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Acceptability and suitability of six fruit fly species (Diptera: Tephritidae) for Kenyan strains of *Psyttalia concolor* (Hymenoptera: Braconidae)

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Abstract

Host acceptability and suitability *Psyttalia concolor* (Szépligeti) is a koinobiont, larval parasitoid of tephritid fruit flies. Individuals of *P. concolor* were field-collected from coffee in the central highlands of Kenya, and cultured initially on Mediterranean fruit fly (medfly), *Ceratitis capitata* (Wiedemann). They were then examined for their ability to oviposit in and develop on five other tephritid species that are pests in Kenya. In addition to the medfly, acceptability for oviposition and suitability for development were tested against the mango fruit fly, *Ceratitis cosyra* (Walker), the Natal fruit fly, *Ceratitis rosa* Karsch, *Ceratitis fasciventris* (Bezzi), *Ceratitis anonae* Graham and the melon fruit fly, *Bactrocera cucurbitae* (Coquillett). *Ceratitis capitata* and *C. cosyra* were accepted as hosts significantly more often than the other species. Superparasitism was recorded only from *C. capitata* and *C. cosyra*. Two days after oviposition, parasitoid eggs in *C. fasciventris* and *B. cucurbitae* were encapsulated, whereas those in *C. rosa* and *C. anonae* were encapsulated, and often melanized. *Ceratitis capitata* was the most suitable host for Kenyan populations of *Psyttalia concolor* in terms of progeny production, and proportion of female progeny.

Keywords: *Fruit flies,* Psyttalia concolor, *acceptability, suitability, host range*

Introduction

Fruit-infesting Tephritidae (Diptera) have an enormous impact on fruit and vegetable production throughout the world. Losses are caused not only by direct damage to the crop, and the cost of the control measures, but also by quarantine restrictions that prevent export (Waterhouse 1993). Two of the genera originating in the Old World tropics, *Ceratitis* MacLeay and *Bactrocera* Macquart, contain several species that pose a constant threat of introduction to the US mainland. The medfly, *Ceratitis capitata*

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(Wiedemann), is already established in Hawaii and in tropical America from Guatemala south (White & Elson-Harris 1992). Additionally, three species of *Bactrocera* are established in Hawaii and a fourth in Suriname. Still another species, the olive fly, *Bactrocera oleae* (Gmelin), became established in California in 1998 (Collier & Van Steenwyk 2003).

Biological control is a potentially useful approach for suppression of fruit fly densities (Willard & Mason 1937; Clausen et al. 1965) and there has been renewed enthusiasm for utilizing natural enemies to reduce fruit fly populations (Knipling 1992; Wong et al. 1992; Headrick & Goeden 1996; Sivinski et al. 1996). Much of the attention in tephritid biological control has been directed towards the medfly and the olive fly. The medfly and several other potentially important tephritid species have their origins in sub-Saharan Africa (De Meyer 1996, 1998; Gasparich et al. 1997). The olive fly, whose origins are less certain, also occurs in this region. Hence, Africa is a logical focus for biological control programs seeking to obtain more effective parasitoids for areas where the medfly and the olive fly have become established (Gilstrap & Hart 1987; Wharton 1989; Messing 1996; Sivinski 1996; Collier & Van Steenwyk 2003).

Numerous parasitoids, representing several genera and at least nine families, are known to attack fruit-infesting Tephritidae (Wharton 1989, 1997; Hoffmeister 1990, 1992). Among these genera, *Psyttalia* Walker contains the largest number of species known to attack fruit-infesting tephritids. Only half of the approximately 50 described species have host records (Fischer 1987; Wharton 1997), but all of these are from Tephritidae. Members of this genus are synovigenic, koinobiont parasitoids (Pemberton & Willard 1918; Wharton 1997), which typically attack late larval instars and kill the host before the latter pupates but after pupariation. Recently, a species morphologically inseparable from *Psyttalia concolor* (Szépligeti) was found to be the dominant larval parasitoid of fruit flies in coffee plantations in the central highlands of Kenya (Wharton et al. 2000; Kimani-Njogu et al. 2001).

Psyttalia concolor is widely used for augmentative biological control of the olive fly in the Mediterranean region (Raspi 1993), but it's host range outside the Mediterranean Region is poorly understood in part because of uncertainties regarding its identity (Kimani-Njogu et al. 2001). Thus, one of the goals of this study is to provide baseline biological information on *P. concolor* from naturally occurring populations attacking the medfly in coffee in Kenya, for eventual comparison with well-studied populations from the Mediterranean region (Biliotti & Delanoue 1959; Arambourg 1962; Cals-Usciati 1982, 1983; Avilla & Albajes 1984; Loni 1997). *Psyttalia concolor* was originally described from material reared from the olive fly in the Tunisia. In other parts of the Mediterranean region, it has subsequently been reared from *Capparimyia savastani* (Martelli) infesting capers (*Capparis spinosa* L.) and *Carpomyia incompleta* (Becker) in the fruits of jujube (*Ziziphus jujuba* Mill.) (Fischer 1971); and the medfly is used as a host in the mass rearing programs for augmentative releases against the olive fly. Other recorded hosts are largely suspect (Wharton & Gilstrap 1983), though *P. concolor* was released and established against *Anastrepha suspensa* (Loew) in Florida (Baranowski et al. 1993). As noted by Canale and Raspi (2000), data on the preferred hosts of *P. concolor* are 'scanty', even in the Mediterranean region.

