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Insectary production and synopsis of *Fopius caudatus* (Hymenoptera: Braconidae), parasitoid of tephritid fruit flies indigenous to Africa

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ABSTRACT

Fopius caudatus (Szépligeti) is an endophagous koinobiont egg-larval parasitoid native to Africa. It has recently been noted as a candidate for augmentative biological control of several Dacinae fruit fly pests (Diptera: Tephritidae), due to its ability to parasitize the egg stage. Previous attempts to establish this parasitoid in Hawaii, Guatemala, and Costa Rica were unsuccessful due to inability to maintain parasitoid colonies under laboratory conditions. A cohort of *F. caudatus* collected from Kenyan fruit flies infesting *Coffea arabica* was successfully colonized in Hawaii at 28 °C and 60–80% RH, resulting in the development of a laboratory-adapted colony amenable for mass production. The parasitoid was successfully developed from eggs of *Ceratitis capitata* and *Bactrocera latifrons* as a factitious host. The wasps were propagated for 15 weeks until the rearing stabilized, at which point > 10,500 adults were produced with an overall sex ratio of 0.52 females and a mean host parasitism rate of 17.3%. It could parasitize Medfly eggs in fruits other than coffee, including papaya, mango, pear, squash, and sweet pepper. Female *F. caudatus* oviposited mainly in 24–48 h old Medfly eggs, although occasionally a few individuals eclosed when first instar fly larvae were exposed. Mean developmental time from egg to adult was 19.8 d for males and 21.5 d for females. Mean longevity was 5.2 d for males and 14.2 d for host-deprived females. This study enabled us to maintain a colony of *F. caudatus* for research and redistribution to other countries for biocontrol programs against Medfly.

Introduction

Members of the genus *Fopius* (Hymenoptera: Braconidae: Opiinae) are koinobiont endoparasitoids of tephritid fruit flies (Diptera: Tephritidae), with 36 described species from the tropics (Wharton, 1999, http://media.eol.org/pages/12064901/names?all=1). They are of great importance to biological control of frugivorous fruit flies because of their mode of parasitism in the host eggs [e.g., *Fopius arisanus* (Sonan), and *F. ceratitivorus* Wharton], or early instars [e.g., *F. vandenboschi* (Fullaway)]. These life stages occur close to the surface of fruits in contrast to more mature larvae that burrow deeper in fruit where they find refuge from parasitism.

Fopius caudatus (= *Opius caudatus* or *Biosteres caudatus*) is characterized and readily identified within this species group by its black head-thorax region, and a distinctive band of setae and punctures on the frons extending between the eye and ocelli (Plates 1, 2). Additional characters are the crenulate notauli that extend to metasomal midpit and a long, strongly narrowed ovipositor with rows of setae on the sheath (Plate 3) (Wharton, 1997).

Fopius caudatus has been frequently reared from ceratitidine tephritid fruit flies in coffee and other fruits (Steck et al., 1986; Wharton et al., 2000) and from *Dacus* species infesting Cucurbitaceae in tropical regions of Western and Eastern Africa (Table 1). Unlike the Asian congener *F. arisanus,* which has a much broader host range of many host plants infested by various *Bactrocera* species, *F. caudatus* has been collected from far fewer numbers of plants, mainly infested with African *Ceratitis* and *Dacus* species (Table 1).

In its native Africa, *F. caudatus* is restricted to wet cool climates and high elevations (1400–1500 m, Trostle Duke, 2005). The original species description (Szépligeti, 1913) was of wasps collected from Nigeria (Silvestri, 1914) and Kenya (Wharton et al., 2000). No fruit collections in the lower and drier areas of Kenya yielded *F. caudatus*; there the parasitoid guild is dominated by *Fopius ceratitivorus* (Trostle Duke, 2005).

Previous attempts to colonize *F. caudatus* outside Africa (i.e., in Hawaii, Guatemala, and Costa Rica (Clancy et al., 1952; Clausen et al.,

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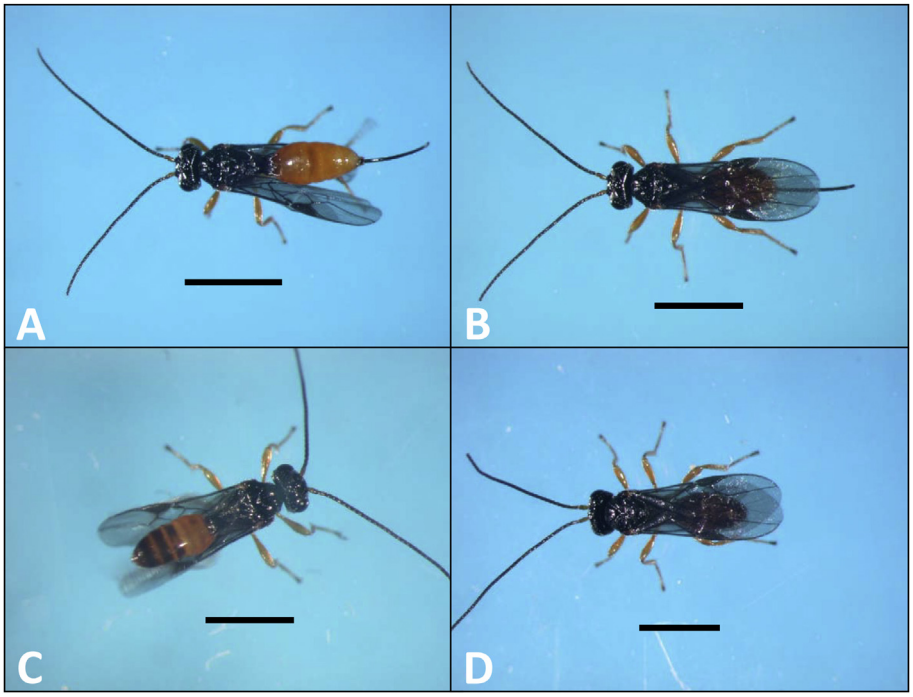

Plate 1. Habitus and color pattern of female (A, B) and male (C, D) *Fopius caudatus* Kenyan strain. Bars = 2 mm.

Plate 2. Female *F. caudatus* Kenyan strain: A) Anterior view of face showing outer surface of clypeus (red rectangle) weakly convex, ventral margin protruding, thickened medially and covering most of labrum. B) Lateral view of head with occipital carina present laterally (red rectangle). C) Deep crenulate natauli complete to midpit. D) Dorsal view of frons showing broad transverse band of punctures and dense minute setae (red rectangle) extending from occeli to compound eyes like arched eye brows (typical of *F. caudatus* only).

1965; Lopez et al., 2003; Wharton, 1989a, 1989b; Steck et al., 1986) failed mainly due to rearing difficulties during exploration and in quarantine (Table 1). During surveys in West Africa in 1912, *F. caudatus* did not survive the trip to Hawaii, because rearing was tried on host larvae rather than eggs (Silvestri, 1914). The second attempt to import *F. caudatus* into Hawaii was made from Sierra Leone and Angola in 1935–36 (van Zwaluwenburg and McGough, 1936); five parasitoid species were transported to Hawaii of which, three (*Opius giffardi* (Silvestri), *F. caudatus* and *Tetrastichus* sp.) reached Honolulu alive (total of 750 adults, Wharton et al., 2000). An undocumented number of *F. caudatus* were released in Hawaii at that time, without any subsequent recovery, apparently in sub-optimal wet habitats and targeted against the wrong host species (van Zwaluwenburg and McGough, 1936). The third attempt to import this parasitoid to Hawaii was made in 1950, against the oriental fruit fly, *Bactrocera dorsalis* (Hendel), and melon fly, *Zeugodacus cucurbitae* (Coquillett). The melon fly was included because of the parasitoid's recovery from cucurbit plants infested with *Dacus* species in West Africa (Table 1). Again, rearing efforts failed in Hawaii, with the production of few progeny and a male biased sex ratio (Clausen et al., 1965). In the 1980's *F. caudatus* was imported to Costa Rica through a Texas quarantine facility for release against Medfly. The parasitoid originated in West Africa but again failed due to rearing problems (Clausen et al., 1965). A recent attempt to rear *F. caudatus* was also made in Guatemala (December 2000) using female wasps from Kenya. This colony also collapsed after seven generations (P. Rendon, J. Sivinski, pers. comm., Lopez et al., 2003). Steck et al. (1986) and

