COLONIZATION OF *FOPIUS CERATITIVORUS*, A NEWLY DISCOVERED AFRICAN EGG-PUPAL PARASITOID (HYMENOPTERA: BRACONIDAE) OF *CERATITIS CAPITATA* (DIPTERA: TEPHRITIDAE)

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ABSTRACT

Fopius ceratitivorus Wharton is a recently discovered braconid parasitoid of the Mediterranean fruit fly (= medfly), *Ceratitis capitata* (Wied.). Unlike other parasitoids previously used in medfly biological control, *F. ceratitivorus* was originally collected from medfly in its purported region of origin, east Africa. Shipments of *Ceratitis* spp. pupae from Kenya to a newly constructed quarantine facility in Guatemala yielded both *F. ceratitivorus* and its congener *F. caudatus* (Szèpligeti). Only the former species was successfully colonized through the use of medfly infested coffee berries. In the process of colonization it was determined that *F. ceratitivorus* oviposited into the eggs and recently hatched larvae of medflies and completed development in the hosts' puparia. This is a relatively rare behavior among fruit fly parasitoids and, because tephritid eggs near the surface of fruits are particularly vulnerable to attack, one that might contribute to its success as a biological control agent.

Key Words: biological control, mass-rearing, medfly

RESUMEN

F. ceratitivorus Wharton es un parasitoide Braconido de la mosca del Mediterráneo (= moscamed), *Ceratitis capitata* (Wied.), recientemente descubierto. A diferencia de otros parasitoides previamente usados en el control biológico de la moscamed, *F. ceratitivorus* fue colectado originalmente de moscamed en su supuesta región de origen, al este de Africa. Envíos de pupa de tephritidos desde Kenia hacia la recientemente construida instalación de Cuarentena en Guatemala, produjeron especimenes de *F. ceratitivorus* y su congener *F. caudatus* (Szepligeti). Solo la primera especie fue colonizada exitosamente mediante el uso de frutos de café infestados por moscamed. En el proceso de colonización se determinó que *F. ceratitivorus* oviposita sobre los huevos y larvas recientemente eclosionadas de moscamed, y que completa su desarrollo en la pupa huésped. Este es un comportamiento relativamente raro dentro de los parasitoides de moscas de la fruta, y debido a que los huevos de los tephritidos cercanos a la superficie del fruto son particularmente vulnerables, ello podría contribuir a su éxito como agente de control biológico.

By the end of the 19th century the Mediterranean fruit fly (= medfly), *Ceratitis capitata* (Wied.), had spread from its African homeland to tropical and subtropical countries around the

world. After finding medfly in the Honolulu area in 1910, the progressive Hawaiian agricultural community of the time financed an African collection of tephritid natural enemies by Silvestri (1914) in order to bring the fly under biological control. By 1918 there were several parasitoids from various parts of the world established in Hawaii, including three species of opiine Braconidae (Pemberton & Willard 1918). Over time, subsequent expeditions resulted in additional Hawaiian establishments (Gilstrap & Hart 1987), the most effective of which for suppression of both medfly and oriental fruit fly (*Bactrocera dorsalis* [Hendel]) proved to be the braconid *Fopius arisanus* (Sonan) (Bess et al. 1961).

While *F. arisanus* is a common parasitoid of medfly in Hawaii, it is an Asian species that was originally obtained from the pupae of oriental fruit fly (Wharton & Gilstrap 1983). In fact, to our knowledge, none of the braconids successfully disseminated for the control of medfly originated from collections of medfly (Wharton & Gilstrap 1983; Ovruski et al. 2000). This shortage of "true-medfly" parasitoids is not due to a lack of candidates since a recent Kenyan survey of *Ceratitis* spp. yielded 10 species of hymenopterous parasitoids (Wharton et al. 2000; see also Steck et al. 1986), but probably reflects the historical difficulty of transporting live insects from Africa to afflicted agricultural areas such as Hawaii or Central America (e.g., van Zwaluwenburg 1937).

We here describe the shipment to Guatemala and subsequent colonization of *Fopius ceratitivorus* Wharton, a recently discovered parasitoid of the medfly that is both a true, African natural enemy of medfly and, like its congener *F. arisanus,* an egg-pupal parasitoid. This combination of characteristics suggests that this species may be a particularly attractive candidate for biological control.