Understanding the relative performance of a parasitoid on the potential hosts that it may encounter in nature is necessary for designing successful biological control programs. Issues of concern include optimizing rearing conditions for laboratory cultures, and assessing the trade-off between the potential for non-target impacts on

the one hand and utility against more than one target pest on the other. Some of the more polyphagous tropical tephritids may co-exist in the same habitat, or even within fruit sampled from the same tree (Wharton et al. 2000; Copeland et al. 2002). Thus, a foraging parasitoid may encounter several species of hosts, and these may differ in their acceptability and/or suitability. Ideally, the parasitoid will be able to distinguish between poor and good quality hosts and accept only the latter (Van Alphen & Janssen 1982; Godfray 1994), but assessment of host quality is not a simple matter (Hemerik & Harvey 1999; Harvey 2000).

The primary objective of the present study was to compare medfly, a native host of *P. concolor* in Kenya, to other Kenyan tephritids relative to their acceptability and suitability as hosts of this parasitoid. If *P. concolor* is relatively host specific, we would expect to find that most if not all other tephritids that we test are unsuitable, resulting in encapsulation of the parasitoid eggs (Salt 1970). We would also expect the parasitoid to lay fewer or no eggs in unsuitable hosts if she is able to discriminate, and that these responses would most likely to be found when tested against a species such as *Bactrocera cucurbitae* (Coquillett). *Bactrocera cucurbitae* is an invasive species in Kenya, belonging to a different genus than the medfly, and it has a well-documented encapsulation response to several parasitoids of fruit-infesting tephritids in Hawaii, where it is also an introduced pest (Nishida & Haramoto 1953). While parasitoids fail to develop in unsuitable hosts (due to nutritional inadequacy or failure to overcome the host's defenses), suitable host species may also vary in quality, and this can be measured in a number of ways. Size is often used as a measure of fitness, and thus larger host species might be judged as more suitable if they produce larger parasitoids (and a female-biased sex ratio) than smaller host species. However, there may be trade-offs between competing fitness parameters such as size and speed of development (Harvey & Strand 2002). In this paper, we use several standard measures to compare suitable hosts to understand patterns of host use by this species.

This information will be of value both for developing augmentative and conservation biological control strategies in Africa and for classical biological control of African fruit flies (especially the medfly and the olive fly) in areas of the world where they are invasive. This study is particularly timely as *P. concolor* is now being released against the olive fly in California (Collier & Van Steenwyk 2003).

Materials and methods

Hosts

The tephritids tested for their potential as hosts included the five most polyphagous species of *Ceratitis* native to Kenya (De Meyer et al. 2002): *C. capitata*, *C. cosyra* (Walker), *C. rosa* Karsch, *C. fasciventris* (Bezzi) and *C. anonae* Graham and one introduced species, *B. cucurbitae* (Coquillett). Colonies of all six fruit fly species were maintained at the International Centre of Insect Physiology and Ecology (ICIPE) in Nairobi, Kenya. Culture conditions and data on original field collections from which cultures were established are provided in Mohamed et al. (2003). All flies originated from Kenya, with cultures established between 1997 and 2001, and these were the only tephritids in culture at ICIPE at the time the experiments were conducted.

Parasitoids

A colony of *P. concolor* was initiated with individuals emerging from tephritids collected from arabica coffee (*Coffea arabica* L., Rubiaceae) at Rurima (0° 38.39′S, 37° 29.69′E and elevation of 1228 m). The three fruit fly species reared from coffee at this location were *C. capitata*, which was the most abundant, *C. fasciventris*, and a very small number of *Trirhithrum coffeae* Bezzi (Diptera: Tephritidae) (Wharton et al. 2000). We did not determine which of these hosts produced the parasitoids used to initiate our cultures. In a subsequent collection, however, examination of isolated puparia from which *P. concolor* emerged demonstrated that at least some individuals from this locality attack *C. capitata* in the field.

The parasitoids were reared in acrylic cages ($40 \times 30 \times 15$ cm, $l \times w \times h$) using methods described by Mohamed et al. (2003). Four round openings (10 cm diameter) were made on the topside of the cage to which pieces of organza material were fixed. Parasitoids were cultured on *C. capitata* larvae, which were placed with a thin layer of their larval diet in a modified Petri dish. The Petri dish, originally measuring 0.5 cm deep and 5.7 cm diameter, was reduced to a depth of 1 mm. This modification enabled the parasitoids, which have relatively short ovipositors, to reach all the larvae. The Petri dish (oviposition unit) was then inverted and placed on the organza-covered opening on the top of the cage for 4–6 h. A 15-g weight was placed on the oviposition unit to prevent the larvae from escaping. Placing the oviposition unit on the top of the cage, rather than inside the cage as is usually done for tephritid parasitoids (Wong & Ramadan 1992), was found to be effective for culturing parasitoids recently obtained from field collections. Before starting the experiments, the parasitoid colony was continuously reared on *C. capitata* for 18 generations.

The parasitoids used in this study were the same ones examined by Kimani-Njogu et al. (2001). Based on morphometrics and mating compatibility, Kimani-Njogu et al. (2001) concluded that the parasitoid was very close to *P. concolor*, originally described from Tunisia in North Africa, but indicated that further work was required. Wharton *et al*. (2000) referred to the Kenya material as *P. concolor*. Voucher specimens have been deposited in the ICIPE collection.

Host acceptability

Five naive, mated female wasps (10–15 days old) were introduced into a small acrylic cage ($10 \times 7 \times 10$ cm) as described by Mohamed et al. (2003). Twenty early third instar larvae of one of the host species were placed with a thin layer of their larval diet in a modified Petri dish (3.7 cm diameter, 1 mm depth). The Petri dish was then inverted and placed on the organza-covered opening on the top of the cage for 3 h. This experiment was conducted with each of the six host species in no choice tests. During the 3-h exposure period, wasp behavior was closely monitored and the number of ovipositor insertions was recorded. After the exposure period, the larvae were dissected in phosphate-buffered saline solution and inspected for the presence of parasitoid eggs. The experimental design was completely randomized, with five replicates for each host.