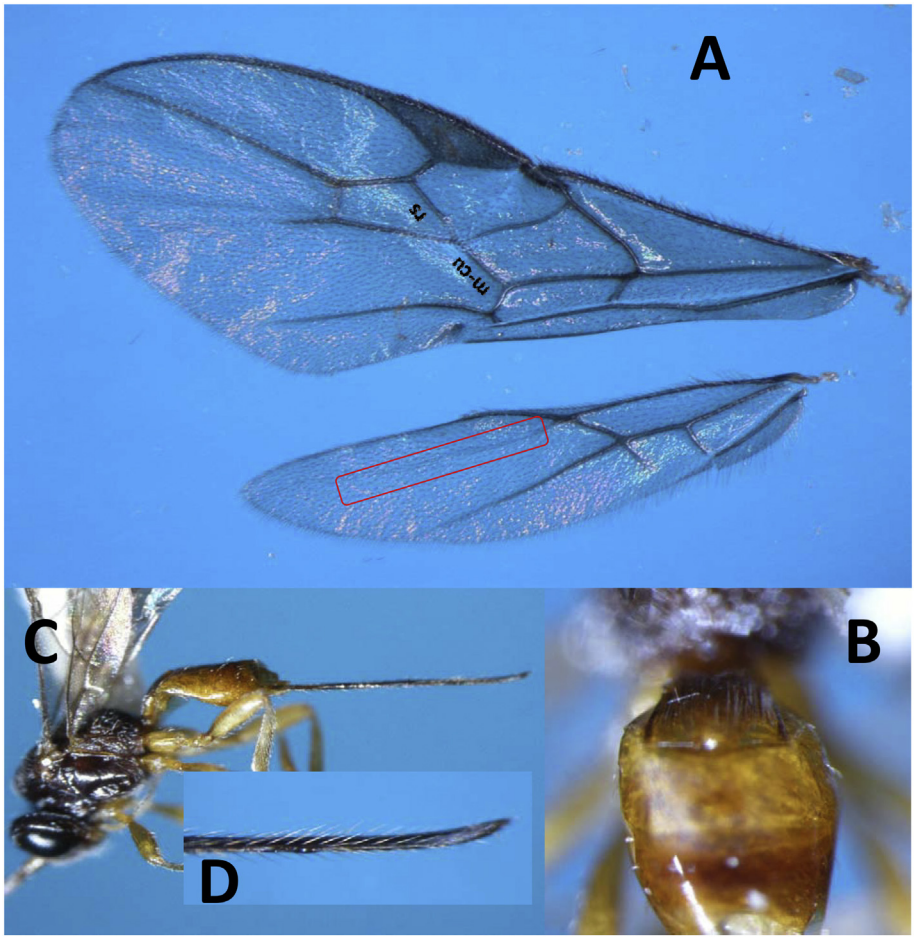

Plate 3. Female *F. caudatus* Kenyan strain. A) Forewing similar to *Fopius* species with short 2nd submarginal cell and m-cu arising directly in line with 2RS. Hind wing with RS represented by barely infumate crease, typical of *F. caudatus* (red rectangle). B) Metasomal terga smooth with no striation, petiole appearing more parallel–sided, with dorsal carina and no ridge. C, D) ovipositor longer than metasoma with rows of densely spaced setae on ovipositor sheath.

Wharton (1999) addressed the problem of *F. caudatus* rearing, suggesting that the species may be an egg-larval parastoid, based on the morphology of its thin ovipositor (like *F. arisanus*). This prediction was tested at the International Center of Insect Physiology and Ecology (ICIPE) in Kenya, and proved to be correct, using eggs of Medfly (Trostle Duke, 2005).

Recently, the Kenyan biotype of *F. caudatus* was imported into Hawaii as part of a renewed effort to control invasive tephritid fruit flies that are serious pests affecting fruit and vegetable production throughout the islands. These include the melon fly, the Medfly, the oriental fruit fly, and the solanaceous fruit fly, *Bactrocera latifrons* (Hendel). Attempts to manage these pests in Hawaii have used bait-spray applications, sanitation, sterile insect technique, and release of parasitoid species. Over 30 parasitoids have been introduced from Asia, Africa and Australia for tephritid control, resulting in some successful examples of classical biological control (Bess et al., 1961; Clausen et al., 1965; Haramoto and Bess, 1970; Wong and Ramadan, 1987; Wharton, 1989a, 1989b; Vargas et al., 1995; Mohamed et al., 2016).

Of these, the braconid *F. arisanus*, introduced to Hawaii in 1948 for control of *B. dorsalis*, successfully established on *C. capitata* (Bess et al., 1961; Haramoto and Bess, 1970) and on *B. latifrons* (Bokonon-Ganta et al., 2007b). Though commonly recovered from *C. capitata* in Hawaii, *F. arisanus* is an Asian species that was originally obtained from the puparia of oriental fruit fly (Wharton and Gilstrap, 1983); it attacks *C. capitata* in mixed infestations at lower elevations. At higher elevations, however, *F. arisanus* is virtually absent where *C. capitata* predominates the fruits (as in Jerusalem cherry, *Solanum pseudocapsicum* L., at Volcanoes National Park). Only the Australian larval parasitoid *Diachasmimorpha tryoni* (Cameron) can be found in wet, high elevation areas of Hawaii dominated by *C. capitata* (M. Ramadan, unpublished data).

The African parasitoids *Psyttalia humilis* (Silvestri), *Diachasmimorpha fullawayi* (Silvestri), and *Tetrastichus giffardii* Silvestri were released but failed to persist at any sites on the Hawaiian Islands (Wharton, 1989a, 1989b). *P. humilis* has not been recovered from any survey in Hawaii after 1933. Only *T. giffardianus* Silvestri (Hymenoptera: Eulophidae) persisted in the field, attacking *B. dorsalis* and *C. capitata* at lower elevations (Ramadan and Wong, 1990). The discovery of two *Fopius* egg-larval parasitoids in African coffee (*F. ceratitivorus*, and *F. caudatus*) renewed interest in their release in Hawaii and other parts of the world against Medfly (Wharton, 1999; Wharton et al., 2000; Steck et al., 1986).

F. caudatus was re-introduced to Hawaii in July 2006 from Central Kenya. After several attempts to rear this parasitoid in Hawaii a successful rearing protocol was developed that led to establishment of a laboratory colony. We describe the steps in establishing this colony and report on aspects of its behavior and reproduction, including the effect of host fruit, host fly species, host instar, and parasitoid density. These data are critical for understanding the evolution of its life-history strategy (Heimpel et al., 1998) and to facilitate mass rearing for research and field colonization in biological control programs.

Table 1
Afro-tropical frugivorous Tephritidae hosts, host plant associations, and natural distribution of *Fopius caudatus*.

Fruit fly species[a] (Subfamily Trypitinae, Tribe Dacini)	Host fruit species and family[a]	Native distribution and locality[a]		Introductions for biocontrol programs	Outcome of introduction
		West Africa	East Africa		
Subtribe Ceratitidini					
Carpophthoromyia tritea (Walker) (8,12,22)	*Pyrenacantha vogeliana* (Icacinaceae) (8,12)	Cameroon (5,7,8,10,13,14,18) Nigeria (Olokomeji 12) (2,5,8,13,14)		Hawaii 1913 via Nigeria (18)	Cohorts died during journey (18)
**Ceratitis anonae* Graham (4, 8,12,14,18,22)	*Annona* sp. (Annonaceae) (8) *Citrus limon* (Rutaceae) (28) *Coffea arabica* (Rubiaceae) (29) *Dovyalis caffra* (Salicaceae) (8,12) *Mangifera indica* (Anacardiaceae) (14,28) *Myrianthus arboreus* (Moraceae) (14,4,18) *Pancovia* sp. (Sapindaceae) (4) *Persea americana* (Lauraceae) (8) *Psidium guajava* (Myrtaceae) (12)	Cameroon (Yaounde 18, Akonolinga 14), (3,7,8,13) Congo (6,8) Nigeria (Olokomeji 12) (2,5,8,14,18) Sierra Leone (8,10,18,22) Zaire (Yangambi 4)	Kenya (Koru 17) (4,8,9) Uganda (Kawanda, Kampala 4, 29) (27)	Hawaii 1950–51 via Zaire (4)	Rearing failed on *Bactrocera dorsalis* and *Zeugodacus cucurbitae*, with limited progeny and low sex ratio on *Ceratitis capitata* (4).
**Ceratitis capitata* (Wiedemann) (3,10,17,21)	*Anacardium occidentale* (Anacardiaceae) (30) *Coffea arabica* (Rubiaceae) (17) *Coffea canephora* (Rubiaceae) (17)	Cameroon (3,5,7,8,10,13,14,18) Congo (4,6,8) Ghana (Nadowli, Tamale, Bawku 30)	Kenya (Koru 17) (4,8,9)	Hawaii 1936 via West Africa (18). Hawaii 1997–2006 via ICIPE Kenya, (17, MMR). Israel 2009 redistribution via Hawaii (32). Guatemala 2001 via ICIPE Kenya, Koru (9, 17).	Hawaii: rearing failed on larvae. Cohorts released with no recovery. Hawaii: rearing success, 17 shipments had *F. caudatus* from Kenya, Koru (MMR). Israel: rearing failed on *Bactrocera oleae*, *Capparimyia savastani*. Released in 2011 for *C. capitata* with limited rearing, < 100 wasps, no recovery (32). Guatemala: rearing success on *C. capitata* eggs for seven generations, colony collapsed, male biased sex ratio. No release (9).
**Ceratitis cosyra* (Walker) (20)	*Anacardium occidentale* (Anacardiaceae) (30) *Mangifera indica* (Anacardiaceae) (19) *Annona senegalensis* (Annonaceae (20) *Landolphia dulcis* (Apocynaceae) (20) *Saba comorensis* (Apocynaceae) (20) *Icacina senegalensis* (Icacinaceae) (20) *Sarcocephalus latifolius* (Rubiaceae) (20,31)	Ghana (Nadowli, Tamale, Bawku 30) Mali (Sikasso, Bougouni 19) Senegal (Casamance 20) Togo (Agomé-Adisitoe 31)			
Ceratitis ditissima (Munro) (4,22)	*Chrusophyllum* sp. (Sapotaceae) (4) *Mangifera indica* (Anacardiaceae) (19) *Terminalia* sp. (Combretaceae) (4)	Mali (Sikasso, Bougouni 19) Zaire (Yangambi 4) (8)	Kenya (Koru 4,9)	Hawaii 1950–51 via Zaire (4)	Rearing failed on *B. dorsalis* larvae (4)
**Ceratitis fasciventris* (Bezzi) (17)	*Coffea arabica* (Rubiaceae) (17) *Mangifera indica* (Anacardiaceae) (19)	Mali (Sikasso, Bougouni 19)	Kenya (Koru 4,8,9,17)	Hawaii 1998–1999 via ICIPE Kenya (MMR)	Rearing failed on *C. capitata*, no offspring (MMR)

