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Life history of *Eretmocerus mundus*, a parasitoid of *Bemisia tabaci*, on tomato and sweet pepper

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Abstract. *Eretmocerus mundus* is native to the Mediterranean region where it is often observed to enter greenhouses to parasitize *B. tabaci* on fruiting vegetables and other host crops. Fecundity on tomato and pepper was evaluated by placing newly emerged pairs ($n = 15$) of *E. mundus* on leaf discs infested with second instar *B. tabaci*, the preferred stage, maintained at 25 °C and changed daily until death of the female. All whitefly nymphs were observed for host feeding and inverted to count parasitoid eggs. Adult longevity was estimated at 7.3 ± 0.8 d on tomato and 10.1 ± 1.0 d on sweet pepper. Fecundity (number of hosts parasitized) was estimated 147.8 ± 12.6 per female on tomato and 171.1 ± 21.5 on pepper. Incidence of host feeding (number of hosts killed) was significantly greater on sweet pepper than on tomato, 15.6 ± 1.9 vs. 10.4 ± 1.3 nymphs per female, respectively. No significant differences were detected in the duration of life stages between sweet pepper and tomato. Preimaginal survivorship in clip cages was estimated at $69.5 \pm 11.9\%$ on tomato and $76.6 \pm 10.5\%$ on sweet pepper, with no statistical differences. Net reproductive rate (R_o) was estimated at 63.8 ± 8.2 and 51.0 ± 4.4 on tomato and sweet pepper respectively. Generation time (T) was significantly greater on sweet pepper (19.3 ± 0.5) than on tomato (17.9 ± 0.4), but the estimate of intrinsic rate of increase (r_m) was not statistically different at 0.216 ± 0.005 and 0.219 ± 0.004 respectively. These values are well above those reported for *B. tabaci* on any crop, indicating the potential of *E. mundus* to control this pest on solanaceous crops in the greenhouse.

Key words: whitefly, biology, augmentative biological control, fecundity, developmental time, life table, demographic parameters, intrinsic rate of increase

Introduction

The sweetpotato whitefly, *Bemisia tabaci* Gennadius (Hom.: Aleyrodidae), is a key pest of vegetables and other horticultural crops in much of the Tropics and Subtropics. Since its detection in southeastern Spain at the beginning of the 1990s, *B. tabaci* biotype "Q" has become a key pest in many greenhouse crops. Injury and loss result from sap removal, reduction of fruit quality due to sooty mold, and plant viruses vectored by the whitefly. Insecticidal control has become problematic in Spain and elsewhere due to resistance against major classes of active ingredient such as neonicotinoids and insect growth regulators (Cahill et al., 1996; Elbert and Nauen, 2000; Horowitz et al., 2003), providing incentive for alternate management strategies, including biological control. The resulting search for parasitoids best suited to control *B. tabaci* has focused on *Eretmocerus* spp., considered the most efficient against this pest (Gerling, 1986; Becker et al., 1992).

Until early 2002, the only species of *Eretmocerus* available commercially for augmentative biological control programs in Spain and elsewhere was *Eretmocerus eremicus* Howard (Hym.: Aphelinidae). However, observations in Spain revealed that native *E. mundus* Mercet (Hym.: Aphelinidae) entering the greenhouse seemed to provide better control of *B. tabaci*, even displacing released *E. eremicus* (Rodríguez-Rodríguez, 1994; Van der Blom, 2002; Stansly et al., 2005a). Greater specificity of *E. mundus* for *B. tabaci* (Greenberg et al., 2002) may provide a competitive advantage over *E. eremicus* when only one whitefly species is present. Consequently, *E. mundus* is now widely available, and its use is expanding in greenhouse crops (Lara and Urbaneja, 2002; Urbaneja et al., 2002a, b; Téllez et al., 2003; Stansly et al., 2004, 2005a, b).

Eretmocerus mundus is biparental, and like all *Eretmocerus* sp. undergoes an ecto- and endoparasitic stage in its life cycle on the whitefly host. Females oviposit externally between the leaf surface and the host nymph, preferably late second or early third instar (Gerling et al., 1998; Jones and Greenberg, 1998; Headrick et al., 1999; Urbaneja and Stansly, 2004). Upon eclosion, the first instar larva enters through a hole bored in the ventral integument of the host to feed internally (Gerling et al., 1991). Pupation occurs after three instars (Hafaz et al., 1978; Headrick et al., 1999), the adult eventually emerging through a circular hole chewed through the dorsum of the empty host. The female wasp also uses her ovipositor to pierce nymphs

through the vasiform orifice to obtain hemolymph, inflicting additional mortality on host populations (Gerling and Freid, 2000).