Host suitability

Twenty larvae of each host species were exposed to five naive, mated wasps, in the same manner as described for the acceptability experiment, and for the same exposure

period. After exposure, larvae were processed as in Mohamed et al. (2003), with puparia held until emergence of adult flies or parasitoids. When parasitoids ceased emerging (at 25 days after exposure), the parasitoids, flies, and uneclosed host puparia were counted. The experiments were replicated 25 times for *C. capitata*, 30 times for *C. cosyra*, 5 times for *C. fasciventris*, and *B. cucurbitae* and 4 times for *C. rosa* and *C. anonae*. Fewer replicates were used for the latter four hosts when it was observed that no parasitoids had emerged from the first sets of replications (a total of 100–120 larvae of each of the latter four species were exposed) (Table I).

To further verify unsuitability of *C. rosa*, *C. fasciventris*, *C. anonae* and *B. cucurbitae*, 100 larvae of each host were exposed to approximately 50 experienced female wasps in rearing cages for 6 h. Larvae were then removed, and *C. rosa*, *C. fasciventris* and *C. anonae* were provided larval diet, while *B. cucurbitae* larvae were provided with small pieces of squash. On the second day after parasitization, a sample of 30 larvae of each species was dissected in a saline solution (phosphate buffer solution) and examined under a binocular microscope. The number of encapsulated and/or melanized eggs was counted in each host.

Developmental time

One hundred and fifty larvae of *C. capitata* and *C. cosyra* were exposed to approximately 50 female parasitoids with previous ovipositional experience on *C. capitata*. Exposures were conducted in rearing cages for 5 h using the same methods described for the parasitoid cultures. After exposure to *P. concolor*, hosts were kept in an incubator at 26±0.5°C, 60–70% R.H, and checked daily. The diet was kept moist by adding a few drops of water as required. Puparia were checked daily for parasitoid emergence, beginning on day 10. Developmental time (in days) for both sexes was recorded. To quantify differences in apparent size between *C. capitata* and *C. cosyra*, thirty newly formed puparia of each species were removed from the colony and weighed individually.

Table I. Number of uneclosed puparia, total parasitoid progeny, percent female progeny and developmental time of *Psyttalia concolor* reared on six fruit fly species.

Host species	Number of replicates	Percent of uneclosed puparia/20 hosts (mean±SE)	Total parasitoid progeny/20 hosts		% female progeny	Developmental time (days) (mean±SE)	
			Range	Mean±S.E.		Female	Male
C. capitata	25	20.6±2.1b	4–17	9.1±0.7a	59.2±5.1a	15.4±0.1a (135)	13.7±0.1a (133)
C. cosyra	30	50.0±2.5a	1–11	5.6±0.5b	29.6±5.8b	17.0±0.1b (75)	15.8±0.1b (70)
C. rosa	4	6.3±4.7c	0	0	–	–	–
C. fasciventris	5	7.0±2.6c	0	0	–	–	–
C. anonae	4	7.5±3.2c	0	0	–	–	–
B. cucurbitae	5	27.0±4.7b	0	0	–	–	–

Means in the same column followed by the same letter are not significantly different ($P=0.05$) (Student–Newman–Keuls test for all comparisons except % female in which a chi-square test was used).

Data analysis

One-way analysis of variance using a general liner model was used to compare the proportion of hosts of each species accepted, number of oviposition probes, the number of total emerged parasitoids, number of superparasitized hosts, proportion of uneclosed hosts, and developmental time between species (PROC GLM, SAS Institute 2000). Proportional data were arcsine square-root transformed prior to analyses, and count data for total number of emerged parasitoids were $\log_{10}$ transformed. Untransformed data are presented in Table I. When ANOVAs were significant, means were separated using Student–Newman–Keuls (SNK) test. The proportion of female progeny was compared between the *C. capitata* and *C. cosyra* using a chi-square test of independence. Pupal weights of *C. capitata* and *C. cosyra* were compared using paired *t*-test.

Results

Host acceptability

An acceptable host was defined as a host containing at least one parasitoid egg. Using this criterion, *P. concolor* females accepted all six fruit fly species tested, however, the proportion of hosts accepted was different among host species ($F=60.4$; df = 5, 24; $P<0.0001$) (Figure 1). There was no difference in acceptance of *C. capitata* and *C. cosyrae*, but both hosts were accepted more often than the other four species. Females were observed to insert their ovipositors in the hosts more frequently than would account for the number of the eggs found at dissection, with *C. capitata* and *C. cosyrae* receiving more probes than the other four hosts ($F=12.3$; df = 5, 24; $P<0.0001$) (Figure 1). Dissections revealed that more *C. capitata* were superparasitized than *C. cosyra* ($t=6.6$; df = 8; $P<0.0002$), while the other four species were not superparasitized. The mean number of eggs per superparasitized larva was not different between *C. capitata* and *C. cosyra* with 2.7 ± 0.2 (SE) and 2.0 ± 0.0 (SE) eggs/host, respectively. All eggs were oviposited in the posterior third of the larval abdomen.

Host suitability

Both *C. capitata* and *C. cosyrae* were suitable for development of *P. concolor*. The total number of progeny successfully reared from *C. capitata* was significantly greater than the number reared from *C. cosyra* ($F=14.1$; df = 1, 53; $P<0.0004$) (Table I). The proportion of hosts that failed to produce parasitoids or flies (uneclosed puparia) was highest for those exposed to *C. cosyra*, not different between *C. capitata* and *B. cucurbitae*, and lowest for those exposed to *C. rosa*, *C. fasciventris* and *C. anonae* ($F=24.1$; df = 5, 24; $P=0.0001$) (Table I). The proportion of female progeny was significantly higher when they were reared on *C. capitata* than when reared on *C. cosyra* ($\chi^2=21.9$; $P=0.0001$) (Table I). The sex ratio of parasitoids emerging from *C. capitata* was slightly female biased (1: 0.81, female: male), while it was distinctly male biased (1: 2.2) in those emerging from *C. cosyra*.

