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This contribution is dedicated to the memory of Prof. Dan Gerling, a scientist, a colleague and a friend

Development duration, longevity and fertility of *Eretmocerus mundus* Mercet and *Encarsia sophia* (Girault & Dodd) (Hymenoptera: Aphelinidae) on *Bemisia tabaci* (Hemiptera: Aleyrodidae) attacking cassava in Uganda

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ABSTRACT

At least one member of the whitefly *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae) species complex is a vector of cassava mosaic geminiviruses and cassava brown streak viruses, which cause serious damage to cassava, *Manihot esculenta* Crantz. The whiteflies are predominantly attacked by *Eretmocerus mundus* Mercet and *Encarsia sophia* (Girault & Dodd) (Hymenoptera: Aphelinidae). These parasitoids had, however, not been able to control *B. tabaci* populations on cassava. This study therefore aimed at elucidating how life history parameters limit the performance of the parasitoids. We conducted the study under fluctuating laboratory conditions to determine the development duration, longevity and fertility of these parasitoids. The initial egg count on emergence and development duration were higher in *E. mundus* than in *E. sophia*. Similarities occurred in the development duration of females and males *E. mundus*, whereas the females of *E. sophia* developed about two days earlier than their males. Mean longevity of females when provided with honey diet was 5.4 days for *E. mundus* and 6.6 days for *E. sophia*, and averaged 5.5 days and 11.3 days, respectively, when developed on whitefly nymphs. Progeny production averaged 25.6 offspring for *E. mundus* and 16.5 for *E. sophia*. The net reproduction rate of *E. mundus* was 13.1 as opposed to 15.5 for *E. sophia*. The intrinsic rate of increase was 0.10 for *E. mundus* and 0.11 for *E. sophia*. Mean generation time was 24.9 and 26.2 days for *E. mundus* and *E. sophia*, respectively. The results suggest that *E. mundus* is the most suitable candidate for high *B. tabaci* population control, whereas *E. sophia* may be effective under low *B. tabaci* populations.

KEYWORDS: Afrotropical, Hemiptera, Aleyrodidae, *Bemisia tabaci*, Hymenoptera, Aphelinidae, *Encarsia sophia*, *Eretmocerus mundus*, parasitoids, demographic fitness, generation time, intrinsic rate of increase, net reproduction rate.

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INTRODUCTION

Whiteflies (Hemiptera: Aleyrodidae) attack various agronomic and horticultural crops throughout the world and may cause devastating damage to national economies (Gerling & Mayer 1996). Members of the *Bemisia tabaci* (Gennadius, 1889) species complex transmit cassava mosaic geminiviruses that cause cassava mosaic disease (Legg & Fauquet 2004; Patil & Fauquet 2009), causing annual losses of 12–34 million tons of cassava in Africa (Thresh *et al.* 1997; Legg *et al.* 2006). The exact identity of the particular species within the *B. tabaci* complex responsible for this unprecedented damage to cassava in East Africa is currently under investigation and is widely referred to as SSA1 (Sub-Saharan Africa 1), which itself represents an assemblage of several distinct biological species (e.g. Tocko-Marabena *et al.* 2017; Wosula *et al.* 2017). *Bemisia tabaci* also transmits the cassava brown streak viruses, which cause cassava brown streak disease (Maruthi *et al.* 2005; Legg *et al.* 2014). Besides virus transmission, high whitefly populations are associated with mould on leaves, petioles and stems, reduction of leaf size, distortion of leaf shape, mottled chlorosis and general stunting (Legg *et al.* 2003). In order to manage *B. tabaci* and the diseases, the four cornerstones of integrated pest management (host plant resistance, biological control, cultural practices and chemical control) can be employed (Hilje *et al.* 2001). To date, however, control of the diseases has mainly relied on host plant resistance, without direct attempts to control the vector. Research in Uganda has focused on identifying the principal parasitoids of *B. tabaci* on cassava and understanding their population dynamics (Otim *et al.* 2005, 2006). The parasitoids, *Eretmocerus mundus* Mercet, 1931 and *Encarsia sophia* (Girault & Dodd, 1915) (Hymenoptera: Aphelinidae) were the most abundant parasitoids of *Bemisia tabaci* on cassava in Uganda. In a follow up study however, Otim (2007) demonstrated that *E. mundus* was considerably more abundant than *E. sophia* in the same locations. Moreover, these two parasitoid species do not offer adequate control of their *B. tabaci* hosts (Otim 2002). The present study was therefore initiated to investigate the life history parameters of the two parasitoids, specifically their development duration, longevity and fertility of *E. mundus* and *E. sophia* attacking *B. tabaci* on cassava. This would help (1) to gain an understanding of the extent to which the life history parameters influence abundance of the parasitoids in the field, and (2) to compare the probabilities that other parasitoids, with different life histories may be used for improving biological control of *B. tabaci* in Uganda.

