Parasitoids of medfly, *Ceratitis capitata*, and related tephritids in Kenyan coffee: a predominantly koinobiont assemblage

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Abstract

Arabica coffee was sampled from two sites in the central highlands of Kenya (Rurima, Ruiru) and one site on the western side of the Rift Valley (Koru). Three species of ceratitidine Tephritidae, *Ceratitis capitata* (Wiedemann), *C. rosa* Karsch and *Trirhithrum coffeae* Bezzi, were reared from sites in the central highlands, and an additional species, *C. anonae* Graham, was recovered from the western-most site. Ten species of parasitic Hymenoptera were reared from these tephritids. The parasitoid assemblage was dominated by koinobionts. Eight of the species are koinobiont endoparasitoids, but only one idiobiont larval ectoparasitoid was reared, and only one idiobiont pupal endoparasitoid. The effects of sampling bias on determination of parasitoid assemblage size associated with concealed hosts are discussed. The potential for use of these parasitoids in biological control is also discussed. Most of the parasitoid species recovered during this study are capable of developing on *C. capitata*, while several also attack *C. rosa*. Both flies are notorious pests of tropical and subtropical fruits.

Introduction

The Mediterranean fruit fly (= medfly), *Ceratitis capitata* (Wiedemann) (Diptera: Tephritidae), is one of the most polyphagous and important pests of edible fruits worldwide (Weems, 1981; Liquido *et al*., 1991). The Natal fly, *Ceratitis rosa* Karsch (Diptera: Tephritidae), is an equally serious regional pest of many edible fruits, but is limited in distribution to Africa, Mauritius and La Réunion (Commonwealth Institute of Entomology, 1985; White & Elson-Harris, 1992). Medfly is indigenous to Africa (Silvestri, 1913), with increasing evidence (in the form of high genetic diversity) pointing to a subsaharan, tropical origin (Steck *et al*., 1996; Gasparich *et al*., 1997). It is the most widespread of the fruit-infesting tephritid pests, having been introduced to Australia, Hawaii, the Mediterranean Region, most of tropical America and numerous islands (White & Elson-Harris, 1992). An enormous amount of information has been published on medfly, but much of our knowledge comes from efforts to control this pest in areas where it has been introduced (see Quaintance (1912) and Back & Pemberton (1918) for earlier studies and Fletcher (1989) for a more recent review). Relatively few studies (e.g. Abasa, 1973) have been conducted in regions of medfly's presumed origin, in part because of its scarcity. As both medfly and Natal fly are native to subsaharan Africa, data on factors that may limit population growth in their aboriginal home should be of some value to pest management programmes.

In East Africa, coffee cherries (especially *Coffea arabica* L.: Rubiaceae) are an important reservoir for both medfly and Natal fly. The occurrence and relative abundance of these

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and other tephritids found in coffee vary regionally and seasonally (Greathead, 1972; Abasa, 1973; Waikwa, 1978; Steck *et al*., 1986; Mukiama & Muraya, 1994). Differences in tephritid species composition among coffee species have also been noted (Greathead, 1972; Mukiama & Muraya, 1994). Coffee is thus a potentially useful host for examining the effects of natural enemies and other factors on populations of these two pests. Further, medfly usually causes little or no economic damage in coffee (Hamilton, 1967; Le Pelley, 1968; Abasa, 1973), facilitating the acquisition of samples under relatively insecticide-free conditions. Nevertheless, some economic damage can occur when beans are not processed in an optimal manner (Gibson, 1970) or when fly populations are so excessively high that a significant amount of oviposition occurs in unripe cherries (a non-preferred stage) (Back & Pemberton, 1918).

Data on the parasitoids and other natural enemies of East African, coffee-infesting tephritids are largely lacking. Greathead (1972) recorded several parasitoids of *Trirhithrum coffeae* Bezzi in robusta coffee (*Coffea canephora* Pierre ex Froehner) from Uganda, and this is undoubtedly the best quantitative data available for East Africa. Unfortunately, there were very few specimens of medfly and Natal fly in his samples. Other reports of parasitoids from coffee samples collected in East Africa are largely anecdotal (Bianchi & Krauss, 1937; Clausen *et al*., 1965; Waikwa, 1978). Steck *et al*. (1986) provided a quantitative assessment of parasitism of tephritids in coffee from West Africa, but medfly was also rare in their samples, and Natal fly was absent.

There has been renewed interest in the biological control of medfly in recent years (Wharton, 1989a; Knipling, 1992; Headrick & Goeden, 1996; Sivinski, 1996; Purcell, 1998), with a focus on reducing source populations that pose a constant threat of introduction to fruit growing regions of Mexico and mainland USA. Outbreaks in Florida in 1997 and 1998, and increasing penetration of the barrier zone along the Mexican/Guatemalan border since 1998 have added urgency to the search for alternative strategies for medfly control. Thus, the demand for more effective natural enemies from the aboriginal home of this pest, as championed by several researchers (Gilstrap & Hart, 1987; Wharton, 1989a,b; Headrick & Goeden, 1996), is as great now as it has ever been. Parasitoids of Natal fly have also been of interest to biological control workers ever since this species was accidentally introduced to Mauritius and La Réunion in the 1950s (Orian & Moutia, 1960; Étienne, 1973).