Previous published studies on the biology of *E. mundus* either did not provide demographic parameters or did not take host plant factors into account. Furthermore, most previous studies were conducted using *B. tabaci* biotype "B", whereas biotype "Q" predominates in much of the Mediterranean basin (Simón, 2002) and appears to be the principal biotype responsible for the stable insecticide resistance observed so far (Horowitz et al., 2003; Rauch and Nauen, 2003). We evaluated life history traits of *E. mundus* on *B. tabaci* biotype "Q", using as plant hosts the two most important protected vegetable crops in southeastern Spain, tomato and sweet pepper.

Material and methods

Plants and insects

Tomato, *Lycopersicon esculentum* L. 'Saskia', and sweet pepper, *Capsicum annuum* 'Spiro', (Seminis Vegetable Seeds Ibérica S.A. Almería; Spain) were sown inside large screened cages located within an air-conditioned greenhouse at the Koppert facility in Águilas (Murcia) Spain. Plants were transplanted individually after 3 weeks into 4 l pots filled with peat until ready for whitefly infestation upon development of four fully expanded leaves.

Adult *B. tabaci* used in the experiments were from a production colony originally obtained in the provinces of Murcia and Almería and identified by polymerase chain reaction (PCR) as biotype "Q" (J.L. Cenís, CIDA La Alberca. Murcia, SP, personal communication). *Eretmocerus mundus* used in the studies were taken from colonies originally collected from multiple locations in the provinces of Murcia and Almería and maintained on *B. tabaci* at the facility in Águilas. Pupae of *E. mundus* were held temporarily in a climate controlled cabinet at 25 ± 1 °C, $75 \pm 5\%$ RH, and 16:8 L:D until sexed under a stereoscopic microscope according to antennal color: dark for males, light for females (Rose and Zolnerowich, 1997). One female pupa and two male pupae were then introduced in a Petri dish (5.2 cm dia.) and held for a day after emergence to allow mating before use in experiments. Therefore, female age upon first exposure to hosts was 24–48 h.

Development and survivorship of immatures

Three clip cages (3.5 cm dia.) per plant were attached to four newly expanded leaves of four plants of sweet pepper and four of tomato. Twenty adults of *B. tabaci* from the colonies (60% female) were introduced into each clip cage. All whiteflies were removed after 4 h and plants held in the climate-controlled cabinet for 11 days when all insects had reached second instar. A single pair of *E. mundus* was introduced into each of eight clip cages on sweet pepper and seven on tomato. Wasps were removed after 24 h and plants with the clip cages were further incubated in the cabinet. Incidence of parasitism was evaluated within 7–8 days when mycetome displacement in parasitized whiteflies could be observed. Apparently unparasitized nymphs were inverted to check for egg remains or unhatched parasitoid eggs indicating unsuccessful parasitism or unviable eggs respectively. Fertility was calculated as the total number of parasitized nymphs divided by the same plus the number of unviable eggs. Parasitized nymphs were held for emergence to estimate developmental time, survivorship (number emerged divided by total number parasitized) and sex ratio, determined by antennal and genital morphology (Rose and Zolnerowich, 1997).

Reproductive parameters

Preoviposition, postoviposition and oviposition periods, fecundity, host feeding and longevity were determined through daily observations on the activities of individual females offered a surplus of the preferred second instar nymphs of *B. tabaci* (Urbaneja and Stansly, 2004). Sweet pepper and tomato plants were exposed to whiteflies in a $2 \times 4 \times 2.5$ m screened compartment used for whitefly production in an air-conditioned greenhouse maintained at 23 ± 2 °C and $60 \pm 5\%$ RH. Plants were removed after 24 h to obtain a uniform cohort of eggs. Vacuumed-cleaned plants were placed in identical cages provisioned with eight yellow sticky cards to capture errant insects. Whitefly development was monitored daily with a stereoscopic binocular microscope until the second nymphal instar was reached at which the time leaf discs were cut.