MATERIALS AND METHODS

Geographical setting

The experiments were conducted in a laboratory at Makerere University Agricultural Research Institute, Kabanyolo (MUARIK) (*ca* 18 km north of Kampala, 0°28'N 32°37'E). The area is about 1200 meters above sea level and receives a mean annual rainfall of 1270 mm in a bimodal pattern, with peaks in April/May and October/November. The maximum temperatures rarely exceed 30 °C, while the minimum ones do not fall below 15 °C.

Culture of *B. tabaci* and source of the parasitoids

The *B. tabaci* used in the study were obtained from colonies raised in a screen house at MUARIK. Cassava plants of the variety Nase 4 were grown in 1-litre buckets containing sterilized soil. When the plants reached 4-leaf stage, adults of *B. tabaci* were introduced to initiate colonies. To obtain adults to initiate the colony, nymphs were collected from cassava fields at Namulonge Agricultural and Animal Production Research Institute in 2004 and held in emergence bottles. Emerging adults were collected daily and introduced on clean plants in the screen house. The colony was maintained on cassava under natural fluctuating conditions [22.8±5.4 °C (range, 15.6–34 °C) and 64±20.2 % relative humidity (range, 25.3–91.7 %).

The parasitoids used for this study were reared from parasitized nymphs collected from the same fields as the *B. tabaci* immatures. The parasitoids were collected a few days before observations and the parasitized nymphs were placed in emergence bottles.

Parasitoid life history

Development duration of E. mundus *and* E. sophia

Twenty to thirty females of *E. mundus* and *E. sophia* (0–24 hrs old) were caged on leaves of five plants bearing 100–200 nymphs of *B. tabaci* each, in a screen house under fluctuating climatic conditions. For *E. mundus*, we used second instar nymphs, whereas for *E. sophia* we used third instar nymphs. We removed the parasitoid females after 24 hours, and the whiteflies were held under similar conditions in the laboratory until the parasitoids pupated. The mean laboratory conditions were as follows: temperature 24.4 °C (range, 19.8–30.3 °C); relative humidity 65.5 % (range, 24.7–87.1). Upon parasitoid pupation, the leaves with pupae were removed from the plant, placed in Petri dishes and monitored daily. The number and sex of the emerging parasitoids were recorded, and the development duration was calculated from the period between parasitoid female introductions and adult emergence.

Longevity

Longevity was determined in the laboratory under similar conditions to the above, for parasitoids maintained on honey diet or on *B. tabaci* nymphs. For the experiment, the inner surface of glass vials (length, 7.8 cm; diameter, 2.3 cm) was streaked with honey and newly emerged (<24 hrs old) females of each species were placed in individual vial. Honey was added when necessary, the parasitoids' presence monitored daily until their death and their longevity recorded. For longevity when exposed to nymphs, the survival duration of parasitoids used in the fertility experiment was used.

Initial egg load and fertility of E. mundus *and* E. sophia

In order to determine the initial egg load on emergence, 50 females of each parasitoid species were dissected shortly after emergence (<24 hrs old) and the number of mature eggs was recorded.