In this paper the occurrence of tephritid parasitoids in coffee in Kenya is documented, including sites where medfly and Natal fly are relatively abundant, thus providing baseline data for biological control efforts directed against these pests. Certain larger issues associated with parasitoid assemblages on concealed hosts are also addressed. In particular, the applicability of the carefully documented findings of Hoffmeister (1992) and Hoffmeister & Vidal (1994), based largely on Holarctic communities, to tropical tephritid systems is explored. Fruit-infesting tephritids are exploited in a variety of ways by numerous parasitic Hymenoptera, most notably those in the families Braconidae, Chalcididae, Diapriidae, Eulophidae, Eupelmidae, Eurytomidae, Figitidae (Eucoilinae), Ichneumonidae, and Pteromalidae (Clausen *et al*., 1965; Wharton *et al*., 1981; Hoffmeister, 1992). Nearly all of these parasitoids attack the host when it is concealed inside the fruit (as an egg or larva) or in the substrate (as a puparium).

Materials and methods

Sampling sites

Ripe cherries of *Coffea arabica* were sampled monthly, depending on seasonal availability, at three principal sites: Rurima, Ruiru, and Koru (fig. 1). Rurima farm is a commercial coffee plantation located in east-central Kenya, near Embu, at 0°38.39′S, 37°29.69′E, and an elevation of *c*. 1228 m. Most of the coffee at Rurima is unshaded. The other two sites are experimental field stations of the government-run, Coffee Research Foundation (CRF). None of the coffee from these two sites is shaded. CRF-Ruiru (hereafter referred to as Ruiru) is located in the central Kenyan highlands at 1°5.72′S, 36°54.22′E, and an elevation of 1609 m. It is approximately 15 km north of the International Centre of Insect Physiology and Ecology (ICIPE) laboratories where all coffee samples were processed. CRF-Koru (hereafter referred to as Koru) is located in the western Kenyan highlands at 0°8.16′S, 35°16.87′E, and an elevation of 1513 m. Rurima and Ruiru are on the eastern side of the Rift Valley and form part of a more or less continuous band of commercial coffee farms that generally experience two rainy seasons. The major coffee season in the Ruiru area is from October to December. A smaller coffee harvesting period occurs from April to July. Koru is located on the western side of the Rift Valley where coffee farming is far less prevalent. Koru has one long coffee season, with most of the coffee produced from July to November. Local agriculture in the Koru area is dominated by vast monocultures of sugarcane. Robusta coffee was available at both Ruiru and Koru, but sampling was restricted to arabica coffee to facilitate among-site comparisons. Earlier reports (e.g. Greathead, 1972) suggest that there are distinct differences in tephritid species composition in robusta and arabica coffee.

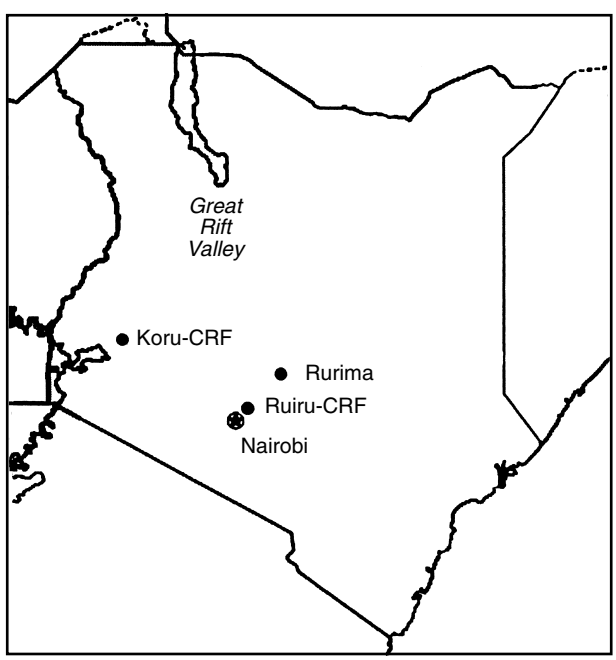

Fig. 1. Map of Kenya showing locations of primary collecting sites.

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Table 1. Monthly rainfall and temperature data for the three primary sample sites, representing means for the last 45 years (Ruiru), 40 years (Koru) and 30 years (Rurima).

Month	Ruiru			Koru			Rurima		
	Rainfall (mm)	Temp. (°C)		Rainfall (mm)	Temp. (°C)		Rainfall (mm)	Temp. (°C)	
		Max.	Min.		Max.	Min.		Max.	Min.
1	50.7	26.1	11.7	108	27.3	13.5	24	28.3	14.2
2	47.2	27.9	12.6	112.3	28.5	14.1	28	31.1	15
3	100.9	27.7	13.7	186.6	29.8	14.3	101	30.2	16.3
4	247.2	25.5	14.7	245.6	26	14.7	231	28.6	17.2
5	168	24.6	13.7	195.2	25.2	14.3	109	27.6	16.5
6	46.8	23.5	12.2	133.7	24.6	14.1	8	26.7	14.9
7	28.3	22.3	11.6	138.1	24.9	13.8	3	25.6	14.5
8	26	22.7	11.6	142	26	13.7	4	26.2	4.5
9	26.6	25.2	11.9	101.8	28	13.5	8	28.2	15
10	74.3	26.3	13.4	113.7	28.6	13.4	96	29.5	16.3
11	163	23.7	13.9	130.2	28.3	13.6	216	27.3	16.4
12	85.7	25	12.9	100.8	28.2	13	74	27.1	15.2
Total rainfall	1064.7			1708			902		
Mean temp		25	12.8		27.1	13.8		28	15.5

Data are from Central Research Farm records at Ruiru and Koru and have been estimated for Rurima using the program ACT-20. Mean rainfall and temperatures are calculated from these data.