(*continued on next page*)

Table 1 (*continued*)

Fruit fly species[a] (Subfamily Trypitinae, Tribe Dacini)	Host fruit species and family[a]	Native distribution and locality[a]		Introductions for biocontrol programs	Outcome of introduction
		West Africa	East Africa		
**Ceratitis giffardi* Bezzi (8,12,22)	*Chrysobalanus ellipticus* (Chrysobalanaceae) (12) *Sarcocephalus esculenta* (Rubiaceae) (8,12,18)	Benin (Kotonou 12) Cameroon (3,5,7,8,10,13,14,18) Guinea (Kakoulima 12) (3,8,13,22) Nigeria (Olokomeji 12) (2,5,8,13,14,18) Senegal (Dakar 12) Sierra Leone (Njala 18) (8,10,22)		Hawaii 1913 via Nigeria (18) Hawaii 1936 via Sierra Leone (18)	Cohorts died during journey to Hawaii for *C. capitata* (18) Reached Hawaii alive (220 adults), released for *C. capitata* with no recovery (18)
Ceratitis rosa Karsch	*Coffea arabica* (Rubiaceae)	–	Kenya, Koru (MMR)	Hawaii 2003 via ICIPE Kenya (MMR)	Rearing failed on *C. capitata* eggs and larvae.
Ceratitis punctata (Wiedemann) (8)	*Conopharyngia* spp. (Apocynaceae) (8) *Theobroma cacao* (Malvaceae) (12)	Cameroon (3,5,7,8,13,14,18)		Hawaii 1936 via Sierra Leone (18)	Reached Hawaii alive, released for *C. capitata* with no recovery (18)
Ceratitis quinaria (Bezzi) (19)	*Mangifera indica* (Anacardiaceae) (19)	Mali (Sikasso, Bougouni 19)			
Ceratitis silvestrii Bezzi (19)	*Mangifera indica* (Anacardiaceae) (19)	Mali (Sikasso, Bougouni 19)			
Ceratitis stictica Bezzi (8,12,22)	*Oxyanthus sulcatus* (Rubiaceae) (8,12)	Nigeria (Olokomeji 12) (2,5,8,13,14,18)			
Subtribe Dacina					
**Dacus bipartitus* Graham (8,12,13)	*Momordica* sp. (Cucurbitaceae) (8,12)	Benin (Segboroue 12) (7,8,10,13) Cameroon (Victoria 12) (3,5,7,8,10,13,14,18)			
Dacus bivittatus (Bigot) (4,12,14)	*Cucurbita* sp. (Cucurbitaceae) (12) *Cucurbita pepo melopepo* (Cucurbitaceae) (14)	Cameroon (Yaounde 14) (3,5,7,8,10,12,13,18) Congo (4,6,8) Togo (Lome 14, 27)	Kenya (Koru 4,8,9)	Hawaii 1913 via Cameroon (14) Hawaii 1950 via Kenya (4)	Cohorts died during journey to Hawaii. Rearing failed on *B. dorsalis* larvae.
**Dacus ciliatus* (Loew) (4,8,10,12,16, 22)	*Momordica charantia* (Cucurbitaceae) (8, 18) *Momordica* sp. (Cucurbitaceae) (12)	Benin (Sigborue 12) (3,10,22) Congo (8) Nigeria (Ibadan 18) (2,5,8,12,13,14) Zaire (Yangambi 4) (11,22)	Kenya (Koru 4,8,9)	Hawaii 1950 via Kenya (4)	Rearing failed on *B. dorsalis* larvae.
Dacus humeralis (Bezzi) (8,10)	?	Cameroon (3,5,7,8,13,14,18)			
Dacus momordicae (Bezzi) (22)	?		Kenya (Koru 8,9)		
**Trirhithrum coffeae* Bezzi (4,22,17)	*Coffea arabica* (Rubiaceae) (17) *Coffea canephora* (Rubiaceae) (29)	Cameroon (14) Congo (6,8) Ivory Coast (27) Togo (Kpalime 14) Zaire (4,11,22)	Kenya (Koru 8,9,17)	Costa Rica (1982) via Togo and Cameroon (14). Hawaii 1950–51 via Zaire (4)	Rearing failed on *Anastrepha* spp. and *C. capitata.* Rearing failed on *B. dorsalis* larvae.
**Trirhithrum nigerrimum* (Bezzi) (8,12,22)	*Euginia uniflorafruits*(Myrtaceae) (8,12)	Cameroon (Victoria 12) (3,5,7,8,10,13,14,18)			

Taxa names with asterisk are natural hosts reported as the main species infesting the fruit with *F. caudatus* the dominant parasitoid. Others need confirmation (Wharton, RA and M.J. Yoder. Parasitoids of Fruit-Infesting Tephritidae. http://paroffit.org. Accessed on Feb. 07, 2016). (1) Back and Pemberton, 1918. (2) Brues, 1926. (3) Canovas, 1940. (4) Clausen et al., 1965. (5) Delucchi, 1957. (6) Fischer, 1962. (7) Fischer, 1967. (8) Gilstrap and Hart, 1987. (9) Lopez et al., 2003. (10) Narayanan and Chawla, 1962. (11) Papp, 1985. (12) Silvestri, 1914. (13) Silvestri, 1939. (14) Steck et al., 1986. (15) Szépligeti, 1913. (16) Thompson, 1953. (17) Trostle Duke, 2005. (18) van Zwaluwenburg and McGough, 1936. (19) Vayssières et al., 2002. (20) Vayssières et al., 2012. (21) Wang et al., 2004. (22) Wharton and Gilstrap, 1983. (23) Wharton, 1987. (24) Wharton, 1989b. (25) Wharton, 1997. (26) Wharton, 1999. (27) Anonymous, 2015. (28) Lux et al., 2003. (29) Greathead, 1972. (30) Badji Kongyeli Benjamin, 2014. (31) Mondjonnesso, 2015. (32) Argov and Gazit, 2012.

[a] Numbers in parenthesis are the references cited for tephritid taxon, host fruits, country of origin, and introductions of *Fopius caudatus*.

Table 2
Records of consignments of tephritid puparia infesting coffee and associated parasitoids sent from ICIPE Kenya, Koru (Nyanza Province, Kisumu District) to Hawaii Department of Agriculture Containment Facility for recovery of *Fopius caudatus*.