The fertility of *E. mundus* and *E. sophia* was studied in the laboratory under similar conditions to those described above. Parasitoid pupae of either species were collected from the field and kept under laboratory conditions in emergence bottles. A freshly emerged female (<24 hrs old) was confined with a conspecific male in a gelatin capsule for 24 hrs. Thereafter, each couple was transferred into an open glass tube (15×5 cm) with a fine insect screen on one side and open on the other end. Upon release of the parasitoids, an infested cassava leaflet was inserted into the tube, and the tube opening was closed using a round piece of foam. The couples were provided with new leaflets every day until the female died. If the male died within the first three days, another male was introduced into the glass tube. The leaves were thereafter monitored until parasitoid pupation. Upon pupation, leaflets with pupae were picked, placed in Petri dishes and monitored for adult parasitoid emergence. The number and sex of the parasitoids were recorded daily until emergences ceased. Parasitoid pupae that failed to develop into adults were included in the calculation of the total fertility. Based on the data on the development duration, longevity, survival and fertility, age-specific fertility (m_x), intrinsic rates of increase (r_m), net reproduction rates (R_0) and generation time (T) were calculated. Age-specific fertility of the adult females (m_x) was expressed as the mean number of female progeny produced by a female of age *x* per day, whilst intrinsic rates of increase, net reproduction rates, and generation time were calculated according to Andrewartha and Birch (1954) as follows:

$$R_0=\sum l_x \cdot m_x$$

$$T=(\sum x \cdot l_x \cdot m_x)(\sum l_x \cdot m_x)^{-1}$$

$$r_m=(\ln R_0)T^{-1}$$

Data analysis

Data on longevity and fertility were subjected to ANOVA, while development duration between species and sexes of species was analyzed using T-statistics (GenStat 2018). In calculating progeny numbers, only ovipositing females were considered. Data on age specific fertility (mean number of female progeny per ovipositing female) were plotted against the age of females, and a regression analysis was performed to test the relationship between numbers of adult progeny and longevity for each parasitoid species.

RESULTS

Development duration of *E. mundus* and *E. sophia*

There was a significant difference between the development duration of the two parasitoid species (t_{364}=14.7; P<0.001) and between the females and males of *E.*

Table 1. Preimaginal development duration of *E. mundus* and *E. sophia* on *B. tabaci*. Data within a column followed by same lower case letters are not statistically different (ANOVA; P>0.05).

		Preimaginal development period (days)		
		N	Mean±SE	Range
E. mundus	♀♀	154	19.7±0.11 a	16–23
	♂♂	131	19.6±0.14 a	16–24
	df		254	
	t		0.56	
	P		0.578	
E. sophia	♀♀	59	16.8±0.10 a	16–19
	♂♂	22	18.7±0.18 b	17–20
	df		79	
	t		-9.17	
	P		<0.001	
Grand mean				
E. mundus		285	19.6±0.09 b	16–24
E. sophia		81	17.4±0.13 a	16–20
	df		14.7	
	t		164	
	P		<0.001	

sophia (t_{19}=-9.17; P<0.001), whilst there was no significant difference in development duration between the sexes of *E. mundus* (t_{254}=10.54; P=0.578) (Table 1). *Encarsia sophia* developed two days earlier than *E. mundus*. The males of *E. sophia* developed two days later than their females from hosts exposed to females for only 24 hours. Peak numbers of *E. mundus* parasitoids emerging occurred at 19 and 20 days for females and males respectively, whereas peak emergence of *E. sophia* occurred at 17 days for females and 19 days for males (Figs 1A, B).

Longevity of *E. mundus* and *E. sophia*

Mean longevity did not vary significantly (P>0.05) between females of both species when provided with honey; longevity averaged 5.5±0.45 days (range, 2–13) for *E. mundus* and 6.6±0.57 days (range, 1–11) for *E. sophia*. Longevity was, however, significantly (P<0.001) higher for *E. sophia* (11.3±1.94 days; range, 1–25) than *E. mundus* (5.5±0.57 days; range, 1–12) when hosts were provided.

Initial egg load and fertility of *E. mundus* and *E. sophia*

Upon emergence, the initial egg count differed significantly (P<0.001) between species. *Eretmocerus mundus* had an average of 35±1.54 (n=50; range, 2–54) mature eggs per female, whereas *E. sophia* had an average of 3±0.22 (n=50; range, 0–7) eggs per female.