Precipitation and mean maximum and minimum temperatures are given in table 1 for the principal sites. Data are listed as 30–45 year means. Ruiru and Rurima have similar rainfall patterns with both a long and a short rainy season each year. Rainfall is higher at Koru, with a distinct peak during the long rainy season from March to May, but otherwise spread more evenly over the year. Rurima is both drier and warmer than the other two sites.

Although mature coffee plants are capable of bearing fruit all year long, coffee cherries are routinely stripped from all plants as a means of reducing coffee-pest populations during non-peak seasons. Stripping occurred in mid-December at all three principal sites, resulting in little or no coffee available for sampling during the first few months of the year. To fill this gap, small samples of arabica coffee were obtained from adjacent farms where stripping was of more sporadic occurrence. Spot samples of *Coffea canephora* were also collected from a small plot maintained by the Ministry of Agriculture in the Shimba Hills during July 1997 and May 1999 for comparative purposes.

Sampling periods

Preliminary samples were taken from Ruiru in 1995 and 1996 to assess potential for recovery of medfly parasitoids for use in biological control. Routine monthly sampling of coffee began in November, 1997 at all three localities. Farms adjacent to the Coffee Research Foundation provided nearly all of the coffee at Ruiru from November 1997 through July 1998.

Sample processing

Coffee cherries were hand-picked and returned to an ICIPE laboratory in Nairobi on the same day (Ruiru and Rurima) or the following day (Koru). Conditions in the laboratory reflected ambient outdoor temperature and relative humidity in the shade. When scales were available at the CRF stations, samples were weighed immediately after picking. Otherwise, weights were estimated as follows: a 5 kg sample was weighed and placed into a 20 l bucket. A fill line was then drawn on the bucket at the level reached by the 5 kg sample. Later measurements using a precision balance showed that both procedures gave an error estimate of about 10%. Samples varying in weight from 1 to 10 kg (depending largely on availability) were held in either 60 × 48 × 60 or 60 × 88 × 60 cm, wooden-bottomed and framed rearing cages covered on three sides and the top with fine white mesh and in the front by a sheet of removable perspex. Fruits were distributed between two stacked, plastic rearing trays, each with slits in the bottom through which larvae could drop to moistened sand at the bottom of the cage. When the fruit started to dry up through time, it was sprayed with water, then rolled and mixed to ensure all fruits were moistened. Sand was sieved at 12–14 days and again five days later. Subsamples of the puparia obtained from the first sieving were shipped to the Hawaii Department of Agriculture (HDOA) quarantine facility for use in biological control. At both ICIPE and HDOA, puparia were transferred to smaller cages with fine mesh on at least two sides. Emerging insects were provided with water-soaked cotton wool, honey droplets, and a yeast/sugar diet. Adult tephritids emerging at ICIPE were held for about five days and then either killed and pinned or identified while alive and used to establish and maintain colonies (medfly and Natal fly, *C. rosa*). In Hawaii, all emerging flies were killed immediately. Hymenopterous parasitoids were killed immediately in 95% ethanol at ICIPE, but some were used to establish laboratory cultures in quarantine in Hawaii. Estimates of infestation rates per fruit were obtained in August 1998 and August–November 1999 by dissecting several hundred field-collected cherries and recording the numbers of tephritid eggs and larvae in each fruit. Estimates were made for each of the three principal sites.

Several hundred puparia were individually isolated in small vials and held for emergence of flies and parasitoids. Using correctly associated fly puparia obtained in this manner, morphological features were scored for the puparia of the four tephritid species reared from coffee. These

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features were then used to identify the isolated puparia that produced parasitoids. Puparia from the monthly samples were not routinely isolated because the additional handling greatly decreased overall % emergence, as did the decrease in humidity associated with the isolation vials.

Additional samples were taken to obtain data on egg and pupal parasitoids. To determine the presence of egg parasitoids, coffee cherries were sampled on four different occasions from Ruiru, twice from Koru, and once from Rurima. Fruits were dissected to recover tephritid eggs, and all recovered eggs were placed in a Petri dish on the associated hull of the coffee cherry from which they were extracted. The Petri dish was then taped shut to prevent escape of any egg parasitoids, and held until eggs hatched. Preliminary attempts to recover pupal parasitoids by extracting puparia from soil beneath coffee bushes were unsuccessful, yielding only flies and koinobiont larval–pupal parasitoids. A separate laboratory colony of medfly was therefore established at ICIPE using flies obtained from the Ruiru samples. During September 1999, fully fed third instar larvae were removed from the laboratory culture, immediately taken to Ruiru, and allowed to enter the soil to pupate. Four hundred and 50 larvae were dispersed in the field at a rate of fifty per coffee bush. Samples beneath five of the bushes were recovered after a 3-day period and the remaining four samples were recovered after a one-week period. Of 450 third instar larvae released under coffee plants, only 249 puparia were recovered, and these were held individually in the laboratory for emergence of flies and parasitoids.