Date shipped to HDOA	No. of shipments	Puparia received at HDOA			Total emerged Tephritids			Total emerged Parasitoids		
		Puparia/shipment (mean ± SEM)	Total puparia	% Uneclosed puparia (mean ± SEM)	Species	Number	%	Species	Number	%
Dec. 8, 1997	1	208	208	4.3	*Ceratitis capitata*	19	9.8	*Fopius caudatus*	6	100.0
					Ceratitis fasciventris	79	41.0			
					Trirhithrum coffeae	95	49.2			
Feb. 2, Apr. 21, May 27, Jul. 8, Sep.8, Oct.8, Dec. 11, and Dec. 15, 1998	8	1169 ± 301	9354	68.4 ± 3.9	*Ceratitis capitata*	751	30.2	*Fopius caudatus*	301	76.0
					Ceratitis fasciventris	1069	43.1	*Fopius ceratitivorus*	2	0.5
					Trirhithrum coffeae	663	26.7	*Diachasmimorpha fullawayi Psyttalia humilis*	2	0.5
									56	14.1
								Tetrastichus giffardianus	35	8.9
Apr. 22, Jun.3, and Jul. 5, 1999	3	993 ± 157	2979	61.4 ± 14.4	*Ceratitis capitata*	750	62.9	*Fopius caudatus*	96	90.6
					Ceratitis fasciventris	426	35.7	*Diachasmimorpha fullawayi Psyttalia humilis*	5	4.7
					Trirhithrum coffeae	16	1.3		2	1.9
								Tetrastichus giffardianus	3	2.8
Jul. 28, 2006	1	9400	9400	83.7	*Ceratitis capitata*	1314	87.1	*Fopius caudatus*	23	92.0
					Ceratitis fasciventris	129	8.5	*Fopius ceratitivorus*	2	8.0
					Trirhithrum coffeae	66	4.4			
Total	13	1687 ± 672	21,941	63.1 ± 6.3	*Ceratitis capitata*	2834	52.7	*Fopius caudatus*	426	79.9
					Ceratitis fasciventris	1703	31.7	*Fopius ceratitivorus*	4	0.8
					Trirhithrum coffeae	840	15.6	*Diachasmimorpha fullawayi Psyttalia humilis*	7	1.3
									58	10.9
								Tetrastichus giffardianus	38	7.1

Materials and methods

Origin of parasitoids

F. caudatus was obtained from mature berries of *C. arabica* collected from the Coffee Research Foundation Farm at Koru (Western Kenyan Highlands) in July 2006 at 0°8, 16′S; 35°16, 87′E (elevation 1513 m). Thirteen consignments of tephritid puparia (> 18,000) of mainly *C. capitata, Ceratitis fasciventris* and *Trirhithrum coffeae* were shipped to the Insect Containment Facility of the Hawaii Department of Agriculture in Honolulu for screening and parasitoid rearing (Table 2).

HDOA Containment Facility and rearing conditions

Puparia were held in 2 L plastic containers (20 cm diam, 20 cm deep) in a double sleeved wooden cage (0.8 × 0.8 × 0.8 m) with plexiglass top. After emergence, all plastic containers were inspected for hyperparasites or diseases, and emerged parasitoids were individually collected and transferred into sleeved, ventilated plexiglass cages (12 × 12 × 12 cm). Emerged parasitoids, flies, and uneclosed puparia from each shipment were counted. Parasitoids and flies were identified using published keys (Wharton, 1999; Wharton and Gilstrap, 1983; White and Elson-Harris, 1992).

General rearing and laboratory conditions

Rearing of *F. caudatus* was achieved using *C. capitata* eggs (USDA Medfly Toliman lab strain), using papaya as host fruit even though the wasp was originally collected from coffee. Papayas were easy to handle, cheap and available year round, and are recorded as host for three of the four fly species studied in Hawaii, and a lab host for *B. latifrons* (Liquido, 1991; Liquido et al., 1990). Papaya fruits were infested with Medfly eggs by exposing them to ~ 500 pairs of adult *C. capitata* in cages for 24 h; the host fly colony was initiated at the University of Hawaii, from puparia provided by the USDA/ARS Pacific Basin Agricultural Research Center in Honolulu. Upon eclosion, adult flies were maintained in wooden cages (25 × 25 × 25 cm) with screen sides and top and a glass front, provided with water in wet cotton wicks, and fed on a diet of sugar and hydrolysate yeast powder in a ratio of 3:1 by volume. Flies were used for fruit infestation when they were 7–10 d-old. Papaya fruits were purchased from local stores, washed and kept in the refrigerator at 7 °C for 3–5 d before used in experiments, to ensure the destruction of any unwanted fruit fly eggs they might contain (Bautista and Harris, 1996). Cages were kept in the insectary at the University of Hawaii at 28 ± 2 °C and 60–80% RH under a 12:12 h L:D regime.

Papaya infested with ≤ 24 h old *C. capitata* eggs were exposed to *F. caudatus* for 48 h in the same small plexiglass cages used to maintain wild wasps at 28 ± 2 °C and 60–80% RH, 12:12 L:D. After exposure to parasitoids, papaya pieces were transferred to incubation units made of plastic cups (9 cm diam, 5 cm deep) with 150 g fresh wheat diet (Tanaka et al., 1969) as supplemental larval food. Each cup was placed in a 2 L plastic container (20 cm diam, 20 cm deep) with a 1-cm layer of moist vermiculite on the bottom. Newly formed host puparia were sieved from the vermiculite after 10 days and kept until adult fly or parasitoid emergence in containers made from 148 ml plastic vials (4.9 cm diam, 8.5 cm deep). Bottoms of the vials were removed and covered with fine-mesh screen for aeration. Emerging parasitoids were aspirated and used to start new colonies. Water and fine drops of pure honey streaked on the top of the rearing cages were provided.

Suitability of Bactrocera and Zeugodacus species

Suitability of two *Bactrocera* and a *Zeugodacus* species were studied in the same small plexiglass cages. Experimental oviposition units were prepared by exposing papaya fruits for 24 h to about 300 pairs of mature (7–10 d old) adults of each of the three-fly species (*B. dorsalis*, *B. latifrons* and *Z. cucurbitae*).

The egg-infested fruits were transported to the quarantine lab for tests. Each infested papaya, excluding the seeds, was cut lengthwise into four equal sections. Each quarter (8 × 6 × 1 cm), representing one experimental unit, was exposed to 20 pairs of *F. caudatus* in cage for 24 h, with water and honey provided. After exposure to parasitoids, the papaya quarters were transferred into incubation units. Newly formed host puparia were placed into plastic vials (4.9 cm diam., 8.5 cm deep) until adult flies or wasps emerged. Each of the three fly species was tested separately, with three replicates for *Z. cucurbitae*, four for *B. dorsalis*, and six for *B. latifrons*.

Effect of host instar on parasitoid acceptance and reproduction

A papaya fruit was infested with *C. capitata* eggs by exposing it to 500 pairs of two-week-old adult flies for 24 h. The fruit was then cut into small pieces (4 cm long × 2 cm wide × 0.5 cm thick), each piece serving as a test unit. We estimated the mean number of *C. capitata* eggs per papaya section by counting the number of oviposition punctures on each fruit section. Dissection of a subsample of 20 oviposition punctures revealed that a mean of 25*C. capitata* eggs were laid per puncture. The parasitism rate (total number of adult parasitoids emerged/total number of hosts × 100) was based on the number of puparia recovered following incubation of fruits for rearing of exposed *C. capitata* eggs. Exposures to *F. caudatus* were prepared in two different sets: (1) infested papaya sections containing eggs (2 d-old) or first instar larvae (4 d-old). First instars were obtained from four d-old infested papaya fruits (egg hatching of *C. capitata* requires 48–72 h at 25 °C: Back and Pemberton, 1918) or (2) standard oviposition units containing *C. capitata* larvae. These were 9 cm diam. and < 0.5 cm deep modified Petri dishes (Wong and Ramadan, 1992) containing 10 g of rearing diet and 200 larvae each of second instar (5 d-old), early third instar (6 d-old), and late third instar (8 d-old). Larvae were reared from the same papaya fruits used in the first set to minimize age difference between larvae. We did not use pieces of papaya for older *C. capitata* instars, because after four days of incubation, papaya fruits decay and *C. capitata* larvae drown.

For each treatment, 5–7 d-old experienced female *F. caudatus* were used. Experiments were replicated 5 times using different sets of parasitoids. After 24 h exposure, exposed and non-exposed units were transferred into incubation units made of plastic cups to rear host eggs using the same methods described above. Newly formed host puparia were recovered and kept until adult fly or parasitoid emergence.