There was no significant difference (P>0.432) between the total progeny across species, and between female and male progeny of *E. mundus*. *Encarsia sophia*, however, produced significantly (P=0.012) more females than males (Table 2). Age-specific fertility was higher for *E. mundus* for the first 10 days, averaging about two daughters per female and gradually declined thereafter (Fig. 1C). For *E. sophia*, age-specific fertility averaged one female per female per day and oscillated between one and two (Fig. 1D).

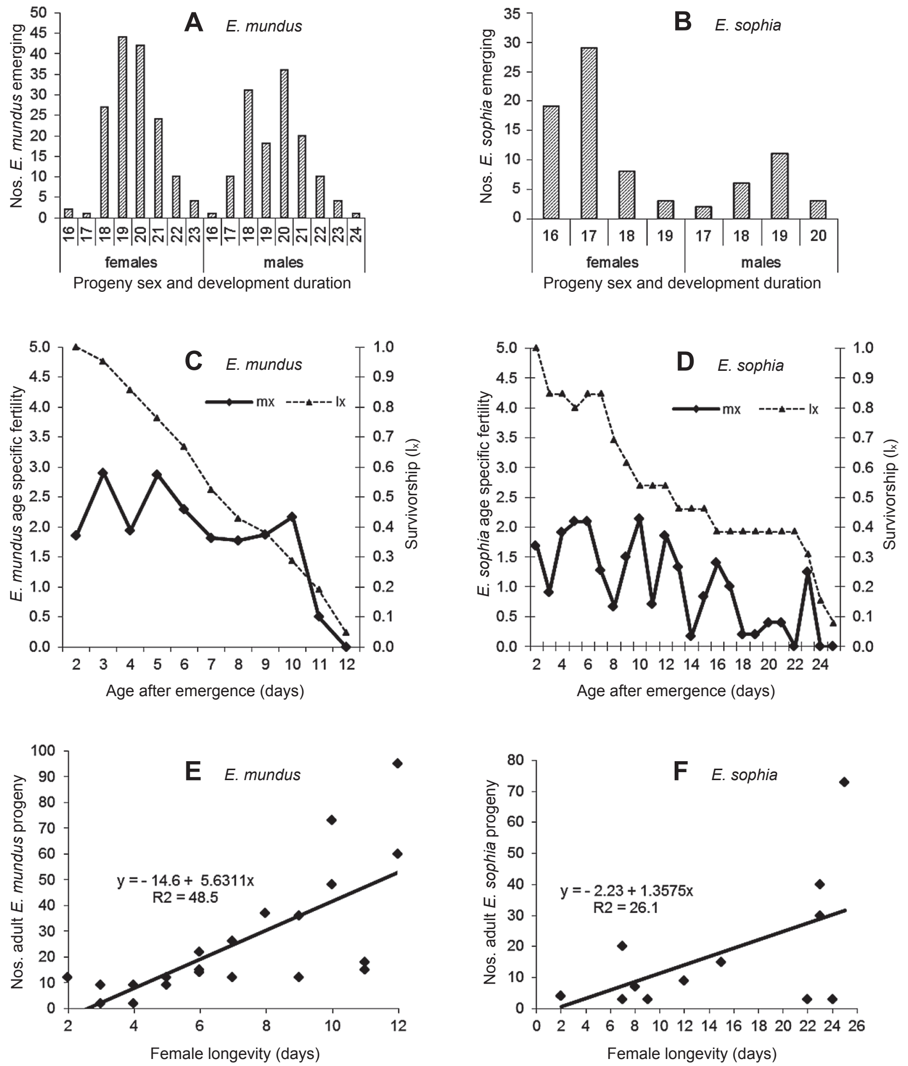

Fig. 1: (A, B) Variations in the development duration (days) of *E. mundus* (A) and *E. sophia* (B); (C, D) age-specific fertility (m_x) and survivorship of females (l_x) of *E. mundus* (C) and *E. sophia* (D); (E, F) relationship between numbers of progeny with female longevity in *E. mundus* (E) and *E. sophia* (F) on *B. tabaci* attacking cassava.

Table 2. Adult female fertility of *E. mundus* and *E. sophia* attacking *B. tabaci* on cassava. Data within a column followed by same lower case letters are not statistically different (ANOVA; P>0.05).