Materials and Methods

Origin of Insects

Fopius ceratitivorus has been obtained only from coffee, *Coffea arabica* L., in central Kenya and in particular from plantations at Ruiru (1°5.72'S, 36°54.22'E at 1609 m) and Rurima (0°38.39'S,37°29.69'E at 1228 m) (Wharton 1999; Wharton et al. 2000). Mean annual rainfalls in these areas are 1.06 m and 0.9 m, respectively, and the mean temperature ranges are 12.8-25 and 15.5-28°C, respectively (Wharton et al. 2000). Collections were made throughout the November-July coffee harvest season. The tephritids in the shipments, in order of abundance, were: *C. capitata, C. rosa* Karsch, and *Trirhithrum coffeae* Bezzi (Wharton 1999).

Insect Arrival

Field collection procedures and handling procedures were described by Wharton et al. (2000). Pupae were shipped by air in lots of 4,000-23,000 insects to the Guatemala International Airport, cleared through customs, and then brought by car to the USDA-APHIS/MOSCAMED quarantine facility at San Miguel Petapa, Guatemala (Table 1).

Quarantine Facility

Packages were brought to the USDA-APHIS / MOSCAMED quarantine facility at San Miguel Petapa outside of Guatemala City, Guatemala. Initially, packages holding pupae were removed from containers in a large (0.8 × 0.8 × 0.8 m) sleeved cage separated from the remainder of the quarantine facility by a locked door. Adult parasitoids were captured individually and transferred to smaller (21 × 21 × 21 cm) cages containing honey and a water-wick while adult flies were placed in 70% ethanol and preserved for latter ex-

Table 1. The dates, sources, and numbers of pupae in shipments of *Ceratitis* spp. pupae from Kenya to the quarantine facility near Guatemala City, Guatemala as well as the numbers of various parasitoids the shipment contained and the % parasitism of the pupae.

				Parasitoids		
Date	Collection	No. Pupae	% Parasitism	F. ceratitivorus	F. caudatus	D. fullaway
9/19/2000	Koru	4,310	4.11	0	177	0
10/31/2000	Koru	10,052	2.14	0	215	0
10/31/2000	Ruiru		0.73	73	0	0
12/22/2000	Koru	22,507	0.46	0	95	8
12/22/2000	Ruiru		1.57	290	0	63
12/22/200	Rurima		0.35	74	0	5
6/26/2001	Koru	15,645	12.77	0	1,998	0
12/21/2001	Koru	8,043	0.20	0	16	0
12/21/2001	Ruiru		3.68	221	0	75

amination. Caged parasitoids were then moved into a larger room within the quarantine facility that had both windows providing natural light and artificial lighting (12L: 12D). Temperature in this room was 26°C and relative humidity 65-75%. All packaging materials and biological wastes were sterilized in an autoclave before removal from the quarantine building. Specimens of all insect species received were preserved in collections at the quarantine facility.

Presentation of Hosts

Several means of host presentation were developed, including artificially placing eggs into slits cut through the skin and pulp of coffee berries. However, the most practical and effective means of presenting hosts to *F. ceratitivorus* consisted of first allowing female medflies to oviposit into firm coffee berries that were mature to the point of color-break. In addition to conserving any host-location cues the ovipositing medfly might leave, this technique minimized fermentation during the presentation. High densities of medflies (~4,000 males and 4,000 females) were kept in $31 \times 31 \times 31$ cm screen cages and allowed to lay eggs in varying numbers of berries for a period of 24 hours. The berries had been previously strung on thread to form "necklaces" of ~180 fruits and then suspended from the ceiling of the cage. Strings of berries were then transferred to screen cages that contained ~600 female parasitoids and a similar number of males. There was an attempt to present infested fruit at a ratio of 3 fruit / female (~120 host egg clutches / female parasitoid). Females at the time of first presentation were ~ 8 days of age and had been kept in the presence of similar aged males since eclosion. During the first 2 days of this mating period cages were placed near windows to approximate a natural light environment. Over the next 6 days the cages were kept under full spectrum lights.

Typically, infested fruits were exposed to parasitoids for 48 hours; however, if berries were small and prone to drying exposures were curtailed after 24 hours. Depending on coffee availability there were 2 to 4 exposures / cage / week. Female survived in the exposure cages for up to 45 days, with 50% percent of females were typically alive after 30 days. Male lifespans were lower in quarantine, with 50% dead after only 15 days.