To determine occurrence of larval ectoparasitoids, smaller samples (0.5 kg) were held in escape-proof cages for several weeks and all parasitoids collected from the cages daily. When ectoparasitoid taxa were recovered, fruits were dissected to verify hosts (since coffee cherries also harbour larval beetles and moths that could serve as hosts of ectoparasitoids).

Analysis

Where appropriate, data for flies and parasitoids are presented by species as the geometric mean monthly number of individuals per kg of coffee.

Identifications

Flies and parasitoids reared from coffee during the first year's collections were all sorted and identified by R.A. Wharton, mostly using available literature, or literature specifically prepared for this purpose at the start of the project (Wharton & Gilstrap, 1983; White & Elson-Harris, 1992; Wharton, 1997, 1999; Wharton *et al*., 1999). Routine identifications of the three most common fly species and four most common parasitoid species were performed in subsequent years either by technical staff at ICIPE trained by Wharton or by Kimani-Njogu and Trostle. Voucher specimens are maintained at ICIPE, Texas A&M University, and the National Museum of Kenya.

Results

Tephritid flies infesting coffee

From November 1997 through to June 1999, 21,433 puparia were obtained from arabica coffee samples collected at Koru, 18,127 puparia from Ruriru, and 12,585 puparia from Rurima. Four species of ceratitidine Tephritidae were reared from these samples: *Ceratitis anonae* Graham, *C. capitata*, *C. rosa*, and *T. coffeae*. Females of *C. anonae* are virtually indistinguishable from *C. rosa*, and it is thus possible to overlook the presence of *C. anonae* in samples where *C. rosa* is abundant. Otherwise, adults of the species recorded here can be readily identified using a combination of the keys in White & Elson-Harris (1992) and Hancock & White (1997). The species of *Trirhithrum* occurring in coffee are relatively darker species with a uniformly black scutellum, and are thus readily separated from the species of *Ceratitis* reported from coffee. *Ceratitis anonae* was recovered only from Koru. *Trirhithrum coffeae* was occasionally abundant at Koru, sporadic at Ruiru, but recovered only very rarely from Rurima (table 2).

Table 2. Geometric mean number of flies per kilogram for each fly species at each site in Kenya.

Site	*Ceratitis capitata*	*Ceratitis rosa*	*Ceratitis anonae*	*Trirhithrum coffeae*
Koru	4.60	21.80	0.19	1.86
Ruiru	32.34	10.12	0	0.98
Rurima	48.77	2.30	0	0.21

Infestation rates (sample means of number of eggs plus larvae per coffee cherry) ranged from 0.87–1.4 at Ruiru, 1.2–1.4 at Rurima, and 0.4–1.5 at Koru over the latter half of 1999. The smaller sample collected in Ruiru on 4 August 1998 was more heavily infested, with a mean of 2.0 individuals per coffee cherry.

Parasitoids of tephritids in coffee

Ten species of parasitoids were reared from the tephritids infesting coffee cherries. Eight of these, the eulophids *Tetrastichus giffardianus* Silvestri and *T. giffardii* Silvestri, and the opiine braconids *Diachasmimorpha fullawayi* (Silvestri), *Fopius ceratitivorus* Wharton, *F. caudatus* (Szépligeti), *F. silvestrii* Wharton, *Psyttalia cosyrae* (Wilkinson), and *Psyttalia* cf. *concolor* (Szépligeti), are all koinobionts that oviposit in the egg or larval stage of the host and emerge from the puparium. All of these were recovered using the standard sampling techniques described above. *Fopius ceratitivorus*, commonly found at least seasonally at the other two sites, was never found at the wetter site in Koru. Similarly, *F. caudatus* was never found at Ruiru or Rurima. The only idiobiont larval ectoparasitoid confirmed as a tephritid parasitoid was *Bracon celer* Szépligeti (Hymenoptera: Braconidae). The tenth species was an idiobiont pupal endoparasitoid belonging to the genus *Coptera* (Hymenoptera: Diapriidae). No egg parasitoids were found; the 211 eggs isolated from 540 field-collected coffee cherries all produced tephritid larvae. Based on isolated puparia and dissections of host remains, *T. giffardianus* and *T. giffardii* were gregarious; all other species were solitary. In terms of species richness, koinobionts dominated the samples. The parasitoid assemblage included egg-prepupal/pupal endoparasitoids (included in the second guild discussed below), larval-prepupal/pupal endoparasitoids (the major component of the second guild), larval ectoparasitoids (guild three), and pupal endoparasitoids (guild four).

The relative abundances of the more routinely sampled parasitoid species are listed by sample locality in table 3. Of the remaining species, two (*P. cosyrae* and *F. silvestrii*) were rare, with fewer than ten individuals each. *Psyttalia cosyrae* was found in coffee only at Rurima and *F. silvestrii* only at

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Table 3. Geometric mean number of parasitoids per kilogram for the four species routinely recovered from coffee samples.