No parasitoid progeny emerged from *C. rosa*, *C. fasciventris*, *C. anonae*, or *B. cucurbitae* (Table I). Eggs deposited in the four unsuitable hosts were all encapsulated. Dissections 2 days after oviposition revealed that eggs deposited in

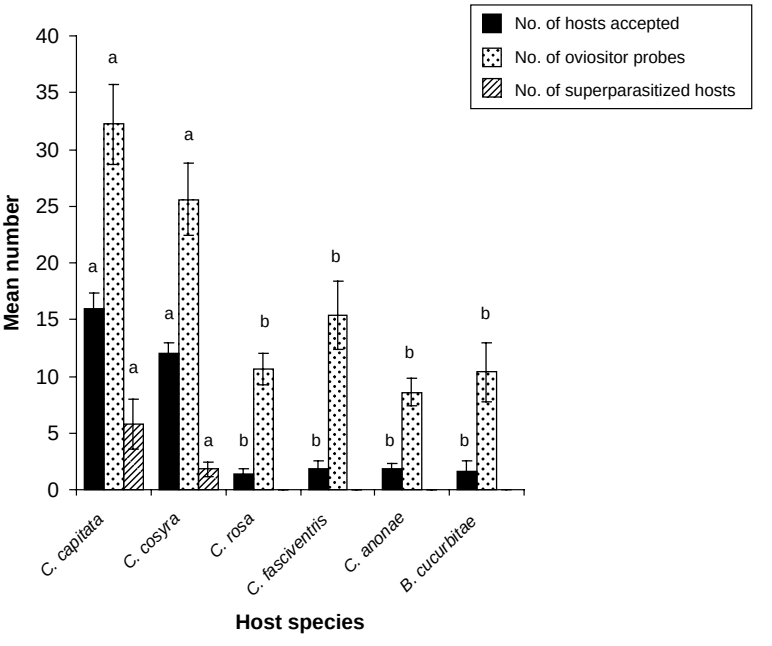

Figure 1. Mean number (±SE) of six fruit fly species accepted, probed and superparasitized by *Psytallia concolor.* The same letter above bars within a category (acceptance, probes, superparasitism) indicates no significant difference ($P > 0.05$, Student–Newman–Keuls procedure).

C. rosa and *C. anonae* were either encapsulated or encapsulated and partially or completely melanized (Figure 2). Those deposited in *C. fasciventris* and *B. cucurbitae*, however, showed no evidence of melanization.

Developmental time

The pre-imaginal developmental time of *P. concolor* was significantly shorter in *C. capitata* (14.5 ± 0.1 days) than in *C. cosyra* (16.5 ± 0.1 days) ($F = 235.4$; df = 1, 408; $P = 0.0001$). Male and female developmental time varied within the same host species ($F = 227.4$; df = 1, 263; $P = 0.0001$ and $F = 84.8$; df = 1, 140; $P = 0.0001$ for *C. capitata* and *C. cosyra,* respectively) and between the species ($F = 183.5$; df = 1, 198; $P = 0.0001$ and $F = 206.8$; df = 1, 205; $P = 0.0001$, for males and females, respectively) (Table I). *Ceratitis capitata* puparia were lighter than those of *C. cosyra* ($t = 2.002$; df = 29; $P < 0.0001$). *Psyttalia concolor* thus developed faster in the smaller host species.

Discussion

Information on the acceptability and suitability of hosts for parasitoid oviposition and development provides insight into the host range of that parasitoid in nature. In this study, acceptance of the six fruit fly species by Kenyan *P. concolor* varied, with unsuitable hosts being accepted far less frequently. These results are similar to those of Duan and Messing (2000) and Quimio and Walter (2001), who also worked with opiine braconids attacking tephritid pests. Quimio and Walter (2001) showed that

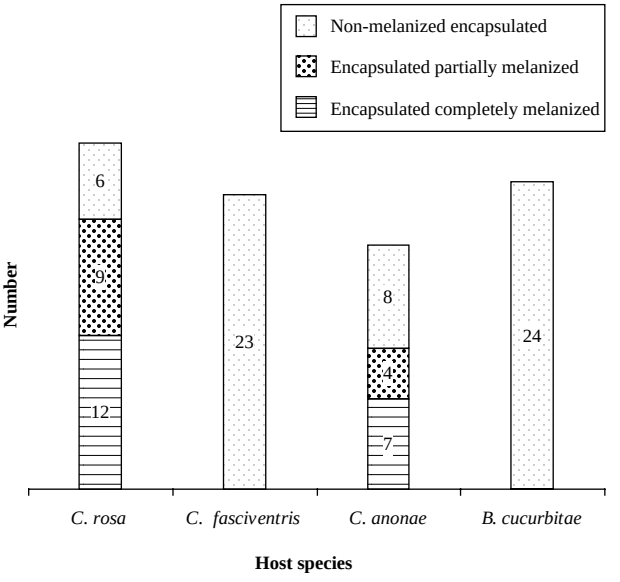

Figure 2. Fate *Psyttalia concolor* eggs oviposited in four unsuitable fruit fly hosts.

Fopius arisanus (Sonan) accepted three of the tested tephritid species but exhibited a stronger preference for *Bactrocera tryoni* (Froggatt) and *B. jarvisi* (Tryon) compared to *B. cucumis* (French). Similarly, Duan and Messing (2000) demonstrated that *Diachasmimorpha kraussii* (Fullaway) exhibited a decided preference for the target pest *Bactrocera latifrons* (Hendel) relative to four non-target tephritids in galls and flower heads. Duan and Messing (2000) also noted that the results were the same regardless of whether hosts were offered under choice or no choice conditions.