In addition to coffee, medflies were allowed to oviposit in several other fruits that were subsequently exposed to *F. ceratitvorus* : mangos (*Mangifera indica* L. var. Tommy Atkins), *Spondias* sp., papaya (*Carica papaya* L.), apple (*Malus pumila* Mill.), peach (*Prunus persica* Batsch), and pear (*Pyrus communis* L.). The treatment of these fruits following exposure was as described above for coffee berries.

Holding of Larvae

Following either 24 or 48 hours of exposure to parasitoids, 180-360 berries were placed in 30×15 cm trays on dampened paper over a 0.5 kg of moist medfly diet obtained from the USDA-APHIS / MOSCAMED rearing facility at El Pino, Guatemala (Schwarz et al. 1985). After spraying the berries lightly with water, the trays were placed in a $0.6 \times 0.4 \times 1.0$ m rack covered with a black plastic sheet, which allowed temperature and relative humidity to increase to 26-27°C and 98-99%, respectively. After 48 hours, the berries were mixed into an additional 0.5kg of diet. Trays were moved into a cooler room at 23°C and 65-75% RH, and held over sawdust for 13 days (day 19 of the process). At the end of this time, mature larvae had left the diet and completed pupation in the sawdust. Puparia were placed in the 31 cm $\times$ 31 cm $\times$ 31 cm cages and emerging medflies removed through aspiration. *Fopius ceratitivorus* males began to eclose on day 24 and females on day 26.

Host Stage Parasitized

Standard rearing methods enabled oviposition into both eggs and newly hatched larvae. However, they did not distinguish between these stages. To better determine what stage(s) of medfly was being parasitized we varied parasitoid-exposure schedules to present either eggs alone or larvae alone (Fig. 1). In one case (Fig 1; A), fruit with eggs were presented 21 hours after the initial exposure to medfly females and then removed after 24 hours. This eliminated the possibility that early-instar larvae where present. In the second case (Fig. 1; B), 69 hours elapsed between the initiation of oviposition and exposure of the fruit to parasitoids, and only larvae were available as hosts. In the third case (Fig.1; C), the standard exposure sequence was modified so that parasitism was limited to a 24 hour period rather than the usual 48 hours. This again resulted in only eggs being present during attacks. D represents the standard sequence where both eggs and early instar larvae are potentially present. There were 3 replications of each of the exposure regimes.

Results

Host Stage Parasitized

In the course of the standard rearing procedure, infested berries were removed from exposure to parasitoids prior to or just following egg hatch and larvae were rarely observed when berries were first placed on dampened paper over diet. To better determine the stage of medfly being attacked the exposure procedure was modified to expose only eggs or only recently hatched first in-