	Koru	Ruiru	Rurima
Braconidae			
Diachasmimorpha fullawayi	0.74	1.15	0
Fopius caudatus	2.61	0	0
F. ceratitivorus	0	1.02	2.62
Psyttalia cf. *concolor*	0.79	1.87	1.67

Koru. The relative abundances of the two *Tetrastichus* species were difficult to estimate in the larger samples due to their gregarious nature in combination with their small size (making recovery of all individuals difficult). *Tetrastichus giffardianus* was found at all three sites. *Bracon celer* and *Coptera* sp. were obtained only by modifying the standard sampling programme (as noted above). Nineteen *B. celer* were reared from 14 separate 0.5 kg samples isolated from Ruiru. In addition to the larval ectoparasitoid *B. celer*, these samples produced a total of 2661 tephritid puparia. *Coptera* sp. was represented by six individuals reared from the 249 medfly puparia recovered from soil samples.

The widespread, polyphagous pupal ectoparasitoid *Pachycrepoideus vindemiae* (Rondani) (Hymenoptera: Pteromalidae), commonly used in augmentative programmes against tephritid pests, was recovered during the sampling period from *Dacus* puparia infesting squash at ICIPE. On occasion, adult wasps of this species were also found crawling on the inside of the rearing room windows (undoubtedly originating from the drosophilids associated with the older coffee samples). However, we never reared *P. vindemiae* from coffee-infesting tephritids during this study.

Discussion

Host flies

White & Elson-Harris (1992) and Hancock & White (1997) summarize the records for tephritid species previously recorded from coffee. We are unaware of any prior records for *C. anonae* from coffee in Kenya, though Greathead (1972) recorded it from Uganda, Crowe *et al*. (1977) noted its occurrence in Ethiopia, and it has been reported sporadically on coffee elsewhere in Africa (Steck *et al*., 1986). *Ceratitis anonae* is a common pest of other edible fruits in western Kenya and elsewhere (White & Elson-Harris, 1992). Only two other native tephritids are commonly reared from coffee berries in subsaharan Africa: *Ceratitis punctata* (Wiedemann) and *Trirhithrum nigerrimum* (Bezzi). Records of *Ceratitis rubrivora* (Coquillett) and *C. colae* Silvestri from Tanzania (Bianchi & Krauss, 1937) are based on misidentifications, as are records of *C. nigra* Graham (Kourti *et al*., 1992). The *C. nigra* (= *T. nigrum*) records from Kenya (Mukiama & Muraya, 1994) most likely refer to *T. coffeae*.

The results reported here are from samples of *Coffea arabica*. Both Waikwa (1978) and Mukiama & Muraya (1994) specifically mention the work by Greathead (1972) in concluding that *T. coffeae* is often the dominant fly in areas where robusta coffee is grown and *C. capitata* is dominant where arabica coffee is grown. However, sufficient detail has not been provided to ascertain whether such differences are regional, seasonal, or due entirely to the variety of coffee grown. The data reported by Steck *et al*. (1986) similarly suggest that *C. capitata* is more prevalent in arabica coffee relative to *T. coffeae*, but Steck *et al*. (1986) also noted that both fly species can be abundant in this type of coffee. The work reported here demonstrates that *T. coffeae* and *C. capitata* regularly co-occur with *C. rosa* in arabica coffee at Koru (and less commonly at Ruiru) at least at certain times of the year, making it difficult to associate parasitoids with a particular host fly species. Thus, the coffee system in the Kenyan highlands differs from most of the work on temperate fruit-infesting tephritid communities, including the excellent studies of Hoffmeister (1992), in which only one fly species is usually present in a given host fruit at any one locality.

The parasitoid assemblage

Medfly

The standard rearing procedures employed in this study precluded assignment of most of the reared parasitoid individuals to a specific host species. In the following discussion, therefore, the parasitoid assemblage is treated as those species attacking a combination of three (Rurima and Ruiru) or four (Koru) ceratitidines in arabica coffee. Nevertheless, through dissections of host remains, laboratory exposure to host cultures, and absence of alternate hosts in a few of our samples, it was possible to ascertain that nearly all of the parasitoid species recovered in our samples can successfully attack medfly. Only the rarely encountered *F. silvestrii* and *T. giffardii* remain unconfirmed as medfly parasitoids. We are therefore confident that the general conclusions about the assemblage of parasitoids on tephritids in coffee can also be applied more specifically to medfly.

Because of the importance of medfly as a major threat to the production of tropical and subtropical fruits worldwide, much has been written about its parasitoids, particularly those attacking medfly where it has become established outside Africa. Medfly has been continuously mass cultured for at least 50 years, and it has thus been available for host suitability tests using a wide range of parasitoids. Many such tests were conducted during the biological control programme directed against the Oriental fruit fly, *Bactrocera dorsalis* (Hendel) (Diptera: Tephritidae), in Hawaii (Clausen *et al*., 1965). Thus, of the 50 parasitoids previously recorded from medfly or fruit samples producing medfly, 13 have only been reared in the laboratory, often with difficulty, and seldom for more than a generation (Clausen *et al*., 1965). An additional 14 species have been reared from medfly in field-collected fruits only in the New World or in Hawaii, and are not indigenous to Africa (Bess *et al*., 1961, Wharton, 1989b; Gilstrap & Hart, 1987). Of the approximately 23 remaining parasitoids that are either indigenous to Africa or widespread synanthropic species, three (*B. celer*, *F. caudatus* and *Coptera* sp.) are recorded for the first time as medfly parasitoids in this publication. Few of the others have been confirmed as medfly parasitoids in field studies, largely because the fruits from which they were reared contained more than one species of fly.

