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ESTABLISHMENT OF THE WEST INDIAN FRUIT FLY (DIPTERA: TEPHRITIDAE) PARASITOID *DORYCTOBRACON AREOLATUS* (HYMENOPTERA: BRACONIDAE) IN THE DOMINICAN REPUBLIC

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ABSTRACT

The West Indian fruit fly, *Anastrepha obliqua* (Macquart), infests numerous fruit species, particularly Anacardiaceae and most importantly mango (*Mangifera indica* L.). Widespread in the Neotropics, it was first reported in Hispaniola nearly 70 years ago. Continental populations are attacked by the opiine braconid parasitoids *Utetes anastrephae* (Viereck) and *Doryctobracon areolatus* (Szépligeti). Largely sympatric, the two species co-exist through microhabitat specializations based on different ovipositor lengths and asymmetries in larval competitive abilities during multiparasitism. *Utetes anastrephae*, but not *D. areolatus*, is apparently native to the Dominican Republic. Since the two parasitoids share an evolutionary history over a substantial portion of their distributions it was proposed that 1) *D. areolatus* would find the Dominican environment suitable, as does *U. anastrephae*; and 2) that there would be no negative interactions when the two species were reunited and overall parasitism would increase. Immediately following releases, *D. areolatus* averaged 9% of adult insects recovered and two years after releases were concluded constituted a mean of 13%. By then the parasitoid had spread up to 50 km from release sites. There was no evidence of competitive exclusion of *U. anastrephae* by *D. areolatus.* Another opiine biological control candidate, *Diachasmimorpha longicaudata* (Ashmead), could be considered for release and establishment. Parasitoids alone are unlikely to provide economic levels of control, but can serve as components of an integrated pest management program established to maintain "fly-free" or "low prevalence" fruit export zones.

Key Words: *Anastrepha obliqua,* mango, biological control, invasive pest

RESUMEN

La mosca de las frutas de las Indias Occidentales, *Anastrepha obliqua* (Macquart), infesta numerosas especies de frutales, principalmente anacardiáceas, siendo el mango (*Mangifera indica* L.) especie de mayor importancia. Aunque este tefrítido está ampliamente distribuido en el Neotrópico fue registrado hace 70 años en La Hispaniola. Las poblaciones continentales de *A. obliqua* son atacadas por los parasitoides bracónidos *Utetes anastrephae* (Viereck) y *Doryctobracon areolatus* (Szépligeti). Las dos especies de parasitoides co-existen a través de especializaciones basados en diferencias en la longitud del ovipositor y asimetrías en las habilidades competitivas durante el multiparasitismo. *Utetes anastrephae*, pero no así *D. areolatus*, es nativo en la República Dominicana donde ataca especies de *Anastrepha* nativas. Como las dos especies de parasitoides comparten una historia evolutiva sobre una porción sustancial de su rango de distribución, se pronosticó que: 1) *D. areolatus* se adaptaría al ambiente dominicano, tal como lo hace *U.*

anastrephae; y 2) no existirían interacciones negativas cuando las dos especies estén juntas y que el parasitismo total se incrementaría. Inmediatamente después de las liberaciones se recuperó un 9% de adultos de *D. areolatus* y dos años después de finalizadas las liberaciones se recobró un 13%. El parasitoide se diseminó por lo menos hasta 50 km de los sitios de liberación. No se observaron evidencias de exclusión competitiva de *U. anastrephae* por *D. areolatus*. Se recomienda a *Diachasmimorpha longicaudata* (Ashmead) como otro posible agente para el control biológico de *A. obliqua*. Los parasitoides por sí solos, probablemente no alcancen niveles económicos de control, pero pueden servir como componentes de un programa de manejo integrado de plagas para mantener zonas de exportación de frutas libres o de baja prevalencia de moscas.

Translation provided by the authors.