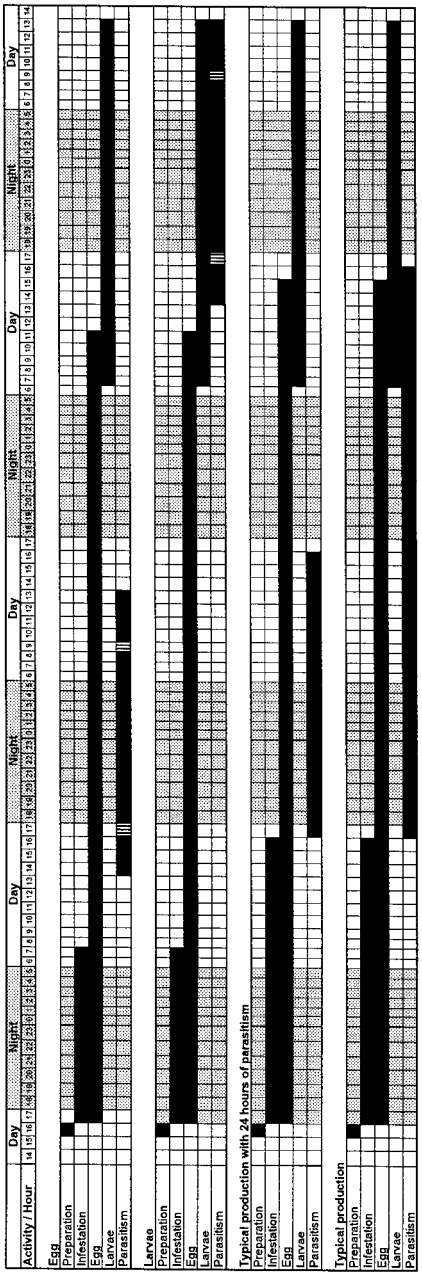

Fig. 1. The timing of exposure of coffee berries containing Mediterranean fruit fly eggs and larvae to the parasitoid *Fopius ceratitivorus.* The various schedules resulted in either eggs (A&C), first instar larvae (B) or both (D) being open to attack. Dark bars refer to time spent in the various activities of preparation of fruit to be exposed to medflies ("prepertion"), exposure of fruit to medflies ("infestation"), the period of egg availability ("egg"), the period during which eggs hatch ("larvae"), and the period of exposure to parasitoids ("parasitism"). The time line in hours is at the top of the chart and the light and shaded areas represent alternating periods of light and darkness.

star larvae to parasitoids. Both stages were vulnerable to attack (Table 2).

In addition to *F. ceratitivorus*, the Kenyan shipments contained other Braconidae including *Fopius caudatus* (Szépligeti). Attempts to rear *F. caudatus* were unsuccessful, although colonies were sometimes maintained for up to 6 generations before increasingly male-biased sex ratios resulted in collapse. *Fopius caudatus* was also an egg-pupal parasitoid and when medfly eggs were presented in slits cut in coffee berries it was relatively easy to observe the penetration of the host egg by the parasitoid's ovipositor. Its capacity to attack early instar larvae is unknown.

Percent Parasitism and Colony Growth

The *F. ceratitivorus* colony increased over time until at present (April 2002) weekly production was 10,000-18,000 adults/week or roughly 2-3 adult parasitoids per berry (Fig. 2). Overall, percent parasitism was 3.5-4%, but was occasionally as high as 21%. Typical sex ratios approximated 1 male:1 female, but were sometimes strongly female or male biased (Fig. 2). For example, in the experiments to identify stage of host attacked only 37% of the adult parasitoids were male. In part, fluctuations in numbers reflected the seasonal changes in the abundance of coffee berries used in the rearing process. *Fopius ceratitivorus* was capable of parasitizing medfly in a variety of fruit species other than coffee (Table 3), and these may be integrated into the rearing program in the future.

Discussion

The establishment of *F. arisanus* in Hawaii is arguably the most successful instance of fruit fly biological control in the world (e.g., Clausen 1978), and it would be useful to employ other parasitoids that possess the characteristics that have made *F. arisanus* so prominent among Hawaiian fruit fly natural enemies. Certainly one the most unusual attributes of *F. arisanus* is that it is an endoparasitic koinobiont that oviposits into the egg, rather than the larva, of its tephritid host (Wharton 1997)). The larval parasitoid persists in the first instar until the host's puparium is formed after which it completes its development (Clausen 1978).The ability to parasitize eggs, as do *F. arisanus, ceratitivorus* and *caudatus,* is otherwise rare among fruit fly parasitoids. We are aware of only one other species known to do so, *Utetes canaliculatus* (Gahan), a North American parasitoid of *Rhagoletis* and another opiine braconid (Prokopy & Webster 1978).

Several reasons have been proposed why egg-parasitism might account for the success of *F. arisanus*, including its early presence inside the host compared to other braconids that attack var-

TABLE 2. THE NUMBER OF *F. ARISANUS* DEVELOPING IN HOST COHORTS OF VARIOUS AGES. (A) "STANDARD EGG" REFERS TO THE COLONIZATION PROCEDURE DESCRIBED IN THE TEXT AS IT WAS APPLIED TO SMALL COFFEE BERRIES. BECAUSE SMALL FRUITS ARE SUBJECT TO DRYING THEY WOULD ONLY BE EXPOSED FOR A 24 HOUR PERIOD A DAY AFTER OVIPOSITION AND AS A RESULT WOULD CONTAIN ONLY EGGS. (D) "TYPICAL EGGS & LARVAE" REFERS TO THE 48 HOUR EXPOSURE EMPLOYED WITH LARGER BERRIES. (A) "EGG" REFERS TO A 24 HOUR EXPOSURE BEGUN EARLIER THAN USUAL TO FURTHER GUARANTEE ONLY EGGS ARE PRESENT, AND (B) "LARVAE" TO A DELAYED 24 HOUR EXPOSURE THAT WOULD CONSIST ENTIRELY OF 1ST INSTAR LARVAE