Response of female Fopius caudatus to host fruit substrates

F. caudatus in Africa is known to attack tephritids infesting 16 families of wild and crop fruits (Table 1). Experiments were designed to demonstrate the ability of *F. caudatus* to accept different Medfly infested substrates in Hawaii, including mango, *Mangifera indica* L. (Anacardiaceae), Bartlett pear, *Pyrus communis* L. (Rosaceae), Italian squash, *Cucurbita pepo* L. (Cucurbitaceae); sweet yellow pepper, *Capsicum annum* L. (Solanaceae), and coffee, *Coffea arabica* L. (Rubiaceae). Papaya, mango, pear, squash and pepper were trimmed into 5 × 4 cm sections to minimize variability of substrate surface area, then exposed to ~ 300 pairs of mature 10 d-old adults *C. capitata* for 24 h and subsequently exposed to *F. caudatus* for 48 h. Tests were replicated 5 times using 10 pairs *F. caudatus* from different parasitoid rearing sets. Inoculated fruit or vegetables were incubated using the methods described above. Newly formed host puparia were recovered and kept until adult fly and parasitoid emergence.

Developmental time and longevity

Developmental time was measured by exposing *C. capitata* egg-infested papaya to ten parasitoid females for 24 h. Methods of exposure

and subsequent handlings of hosts were the same as those described above. Puparia were collected and isolated individually in 59 ml plastic cups under the same environmental conditions. Emerged parasitoids were fed fine drops of honey. Developmental time (in days) for both sexes was recorded, and emerging wasps were set aside for subsequent observations on parasitoid longevity. Emergence and mortality were recorded once daily between 5 and 6 p.m.

Progeny production of Fopius caudatus with increasing parasitoid density

Several studies have shown that the influence of braconid parasitoid density on progeny sex ratio may affect parasitoid propagation under laboratory condition (Ramadan et al., 1992, 1994b). Six densities of parasitoids (1, 5, 10, 20, 40 and 80 females per cage) could oviposit into *C. capitata* -egg infested papaya sections for 24 h. Papaya fruit sections were prepared as in experiment 2.5 above. Experiments were replicated five times using different sets of parasitoids, 4–7 d-old experienced female *F. caudatus*. Exposed papaya units were transferred into incubation units made of plastic cups to rear host eggs using the same methods described above. Newly formed host puparia were recovered and kept until adult fly or parasitoid emergence.

Data analysis

Analysis of variance using a general linear model was performed for number of puparia and number of adult parasitoids (PROC GLM, SAS Institute, 2000). Corresponding treatment means were separated using the Student-Newman-Keuls (SNK) test (Zar, 1999). Percent parasitism was calculated, transformed by arcsin square root before analysis and subjected to a one-way ANOVA for comparisons among mean values (SAS JMP 4.0 Gary NC). Voucher specimens of *F. caudatus* are deposited in the insect collections of the Department of Plant and Environmental Protection Sciences, University of Hawaii at Manoa, Honolulu, Hawaii, and the Hawaii Department of Agriculture.

Results

Parasitoid rearing and colony growth

Shipments of tephritid puparia received in Hawaii from ICIPE Kenya started in 1996 and continued until 2006. Puparia were collected by Sunday Ekesi and Samira Mohamed of the ICIPE, Nairobi, Kenya. Only shipments originated from Koru are reported in Table 2. The last shipment that led to a successful colonization consisted of 9400 puparia collected from coffee on July 17, 2006. The shipment took five days to reach Hawaii, and most of the puparia were uneclosed. Three species of tephritids emerged from this lot: *C. capitata* (87.1% of flies), *C. fasciventris* (8.5%) and *Trirhithrum coffeae* Bezzi (4.4%). Parasitoids recovered were *F. caudatus* (1.5%) and *F. ceratitivorus* (0.1%). Thus, the Hawaiian colony of *F. caudatus* was most likely initiated from *C. capitata*, the predominant fly during this time of the year at Koru (Trostle Duke, 2005). A total of 2501 *F. caudatus* emerged from 19,955 puparia with parasitism ranging from 4.1 to 12.8% (average 12.5% M. Ramadan unpublished data). *F. caudatus* was also recorded from other fruit flies in previous shipments and from West Africa (Table 1).

The Hawaiian colony of *F. caudatus* was initiated from 9 females and 14 males (23 founding adults, July 28, 2006) and increased during 15 weeks to a total of 2249 females and 7583 males. The colony grew through three distinct periods (Figs. 1,2), that can be summarized as follows: (1) from the 1st-3rd week, there were great fluctuations in progeny/female, with means being < 10 parasitoids, percent parasitism, with means < 10%, and a male-biased sex ratio; (2) from the 4th–7th week, there was more stable parasitoid production with a mean progeny/female of ~10 parasitoids, mean percent parasitism reaching 20%, and a male biased sex ratio; and (3) from the 8th–15th week, mean progeny/female exceeded 10 parasitoids, mean percent parasitism reaching 50%, and a more balanced sex ratio (0.3–0.5 females).

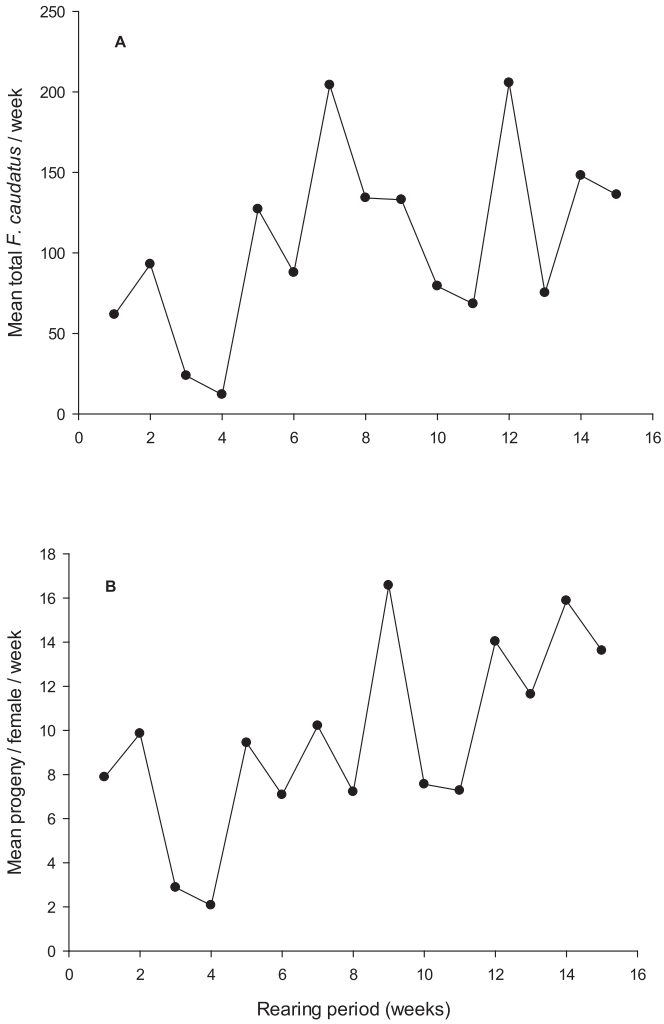

Fig. 1. Patterns of *F. caudatus* total production (A) and production per female per week (B) when reared over a 15-week period on *C. capitata*.

Host acceptance and suitability of Bactrocera species

Observations on host acceptance and suitability of the three *Bactrocera* and *Zeugodacus* species in Hawaii revealed that no *F. caudatus* were obtained from *Zeugodacus cucurbitae* nor any from *B. dorsalis*. In contrast, some development was recorded from *B. latifrons,* with 43 emerged parasitoids out of 1996 puparia recorded (2.1% parasitism), Table 3.

Effect of host instar on parasitoid acceptance and reproduction

F. caudatus reproduced almost exclusively on the egg stage of *C. capitata* (Table 4). Very limited development was observed on first instar *C. capitata* (23 parasitoids out of 2500 exposed hosts, 0.9%). No offspring were produced by *F. caudatus* from second or third instars.