Neotropical and subtropical tephritid fruit flies infest hundreds of fruit and vegetable species (White & Elson-Harris 1992; Foote et al. 1993). Several polyphagous species are particularly destructive and responsible for trade restrictions wherever they occur (Siebert 1999; Siebert & Cooper 1995). *Anastrepha obliqua* (Macquart), the West Indian or Mango fruit fly, is one of the foremost of these pests and most frequently infests species of Anacardiaceae (Hernández-Ortíz and Aluja 1993). *Spondias* spp. ("tropical plums") are particularly favored among native plants, but mango (*Mangifera indica* L.) is economically the most important host. Widespread, the fly occurs from the Greater (including Hispaniola) and Lesser Antilles to Mexico and south through Ecuador and parts of Brazil (Stone 1942; Foote et al. 1993). Wherever it exists, *A. obliqua* threatens both mangoes grown for local consumption, and complicates or precludes mango exports. Population levels in the Dominican Republic can be extremely high. For instance, up to 60 flies per trap have been captured in a single day in the mango orchards of Hato Damas (Serra et al. 2005a; Ogando & Serra 2006; Thomas et al. 2008). These high levels may be due to both a lack of sanitation measures and a depauperate natural enemy guild (Ovruski et al. 2000; Castillo et al. 2006).

The natural enemies of *A. obliqua* in Mexico have been investigated in detail (Sivinski et al. 1997, 1998; Aluja et al. 1998; Lopez et al. 1999), and 2 largely sympatric species of opiine braconids, *Utetes anastrephae* (Viereck) and *Doryctobracon areolatus* (Szépligeti), inflict high levels of mortality on *A. obliqua* in *Spondias* spp. Both *U. anastrephae* and *D. areolatus* attack late-instar *Anastrepha* spp larvae, but because of a significantly shorter ovipositor, *U. anastrephae* is only efficient at reaching hosts in small fruit (Sivinski et al. 1998, 2001). *Doryctobracon areolatus* on the other hand is a major natural enemy of a variety of *Anastrepha* spp. larvae in a large number of fruit. In Florida, where biological control introductions have reunited the two species, only *D. areolatus* is found in *Psidium guajava* L. but both species occur in the much smaller *Eugenia uniflora* (Sivinski et al. 1998). Even within a fruit species the mean size of fruit containing *U. anastrephae* can be smaller than that of fruits containing *D. areolatus.* In spite of its shorter ovipositor, limited host range, lower fecundity and shorter adult life span (Sivinski et al. 2000), *U. anastrephae,* appears to persist because of its superior ability as an "intrinsic competitor" in instances of multiparasitism (Aluja et al., unpublished data).

Utetes anastrephae, but not *D. areolatus*, historically has parasitized native *Anastrepha* spp. on Hispaniola and occasionally parasitizes up to 90% of *A. obliqua* locally in *Spondias* spp. (Serra et al. 2005b). Because the two species co-occur commonly on the American mainland, it was predicted that 1) *D. areolatus* would find the Dominican environment suitable, as does *U. anastrephae*; and 2) there would be no negative interactions between 2 closely co-evolved species; and overall parasitism would increase with the introduction of *D. areolatus,* particularly among flies developing in larger fruits.

Two regions of the Dominican Republic were chosen for parasitoid releases: Hato Damas in the southern part of the country and Mata Larga in the northeast. Evidence of *D. areolatus* recovery, offspring of released parasitoids collected in the same fruiting season, and of establishment (*D. areolatus* collected in a subsequent fruiting season), are presented in the following. In addition, we discuss *U. anastrephae* parasitism, the effects of fruit size and host density on parasitism by both species and search for any indication of *D. areolatus* excluding *U. anastrephae* from hosts. The introduction of another opiine braconid species, *Diachasmimorpha longicaudata* (Ashmead), is considered and we argue that, in this particular case, sequential introductions might be more efficacious than simultaneous.