Freshly cut leaf discs 5.2 cm in diameter were examined under a stereoscopic binocular microscope to ascertain that each held between 30 and 60 nymphs of the appropriate stage. Excess nymphs were removed with a small brush. Leaf discs were then placed in a petri dish of the same diameter on a fine (ca. 2 mm) layer of agar (2% w/v). A

single couple of *E. mundus* was introduced into the petri dish which was held in the climate-controlled cabinet ($n = 15$ per crop). Parasitoids were transferred daily into a Petri dish provided with a fresh leaf disc and nymphal hosts. All nymphs on the old disc were observed under a stereoscopic binocular microscope for evidence of host feeding indicated by exuded hemolymph (McAuslane and Nguyen, 1996) and inverted to check for the presence of parasitoid eggs. Host replacement continued as long as females survived, and males that died were replaced. Parasitoids were fed ad libitum with small drops of a mixture of honey and *Typha* spp. pollen deposited on the leaves.

Data analysis

Values for age-specific survivorship beginning with 1-day-old eggs and age-specific fecundity for females were use to construct life tables. The intrinsic rate of increase (r_m) was computed using the Euler equation,

$$\sum e^{-r_m} l_x m_x \tag{1}$$

where l_x is survivorship of the original cohort over the age interval from day $x-1$ to day x, and m_x is the mean number of female offspring produced per surviving female during the age interval x (Birch, 1948). Values of m_x for the population were calculated from the mean number of eggs laid per female per day. Other parameters, including reproductive rate (R_0) and generation time (T) were calculated as described by Birch (1948) using a statistical jackknife (Maia et al., 2000). Doubling time was calculated from the equation

$$\mathrm{DT} = (\ln 2)/r \tag{2}$$

(Mackauer, 1983)

Where appropriate, parameters such as development time, survivorship and fecundity were subjected to either one- or two-way analysis of variance and Fisher's protected LSD test was used for mean separation ($p < 0.05$) (SPSS, 1999). When the assumptions of normality and homogeneity of variance could not be fulfilled and data could not be transformed to meet those assumptions, the non-parametric Mann–Whitney test was applied. Significance of differences between mean values of life table parameters was determined using Student's t test (Maia et al., 2000) (SAS 1995).

Results

Development and survivorship of immatures

No statistical differences in developmental time of the immature stages of *E. mundus* were found between crops ($df = 1, 96$; $F = 0.632$; $p = 0.429$) (Table 1). However, males developed approximately 1 day faster than females (16 vs. 17 d) ($df = 1, 96$; $F = 12.3$; $p = 0.001$) on both crops. No interaction was found between crop and sex ($df = 1, 96$; $F = 0.067$; $p = 0.796$).

No statistical differences were observed between crops in either parasitoid egg fertility or survival of parasitoid larvae and pupae (Table 2). Survivorship from egg to adult tended to be lower on tomato ($69.5 \pm 11.9\%$) compared to pepper ($76.6 \pm 10.5\%$), although the difference was not significant ($df = 1, 13$; $F = 0.198$; $p = 0.664$).

Reproductive parameters

No preoviposition period for *E. mundus* was observed on tomato or sweet pepper. Host plant had no significant effect on either oviposition or postoviposition period ($df = 1, 29$; $F = 1.979$; $p = 0.170$ and $df = 1,29$; $F = 0.100$; $p = 0.754$, respectively) (Table 3). Longevity of females tended to be less on tomato (8.5 ± 0.9 d) compared to pepper (10.5 ± 0.9 d), but again, the differences were not significant ($df = 1,29$; $F = 2.221$; $p = 0.147$).

Table 1. Mean ± SE (min–max) development time (days) for *E. mundus* on tomato and sweet pepper when reared on *B. tabaci* in clip cages at 25 °C

Sex	Stage	Tomato	Sweet pepper
Male	Egg–Pupa	10.93 ± 0.18 b (9–13)	10.95 ± 0.19 b (9–14)
	Pupa–Adult	5.50 ± 0.13 b (4–7)	5.00 ± 0.10 b (4–6)
	Egg–Adult	16.30 ± 0.19 b (15–19) ($n = 42$)	15.97 ± 0.21 b (13–19) ($n = 34$)
Female	Egg–Pupa	11.23 ± 0.20 a (10–12)	11.33 ± 0.46 a (10–14)
	Pupa–Adult	6.00 ± 0.31 a (4–7)	5.77 ± 0.15 a (5–6)
	Egg–Adult	17.27 ± 0.28 a (16–19) ($n = 9$)	17.11 ± 0.32 a (16–19) ($n = 11$)

Means followed by the same letter between sexes within the same host plant were not statistically different (LSD, $p < 0.05$).