Effect of host fruit species on parasitoid reproduction

F. caudatus could parasitize *C. capitata* eggs in all fruit substrates tested, including mango, sweet pepper, pear, and squash, as well as papaya (used for maternal rearing) and coffee (primary host fruit of the parent colony in Kenya). Significant differences were found among the

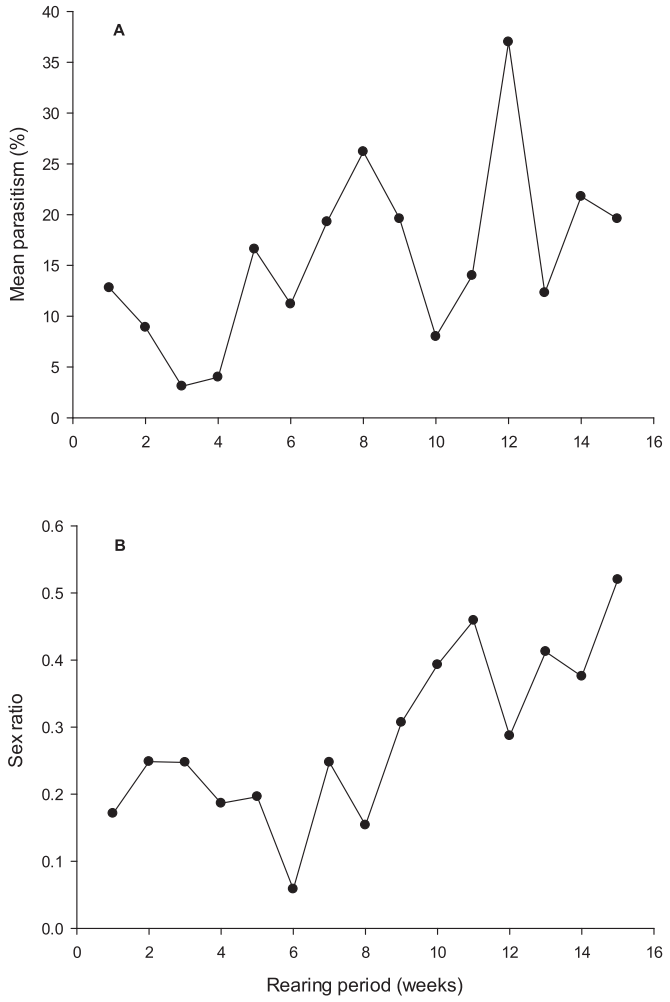

Fig. 2. Patterns of *F. caudatus* percent parasitism (A) and sex ratio (proportion of females, B) when reared over a 15-week period on *C. capitata*.

Table 3
Mean number of host puparia per replicate and percent parasitism by *Fopius caudatus* (20 pairs) exposed to eggs of *Zeugodacus cucurbitae*, *Bactrocera dorsalis* and *Bactrocera latifrons* for 24 h.

Host fly species	Host exposed as eggs		Host exposed as larvae
	Host puparia / replicate	Parasitism (%)	Parasitism (%)[a]
	$\bar{x}$ ± SEM	$\bar{x}$ ± SEM	
Zeugodacus cucurbitae	285.0 ± 40.1 a	0	0
Bactrocera dorsalis	259.3 ± 6.4 a	0	0.02
Bactrocera latifrons	332.7 ± 15.4 a	2.1 ± 0.3	–

[a] Data calculated from Clausen et al., 1965. Means connected by same letters are not significantly different ($P > .05$).

six host fruit species in progeny production/female ($F = 7.96$; df = 5, 24; $P = .002$), and percent parasitism ($F = 3.34$; df = 5, 24; $P = .0198$). However, no significant differences were observed in progeny sex ratio ($F = 1.41$; df = 5, 24; $P = .2570$) (Table 5). This is like observations of *F. arisanus* discrimination among fruit varieties inoculated with eggs of *B. dorsalis* and *C. capitata* (Bautista and Harris, 1996; Harris et al., 1991).

Developmental time and longevity

Mean ± SEM developmental period from deposition of the egg until adult emergence for *F. caudatus* was 21.8 ± 1.1 d for females ($n = 92$), and 20.0 ± 0.4 d for males ($n = 76$) at 28 ± 2 °C, 60–80% RH, and a 12:12 h L:D regime. Mean longevity of host-deprived females was 14.8 ± 0.8 d ($n = 91$) and of mated males was 5.2 ± 0.4 d ($n = 43$).

F. caudatus males emerge two days earlier than females as do two other egg-larval parasitoids *F. arisanus* and *F. ceratitivorus* (Bokonon-Ganta et al., 2007a; Bautista et al., 1998).

Progeny production of Fopius caudatus with increasing density

The response of *F. caudatus* exposed either singly or in groups to *C. capitata*- infested papaya is presented in Fig. 3. Significant differences were found among the six parasitoid densities tested in progeny production per female ($F = 8.00$; df = 5, 24; $P < .0001$), which decreased from 22.2 to 1.0 when the number of parasitoids increased from 1 to 80 (Fig. 3B). Parasitoid density had a significant effect on the sex ratio ($F = 23.95$; df = 5, 24; $P < .0001$). More male progeny were produced when the parasitoids were foraging in groups of 80 than any other density (Fig. 3D). There were significant differences in the percent parasitism ($F = 14.21$; df = 5, 24; $P < .0001$), with increasing parasitoid density. Percent parasitism varied from 2.4–27.8% (Fig. 3C). Densities of 10, 20 and 40/cage resulted in the highest percent parasitism of 27.8, 25.5 and 24.7% respectively. A density of 10 females/cage yielded the most balanced progeny/female (16.6 ± 3.7), percent parasitism (27.8 ± 5.7%) and sex ratio (0.46 ± 0.03 females).

Discussion

Reports on morphological variation, development, and host associations in West and East Africa suggest two different biotypes of *F. caudatus*. In fact, the original specimen of West African *F. caudatus* was described as a new species [*Rhinoplus fuscipennis*Szépligeti, 1913] and later reported by several authors as *Opius fuscipennis* (Szépligeti) or *Biosteres fuscipennis* (Szépligeti) until type specimens were recognized as misidentifications of *Fopius caudatus* (Szépligeti) (Wharton, 1999).

Also, Silvestri (1914) reported that *F. caudatus* from several tephritid hosts in West Africa (Southern Nigeria, Olokomeji, ex. *Ceratitis giffardi*, *C. stictica*, *C. anonae*, Table 1) were much larger than Kenyan *F. caudatus* in body size (3–4.5 mm), ovipositor length (1.7–3.5 mm), and length of antenna (37–40 segments) (Table 6). Other specimens obtained from Victoria (Cameroon, ex. *Ceratitis nigerrima*) have the first abdominal segment more deeply striate. *F. caudatus* from the same locality (ex. *Dacus bipartitus*), were larger (body length = 4 mm) and had longer ovipositors (length = 3 mm) than the Kenyan biotype with the first abdominal segment barely striate. Individuals from Southern Nigeria (Olokomeji, ex. *Ceratitis anonae* and *C. antistictica*) and Segborue, Dahomey (ex. *Dacus brevistylus*) were lighter in color (brick-red ferruginous) than the dark brown mesosoma of Kenyan *F. caudatus* (Plates 1, 2). They were also larger than Kenyan specimens (body length = 4.5 mm, ovipositor length = 3.5 mm, antenna = 37–40 segments). We found that body size and ovipositor length of *F. caudatus* can be significantly greater when eclosed from larger fruit fly hosts ($P < .0001$, Table 6). Moreover, the West African biotype differed in developmental period (modal time 19 d, range 14- 21d) from Cameroon samples (ex. coffee infested with *Trirhithrum coffeae*, Steck et al., 1986).

F. caudatus has a long history of introductions into Hawaii starting in 1913 when it was recognized as a potential biocontrol agent of *C. capitata* (Silvestri, 1914). It was recovered numerous times during explorations (Silvestri, 1914; Clausen et al., 1965; Steck et al., 1986), yet due to unknown factors it has never been successfully reared in substantial numbers and has not established anywhere in Hawaii (Trostle Duke, 2005). In the 1913 shipments several *Ceratitis* species were

Table 4
Percent parasitism of eggs and larval instars of *Ceratitis capitata* during 24-h exposure period to 10 females (5–7 d old) *Fopius caudatus* under laboratory conditions (28 °C, 60–80% RH).

C. capitata exposed to parasitoid ($\bar{x}$ ± SEM)			*F. caudatus* ($\bar{x}$ ± SEM)	
Developmental stage	Age at beginning of exposure	Total puparia / replicate	Total parasitoid offspring	Parasitism (%)
Egg	48 h	539.8 ± 26.2 a	92.6 ± 8.3 a	17.3 ± 1.7 a
First instar	4 d	192.0 ± 4.1 b	2.0 ± 0.5 b	1.0 ± 0.3 b
Second instar	5 d	199.6 ± 0.4 b	0	0
Early third instar	6 d	197.6 ± 1.6 b	0	0
Late third instar	8 d	197.8 ± 0.8 b	0	0

Means connected by the same letters are not significantly different (P > .05).

Table 5
Offspring and sex ratio of *F. caudatus* during 48 h exposure to *C. capitata* eggs in various fruit substrates.