Materials and Methods

Origin of Parasitoids

Doryctobracon areolatus were reared at the Instituto de Ecologia, Xalapa, Veracruz, Mexico on larvae of *Anastrepha ludens*. Details on the facilities, equipment and procedures are available in Aluja et al. (2009).

Release Sites

Parasitoids were periodically released at sites chosen on the basis of relatively high *Anastrepha* spp. densities and large numbers of *Spondias* spp., particularly *S. mombin* L. host trees in the Hato Damas area near San Cristóbal (18°24'59.51"N: 70°06'27.98"W) and in the Mata Larga area, and the rural surroundings of San Francisco de Macoris (19°18'01.83"N: 70°15'15.33"W). At each site there were initially 20 host tree-release points.

Release Schedule

Twenty one *D. areolatus* releases were made at approximately weekly intervals over the period, 17 Jun to 15 Dec 2005. Mortality and sex ratio of newly arrived parasitoids were recorded. They were then provided with honey and water, held for a min of 24 h, and separated into lots of 20 individuals (ca. 1 male: 2 females) each for transport to release sites. In total, 16,973 *D. areolatus,* 58% of them female, were taken into the field. Of these, 87% (14,791) were released in the Hato Damas region. Five releases totaling 2,182 (67% female) insects were made in the Mata Larga region from 22 Jul to 30 Sep 2005.

Fruit Sampling and Parasitoid Recovery

Freshly fallen fruit and fruit from the canopy - when fallen fruits were absent - were collected, counted and weighed on the day of release, 2 days after and ~1 week after release. Sample sizes were based on estimates of available fruit (Sivinski et al. 1996; Sivinski et al. 1998). Larvae were allowed to emerge from fruit for a minimum of 10 d. They were then transferred to cups containing moistened sand as a pupation medium and held for another mo. Adult insect eclosion was noted over this period and insect identities were confirmed.

Statistical Analysis

With the most extensive data sets (insects from *S. mombin*; 2005, release year and 2007, a post-release year), the General Linear Models (GLM) procedure of the Statistical Analysis System (SAS Inst. 2004) was used to examine the following effects on parasitism by *U. anastrephae* and *D. areolatus;* estimated fruit size (= sample weight/number of fruit in the sample), mean numbers of hosts in the sample, mean parasitoid density (numbers of parasitoids / weight of fruit), and parasitism by the other parasitoid species. Parasitism data, being proportional, was log-arcsine transformed prior to analysis. Separate analyses were used to examine the effects of the following abiotic parameters on parasitism by both species: sample site (a class variable), Julian date and the quadratic of Julian date (to examine any possible non-linear relationships). In order to determine if parasitism by *D. areolatus* supplanted that of *U. anastrephae,* a Student t-test, with a Satterthwaite correction due to unequal variance, compared fruit samples that contained *U. anastrephae* and in which *D. areolatus* were either present or not. Lower mean parasitism by *U. anastrepahae* in the presence of *D. areolatus* could indicate competition for hosts, but similar levels of *U. anastrephae* parasitism in the 2 categories would suggest that *D. areolatus* was providing additional parasitism.

Results

Evidence of Establishment and Spread of *Doryctobracon areolatus*

In 2007, 2 years following parasitoid releases, *D. areolatus* was recovered from 17 of 18 of the monitored localities in the Hato Damas region. Where parasitism occurred, percent parasitism ranged from 1.1 to 100% (Fig. 1, derived from 18 *Spondias* spp. trees). In addition to being collected from *S. mombin*, *D. areolatus* was also collected from *Anastrepha* spp. in "tropical plum/ciruela" (*S. purpurea* L. var. 'flava' and var. 'purpurea', Anacardiaceae), golden apple/manzana de oro (*S. cytherea* Sonn., Anacardiaceae), guava/guayaba (*Psidium guajava* L., Myrtaceae), Malay apple/manzana malaya (*Syzygium malaccense* (L.) Merril & Perry, Myrtaceae), bilimbi/vinagrillo (*Averrhoa bilimbi* L., Oxalidaceae), carambola (*A. carambola* L., Oxalidaceae), and tropical almond/almendro tropical (*Terminalia catappa* L., Combretaceae). In the Mata Larga area establishment was finally confirmed by 2007 in collections of *S. mombin* (Table 1), although parasitism was typically less than 10%. This relatively low level may have been due to the lower number of released parasitoids and fewer alternative fruit fly hosts.