Female *P. concolor* were observed to insert their ovipositors into hosts more frequently than the number of the eggs found in these hosts. Thus, some hosts appear to have been rejected following exploratory host probing with the ovipositor. Host rejection by parasitoids in general, following ovipositor insertion, is a well-documented phenomenon (Vinson & Iwantsch 1980). Canale and Raspi (2000) reported the presence of a dome-shaped sensillum on the ovipositor of *P. concolor*. They suggested it might facilitate detection of chemical composition of the hosts, and hence the detection of their quality. Chemosensory sensilla of this nature were first observed on ovipositors of opiine parasitoids of tephritids by Greany et al. (1977), but the nature of the chemicals being detected is still unknown. Several possibilities exist (Fisher 1971; Thompson 1986). For *B. curcurbitae*, *C. rosa*, *C. fasciventris*, and C. *anonae*, there may be species-specific chemicals that enable *P. concolor* to recognize and therefore reject these as unsuitable hosts. From an evolutionary point of view, it is understandable that *B. cucurbitae*, being an introduced pest in Africa, was not a compatible host for *P. concolor*. It is less obvious why *C. rosa*, *C. fasciventris*, and *C. anonae*, which are native to Africa, and members of the same genus as the suitable hosts, were unsuitable. *Ceratitis fasciventris*, in particular, was found in the same geographic area, and breeding in the same habitat (coffee berries) as that of the parasitoid (Wharton et al. 2000). All three of these unsuitable and rarely accepted species belong to the subgenus *Pterandrus*. Detection of unsuitable hosts within the

genus *Ceratitis* might therefore have a phylogenetic component since neither of the suitable hosts are members of this subgenus.

Eggs were consistently laid in the posterior third of the host's abdomen, which is in contrast to findings of Pemberton and Willard (1918), who stated that females of *Psyttalia* (reported as *Opius*) *humilis* (Silvestri) selected no particular location on the host for oviposition. *Psyttalia humilis* from South Africa is virtually indistinguishable morphologically from *P. concolor*, and may represent a sibling species or a geographically distinct population of the same species (Fischer 1958, 1971; Wharton & Gilstrap 1983). Our results showed that although there was no significant difference between the acceptance of *C. capitata* and *C. cosyra*, the survival of the parasitoid was low in *C. cosyra*. The Kenyan *P. concolor* was originally collected from tephritids in coffee (Wharton et al. 2000), where it is highly likely that *C. capitata* was the primary if not exclusive host. In Kenya, *C. cosyra* attacks primarily mango and wild host plants such as *Sclerocarya birrea* (A. Rich.) Hochst. where *P. concolor* is not known to occur. Similarly, Ramadan et al. (1992) found that although *F. arisanus* females did not discriminate between *Bactrocera dorsalis* (Hendel) and *C. capitata*, significantly fewer progeny were obtained when the parasitoid was reared from the adventitious host *C. capitata*.

Host suitability is reported to have a strong influence on the sex ratio of arrhenotokous parasitoids (Waage 1982; Wong et al. 1990; Ramadan et al. 1995). Unsuitable or poor quality hosts may result in a male-biased sex ratio (Charnov & Skinner 1985). This has been observed in other opiine parasitoids of tephritid pests. For example, a higher proportion of male progeny was obtained from *Diachasmimorpha longicaudata* (Ashmead) when the ovipositing parasitoid had developed in *Anastrepha obliqua* than when it had developed in *A. ludens* (Eben et al. 2000). In our study, the parasitoid progeny were male biased when *C. cosyra* was the host. Since there was a relatively high percentage of uneclosed puparia when larvae of *C. cosyra* were exposed to ovipositing female wasps (Table I), the male biased sex ratio from this host could have been due to a high mortality of immature females in the host. Differential parasitoid mortality in which females suffered higher mortality than males has been reported by several authors (e.g. Benson 1973; Rotary & Gerling 1973; Wellings et al. 1986). A more detailed experiment would be required to test the alternative explanation that the female wasps laid more unfertilized eggs in hosts that were perceived to have been of lower quality.

Our results agree with previous studies showing that host species may influence the duration of the developmental time in parasitoids (Moratorio 1987; Harvey & Thompson 1995). Parasitoid development proceeded faster on *C. capitata* than on *C. cosyra*. *Ceratitis capitata* larvae are smaller than *C. cosyra* and thus form smaller, lighter puparia (6.1 ± 0.14 mg) compared to those of *C. cosyra* (10.4 ± 0.23 mg). A similar relationship between host size and the duration of pre-imaginal developmental was reported by Harvey and Thompson (1995) for an ichneumonid parasitoid of pyralid (Lepidoptera) larvae, but the opposite trend was noted by Mochiah et al. (2001) for a braconid attacking a pyralid. Harvey et al. (1999), Hemerik and Harvey (1999), and Harvey and Strand (2002) provide a discussion of other factors that should be considered when assessing host size and development time in koinobiont species. Development time for Kenyan *P. concolor* was a little shorter than that reported by Raspi and Loni (1994) and Loni (1997) for Italian *P. concolor* reared on the medfly.

Parasitoid eggs deposited in an unsuitable tephritid host are routinely encapsulated (Pemberton & Willard 1918; Nishida & Haramoto 1953) or encapsulated and melanized (Ramadan et al. 1994). In this study, Kenyan *P. concolor* was unable to evade the cellular immune system of *B. cucurbitae*, *C. fasciventris*, *C. rosa* and *C. anonae* as all eggs deposited in these hosts were encapsulated. In the latter two hosts some eggs were also melanized. Almost nothing is known about the immune response of the three unsuitable species of *Ceratitis* since they have only rarely been tested against other parasitoids (Mohamed et al. 2003). *Bactrocera cucurbitae* and *C. capitata*, however, have been tested against a variety of parasitoid species over the past 85 years and provide an interesting contrast. Most of the parasitoids tested against *B. cucurbitae* have been encapsulated (Pemberton & Willard 1918; Nishida & Haramoto 1953). These same species develop readily on *C. capitata*, regardless of whether they are co-evolved (Pemberton & Willard 1918; Clausen et al. 1965).