Fruit species	Family	Puparia of *C. capitata* / gram of fruit substrate	Parasitoid progeny production /female	Parasitism (%)	Sex ratio[a]
		$\bar{x}$ ± SEM	$\bar{x}$ ± SEM	$\bar{x}$ ± SEM	$\bar{x}$ ± SEM
Coffea arabica L. (Coffee)	Rubiaceae	0.2 ± 0.1 d	0.7 ± 0.2 d	10.4 ± 1.4 b	0.4 ± 0.1 a
Mangifera indica L. (Mango)	Anacardiaceae	1.2 ± 0.2 bc	4.5 ± 0.7 c	8.3 ± 1.5 b	0.3 ± 0.1 a
Carica papaya L. (Papaya)	Caricaceae	2.9 ± 0.9 a	11.5 ± 3.2 a	27.1 ± 4.9 a	0.4 ± 0.1 a
Pyrus communis L. (Bartlett pear)	Rosaceae	0.2 ± 0.1 d	0.9 ± 0.2 d	13.9 ± 3.6 b	0.4 ± 0.1 a
Capsicum annuum L. (Sweet yellow pepper,)	Solanaceae	0.7 ± 0.1 cd	2.1 ± 0.3 d	26.7 ± 5.0 a	0.4 ± 0.1 a
Cucurbita pepo L. (Italian squash)	Cucurbitaceae	1.8 ± 0.4 b	7.3 ± 1.6 b	19.3 ± 7.2 ab	0.4 ± 0.1 a

Levels connected by same letters are not significantly different (*P* > .05).
[a] Sex ratio expressed as proportion of emerged females (females / total parasitoids).

reported as hosts as were some *Dacus* infesting cucurbit plants (*D. ciliatus*, *D. biparititus*, and/or *D. bivittatus*). But, it was not known that this species attacks the egg stage, and as a result, few *F. caudatus* reached Hawaii alive, and none were released (Silvestri, 1914). Another importation was attempted in 1936 to secure additional cohorts from West Africa. Field parasitism by *F. caudatus* during this survey was 21.7% in Njala, Sierra Leone (64.9% ♀♀, ex. *C. giffadi*), (van Zwaluwenburg and McGough, 1936). Some unreported numbers were released then, but there was no subsequent recovery. In the 1950s, exact numbers of introduced *F. caudatus* and its propagation in the laboratory were reported with 56 individuals from Kenya (82.0% ♀♀, ex. *D. ciliatus* and *D. bivittatus*) and 236 individuals from Congo with 78.0% ♀♀ (81 ex. *Ceratitis ditissima*, 147 ex. *C. anonae*, and 8 ex. *Trirhithrum coffeae*) (Clausen et al., 1965). Additional records were reported from the same locality in the Congo under the synonym *Opius fuscipennis* (Szépligeti) with a total of 557 individulas (68.6% ♀♀), primarily emerged from *C. ditissima* and *C. anonae* (Clausen et al., 1965).

This study confirms that *F. caudatus* from Kenya successfully oviposits into *C. capitata* eggs (Wharton, 1999; Wharton et al., 2000), like *F. ceratitivorus* (Lopez et al., 2003; Bokonon-Ganta et al., 2005) and *F. arisanus* (Bautista et al., 1998; Bess et al., 1961). Most opiine parasitoids of tephritids are larval endoparasitoids (Wharton, 1989a, 1989b). The few well-known exceptions are *F. arisanus* and *F. ceratitivorus* (Wharton, 1999; Wharton et al., 2000; Lopez et al., 2003; Bokonon-Ganta et al., 2005).

Of the three *Bactrocera* species in Hawaii (*Z. cucurbitae*, *B. latifrons*, and *B. dorsalis*) only *B. latifrons* was found to be a suitable host for the development of *F. caudatus*. This represents the first account of parasitism of solanaceous fruit fly, *B. latifrons,* by *F. caudatus*. The possibility of attacking this fly in the field stems from results of *F. caudatus* emerging from solanaceous and cucurbit plants in Africa (Tables 1, 5). However, since the establishment of *B. latifrons* in Kenya and Tanzania there is no information of *F. caudatus* attacking this host in the field (Mwatawala et al., 2007; Mziray et al., 2010).

Although there is a record of *F. caudatus* emerging from the oriental fruit fly, *B. dorsalis*, this host proved to be unsuitable for development, as shown by the paucity of individuals reared in the 1950's (Clausen et al., 1965), as well as our experiments). Clausen et al. (1965) report on rearing this parasitoid using *B. dorsalis* failed, with only a single male offspring (*n* = 9; 51 ♀♀ / cage; 6390 host puparia; 0.02% parasitism). Most likely larvae were exposed for parasitism instead of eggs. In contrast, rearing results on *C. capitata* produced 48 males (*n* = 15; 68 ♀♀/cage; 4983 host puparia; 0.96% parasitism). Apparently, the *C. capitata* larvae had some first instars present that allowed limited parasitoid development. Still, no females were produced from either host. Completely negative results were obtained using the melon fly, *Z. cucurbitae*, as a host (Clausen et al., 1965). All *F. caudatus* eggs laid in *Z. cucurbitae* and *B. dorsalis* died, probably killed by the host's immune system via encapsulation of eggs (Ramadan et al., 1994a). Endoparasitoid eggs or larvae may be killed by a tephritid hosts's immune system as in *F. ceratitivorus* (Bokonon-Ganta et al., 2007a; Jervis and Copland, 1996), mainly through encapsulation (Salt, 1970). Similar observations have been described with other opiine parasitoids of *C. capitata* encapsulated in *Bactrocera* species (Bokonon-Ganta et al., 2005; Mohamed et al., 2003; Pemberton and Willard, 1918; Ramadan et al., 1994a, 1994b).

Fopius caudatus is of African origin and has no co-evolutionary history with *Bactrocera* species of Asian origin (Wharton and Gilstrap, 1983). With the recent spread of *B. dorsalis* (42 nations since 2003) and *Z. cucurbitae* (21 nations since 2004) in West and East Africa, there have been no reports of field or laboratory studies documenting indigenous African opiines successfully attacking the Asian *Bactrocera* and *Zeugodacus* flies (Mohamed et al., 2016, Vayssières et al., 2007, http://www.cabi.org/isc/datasheet/17683, http://www.cabi.org/isc/datasheet/17685).

There was a significant reduction in progeny of *F. caudatus* with increasing number of female parasitoids foraging per cage, which is indicative of mutual interference among foraging adult wasps. Such reduction was observed in many parasitoids, including *Anagyrus sinope* Noyes & Menezes (Hymenotera: Encyrtidae) parasitizing the Madeira mealybug, *Phenacoccus madeirensis* Green (Hemiptera: Pseudococcidae) (Chong and Oetting, 2007). Mutual interference is a form of parasitoid