Following post-release collections at release sites in 2007, additional fruits were collected in 2007-2008 at distances of 2.5 to 50 km from the nearest point of release. *Doryctobracon areolatus* was obtained from *S. mombin*, S. *purpurea, A. carambola* and *P. guajava* (Table 2; Fig. 2). The farthest of these points was in a commercial guava (cv. 'Cubano') orchard located in Piedra Blanca, Monseñor Nouel province, 50 km northeast of the nearest release site in the Hato Damas area. We have no way of knowing if the parasitoid dispersed there on its own or was carried by humans. Additional data on emergence of fruit flies

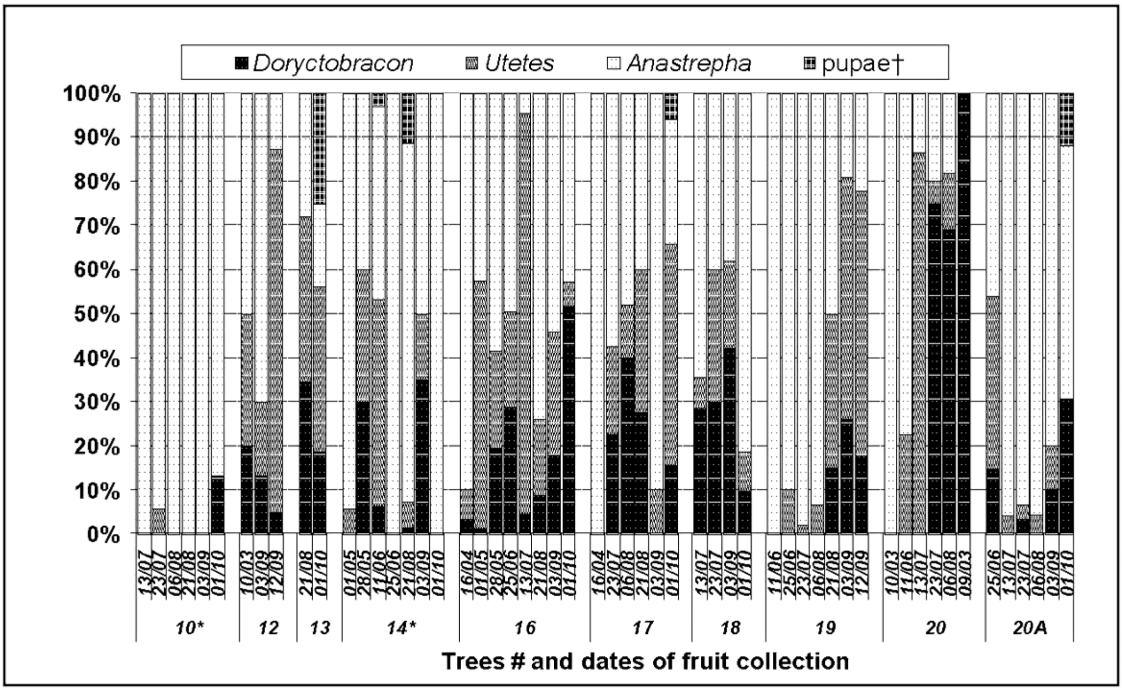

Fig. 1. Pupal mortality and emergence of *Anastrepha* spp., *Doryctobracon areolatus* and *Utetes anastrephae* from fruits of 8 of the 16 local *Spondias mombin* trees and 2 *Spondius purpurea**, i.e., # 10 & 14, at Hato Damas, San Cristóbal, 2 Apr to 10 Oct 2007.

and parasitoids during a 3.5-mo period in 2008 are presented in Fig. 2. Besides one specimen of *U. anastrephae*, all recovered parasitoids were *D. areolatus*, which attacked up to 60% of the available hosts.