Our data partially support the hypothesis that a female wasp selects a host that provides the best environment for the development of her offspring (Van Alphen & Janssen 1982; Brodeur et al. 1998). Acceptance of *C. capitata* and *C. cosyra* was not significantly different, even though *C. capitata* was a better host for parasitoid survival. However, *Ceratitis rosa*, *C. fasciventris*, *C. anonae* and *B cucurbitae*, where oviposition did not lead to a reproductive gain, were rarely accepted as hosts.

Negative environmental impacts of introduced biocontrol agents, mainly through the effect on non-target species, have recently received a great deal of attention (e.g. Howarth 1991; Follett et al. 2000). Our results indicate that the Kenyan population of *P. concolor* has a narrow host range, which is a positive attribute when selecting natural enemies for classical biological control (Van Lenteren 1986). Therefore, we would expect this parasitoid to have minimal impact on non-target species. However, we are currently investigating the foraging behavior of the parasitoid in relation to different habitats, which will provide more insight into the potential risk to non-target species.

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References

Arambourg Y. 1962. Observations sur la biologie de *Dacus oleae* Gmel. (Diptera: Trypetidae) et de son parasite *Opius concolor* Szépl. (Hymenoptera: Braconidae) dans la région de Sfax en 1961–1962. Bulletin de la Société Entomologique de France 67:197–203.

Avilla J, Albajes R. 1984. The influence of female age and host size on the sex ratio of the parasitoid *Opius concolor*. Entomologia Experimentalis et Applicata 35:43–47.

Baranowski RM, Glenn H, Sivinski J. 1993. Biological control of the carib fruit fly (Diptera: Tephritidae). Florida Entomologist 76:245–251.

Benson JF. 1973. Interspecific competition in the population dynamics of *Bracon hebetor* Say (Hymenoptera: Braconidae). Journal of Animal Ecology 42:105–124.

Biliotti E, Delanoue P. 1959. Contribution a l'étude biologique d'*Opius concolor* Szepl., (Hym. Braconidae) en élevage de laboratoire. Entomophaga 4:7–14.

Brodeur J, Geervliet JBF, Vet LEM. 1998. Effect of *Pieris* host species on life history parameters in a solitary specialist and gregarious generalist parasitoid (*Cotesia* species). Entomologia Experimentalis et Applicata 86:145–152.

Cals-Usciati J. 1982. Les stratégies alimentaires de la larve primaire dominante du parasitoïde *Opius concolor* (Hyménoptère: Braconidae) et les mécanismes d'attaque des tissus de l'hôte, *Ceratitis capitata* (Diptère: Trypetidae). Comptes Rendus de l'Academie de Sciences Paris, série III, 294:379–384.

Cals-Usciati J. 1983. Succession des modes de vie et des stratégies alimentaires des larves d'un insecte entomophage endoparasitoide, *Opius concolor* Szepl. (Hyménoptère, Braconidae). Bulletin de la Société Zoologique de France 108:415–422.

Canale A, Raspi A. 2000. Host location and oviposition behaviour in *Opius concolor* (Hymenoptera: Braconidae). Entomological Problems 31:25–32.

Charnov EL, Skinner SW. 1985. Complementary approaches to the understanding of parasitoid oviposition decision. Environmental Entomology 14:383–391.

Clausen CP, Clancy DW, Chock QC. 1965. Biological control of the oriental fruit fly (*Dacus dorsalis* Hendel) and other fruit flies in Hawaii. United States Department of Agriculture Technical Bulletin 1322:1–102.

Collier TR, Van Steenwyk RA. 2003. Prospects for integrated control of olive fruit fly are promising in California. California Agriculture 57(28–30):32.

Copeland RS, Wharton RA, Luke Q, & De Meyer M. 2002. Indigenous hosts of *Ceratitis capitata* (Diptera: Tephritidae) in Kenya. Annals of the Entomological Society of America 95:672–694.

De Meyer M. 1996. Revision of the subgenus *Ceratitis* (*Pardalaspis*) Bezzi, 1918 (Diptera, Tephritidae, Ceratitini). Systematic Entomology 21:15–26.

De Meyer M. 1998. Revision of the subgenus *Ceratitis* (*Ceratalaspis*) Hancock (Diptera: Tephritidae). Bulletin of Entomological Research 88:257–290.

De Meyer M, Copeland R, Lux SA, Mansell M, Quilici S, Wharton R, White IM, Zenz NJ. 2002. Annotated check list of host plants for Afrotropical fruit flies (Diptera: Tephritidae) of the genus *Ceratitis*. Koninklijk Museum voor Midden-Afrika Tervuren, België. Zoölogische Documentatie 27:1–91.

Duan JJ, Messing RH. 2000. Host specificity test of *Diachasmimorhpa kraussii* (Hymenoptera: Braconidae), a newly introduced opiine fruit fly parasitoid with four nontarget tephritids in Hawaii. Biological Control 19:28–34.

Eben A, Benrey B, Sivinski J, Aluja M. 2000. Host species and host plants effects on preference and performance of *Diachasmimorpha longicaudata* (Hymenoptera: Braconidae). Environmental Entomology 29:87–94.

Fischer M. 1958. Ueber die Variabilitaet von Taxonomisch Wichtigen Merkmalen bei *Opius concolor* Szepl. (Hym. Braconidae). Entomophaga 3:55–66.

