Aluja, M., 2006. The effects of sterile males and two braconid parasitoids, *Fopius arisanus* (Sonan) and *Diachasmimorpha kraussii* (Fullaway) (Hymenoptera), on caged populations of Mediterranean fruit flies, *Ceratitidis capitata* (Wied.) (Diptera: Tephritidae) at various sites in Guatemala. *Biol. Control* 36, 224–231.
- Rousse, P., Harris, E.J., Quilici, S., 2005. *Fopius arisanus*, an egg-pupal parasitoid of Tephritidae Overview. *Biocontrol News Info.* 26, 59N–69N.
- Samways, M.J., 1997. Classical biological control and biodiversity conservation: what risks are we prepared to accept? *Biodiversity and Conserv.* 6, 1309–1316.
- Silvestri, F., 1914. Report of an expedition to Africa in search of the natural enemies of fruit flies (Trypaneidae) with descriptions, observations and biological notes. Territory of Hawaii Board of Agriculture and Forestry. Division of Entomology Bulletin 3 (1–146), 167–176.
- Sivinski, J.M., Calkins, C.O., Baranowski, R., Harris, D., Brambila, J., Diaz, J., Burns, R.E., Holler, T., Dodson, G., 1996. Suppression of a Caribbean fruit fly (*Anastrepha suspensa* (Loew) Diptera: Tephritidae) population through augmented releases of the parasitoid *Diachasmimorpha longicaudata* (Ashmead) (Hymenoptera: Braconidae). *Biol. Control* 6, 177–185.
- van den Bosch, R., Haramoto, F.H., 1953. Competition among the parasites of the oriental fruit fly. *Proc. Hawaii Entomol. Soc.* 15, 201–206.
- van den Bosch, R., Bess, H.A., Haramoto, F.H., 1951. Status of oriental fruit fly parasites in Hawaii. *J. Econ. Entomol.* 44, 753–759.
- van Zwaluvenburg, R.H., 1947. Notes and exhibitions. *Proc. Hawaii Entomol. Soc.* 13, 8.
- Vargas, R.I., Long, J., Miller, N.W., Delate, K., Jackson, C.G., Uchida, G.K., Bautista, R.C., Harris, E.J., 2004. Releases of *Psytalia fletcheri*

- (Hymenoptera: Braconidae) and sterile flies to suppress melon fly (Diptera: Tephritidae) in Hawaii. *J. Econ. Entomol.* 97, 1531–1539.
- Vargas, R.I., Jang, E.B., Klungness, L.M., 2003. Area-wide pest management of fruit flies in hawaiian fruits and vegetables. *Proc. Res. Inst. Subtropics Meeting Fruit Flies*, 37–46.
- Vargas, R.I., Peck, S.L., McQuate, G.T., Jackson, C.G., Stark, J.D., Armstrong, J.W., 2001. Potential for area wide integrated management of Mediterranean fruit fly (Diptera: Tephritidae) with a braconid parasitoid and a novel bait spray. *J. Econ. Entomol.* 94, 817–824.
- Vargas, R.I., Nishida, T., 1985a. Survey for *Dacus latifrons* (Diptera: Tephritidae). *J. Econ. Entomol.* 78, 1311–1314.
- Vargas, R.I., Nishida, T., 1985b. Life history and demographic parameters of *Dacus latifrons* (Diptera: Tephritidae). *J. Econ. Entomol.* 78, 1242–1244.
- Wagner, W.L., Herbst, D.R., Sohmer, S.H., 1990. Manual of the flowering plants of Hawaii. Bernice P. Bishop Museum special publication 83, University of Hawaii Press, Honolulu, HI.
- Wang, X.G., Messing, R.H., 2002. Newly imported larval parasitoids pose minor competitive risk to the extant egg-larval parasitoid of fruit flies in Hawaii. *Bull. Entomol. Res.* 92, 423–429.
- Wang, X.G., Messing, R.H., 2003. Intra- and interspecific competition by *Fopius arisanus* (Hymenoptera: Braconidae) and *Diachasmimorpha tryoni* (Hymenoptera: Braconidae), parasitoids of the Mediterranean fruit fly *Ceratitis capitata* (Diptera: Tephritidae). *Biol. Control* 27, 251–259.
- Wang, X.G., Messing, R.H., Bautista, R.C., 2003. Competitive superiority of early acting species: a case study of opiine fruit fly parasitoids. *Biocontrol Sci. Tech.* 16, 391–402.
- Wang, X.G., Messing, R.H., 2004a. The ectoparasitic pupal parasitoid, *Pachycrepoideus vindemmia* (Hymenoptera: Pteromalidae), attacks other primary tephritid fruit fly parasitoids: host expansion and potential non-target impact. *Biol. Control* 31, 227–236.
- Wang, X.G., Messing, R.H., 2004b. Potential interactions between pupal and egg- or larval-pupal parasitoids of tephritid fruit flies. *Environ. Entomol.* 33, 1313–1320.
- Weld, L.H., 1951. A new species of *Trybliographa* (Hymenoptera: Cynipidae). *Proc. Hawaii Entomol. Soc.* 14, 331–332.
- Wharton, R.A., 2005. Parasitoids of Fruit-infesting Tephritidae. <http://hymenoptera.tamu.edu/paroffit/>.
- Wharton, R.A., 1997. Generic relationships of opiine Braconidae (Hymenoptera) parasitic on fruit-infesting Tephritidae (Diptera). *Contrib. Am. Entomol. Inst.* 30, 1–53.
- Wharton, R.A., 1989. Classical biological control of fruit infesting Tephritidae. In: Robinson, A. S., Hooper, G. (Eds.), *World Crop Pests*, vol. 3B, Elsevier, New York, pp. 303–313.
- Wharton, R.A., Gilstrap, F.E., 1983. Key and status of opiine braconid (Hymenoptera) parasitoids used in biological control of *Ceratitis capitata* and *Dacus*, s.l. (Diptera: Tephritidae). *Ann. Entomol. Soc. Am.* 76, 721–742.
- Wharton, R.A., Gilstrap, F.E., Rhode, R.H., Fischel-M, M., Hart, W.G., 1981. Hymenopterous egg-pupal and larval-pupal parasitoids of *Ceratitis capitata* and *Anastrepha* spp. (Diptera: Tephritidae) in Costa Rica. *Entomophaga* 26, 285–290.
- White, I.M., Elson-Harris, M.M., 1992. *Fruit Flies of Economic Significance: Their Identification and Bionomics*. C.A.B. International, Wallingford, UK.
- Willard, H.F., 1937. Parasitization of the Mediterranean Fruitfly in Hawaii, 1914–33. *USDA Circular No.* 439.
- Wong, T.T.Y., Ramadan, M.M., 1987. Parasitization of the Mediterranean and oriental fruit flies (Diptera: Tephritidae) in the Kula area of Maui, Hawaii. *J. Econ. Entomol.* 80, 77–80.
- Wong, T.T.Y., Mochizuki, N., Nishimoto, J.I., 1984. Seasonal abundance of parasitoid of the Mediterranean and Oriental fruit flies (Diptera: Tephritidae) in the Kula area of Maui. *Hawaii. Environ. Entomol.* 13, 140–145.
- Wong, T., Ramadan, M., McInnis, D., Mochizuki, N., Nishimoto, J., Herr, J., 1991. Augmentative releases of *Diachasmimorpha tryoni* (Hymenoptera: Braconidae) to suppress a Mediterranean fruit fly (Diptera: Tephritidae) population in Kula. *Hawaii. Biol. Cont.* 1, 2–7.