Table 2. Mean ± SE stage specific survivorship of *E. mundus* on tomato and sweet pepper when reared on *B. tabaci* in clip cages at 25 °C

Stage	Tomato (%)	Sweet pepper (%)
Egg	90.9 ± 3.1	93.6 ± 5.3
Larva	77.5 ± 9.9	79.0 ± 8.9
Pupa	98.5 ± 1.5	100.0 ± 0.0
Total	69.5 ± 11.9	76.6 ± 10.5

Fecundity (number of hosts parasitized) was estimated at 171.1 ± 22.8 per female on sweet pepper and 147.8 ± 13.5 on tomato, and oviposition rate (viable eggs/days) was 19.0 ± 1.5 on tomato and 17.0 ± 1.0 on sweet pepper. Although these differences were not statistically significant (df = 1,29; F = 0.869; p = 0.359 and df = 1,29; F = 1.498; p = 0.231, respectively), the shape of the oviposition curve was distinctly flatter (except for a peak at 4 d) on pepper than tomato indicating a delayed cycle of oviposition but greater longevity on pepper (Figure 1). Consequently, 90% of all eggs were laid by day 8 on tomato, whereas on sweet pepper this point was not reached until day 12. A similar pattern was seen for host feeding, with more nymphs fed upon per female on sweet pepper (15.6 ± 0.98) compared to tomato (10.7 ± 1.3) (df = 1,29; F = 5.271; p = 0.029). Nevertheless, the host feeding rate, 1.5 ± 0.5 (nymphs/day) was the same on both plant hosts, again reflecting greater longevity on pepper (Figure 1).

Superparasitism was rare, being seen on only 1.7% of the cases on tomato and 2.2% on pepper (Table 4). No instances were observed of successful development of more than one parasitoid per host.

Demographic parameters

Generation time (T) was significantly greater on pepper (19.3 ± 0.5) than on tomato (17.9 ± 0.4) (t = 2.317; p = 0.028), reflecting more accelerated reproduction on tomato mentioned above (Table 5). The estimated reproductive rate (R_o) on tomato (51.0 ± 4.4), was not statistically different from 63.8 ± 8.7 on sweet pepper (t = 1.378; p = 0.182). However, this factor appeared to compensate for the difference in generation time because the estimated intrinsic rates of increase (r_m), were very similar for both plant hosts (t = –0.513; p = 0.611).

Table 3. Reproductive parameters of *E. mundus* reared on leaf disks of tomato and pepper infested with *B. tabaci* 2nd instar nymphs (mean ± SE and range)

	Tomato (n = 15)		Sweet pepper (n = 15)	
Longevity (days)	8.5 ± 0.9 a	(6–17)	10.5 ± 0.9 a	(6–18)
Oviposition (days)	8.1 ± 0.9 a	(6–16)	10.0 ± 1.0 a	(5–17)
Post-oviposition (days)	0.4 ± 0.1 a	(0–1)	0.4 ± 0.2 a	(0–2)
Fecundity[1] (viable eggs)	147.8 ± 12.6 a	(69–236)	171.1 ± 21.5 a	(102–387)
Host feeding (nymphs)	10.4 ± 1.3 b	(4–24)	15.6 ± 1.9 a	(6–27)
Oviposition rate (viable eggs/day)	19.0 ± 1.5 a	(7.7–26.8)	17.0 ± 1.0 a	(11.7–24.4)
Host feeding rate (nymphs/day)	1.5 ± 0.1 a	(0.6–2.8)	1.5 ± 0.1 a	2(0.9–2.5)

Means followed by the same letter within the same row were not statistically different (LSD; $p < 0.05$).
[1]Non-parametric Mann–Whitney test was applied.