	Adult life time fertility (adult progeny)		
	Sex	Mean±SE	Range
E. mundus (n = 21)	♀♀	13.1±2.9 a	1–49
	♂♂	10.1±2.5 a	0–46
P		0.432	
E. sophia (n = 13)	♀♀	15.5±5.6 b	1–72
	♂♂	0.2±0.0 a	0–2
P-value		0.012	
Grand mean			
E. mundus		25.6±5.4 a	2.95
E. sophia		16.5±5.7 a	3–73
P		0.272	

A regression of fertility on female longevity showed that the longer a female lived, the more eggs were laid (Figs 1E, F). On average, an ovipositing female *E. mundus* lived for seven days (range, 2–12 days), whereas those that never laid lived for 3 days (range, 2–6 days). *Encarsia sophia* that oviposited lived for 13.8 days (range, 2–25), and those that never laid eggs lived for 7.4 days (range, 2–25).

Life table parameters of *E. mundus* and *E. sophia*

The net reproduction rates (R_0) were 13.1 and 15.5 daughters per female per generation for *E. mundus* and *E. sophia*, respectively. Generation time was 24.9 days and 26.2 days for *E. mundus* and *E. sophia*, respectively, and intrinsic rates of increase were 0.10 daughters per female per day for *E. mundus* and 0.11 daughters per female per day for *E. sophia*.

DISCUSSION

The study showed differences in development duration between *E. mundus* and *E. sophia*, and the females and males of *E. sophia*, initial egg load at emergence and longevity when the parasitoids were provided hosts. The two parasitoid species, however, lived for a similar duration when fed on honey. *Eretmocerus mundus* had more eggs and lived for shorter period than *E. sophia*, whilst *E. sophia* developed two days earlier than *E. mundus*. It was also observed that males of *E. sophia* developed from hosts that were exposed to parasitoids for a period of 24 hrs. There is no published information on the life history of parasitoids attacking *B. tabaci* on cassava. However, the present results can be compared with those on the same species attacking whitefly on other plants (Tables 3–5).

Shorter duration of *E. sophia* development compared to *E. mundus* on *B. tabaci* was reported by Kapadia and Puri (1990). In the present study, *E. sophia* females developed in 16.8 days, which is longer than the period observed for this species on sow thistle, cotton, sweet potato, tomato and green bean (Gerling 1983; Kapadia

Table 3. Preimaginal development duration of *E. mundus* and *E. sophia*. Explanations: [t] & [a] – development duration of the thelytokous and arrhenotokous populations of *E. mundus*, respectively; [N1], [N2] & [N3] – first, second and third nymphal instars.

Reference	Host whitefly	Test plant	Development time (days)	Temp., °C
		E. mundus		
Present study	*B. tabaci*	cassava	19.8	24.4
Gameel (1969)		cotton	30	29.5
Tawfik *et al.* (1978)	*B. argentifolii*	sweet potato	17.9	29.8
Sharaf & Batta (1985)	*B. tabaci*	tomato tomato	44 16	14 25
Kapadia & Puri (1990)	*B. tabaci*	cotton cotton cotton	17.1 16.7 15.9	21.4 19.4 21.1
Jones & Greenberg (1998)	*B. argentifolii*	sweet potato	15.4	26
De Barro *et al.* (2000)	*B. argentifolii*	cotton rock melon tomato soybean hibiscus	19–22 (unspecified for crops)	18–30
Ardeh (2004)		gerbera tomato poinsettia gerbera tomato poinsettia	15.4[t] 16.1[t] 15.6[t] 15.3[a] 15.2[a] 15.6[a]	26
Qiu *et al.* (2004)	*B. argentifolii*	poinsettia poinsettia poinsettia poinsettia	64 29.1 17.1 14	15 20 25 32
Urbaneja *et al.* (2007)	*B. tabaci*	tomato & sweet pepper	16–17	25
		E. sophia		
Present study	*B. tabaci*	cassava	18	24.4
Gerling (1983)	*T. vaporariorum*	sowthistle	15	24–26
Kapadia & Puri (1990)	*B. tabaci*	cotton cotton cotton cotton	8.1 10.6 14.3 18.7	28.9 21.4 19.4 21.1
Antony *et al.* (2003)	*B. tabaci*	sweet potato	11.3–15.1	25–30
Zhou *et al.* (2010)	*B. tabaci*	tomato	12.8	25
Luo & Liu (2011)	*B. tabaci*	green bean	11.5	27
Xu *et al.* (2018)	*B. tabaci*	cotton	12.9	26