		A	B	C	D
		Egg	Larvae	Standard Egg	Standard Egg & Larvae
Exposed intervals (h)	Replicates	21-45	69-93	24-48	24-72
Adults reared	1	30	7	24	248
	2	143	51	21	92
	3	72	7	123	333
Pupae recovered (cc)	1	120	280	103	153
	2	400	250	68	62
	3	65	80	98	110
% Parasitism	1	0.4	0.0	0.4	2.6
	2	0.8	0.3	0.5	2.5
	3	1.9	0.1	2.1	5.1

ious larval instars (Bess et al. 1961). Because it is the first parasitoid present, a *F. arisanus* larva would be in a position to eliminate or suppress the growth of its competitors. In addition, tephritid eggs located near the surface of a fruit or vegetable are particularly vulnerable to parasitism. Fruit fly larvae that feed in the pulp or seeds of fruit can be difficult for parasitoids to reach with their ovipositors, and there is a well established negative relationship between fruit size and parasitism by larva-attacking braconids (e.g., Sivinski et al. 1997, Lopez et al. 1999).

Thus the capacity to parasitize vulnerable eggs and early instar larvae is potentially a valuable trait for a biological control agent (Bess et al. 1961), and medfly control in Central America may particularly benefit from the availability of an effective natural enemy. At present, there is little parasitism of medfly in the New World by native tephritid parasitoids, and only local and sporadic parasitism by introduced species such as *Diachasmimorpha longicaudata* (Ashmead) (Eskafi 1990; Sivinski et al. unpublished data). Unlike its exemplary performance in Hawaii, *F. arisanus* has either failed to become established in the Americas (Ovruski et al. 2000) or failed to flourish after establishment (Wharton et al. 1981).

In addition to being a potential candidate for establishment, *F. ceratitivorus* might prove to be important in regional eradication programs. Medfly is now widely distributed across the Latin American tropics and subtropics. The northward spread of medfly into Mexico, and ultimately into the United States, has been prevented by a Sterile Insect Technique (= SIT) / insecticide-bait spray barrier maintained along the Mexican / Guatemalan border by the international organization MOSCAMED (United States, Mexico, and Guatemala). Recently, this barrier has been expanded and the possibility of regional eradication of the medfly is under consideration (P. Rendon, personal communication.).

In a region-wide eradication program the medfly must be attacked in a variety of environments, some of which may not be amenable to repeated applications of insecticide-bait sprays, such as organic growing areas, urban / suburban locations, water-sheds, and national parks. In these areas it will be important to maximize the impact of the biological components of the various control options. There is accumulating evidence that augmentative parasitoid releases may be an efficacious means of suppressing fruit fly populations, perhaps to a level where SIT can then be used to complete eradication (e.g., Wong et al. 1991, Sivinski et al. 1996, Montoya et al. 2000).

The potential of *F. ceratitivorus* for mass-rearing and augmentative release is unknown. The mean parasitism rate in the present colony of ~4% is an order of magnitude or more lower than the laboratory parasitism rates of better established medfly parasitoids (e.g., Baeza et al. 2002). However, experience suggests that greater familiarity with the species' requirements will improve production. In the meantime a stable colony in Guatemala will allow the experiments to be accomplished that will clarify its usefulness in medfly biological control. These include determination of host range and capacity to persist through seasonal declines in Guatemalan medfly populations when eggs are rare.