Differentiation

The year-round availability of coffee makes this an ideal host for acquiring parasitoids needed in biological control, and for studying various aspects of parasitoid ecology and behaviour. A brief synopsis of the parasitoids is therefore provided in appendix 1 to facilitate future work along these lines. Most of the parasitoids reared from coffee-infesting

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tephritids are readily separated from one another, but a few of them are superficially similar and could therefore be confused in routine surveys. The diversity of parasitoids recorded here facilitates exploration of a number of issues associated with parasitoid assemblages on concealed hosts. Several of these are treated in the following sections.

Composition by guilds

For the purposes of this section, four guilds are considered, though it is recognized that some of these can be further divided. The first guild to be considered contains idiobiont egg parasitoids (i.e. those that oviposit into and emerge from the egg). In most surveys of tephritid parasitoids, eggs (perhaps because they are buried in the fruit) have not been sampled. Partly as a consequence, there are few, if any, legitimate records of tephritid egg parasitoids. The results reported here confirm the paucity of strict egg parasitoids, since no egg parasitoids were recovered from the isolation of 211 eggs segregated from field-collected fruits. If egg parasitoids are present, they are either seasonal or occur in extremely low frequency.

The second guild consists of koinobiont parasitoids developing at least in part on the larval stage of the host and emerging from the host puparium. Koinobiont parasitoids of *Ceratitis* and *Trirhithrum* have been recorded on numerous occasions, both within Africa (e.g. Marchal, 1910; Silvestri, 1913; Bianchi & Krauss, 1937; Van Zwaluwenburg, 1937; Féron, 1952; Clausen *et al*., 1965; Greathead, 1972; Steck *et al*., 1986) and in other areas where either medfly or Natal fly have been introduced (Willard & Mason, 1937; Orian & Moutia, 1960; Clausen *et al*., 1965; Étienne, 1973; Wharton *et al*., 1981; Wharton *et al*., 1999). Fruits from an exceptionally large number of host plant species are attacked by both medfly (Liquido *et al*., 1991) and Natal fly (White & Elson-Harris, 1992). As a consequence, many of the parasitoid records for these species are from host plants other than coffee. Some of these parasitoids are exceptionally well-known, especially *P. concolor*, mass reared on medfly for augmentative programmes in the Mediterranean region (Biliotti & Delanoue, 1959; Monastero & Delanoue, 1966; Kapatos *et al*., 1977; Raspi & Loni, 1994; Loni, 1997). Several species introduced to Hawaii for biological control programmes have also been studied in considerable detail (Pemberton & Willard, 1918; Clausen *et al*., 1965; Ramadan *et al*., 1989). The literature on koinobiont parasitoids attacking medfly outside subsaharan Africa is voluminous.

Nearly all of the eight koinobiont species reared during this study have previously been recorded from tephritids infesting coffee in subsaharan Africa. Prior to this study, however, *F. ceratitivorus* was completely unknown and confusion surrounding the identity of *T. giffardii* precluded confirmation of its host associations. The simultaneous discovery of *F. ceratitivorus* during preliminary surveys for this project and an International Institute of Biological Control-sponsored programme on the biological control of coffee berry borer provided the material for the original description of this newly discovered species (Wharton, 1999). The discovery of this species demonstrates quite clearly that there is still a great deal to be learned about the natural enemies of medfly in Africa.

Silvestri (1913) was perhaps the first to record parasitoids of tephritids in coffee when he reared *P. perproximus* from *T. nigerrimum* in Benin. In samples dominated by *T. coffeae*, Steck *et al*. (1986) reared *P. perproximus*, *D. fullawayi*, *F. caudatus*, *F. silvestrii*, and at least two undetermined opiine species from Togo and Cameroon. Many of the same species have been reported from East Africa (Ritchie, 1935; Bianchi & Krauss, 1937; Clausen *et al*., 1965; Ingram, 1965; Greathead, 1972; Waikwa, 1978) though the species have frequently been incompletely identified or misidentified (Wharton, 1989a,b). The *Psyttalia* species recorded as *Opius humilis* reared from *C. capitata* on arabica coffee in Kenya (Bianchi & Krauss, 1937) is the same as that reported as '*concolor* var. ?' from coffee in the Congo (Clausen *et al*., 1965). This is the species tentatively identified as *P. concolor* in the present study, and is probably also the species recorded as *P. cosyrae* by Greathead (1972). As noted in appendix 1, *P. concolor* differs only slightly from *P. perproximus*, the species more commonly recorded from coffee in West Africa. If Greathead's (1972) record is correct, ours is only the second rearing of *P. cosyrae* from coffee. *Psyttalia cosyrae* is normally associated with *Ceratitis cosyra* (Walker) on Anacardiaceae and other hosts.

The most detailed reports on parasitoids of coffee tephritids from East Africa are those of Greathead (1972) and Clausen *et al*. (1965). Greathead (1972) found *F. caudatus* (as 'sp. near *desideratus*.') to be the dominant parasitoid on *T. coffeae* infesting robusta coffee, and also recorded two species of tetrastichine Eulophidae. Clausen *et al*. (1965) recorded *Utetes africanus* (Szépligeti) from arabica coffee in Kenya and *F. silvestrii*, *F. caudatus*, *P. concolor*, and *D. fullawayi* from robusta coffee in the Congo.