Effects of Biotic and Abiotic Variables and of Potential Competition on Parasitism

In 2005, during *D. areolatus* releases, 129 samples of *S. mombin* taken from 20 sites yielded 2958 fruits (mean = 22.9 [stderr = 1.4]) weighing a total of 26.8 kg (mean = 207.1 g [15.5]) and producing 16,074 *Anastrepha* sp. pupae, probably all *A. obliqua* (mean = 124.6 [11.0]). In 2007, a year following *D. areolatus* releases, 85 samples of *S. mombin* taken from 20 sites yielded 1625 pieces of fruit (mean = 19.1 [stderr = 1.1]) weighing a total of 16.3 kg (mean = 192 g [15.0]) and producing 4274 *Anastrepha* sp. pupae, probably all *A. obliqua* (mean = 50.3 [5.9]).

In 2005, mean parasitism (# parasitoid $sp._1$ / # parasitoid $sp._1$ + # parasitoid $sp._2$ + # adult *A. obliqua*) by *U. anastrephae* was 0.34 (0.02), and 0.09 (0.01) by *D. areolatus.* In 2007, mean parasitism by *U. anastrephae* was 0.18 (0.02) and by *D. areolatus* 0.13 (0.02). Among sites, parasitism by *U. anastrephae* ranged from 0-1.0 in 2005 and from 0-0.90 in 2007. Among sites/dates, parasitism by *D. areolatus* ranged from 0-1.0 in 2005 and from 0-0.75 in 2007.

The following pertains only to insects obtained from *S. mombin* collected in 2005 (release year) and 2007 (2 years post-release). In 2005, during *D. areolatus* releases, parasitism by *U. anastrephae* was significantly and negatively related to mean estimated fruit size (F = 5.5, df = 1, $P < 0.02$). Parasitism by *D. areolatus* was not influenced by fruit size nor by host density or parasitism by *U. anastrephae* (F = 1.63, *dfmodel* = 7, *dferror* = 121, P = 0.13). It was subject to the effects of release sites (F = 2.0, df = 12, P = 0.03) and the interaction between release site and Julian date (F = 2.1, df = 12, P = 0.03). In 2007, subsequent to *D. areolatus* releases, there were no effects of fruit size, host density or parasitism by a competitor on either species (F *D. areolatus* = 1.1, *dfmodel* = 7, *dferror* = 77, P = 0.40; F *U. anastrephae* = 1.0, *dfmodel* = 7, *dferror* = 77, p = 0.46). Parasitism by *U. anastrephae* was affected by sample site (F = 2.2, df = 1, $P < 0.02$) and that by *D. areolatus* by Julian date (F = 11.3, df = 1, $P < 0.002$).

There was no evidence that *D. areolatus* excluded *U. anastrephae* from hosts during either year. In 2005 and 2007, there were no differences in *U. anastrephae* parasitism in samples with and

TABLE 2. COLLECTIONS OF FRUIT FROM NON-RELEASE SITES IN 2007-8 THAT YIELDED *DORYCTOBRACON AREOLATUS*. LOCATION REFERS TO THE DISTANCE (KM) AND DIRECTION FROM THE NEAREST RELEASE POINT.