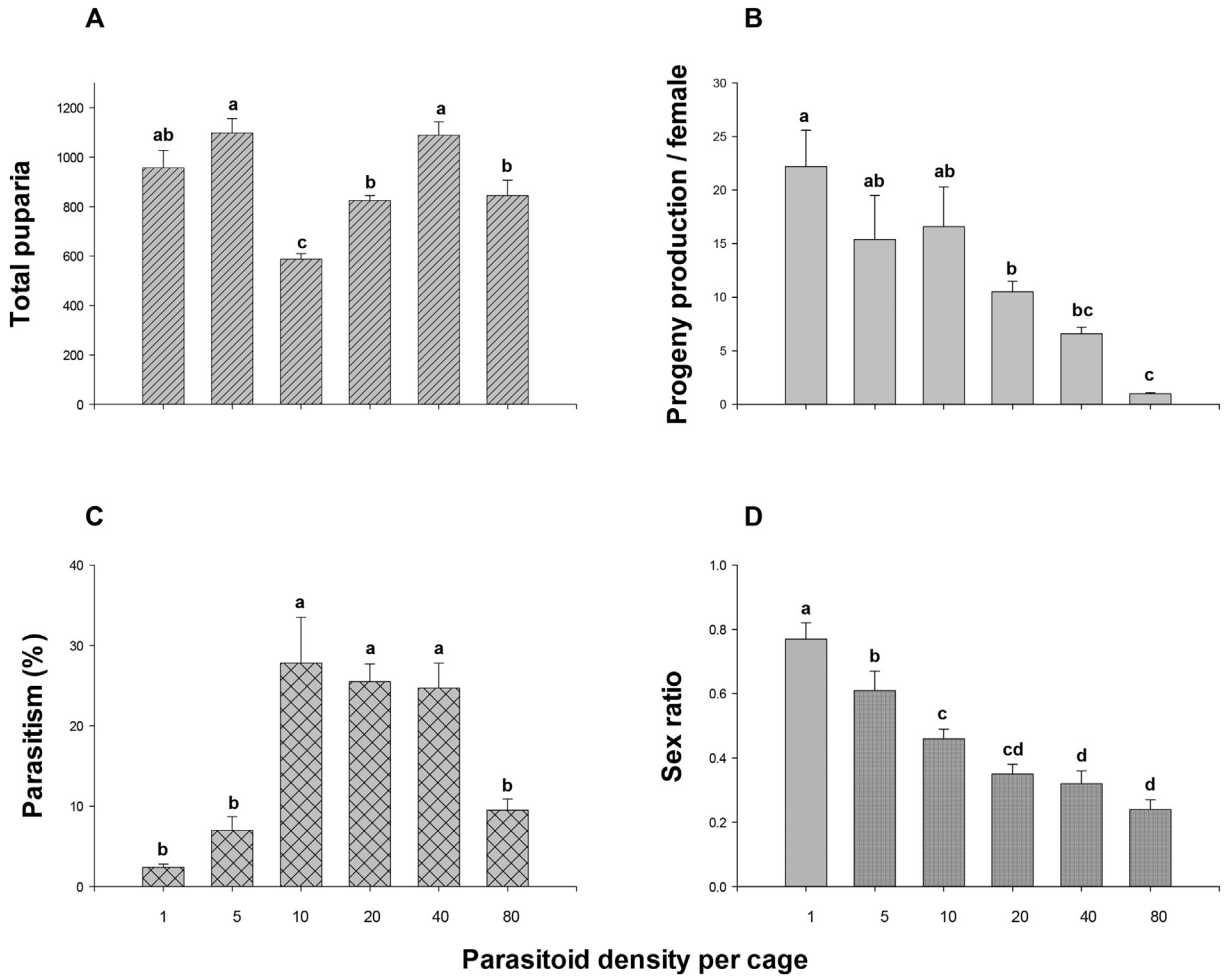

Fig. 3. Mean (± SEM) number of total host puparia (A), progeny produced per female (B), percent parasitism (C) and sex ratio (females / total parasitoids) (D) of *F. caudatus* exposed either singly or in groups to *C. capitata*- infested papaya. Each parasitoid density was replicated 5 times using females from a different parasitoid rearing cohort. Bars topped by the same letters are not significantly different (ANOVA $P > .05$).

density dependence and contributes to the stabilization of a parasitoid-host population dynamics (Hassell and Varley, 1969).

Other researchers also reported difficulty in rearing *F. caudatus* when obtained from a field colony and reared under quarantine conditions (Steck et al., 1986). Parasitoid density in rearing cages may be a factor for this failure. Apparently, this parasitoid needs adequate airflow and an outdoor sunlight source for successful mating. Based on observations made in Kenya and Guatemala, the lack of these two influences probably had the greatest impact on the difficulty of rearing (Trostle Duke, 2005).

As the density of conspecifics increases, each parasitoid spends less time searching for hosts and more time interacting with the conspecifics (Hassell and Varley, 1969). The estimated maximum number of eggs parasitized per parasitoid and the per capita search rate were lower

Table 6
Size differences among dry specimens of female *Fopius caudatus* in relation to tephritid host species and origin.

Tephritid host	Colony origin	No. antennal segments		Mean ± SEM female size (length mm)[a]		
		Range (n = 4–10)	Median	Body (n = 10)	Forewing (n = 10)	Ovipositor (n = 10)
Ceratitis capitata	Hawaii, USDA 2006	36–40	38.0 bc	3.0 ± 0.1 bc	3.4 ± 0.1 abc	2.0 ± 0.1 c
	Guatemala, Petapa 2005	37–41	38.0 abc	3.2 ± 0.1 ab	3.1 ± 0.1 cd	1.7 ± 0.1 de
	Kenya, Koru 1998.	36–38	37.0 cd	3.0 ± 0.1 c	3.3 ± 0.1 bcd	1.9 ± 0.1 cd
Ceratitis anonae	Cameroon, Yaounde 1951.	38–41	40.0 a	2.9 ± 0.1 c	3.6 ± 0.1 ab	2.6 ± 0.1 a
Ceratitis giffardi	Sierra Leone, Njala 1936.	36–38	37.5 bcd	2.8 ± 0.1 c	3.3 ± 0.1 bcd	2.3 ± 0.1 ab
Ceratitis fasciventris	Kenya, Koru 1998.	34–38	36.5 d	2.7 ± 0.1 c	3.1 ± 0.1 d	1.8 ± 0.1 cd
Trirhithrum coffeae	Kenya, Koru 2003.	33–35	34.0 e	2.2 ± 0.1 d	2.7 ± 0.1 e	1.5 ± 0.1 e
Bactrocera latifrons	Hawaii, USDA 2006	37–39	39.0 ab	3.3 ± 0.1 a	3.7 ± 0.1 a	2.1 ± 0.1 bc
F			22.0251	27.3497	18.1992	28.0682
df			7,56	7,72	7,72	7,72
P			< 0.0001	< 0.0001	< 0.0001	< 0.0001

[a] Body length is lateral measurement from head to tip of abdomen, length of forewing from tegula to tip of forewing, ovipositor length is the portion of exposed ovipositor sheath uncovered by hypopygium in lateral view, at the end of metasoma. *C. capitata* from Hawaii and Guatemala are Toliman strain. Mean comparisons for all pairs using Tukey-Kramer HSD. Levels not connected by same letters are significantly different.

when *Trichogramma minutum* Riley (Hymenotera: Trichogrammatidae) were searching in groups of three than when searching alone (Mills and Lacan, 2004). However, *Diachasmimorpha longicaudata* parasitized more fly larvae when foraging in groups of five than singly (Montoya et al., 2000). Without complementary behavioral observations on detailed parasitoid reproductive attributes including handling time, functional response, and competition for limited number of hosts at a higher parasitoid density, the effect of mutual interference on the oviposition behavior of *F. caudatus* remains speculative.

The ability of *F. caudatus* to parasitize eggs suggests significant potential for the biological control of tephritid fruit fly pests. It can attack eggs located near the surface of infested fruits and vegetables, which are particularly vulnerable. Other opiines attack the larval stages but their effectiveness is limited by the length of ovipositor, size of fruit, and inability to reach the larvae before they tunnel deep into the flesh of fruits. In addition, the early presence of the parasitoid inside the hosts gives it a competitive edge over larval-attacking species arriving later into the system. It could therefore play an important role in population management of *C. capitata* in Hawaii and other tropical and subtropical countries around the world.

In conclusion, *F. caudatus* is an egg-larval parasitoid that can be reared successfully on Hawaiian populations of *C. capitata* and *B. latifrons*. It significantly attacks hosts in fruit substrates of Solanaceae and Cucurbitaceae under laboratory conditions and may cue to the same hosts as *B. latifrons* if released in Hawaii. We encourage further investigations into using *F. caudatus* to attack invasive populations of *B. latifrons* in Tanzania and Kenya. The successful colonization of *F. caudatus* together with data presented here on reproductive capacity, and procedures reported on mass production of related opiines (Ramadan et al., 1989; Ramadan et al., 1994b; Ramadan, 2004; Wong and Ramadan, 1992; Bokonon-Ganta et al., 2007a) can help towards the development of an effective mass production system. Other aspects of the biology of the parasitoid remained to be investigated, including the survival, reproductive biology, competition with other parasitoids, and the capacity of *F. caudatus* to persist through mass rearing process.

Distribution records showed that *F. caudatus* is known from tropical regions of 14 countries in Western Africa and two in Eastern Africa (Table 1). It has thus far been reared exclusively from ceratitidine Tephritid fruit flies (Steck et al., 1986; Wharton et al., 2000). It is the most abundant parasitoid of tephritids infesting a variety of fruits in Benin and Mali (Vayssières et al., 2002). It was recently reported as the dominant biological control agent of *C. cosyra* and *C. punctata* in Senegal (Ousmane et al., 2015).

This parasitoid also competes with released *F. arisanus* for biological control of native *Ceratitis* and invasive *B. dorsalis* in Africa. *F. caudatus* parasitized *Ceratitis cosyra*, *C. sylvestrii*, and *C. punctata* (Gilstrap and Hart, 1987) exclusively, while *F. arisanus* preferred mostly the exotic *B. dorsalis* (Ousmane et al., 2015).

Records of *F. caudatus* indicate 12 species in the tribe Ceratidini and 7 species of Dacini fruit flies among hosts in Africa. This parasitoid is not a Medfly specific parasitoid; it prefers *Ceratitis fusciventris* (see Table 1 for references). The success in rearing *F. caudatus* in good numbers for research may stimulate further evaluation of its efficacy against *Ceratitis rosa* in Africa and the Indian Ocean Islands of Mauritius and La Reunion. Also, Medfly and *Anastrepha* species in Latin America are targets of long standing biological control projects and may benefit from *F. caudatus* introductions. However, *F. caudatus* must be tested for non-target effects on native *Anastrepha*, as our results show that is it not a Medfly-specific parasitoid and may compete with other native opiines. Given the well-documented environmental safety of opiine egg-larval endoparasitoids, we conclude that the release of the Kenyan biotype of *F. caudatus* in the Hawaiian Islands would have excellent potential to enhance biological control of Medfly populations, particularly in cooler wet areas where *F. arisanus* is absent.

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