& Puri 1990; Antony *et al.* 2003; Zhou *et al.* 2010; Luo & Liu 2011) (Table 3). A longer development (18.7 days) of *E. sophia* was reported by Kapadia and Puri (1990) at 21.1 °C and 53.3 % relative humidity. The development duration of *E.*

Table 4. Longevity of *E. mundus* and *E. sophia*. Explanations: [t] & [a] – longevity of the thelytokous and arrhenotokous populations of *E. mundus*, respectively; [ann] – cultivar *Annette Hegg Brilliant Diamond*; [lilo] – cultivar *Lilo*; * – control and in presence of sesame flowers, respectively.

Reference	Host whitefly	Test plant	Longevity (days)	Temp., °C
		E. mundus		
Present study	*B. tabaci*	cassava	5.5	24.4
Tawfik *et al.* (1978)	*B. argentifolii*	cotton cotton	6.1 3.2	10 23
Tawfik *et al.* (1978)	*B. tabaci*	tomato tomato	7.6 10.5	18 30
Sharaf & Batta (1985)	*B. tabaci*	tomato tomato	11.3 9.1	14 25
Qiu *et al.* (2004)	*B. argentifolii*	poinsettia poinsettia poinsettia	14.4 11.3 12.4	15 20 25
Ardeh (2004)		gerbera tomato poinsettia gerbera tomato poinsettia	8.4[t] 9.2[t] 7.6[t] 9.2[a] 11[a] 8.0[a]	26
Urbaneja *et al.* (2007)	*B. tabaci*	tomato sweet pepper	8.5 10.5	25
		E. sophia		
Present study	*B. tabaci*	cassava	11.3	24.4
Heinz & Parella (1994)	*B. tabaci*	poinsettia[anne]	4.2	
Heinz & Parella (1994)	*B. tabaci*	poinsettia[lilo]	5.4	
Zhou *et al.* (2010)	*B. tabaci*	tomato	21.9	25
Luo & Liu (2011)	*B. tabaci*	green bean	1.8	27
Kidane *et al.* (2015)	*B. tabaci*	cotton	18	26
Liu *et al.* (2017)			<12 or >15*	
Xu *et al.* (2018)	*B. tabaci*	cotton	21.3	26

mundus (19.6 days) is within the range established by De Barro *et al.* (2000), whereas Gameel (1969) and Sharaf & Batta (1985) documented 30 days at 29.5 °C and 44 days at 14 °C for this species. Similarly, Qiu *et al.* (2004) reported longer development of *E. mundus*, 64 days at 15 °C and 29.1 days at 20 °C. In contrast, shorter durations were reported for *E. mundus* by other authors depending on temperature, *E. mundus* strain and host stage attacked (Table 3). The development of both parasitoid species is quicker than 33.3 days reported for *B. tabaci* on cassava (Legg 1995), which means that the parasitoids are capable of multiplying at a faster rate than their host. Nevertheless, longevity and fertility also affect the performance of parasitoids in the field.

Our observations that male-producing eggs of *E. sophia* developed from nymphs exposed to females for only 24 hours seem to be inconsistent with the autoparasitic habit of that insect, which required that male-producing eggs be deposited when female larvae are already in the host, thus enabling the autoparasitic life mode (Gerling 1983; Hunter & Kelly 1998). Gerling and Rejouan (2004) observed that eggs laid two days after female producing eggs developed into males. The present results seem to suggest that male eggs can be laid the same day as their female counterparts.