Fischer M. 1971. *Hym. Braconidae. World Opiinae.* Index of entomophagous insects. Le Francois, Paris, p. 189.

Fischer M. 1987. Hymenoptera: Opiinae III-Äthiopische, orientalische, australische und ozeanische Region. Das Tierreich 104:1–734.

Fisher RC. 1971. Aspects of the physiology of endoparasitic Hymenoptera. Biological Review 46:243–278.

Follett PA, Duan J, Messing RH, Jones VP. 2000. Parasitoid drift after biological control introductions: re-examining Pandora's Box. American Entomologist 46:82–94.

Gasparich GE, Silva JG, Han JY, McPheron BA, Steck GJ, Sheppard WS. 1997. Population Genetic Structure of Mediterranean fruit fly (Diptera: Tephritidae) and its implications for worldwide colonization patterns. Annals of the Entomological Society of America 90:790–797.

Gilstrap FE, Hart WG. 1987. Biological control of the Mediterranean fruit fly in the Unite States and Central America. United States Department of Agriculture, Agriculture Research Service ARS-56:1–68.

Godfray HCJ. 1994. Parasitoids, behavioral and Evolutionary Ecology. Princeton, NJ: Princeton University Press. pp 473.

Greany PD, Hawke SD, Carlysle TC, Anthony DW. 1977. Sense organs in the ovipositor of *Biosteres* (*Opius*) *longicaudatus*, a parasite of the Caribbean fruit fly *Anastrepha suspensa*. Annals of the Entomological Society of America 70:319–321.

Harvey JA. 2000. Dynamic effects of parasitism by an endoparasitoid wasp on the development of two host species: implications for host quality and parasitoid fitness. Ecological Entomology 25:267–278.

Harvey JA, Strand MR. 2002. The developmmental strategies of endoparasitoid wasps vary with host feeding ecology. Ecology 83:2439–2451.

Harvey JA, Thompson DJ. 1995. Developmental interactions between the solitary endoparasitoid, *Venturia canescens* (Hymenoptera: Ichneumonidae) and two of its hosts, *Plodia interpunctella* and *Corcyra cephalonica* (Lepidoptera: Pryalidae). European Journal of Entomology 92:427–435.

Harvey JA, Jervis MA, Gols R, Jiang NQ, Vet LEM. 1999. Development of the parasitoid, *Cotesia rubecula* (Hymenoptera: Braconidae) in *Pieris rapae* and *Pieris brassicae* (Lepidoptera: Pieridae): evidence for host regulation. Journal of Insect Physiology 45:173–182.

Headrick DH, Goeden RD. 1996. Issues concerning the eradication or establishment and biological control of the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann) (Diptera: Tephritidae), in California. Biological Control 6:412–421.

Hemerik L, Harvey JA. 1999. Flexible larval development and the timing of destructive feeding by a solitary endoparasitoid: an optimal foraging problem in evolutionary perspective. Ecological Entomology 24:308–315.

Hoffmeister T. 1990. Zur Struktur und Dynamik des Parasitoidenkomplexes der Kirschfruchtfliege *Rhagoletis cerasi* L. (Diptera: Tephritidae) auf Kirschen und Heckenkirschen. Mitteilungen der Deutschen Gesellschaft fuer Allgemeine und Angewandte Entomologie 7:546–551.

Hoffmeister T. 1992. Factors determining the structure and diversity of parasitoid complexes in tephritid fruit flies. Oecologia 89:288–297.

Howarth FG. 1991. Environmental impact of classical biological control. Annual Review of Entomology 36:485–509.

Kimani-Njogu SW, Trostle MK, Wharton RA, Woolley JB, Raspi A. 2001. Biosystemics of the *Psyttalia concolor* species complex (Hymenoptera: Braconidae: Opiinae): The Identity of the populations attacking *Ceratitis capitata* (Diptera: Tephritidae) in coffee in Kenya. Biological Control 20:167–174.

Knipling EF. 1992. Principles of insect parasitism analyzed from new perspectives. Practical implications for regulating insect populations by biological means. United States Department of Agriculture, Agriculture Research Service, Agricultural Hand Book 693:1–337.

Loni A. 1997. Developmental rate of *Opius concolor* (Hymenoptera: Braconidae) at various constant temperatures. Entomophaga 42:359–366.

Messing RH. 1996. Status and needs for biological control research for tephritid flies. In: McPheron BA, Steck JG, editors. Fruit fly pests: a world assessment of their biology and management. Delray Beach: St. Lucie Press. pp 365–367.

Mochiah MB, Ngi-Song AJ, Overholt WA, Botchey M. 2001. Host suitability of four stem borers (Lepidoptera: Crambidae, Noctuidae) for different geographic populations of *Cotesia sesamiae* (Cameron) (Hymenoptera: Braconidae). Biological Control 21:284–292.

Mohamed SA, Overholt WA, Wharton RA, Lux SA, Eltoum EM. 2003. Host specificity of *Psyttalia cosyrae* (Hymenoptera: Braconidae) and the effect of different host species on parasitoid fitness. Biological Control 28:155–163.

Moratorio MS. 1987. Effect of host species on the parasitoids *Anagrus mutans* and *Anagrus silwoodensis* Wakker (Hymenoptera: Mymaridae). Environmental Entomology 16:825–827.

Nishida T, Haramoto F. 1953. The immunity of *Dacus cucurbitae* to attack of the parasites of *Dacus dorsalis*. Journal of Economic Entomology 46:61–64.

Pemberton CE, Willard HF. 1918. A contribution to the biology of fruit fly parasites in Hawaii. Journal of Agricultural Research 15:419–466.