Eucoiline figitids were notably absent from our samples, and have not previously been reared from tephritids attacking coffee in Africa. Eucoilines have, however, been recorded from medfly on coffee in Latin America (Wharton *et al*., 1981), and are routinely reared from native frugivorous tephritids in the Neotropics (Jiron & Mexzon, 1989; Lopez *et al*., 1999). Conversely, while tetrastichine eulophids are frequently reared from tephritids in coffee and other fruits in subsaharan Africa, the only tetrastichines recorded from the Neotropical fruit-infesting tephritids are introduced species such as *Aceratoneuromyia indica* (Silvestri) and *T. giffardianus*. This suggests an interesting difference between the new and old world tropics in the guild of parasitoids attacking late instar larvae (particularly those parasitoids capable of crawling into wounds or openings in the fruit). However, several eucoilines (besides the commonly occurring *Leptopilina* Foerster) have been reared from fruit infested with tephritids in subsaharan Africa, and this potential difference in composition needs to be further explored with more extensive sampling designed specifically to recover such species. Like *Leptopilina*, these other eucoilines may simply be parasitoids of Drosophilidae (Nordlander, 1982).

The third guild consists of idiobiont ectoparasitoids of the larval stages. Only one species, *Bracon celer*, was reared. This is the first record to our knowledge for *B. celer* on coffee. It has previously been recorded as a parasitoid of olive fly (Silvestri, 1913; Neuenschwander, 1982), and from an unidentified fruit in Kenya (Clausen *et al*., 1965: p. 63). Hoffmeister (1992) noted a high number of ectoparasitoid species in his work on Palaearctic *Rhagoletis*, *Anomoia*, and *Myoleja*, but the larval ectoparasitoids were only associated with two tephritid species that fed on seeds. Thus, larval ectoparasitoids of frugivorous tephritids appear to be rare. Although the protocol used here to process most of the coffee samples was biased against ectoparasitoids, several

samples were isolated and held specifically for ectoparsitoids. Thus, there is good evidence to suggest that additional species either do not exist, or they are very rare and/or seasonal.

The fourth guild consists of pupal parasitoids. Only a single pupal parasitoid (*Coptera* sp.) was recovered from coffee plantations, though during the same period two other pupal parasitoids (in the genera *Pachycrepoideus* and *Dirhinus*) were reared from *Dacus* hosts in the vicinity of Nairobi. Previously, Silvestri (1913) recorded *Coptera silvestrii* (Kieffer) from coffee in the Gold Coast and Greathead (1972) reared a staphylinid beetle in the subfamily Aleocharinae from puparia of *T. coffeae*. Hoffmeister (1992) found a higher percentage of pupal parasitoids in the tephritids he studied, but most of these records were from the exceptionally well-studied *Rhagoletis cerasi* (Linnaeus), for which a number of polyphagous parasitoids had been recorded. Based on the very limited data available worldwide on pupal parasitoids of frugivorous tephritids, ichneumonids are more commonly found in temperate regions whereas *Dirhinus* (Chalcididae) is one of the more commonly encountered pupal parasitoids of multivoltine species in tropical regions.

In addition to these records, Waikwa (1978) reared an ephydrid fly in the genus *Desmometopa* from medfly in coffee. It is difficult to determine whether this is a parasitoid or predator without more detailed information.

Assemblage size

Despite the fact that several guilds were inadequately sampled, the results reported here fully support and complement the findings of Hoffmeister (1992) and Hoffmeister & Vidal (1994), based on Palaearctic and Holarctic species respectively, that fruit-infesting tephritids support a large assemblage of parasitoids. In coffee infested with four species of ceratitidine tephritids, ten species of parasitoids were recovered, at least eight of which are capable of attacking medfly. These totals are much higher than the means reported by Hawkins (1988) in his comparisons of non gall-making tephritids (m = 1.9) with gall makers (m = 4.5), but compare more favourably with the work of Hoffmeister (1992) (m = 6.7), which focused on more intensively studied frugivorous species. As Hoffmeister & Vidal (1994) so clearly note, earlier conclusions about parasitoid assemblages attacking frugivorous tephritids were almost certainly biased by the inclusion of a large percentage of poorly sampled hosts, despite the perception that fruit-infesting tephritids of economic importance are 'well-known'. The results reported here confirm this, since two of the parasitoid species were recovered using techniques not routinely employed for sampling tephritid parasitoids and two other species were rare and would easily have been missed in a less-intensive sampling programme. Two of the most abundant species were relatively site specific.

There are two important differences between the tropical system studied here and the majority of those used as models by Hoffmeister (1990, 1992). One is the number of tephritid species per host plant species, since this rarely exceeded one for any locality in Hoffmeister's study. The second is the multivoltine nature of the four tephritid species from Kenya vs. the univoltine temperate species. In the Kenyan coffee system, species packing may be enhanced by cultivation and the consequent elimination of some alternate wild hosts for multivoltine species that lack a diapause. Despite these differences, comparison of the results presented here with those of Hoffmeister (1992) and Hoffmeister & Vidal (1994) indicate that assemblages of parasitoids on tropical fruit-infesting tephritids share many similarities with those of temperate systems, especially with regard to overall assemblage size, variation in composition of parasitoid complexes among sites, and the relatively high percentage of koinobionts. Similar to the findings of Hoffmeister & Vidal (1994) for fruit-infesting tephritids as a whole, medfly in coffee is attacked primarily by koinobiont larval parasitoids. The results presented here also support their observation that idiobiont larval parasitoids are rare in this host/host plant system. The sampling programme employed here (one commonly used for tephritids and their parasitoids) was decidedly biased in favour of koinobionts. Nevertheless, considerable effort was made to obtain larval ectoparasitoids during the latter half of 1999, and only a single species was recovered from over 100 kg of coffee.