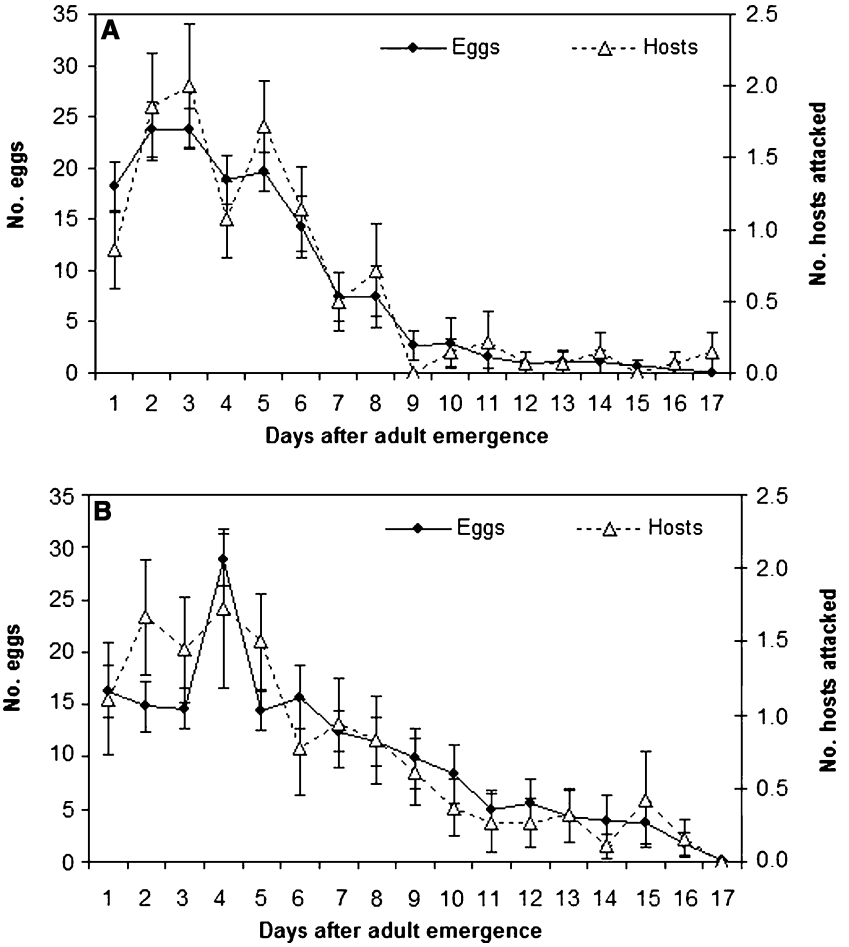

Figure 1. Rates of oviposition and host-feeding for adult *E. mundus* on tomato (A) and sweet pepper (B) when reared on *B. tabaci*.

Discussion

Few differences between tomato and sweet pepper were observed in the life history of *E. mundus*. Developmental time on second nymphal instars of *B. tabaci* was 16 and 17 days on both crops for the male and the female, respectively. Similar results have been reported on various plant hosts (Burnett, 1949; Gameel, 1969; Sharaf and Batta, 1985; Gerling and Fried, 2000; Ardeh, 2004; Qui et al., 2004). In contrast, Greenberg et al. (2002) reported more rapid development of *E. mundus* on *B. tabaci* (biotype "B") on cotton (*Gossypium hirsutum* L.) compared to bean (*Phaseolus vulgaris* L.) at 25 °C.

Table 4. Mean ± SE clutch size frequency of *E. mundus* eggs in *B. tabaci* nymphs on tomato and sweet pepper

Clutch size	Tomato	Sweet pepper
1	145.7 ± 12.5	163.0 ± 21.5
2	0.9 ± 0.3	3.5 ± 1.2
3	0.1 ± 0.1	0.1 ± 0.1
4	–	0.3 ± 0.3

Gerling and Fried (2000) reported parasitoid pupal survivorship at 74% and 84%, depending upon whether pupae were placed in gelatin capsules or left on leaves. Greenberg et al. (2002) observed 84.9% emergence of *E. mundus* from visibly parasitized nymphs, presumably identified by displacement of the mycetomes. We saw no effect of host plant on preimaginal survivorship, with most mortality occurring in the larval stage. In a previous study on sweet pepper under the same climatic conditions, Urbaneja and Stansly (2004) observed preimaginal survivorship of 84.2% with no effect of host stage, and most mortality (14.7%) occurring in the pupal stage. This apparent discrepancy is probably due to different methodologies used to evaluate survivorship: clip cages in this study vs. leaf discs on agar in the previous study. The methodology was changed for the present study because of deterioration of tomato leaf discs toward the end of the incubation period. Clip cages appear to be the better method to estimate developmental time and survivorship on different types of plants, and moreover, create a more realistic environment.