Quimio GM, Walter GH. 2001. Host preference and suitability in an egg-pupal fruit fly parasitoid, *Fopius arisanus* (Sonan) (Hymenoptera: Braconidae). Journal of Applied Entomology 125:135–140.

Ramadan MM, Wong TTY, Beardsley JW. 1992. Reproductive behavior of *Biosteres arisanus* (Sonan) (Hymenoptera: Braconidae), an egg-larval parasitoid of the oriental fruit fly. Biological Control 2:28–34.

Ramadan MM, Wong TTY, McInnis DO. 1994. Reproductive biology of *Biosteres arisanus* (Sonan) (Hymenoptera: Braconidae), an egg-larval parasitoid of the oriental fruit fly. Biological Control 4: 93–100.

Ramadan MM, Wong TTY, Messing RH. 1995. Reproductive Biology of *Biosteres vandenboschi* (Hymenoptera: Braconidae), a parasitoid of early-instar oriental fruit fly. Annals of the Entomological Society of America 88:189–195.

Raspi A. 1993. Lotta biologica in olivicoltura. Atti del convegno su: Techniche, norme e qualita in Olivicoltura, Potenza, 15–17 Dicembre 1993, pp. 483–495

Raspi A, Loni A. 1994. Alcune note sull'allevamento massale di *Opius concolor* (Szépl.) (Hymenoptera Braconidae) e su recenti tentativi d'introduzione della specie in Toscana ed in Liguria. Frustula Entomologica 17:133–145.

Rotary N, Gerling D. 1973. The influence of some external factors upon the sex ratio of *Bracon hebetor* Say (Hymenoptera: Braconidae). Environmental Entomology 2:134–138.

Salt G. 1970. The cellular defense reactions of insects. London: Cambridge University Press. 118 pp.

SAS Institute 2000. SAS user's guide. Release 8.1, Cary, SAS Institute, USA.

Sivinski JM. 1996. The past and potential of biological control of fruit flies. In: McPheron BA, Steck GJ, editors. Fruit fly pests: a world assessment of their biology and management. Delray Beach: St. Lucie Press. pp 369–375.

Sivinski JM, Calkins CO, Baranowski R, Harris D, Brambila J, Diaz J, Burns RE, Holler T, Dodson G. 1996. Suppression of a Caribbean fruit fly *Anastrepha suspensa* (loew) (Tephritidae: Diptera) population through augmented releases of the parasitoid *Diachasmimorpha longicaudata* (Ashmead) (Hymenoptera: Braconidae). Biological Control 6:177–185.

Thompson SN. 1986. Nutrition and in vitro culture of insect parasitoids. Annual Review of Entomology 31:197–219.

Van Alphen JJM, Janssen ARM. 1982. Host selection by *Asobara tabida* Nees (Braconidae: Alysiinae), a larval parasitoid of fruit inhabiting *Drosophila* species. II. Host species selection. Netherlands Journal of Zoology 32:215–231.

Van Lenteren JC. 1986. Parasitoids in the greenhouses: Successes with seasonal inoculative release systems. In: Waage J, Greathead D, editors. Insect parasitoids. London: Academic Press. pp 341–374.

Vinson SB, Iwantsch GF. 1980. Host suitability for insect parasitoids. Annual Review of Entomology 25:397–419.

Waage JK. 1982. Sex ratio and population dynamics of natural enemies: Some possible interactions. Annals of Applied Biology 101:159–164

Waterhouse DF. 1993. Pest fruit flies in the Oceanic Pacific. In: Biological control – Pacific prospects. Canberra: Australian Centre for International Agricultural Research. pp 4–47.

Wellings PW, Morton R, Hart PJ. 1986. Primary sex ratio and differential progeny survivorship in solitary haplo-diploid parasitoids. Ecological Entomology 11:341–348.

Wharton RA. 1989. Classical biological control of fruit-infesting Tephritidae. In: Robinson AS, Hooper G, editors. World crop pests. Fruit flies: their biology, natural enemies and control. Amsterdam/New York: Elsevier. pp 303–313.

Wharton RA. 1997. Generic relationships of opiine Braconidae (Hymenoptera) parasitic on fruit infesting Tephritidae (Diptera). Contributions to American Entomological Institute 30:1–53.

Wharton RA, Gilstrap FE. 1983. Key to and status of opiine braconid (Hymenoptera) parasitoids in biological control of *Ceratitis* and *Dacus s.l.* (Diptera: Tephritidae). Annals of the Entomological Society of America 76:721–742.

Wharton RA, Trostle MK, Messing RH, Copeland RS, Kimani-Njogu SW, Lux S, Overholt WA, Mohamed S, Siviniski J. 2000. Parasitoids of medfly, *Ceratitis capitata* and related tephritids in Kenyan coffee: a predominantly koinobiont assemblage. Bulletin of Entomological Research 90:517–526.

White IM, Elson-Harris MM. 1992. Fruit flies of economic significance: their Identification and bionomics. C.A.B International and Australian Centre for International Agricultural Research. 601 pp.

Willard HF, Mason AC. 1937. Parasitization of the Mediterranean fruit fly in Hawaii, 1914–1933. United States Department of Agriculture Circular 439:1–18.

Wong TYY, Ramadan MM. 1992. Mass rearing biology of larval parasitoids (Hymenoptera: Braconidae: Opiinae) of tephritid flies (Diptera: Tephritidae) in Hawaii. In: Anderson TE, Leppla NC, editors. Advances in insect rearing for research and pest management. Boulder, CO: Westview. pp 405–426.

Wong TTY, Ramadan MM, McInnis DO, Mochizuki N. 1990. Influence of the cohort age and host age on oviposition activity and offspring sex ratio of *Biosteres tryoni* (Hymenoptera: Braconidae:) of *Ceratitis capitata* (Diptera: Tephritidae). Journal of Economic Entomology 83:779–783.