The longevities of the two parasitoids under various conditions differ remarkably (Table 4). The longevity of *E. mundus* on whitefly nymphs was similar to those provided with honey, while *E. sophia* lived longer on hosts than on the honey diet (11.3 *vs* 6.6 days). Contrary to the present observation, Qiu *et al.* (2004) reported a shorter longevity of *E. mundus* in the presence rather than absence of hosts. They attributed the differences to the effect of transferring parasitoids to fresh hosts and loss in quality of leaf disks. In the current study, fresh and intact leaves were provided daily and the quality of leaves might not have influenced parasitoid longevity. Yet again the effect of transfer might have been minimal since the parasitoids were tapped off the leaf onto the glass and they were moved with the glass. Powell and Bellows (1992) observed greater longevity of *E. eremicus* on cotton in the presence of hosts than in their absence and attributed this to a better nutritional quality of the honeydew secreted by the host nymphs. This argument may be true but does not answer the question why *E. mundus* lived for a similar duration both in the presence and absence of hosts. Therefore, the reasons for the similarity in the longevity of *E. mundus* in the presence and absence of hosts, and greater longevity of *E. sophia* when provided with hosts seems to be also due to inherent factors that affect their biology.

The mean longevity of *E. mundus* with access to hosts (5.5 days) in the present experiment corresponds to 6.1 days at 10 °C and higher than the 3.1 days at 23 °C, found by Tawfik *et al.* (1978) on cotton. All other authors, however, reported higher longevity values compared to ours (Table 4). The longevity of *E. sophia* during our study exceeds 4.2 and 5.4 days reported by Heinz and Parella (1994) on two poinsettia varieties, and remarkably so 1.8 days documented by Luo and Liu (2011) on green bean; on the other hand, it is considerably shorter compared to data obtained by Zhou *et al.* (2010) and Kidane *et al.* (2015) on tomato (21.9 days) and cotton (18 days), respectively. Since longevity is positively related to efficiency (Godfray 1994), it is important to increase the longevity of the parasitoids.

The mean fertility in the present study (Table 5) was measured as the number of progeny that emerged plus those that reached pupal stage. In most studies, however, the numbers of eggs laid were used to assess the reproductive potential of the parasitoids. Powell and Bellows (1992) argued that measurements based on egg counts do no take into account mortality before adult emergence and may therefore lead to over-representation of the reproductive potential. The mean fertility of *E. mundus* and *E. sophia* in our study were 25.6 and 16.5 progeny per female, res-

Table 5. Fecundity/fertility of *E. mundus* and *E. sophia*. Explanations: [t] & [a] – fecundity of the thelytokous and arrhenotokous populations of *E. mundus*, respectively.

Reference	Host whitefly	Test plant	Fecundity / Fertility	R_0	r_m	Temp., °C
			E. mundus			
Present study	*B. tabaci*	cassava	25.6	13.1	0.10	24.4
Tawfik *et al.* (1978)	*B. tabaci*	sweet potato	14.5			18
	B. argentifolii	sweet potato	48			20
Sharaf & Batta (1985)	*B. tabaci*	tomato	20			14
		tomato	27.4			25
De Barro *et al.* (2000)	*B. argentifolii*	cotton	97.8			18–30
		rock melon	138.3			
		tomato	107.8			
		soybean	96			
		hibiscus	105.3			
Ardeh (2004)		gerbera	19[t]	17	0.17	26
		tomato	54.6[t]	51	0.23	
		poinsettia	28.6[t]	26	0.20	
		gerbera	26.8[a]	12	0.15	
		tomato	117.5[a]	55	0.23	
		poinsettia	49.4[a]	23	0.19	
Qiu *et al.* (2004)	*B. argentifolii*	poinsettia	10.7			15
		poinsettia	43.4			20
		poinsettia	42.5			25
Urbaneja *et al.* (2007)	*B. tabaci*	tomato	147.8			25
		sweet pepper	171.1			25
			E. sophia			
Present study	*B. tabaci*	cassava	16.5	15.5	0.11	24.4
Xu *et al.* (2018)	*B. tabaci*	cotton	101.6	57.5	0.22	26

pectively. The fertility of *E. mundus* in this study is close to the fecundity values reported by Sharaf and Batta (1985) (20 eggs per female at 14 °C, 27.4 eggs per female at 25 °C) and by Ardeh (2004) on gerbera (19 and 26.8 eggs per female for the thelytokous and arrhenotokous populations of *E. mundus*, respectively). Similarly, Ardeh (2004) reported a fecundity value of 28.6 eggs per female for the thelytokous population of *E. mundus* on poinsettia. The fertility of *E. mundus* in this study falls within the mean fertility range reported by Powell and Bellows (1992) for an unknown *Eretmocerus* sp., which ranged from 20 to 47 progeny per female depending on source of the *Eretmocerus*, and the host plant used.