Site, Host	Where fruit was collected Km and direction from nearest release site	Date	Number of fruit	Weight of fruits	Pupae/kg	# pupae	% Emergence			Parasitism
							Anastrepha	*D. Areolatus*	*U. Anastrepahae*	
La Cruz B, *S. mombin*	3,SW	21/08	25	155	97	15	68.0	4.0	28.0	32.0
La Cruz D, *S. mombin*	6,SW	1/10	25	198	250	40	100.0	0.0	0.0	0.0
Los Cocos, *S. mombin*	2.5,SE	3/09	85	335	314	85	45.9	2.4	51.8	54.1
Los Mameyes, *S. purpurea*	4.5,SE	21/08	16	400	100	40	90.0	10.0	0.0	10.0
Feliciano, *S. mombin*	5.5,SE	21/08	20	155	452	70	78.6	8.6	12.9	21.4
La Pared, *S. mombin*	7,SE	21/08	20	240	146	35	94.3	0.0	5.7	5.7
Piedra Blanca, *P. guajava*	50,NW	18/10	1	300	83	25	72.0	28.0	0.0	28.0

without *D. areolatus* ($t(2005) = 1.0$, df = 66.8, $P = 0.32$; $t(2007) = 1.4$, df = 61, $P = 0.15$).

DISCUSSION

Doryctobracon areolatus emerged from the puparia of *A. obliqua* following their release in the vicinity of fruiting *S. mombin, S. purpurea*, and *P. guajava* (infested with *A. suspensa*) and gave evidence of establishment when it was recovered from these same sites 2 years after releases had been concluded. Its ultimate distribution, density and capacity to control *A. obliqua* remain to be determined. This may not be the end of biological control efforts. Another candidate opiine parasitoid, *Diachasmimorpha longicaudata* (Ashmead), was not immediately released. It is an Indo-Malaysian exotic that has been introduced worldwide for tephritid control, and is a particularly effective natural enemy of *Anastrepha suspensa* (Loew) (Sivinski et al. 1996) We were concerned that it might suppress a critical alternative host for *D. areolatus* and so we postponed its establishment.

If *D. longicaudata* is also released the range of *D. areolatus* may shrink. In Mexico, *D. longicaudata* is more abundant than *D. areolatus* at higher altitudes (Sivinski et al. 2000) and in larger, commercial fruits (Lopez et al. 1999). It is unclear if the altitudinal distributions are the result of interspecific competition leading to habitat subdivision, but in Florida where first *D. areolatus* and then *D. longicaudata* was introduced to control *A. suspensa,* there is evidence of displacement (Eitam et al. 2004). Both species were originally established in southern Florida, but at present *D. areolatus* occurs in the northern portion of the peninsula (in spite of being more abundant at lower, warmer altitudes in Mexico) and *D. longicaudata* occurs in the southern portion with only a narrow range of overlap. One explanation for this distribution is that *D. areolatus* is better able to persist during periods of host scarcity and in areas with lower host-plant diversity. Thus the northern part of *A. suspensa*'s range provides a refuge from an otherwise superior competitor. In terms of biological control, parasitism levels were not noticeably affected by the replacement of one species by the other (Baranowski et al. 1993). There appears to be little reason for concern about the effects of *D. longicaudata* on the endemic *U. anastrephae.* It is widespread in Florida and occurs in the ranges of both introduced species (Eitam et al. 2004).

The possible effects of *D. areolatus*, a parasitoid with a broad host range within the genus *Anastrepha,* on native, non-target tephritids was also considered by the Ministry of Agriculture prior to release. In addition to *obliqua* and *suspensa* another 5 species of *Anastrepha* occur on

TABLE 1. RECOVERY OF *DORYCTOBRACON AREOLATUS* FROM *ANASTREPHA OBLIQUA* INFESTING *SPONDIAS MOMBIN* FRUITS COLLECTED IN THE MATA LARGA AREA IN 2007.