Biological control

Medfly is of considerable economic importance worldwide; hence the interest in factors that impact its populations in areas of endemicity. We record here at least eight species that can attack medfly in *Coffea arabica*. The apparent preference of medfly for arabica coffee over robusta coffee suggests that the concerns expressed by Hoffmeister (1992) regarding habitat specificity relative to host specificity of parasitoids are appropriate considerations in this system. Similarly, when *Psyttalia humilis* was introduced from South Africa to Hawaii in 1913 to control medfly, it was seldom found in coffee (Willard & Mason, 1937). Thus, even though the species of *Psyttalia* that we routinely recovered from coffee in Ruiru is virtually identical to *P. humilis* and to the *P. concolor* mass-reared in Europe, its utilization of medfly in coffee makes it of value in those areas outside Africa where coffee is an important reservoir for medfly.

It is quite clear from these studies on only a single host plant that much remains to be learned about medfly and its natural enemies in its native home.

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Appendix 1

Differentiation of parasitoids reared from coffee in Kenya.

Six of the parasitoids recorded here (belonging to the genera *Fopius*, *Diachasmimorpha*, and *Psyttalia*) are in the braconid subfamily Opiinae. The three species of *Fopius* all have a short second submarginal cell, distinctly crenulate notauli ending posteriorly in a well-defined median pit, and a large clypeus that lacks median tubercles on its ventral margin (Wharton, 1997, 1999). Two of the species (*F. silvestrii* and *F. caudatus*) are predominantly dark in colour whereas *F. ceratitivorus* is orange. *Fopius caudatus* is readily separated from *F. silvestrii* by the band of punctures extending on each side of the top of the head between the ocelli and the eye (Wharton, 1987). The other three opiines, *D. fullawayi* and the two species of *Psyttalia*, are also predominantly orange, though the *Psyttalia* from Koru tend to have a somewhat darker abdomen. *Psyttalia* differs from *Diachasmimorpha* and *Fopius* in the possession of a longer second submarginal cell, the absence of a median pit or groove near the posterior

margin of the mesoscutum, and the presence of a distinct gap between the clypeus and the mandibles when the mandibles are closed (Wharton, 1997). *Diachasmimorpha fullawayi* most closely resembles *F. ceratitivorus* because of the coloration, but has two very small tubercles medially on the ventral margin of the clypeus and also has the m-cu cross-vein entering the second submarginal cell. Nearly all previous biological information on these six species has been published using the generic names *Opius* or *Biosteres*.

Two species of *Psyttalia* were reared. A few individuals of *P. cosyrae* were collected from coffee fields in which mangoes were growing nearby, but the dominant parasitoid in many of our samples was a species of *Psyttalia* morphologically indistinguishable from *P. concolor* (Szépligeti). In previous collections of parasitoids from various fruits in Kenya, this latter species has been referred to as either *Opius concolor*, *O. humilis* Silvestri (Bianchi & Krauss, 1937), *O. perproximus* (Clausen *et al*., 1965) or *O.* sp. The difference between *concolor* and *humilis* is subtle at best (Fischer, 1958; Wharton & Gilstrap, 1983), and the two have been variously treated as either synonyms or separate species, with *perproximus* also sometimes included in the synonymy (Fischer, 1972). *Psyttalia concolor* was described from Tunisia in 1910, *P. humilis* from South Africa in 1913, and *P. perproximus* from West Africa, also in 1913. For the purpose of this paper, we tentatively refer to our common species as *P. concolor*, pending the outcome of studies currently being conducted on its specific status by Kimani-Njogu and Trostle. Both *P. cosyrae* and *P. perproximus* have longer ovipositors than *P. concolor*, with that of *cosyrae* extending distinctly beyond the tip of the wings when the wasp is at rest.

Three species of *Bracon* were collected in sweep net samples in coffee fields, but only one (*B. celer*) was repeatedly reared from coffee berries and verified as a parasitoid of tephritids. This is a colour-variable species superficially similar to *Psyttalia*. In *Bracon*, the subbasal cell of the hind wing is much smaller than in the opiines.

We reared only three species of parasitoids that were not members of the family Braconidae. The pupal parasitoid in the genus *Coptera* can be readily distinguished from all other parasitoids by the greatly reduced venation, with only a weak submarginal vein confined to the basal half of the wing. Our species is definitely not *C. silvestrii* (Kieffer), a species previously reared on medfly (Silvestri, 1913). The gregarious eulophid parasitoids in the genus *Tetrastichus* have only four tarsomeres, whereas tephritid parasitoids in all other families (including the gregarious pteromalid *P. vindemiae*) have five tarsomeres. *Tetrastichus giffardianus* has a distinct bare patch (devoid of setae) near the base of the wing whereas *T. giffardii* does not. The latter is difficult to differentiate from both *T. oxyura* Silvestri and *T. dacicida* Silvestri, and this taxonomic problem is currently being addressed by J. LaSalle as part of this programme.

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