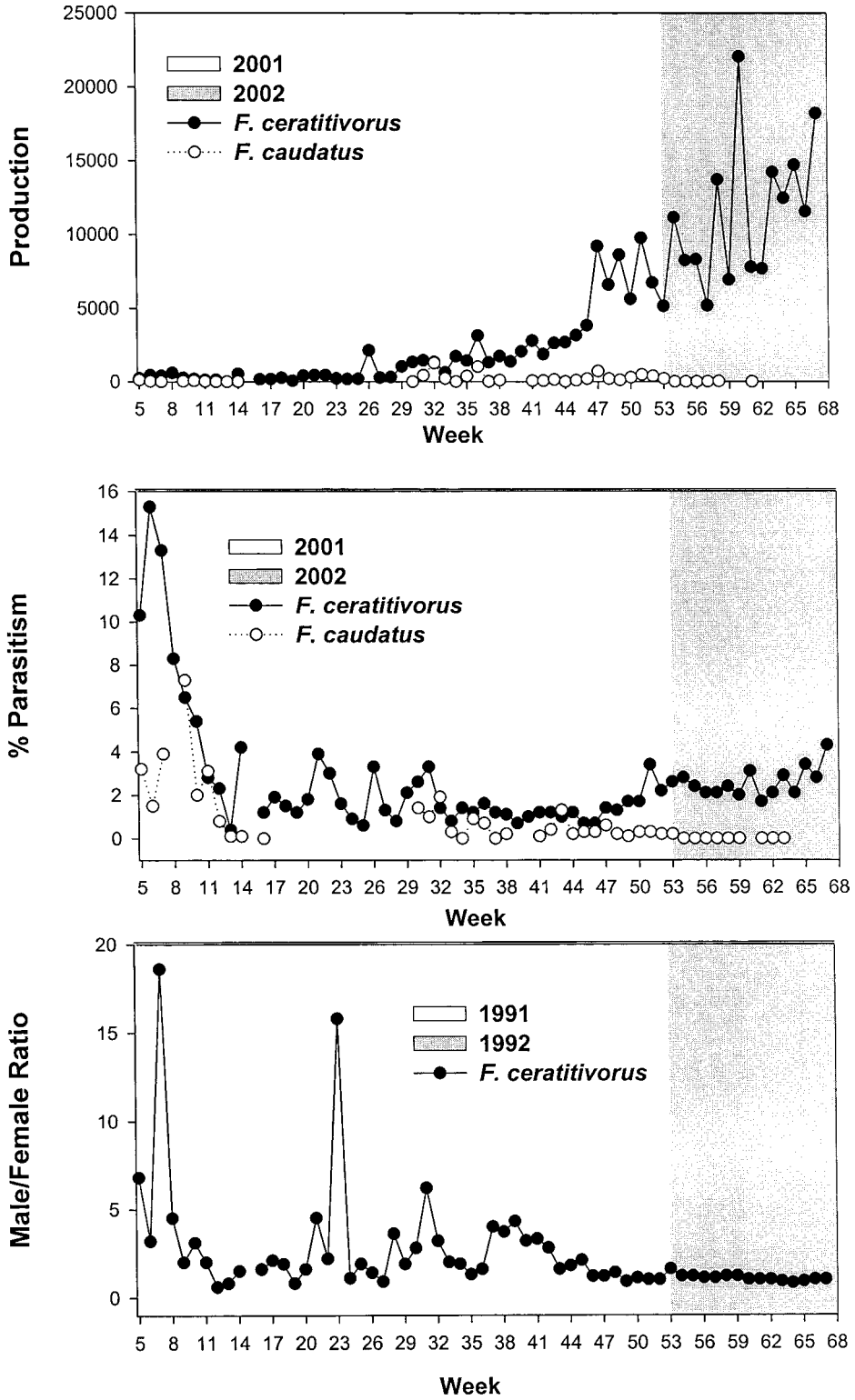

Fig 2. The production, % parasitism, and sex-ratio of *Fopius ceratitivorus* and *F. caudatus* in the Guatemalan quarantine facility over time. Sharp declines are typically due to temporary shortages of coffee berries.

TABLE 3. THE PRODUCTION OF *F. CERATITIVORUS* IN VARIOUS FRUITS INCLUDING THE MEAN NUMBERS OF PUPAE RECOVERED/FRUIT (1 ML = ~50 PUPAE), THE NUMBER OF PARASITOIDS TO EMERGE FROM THE SUMMED FRUITS OF EACH SPECIES AND THE SEX RATIOS OF THE PARASITOIDS.

Host Fruit	Number of Fruit	Pupae per Fruit (ml)	Emerged Parasitoids ♂	Emerged Parasitoids ♀	% Parasitism	♂:♀ Ratio
Mango	60	20	2,398	1,359	5.3	1.8
Pear	46	40	4,254	2,593	6.4	1.6
Coffee	1,260	1	1,511	1,343	3.3	1.1
Spondias sp.	32	2	235	99	7.2	2.4
Papaya	12	9	226	84	4.7	2.7
Peach	1	3	7	0	4.0	
Apple	1	8	0	0		

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