			% of emerged insects			
Tree #	Date	Pupae	*D. areolatus*	*U. anastrephae*	*Anastrepha*	*Parasitism*
2	21/8	70	1.4	11.4	87.1	12.9
3	21/8	39	2.6	15.4	82.1	17.9
4	21/8	65	3.1	0.0	96.9	3.1
4	3/9	32	9.4	6.3	84.4	15.6
9	3/9	69	6.3	25.0	68.8	31.3
9	26/9	32	5.0	0.0	95.0	5.0
10	26/9	24	6.0	0.0	94.0	6.0
12	21/8	44	4.5	4.5	90.9	9.1
15	21/8	83	7.3	0.0	92.7	7.3

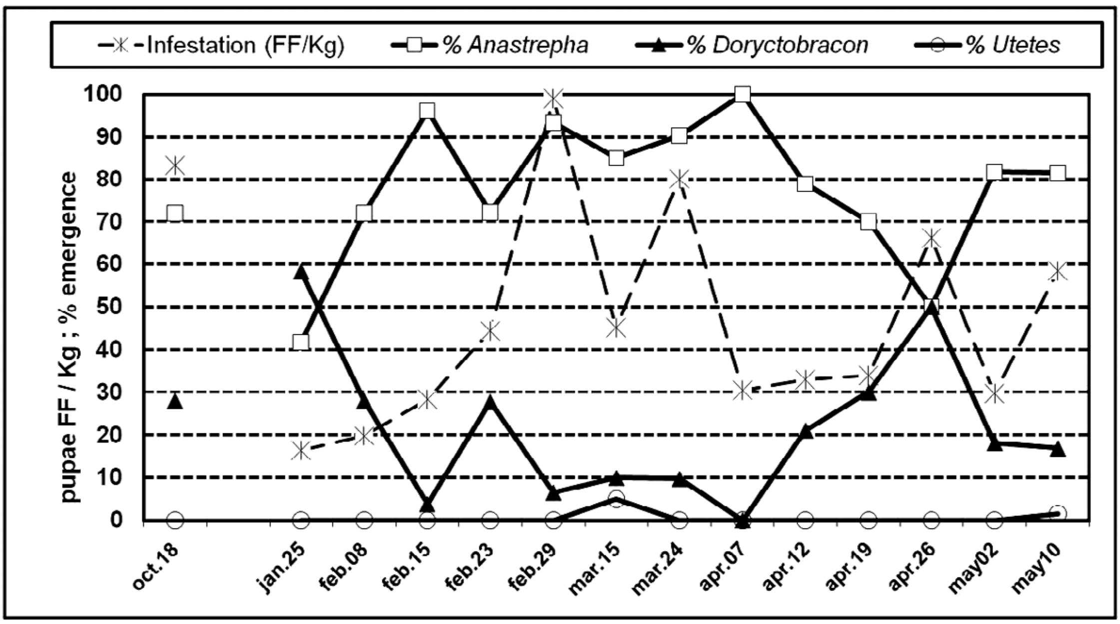

Fig. 2. Infestation of *Psidium guajava* fruits, and the emergence of *Anastrepha* (probably *suspensa*) and braconid parasitoids at Piedra Blanca, Monseñor Nouel on 18 Oct 2007 (first detection) and between 25 Jan and 10 May 2008.

Hispaniola: *A. dissimilis* Stone, *A. insulae* Stone, *A. ocresia* Walker, *A. antillensis* Norrbom and *A. stonei* Steyskal (Stone 1942; Norrbom 1998). While there was no guarantee that *D. areolatus* would not attack these species as well, typically *D. areolatus* parasitism rates of uncommon, non-pestiferous flies are very low (<1%; e.g., Aluja et al. 2000; Aluja et al. 2003; Pereira et al. 2007; Rull et al. 2009).

Biological control, even with the addition of *D. areolatus*, is unlikely to unilaterally solve the economic problems created by *A. obliqua.* However, it could serve as a component of an integrated pest management program designed to protect “fly-free export” or “low-prevalence” zones, particularly if high fly populations in non-commercial *Spondias* spp. could be suppressed leaving fewer flies to disperse into agricultural environments (Sivinski et al. 1996).

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