The only available study of demographic fitness of *E. sophia* (Xu *et al.* 2018) reports much higher number of eggs per female compared to our data (101.6 *vs* 16.5), as well as a higher net reproduction rate and intrinsic rate of increase. No satisfactory explanation of such a drastic difference can be given, but the existence of two (or more) cryptic species—with distinct biological features—under the name of *E. sophia* cannot be ruled out (Giorgini & Baldanza 2004).

There are many scenarios that could explain differences between fecundity and fertility values. The number of eggs laid per female varies depending on host plant, experimental procedure and conditions (Heinz & Parella 1994; De Barro *et al.* 2000; Ardeh 2004; Urbaneja *et al.* 2007). In order to oviposit, *E. mundus* females stand beside their host and locate a suitable position between the nymph and the leaf surface where they can lay their eggs (Gerling 1990). Therefore, a host plant with smooth leaves like gerbera, where the margin of the nymph is flat on the leaf surface, results in difficulties during oviposition for the females (Headrick *et al.* 1996*a*, *b*; Ardeh 2004). On the contrary, plants with hairy foliage like poinsettia, tomato and melon make placement of the eggs under the nymph easier since it does not rest flat on the leaf surface (De Barro *et al.* 2000; Ardeh 2004). In addition, the length and density of leaf hairs can interfere with the movement of the parasitoids and reduce parasitism level (van Lenteren *et al.* 1995; De Barro *et al.* 2000). While it is evident that host plant species affects fecundity and fertility of parasitoids, experimental procedures could also have contributed to the differences between published results and the present study. For instance, De Barro *et al.* (2000) observed the parasitoids over a ten day period, while Ardeh (2004) and ourselves assessed the numbers of progeny per female until the female died. Furthermore, as noted by Sharaf and Batta (1985), the fecundity of *E. mundus* increased with elevating temperatures (Table 5). Cassava (a glabrous variety) was the only host plant used in the current study and no other host plant was suitable for fecundity studies because attempts to rear this specific *B. tabaci* biotype on cotton and sweet potato failed. Since survival was positively related to progeny production, improvement of the survival of the parasitoids could enhance *B. tabaci* control on cassava.

The demographic parameters calculated for *E. mundus* (R_0=13.1; T_C=24.9; r_m= 0.10) are lower than the values for *E. sophia* (R_0=15.1; T=26.2; r_m=0.11). The net reproduction rate of *E. mundus* in the current study compares with that reported for the arrhenotokous population of *E. mundus* on gerbera by Ardeh (2004), but is lower than values on tomato and poinsettia (Ardeh 2004). The higher intrinsic rate of increase of *E. sophia* compared with that of *E. mundus* may be partly attributable to the greater longevity and highly female biased sex ratio (*ca* 99% female *E. sophia* progeny compared to *ca* 59% female *E. mundus* progeny in the entire experiment). The intrinsic rate of increase of *E. mundus* is lower than the values reported for the different populations of *E. mundus* on the various plants (Ardeh 2004). This is expected because of differences in populations of *E. mundus*, host plants and the numbers of eggs laid used for calculating r_m. For comparison between *B. tabaci* and its parasitoids on cassava, there is a need to gather information on the development duration, longevity and fertility of *B. tabaci*.

From the life history parameters, it is evident that *E. mundus* may be a good candidate to reduce a high population of *B. tabaci*, for it lives for a shorter time (5.5 days) and produces a little more offspring than *E. sophia*. *Encarsia sophia*, on the other hand, would work better with low density *B. tabaci* populations, because it lives for a longer period (*ca* 11 days) and produces fewer eggs per day. The collected data may be of use in future if parasitoids are to be imported for control of *B. tabaci* on cassava.

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