We estimated longevity of *E. mundus* females at 10.1 and 7.3 days on sweet pepper and tomato, respectively. Similar results were also obtained on tomato by Sharaf and Batta (1985), on tomato, gerbera (*Gerbera jamesonii* Bolus) and poinsettia (*Euphorbia pulcherrima*

Table 5. Life table parameters for *E. mundus* when reared on *B. tabaci* using tomato and sweet pepper

	Tomato	Sweet pepper
T	17.9 ± 0.4 b	19.3 ± 0.5 a
R_0	51.0 ± 4.4 a	63.8 ± 8.2 a
D	3.2 ± 0.1 a	3.2 ± 0.1 a
r_m	0.219 ± 0.004 a	0.216 ± 0.005 a

Means followed by the same letter within the same row were not statistically different (*t*-Student, using a statistical jackknife technique; $p < 0.05$).

Willd. ex Klotzsch) by Ardeh (2004) and on cotton by Gerling and Fried (2000), but not by Tawfik et al. (1978) who estimated longevity at 3.5 days on tobacco (*Nicotiana tabacum* L.) at 26.8 °C. We observed *E. mundus* to exhibit no preoviposition period. Although the mean age of females at first exposure to a host was 24–48 h, we have independently observed females to attack *B. tabaci* nymphs within minutes of emergence. Gerling and Fried (2000) on cotton and Ardeh (2004) on tomato, poinsettia and gerbera obtained similar results.

We estimated fecundity at 171.1 and 147.8 eggs per *E. mundus* female on sweet pepper and tomato, respectively. This difference was due, at least in part, to longer survival on pepper compared to tomato. Ardeh (2004) found a large variation in fecundity on different host plants (26.8 eggs per female on gerbera, 49.4 on poinsettia and 117.5 on tomato). Gerling and Fried (2000) observed from 81.1 to 247.5 eggs per female during the first 9 days after emergence. In contrast, Sharaf and Batta (1985) reported only 24 eggs/female on tomato and Tawfik et al. (1978) 48 eggs at 30 °C on cotton. We can only attribute these later results to differences in experimental conditions during the course of the studies.

We noted above that fecundity was accelerated on tomato compared to pepper. This may be due to differences in oviposition time related to the shape of the nymphal host—thick on a pubescent surface such as tomato vs. thin and appressed to a glabrous surface such as pepper (Gelman and Gerling, 2003). Thus the female could require more time to force the ovipositor between the tightly adhering nymphal venter and the leaf surface on pepper compared to tomato. The result would be delayed reproduction and longer generation time (T) on sweet pepper. The same differences in host morphology could explain higher incidence of parasitism by *E.* nr. *californicus* (= *E. eremicus*) in pubescent or hirsute varieties of soybean *Glycine max* (L.) compared to glabrous varieties (McAuslane et al. 1995) and by *E.* sp. nr. *furuhashii* on crops with different density of leaf hairs (Qiu et al., 2005).

Stansly et al., (2005b) found that higher release rates of *E. mundus* were necessary to control *B. tabaci* on tomato compared to sweet pepper. Our results indicating similar inherent rates of increase r_m on these crops would tend to support their suggestion that differences observed in control capability were due to greater reproductive capacity of *B. tabaci* on tomato compared to pepper rather than a direct response of *E. mundus* to either crop.

Intrinsic rate of increase (r_m) estimated for *E. mundus* from this study was generally higher than previously reported for other *B. tabaci* parasitoids. Headrick et al. (1999) estimated an r_m at 28 °C for *E. eremicus* on *B. tabaci* biotype "B" of 0.055 using sweet potato (*Ipomoea batatas* L.) which is glabrous and 0.096 using a hirsute cotton cultivar, 'Delta Pine 61'. Gerling and Fried (2000) reported an r_m on cotton for *E. mundus* on *B. tabaci* (biotype not mentioned) of 0.191 females/female/day, while Ardeh (2004) obtained an r_m on tomato of 0.23, 0.19 on poinsettia and 0.15 on gerbera. Our estimates for *E. mundus* of 0.216 on tomato and 0.219 on pepper are well above published estimates of r_m for *B. tabaci* at the same temperature of 25 °C: 0.124 on tomato and cucumber (*Cucumer sativus* L.) (Powell and Bellows, 1992), 0.087 on poinsettia (Enkegaard, 1993), and 0.123 on cotton (Powell and Bellows, 1992). These results lend credence to reports that augmentative biological control of *B. tabaci* biotype "Q" with *E. mundus* can be effective in greenhouse tomato and pepper crops (Stansly et al., 2004, 2005a, b).

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