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## Biocontrol Science and Technology

Publication details, including instructions for authors and subscription information:

<http://www.informaworld.com/smpp/title~content=t713409232>

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Online Publication Date: 01 January 2007

To cite this Article: Naranjo, Steven E. , (2007) 'Intraguild predation on **Eretmocerus** sp. nr. **emiratus**, a parasitoid of **Bemisia tabaci**, by three generalist predators with implications for estimating the level and impact of parasitism ', Biocontrol Science and Technology, 17:6, 605 - 622

To link to this article: DOI: 10.1080/09583150701408816

URL: <http://dx.doi.org/10.1080/09583150701408816>

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# Intraguild predation on *Eretmocerus* sp. nr. *emiratus*, a parasitoid of *Bemisia tabaci*, by three generalist predators with implications for estimating the level and impact of parasitism<sup>1</sup>

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(Received 31 October 2006; returned 11 February 2007; accepted 16 February 2007)

## Abstract

Intraguild predation (IGP) is pervasive in many managed and unmanaged ecosystems and may have negative, neutral or positive effects on the biological control of pest insects. Both generalist predators and aphelinid parasitoids attack *Bemisia tabaci* (Gennadius) Biotype B (= *B. argentifolii* Perring & Bellows) on cotton in the southwestern USA. Free-choice and no-choice laboratory assays were conducted to quantify prey consumption patterns and preference by three representative generalist predators, *Geocoris punctipes* (Say), *Orius insidiosus* (Say), and *Hippodamia convergens* Guérin-Ménéville, offered fourth instar *B. tabaci* nymphs and nymphs parasitized by *Eretmocerus* sp. nr. *emiratus*. All three predators showed a significant preference for larval and pupal stage parasitoids over early fourth instar nymphs, but *G. punctipes* and *O. insidiosus* were non-discriminating when offered a choice of larval parasitoids and late fourth instar nymphs. The potential implications of these observed patterns for the field were examined through sensitivity analyses of existing field life table data. First, preference for parasitized hosts alters the methods required for calculating marginal rates of parasitism. Incorporating a preference variable in the estimation procedure had a very small positive effect (0.02–1.13% change) on total generational mortalities observed in previous life table studies. However, further hypothetical analyses suggested that under circumstances of lower generational mortality and higher levels of either apparent parasitism or predation, high levels of predator preference for parasitized prey could alter estimates of total mortality as much as 14%. Second, although intraguild predation was demonstrated, the implications for biological control are unclear. Based on field life table data the rate of IGP ranged from 0.019 to 0.126 depending on predator species and prey comparison, but accounting for these levels of IGP had only small negative effects on total generational mortalities (0.193–1.278% change).

**Keywords:** *Bemisia tabaci*, generalist predators, aphelinid parasitoids, prey preference, life tables, marginal mortality rates

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First published online 1 June 2007

ISSN 0958-3157 print/ISSN 1360-0478 online © 2007 Taylor & Francis

DOI: 10.1080/09583150701408816

## Introduction

Intraguild predation (IGP) is an emergent outcome of species simultaneously engaged in competition and predation and is defined as a trophic interaction between species using a shared prey resource. IGP is pervasive in many managed and unmanaged ecosystems (Polis et al. 1989; Rosenheim et al. 1995) and has been of particular interest in insect biological control because a variety of natural enemies may compete for and attack a given pest species, and interactions between these natural enemies may have negative, neutral or positive effects on overall pest suppression (Press et al. 1974; Roland 1990; Rosenheim et al. 1993; Ferguson & Stiling 1996; Heinz & Nelson 1996; Colfer & Rosenheim 2001; Snyder & Ives 2001; Kaplan & Eubanks 2002). Defining the nature, extent, and impact of IGP in agricultural systems characterized by multiple natural enemies is central to the design and implementation of effective and efficient biological control programs.

*Bemisia tabaci* (Gennadius) biotype B (= *B. argentifolii* Perring & Bellows), a major pest and virus vector of numerous crops worldwide, is attacked by a large assemblage of predators, parasitoids and fungi (Lopez-Avila 1986; Gerling 1990; Breene et al. 1994; Lacey et al. 1996; Nordlund & Legaspi 1996; Gerling et al. 2001). The effect of these natural enemies on populations of *B. tabaci* is not completely understood; however, studies have documented resurgence of *B. tabaci* in cotton with use of broad-spectrum insecticides (e.g. Abdelrahman & Munir 1989; Devine et al. 1998), and several recent studies suggest that generalist predators and aphelinid parasitoids may act as key factors in the population dynamics of this pest in several crops (Naranjo & Ellsworth 2005; Asiimwe et al. 2007; Cañas et al., unpubl.).

Both generalist predators and aphelinid parasitoids attack *B. tabaci* on cotton in the southwestern USA. Examination of predator gut contents has definitively identified nearly 20 species of generalist predators feeding on *B. tabaci* in the field (Hagler & Naranjo 1994a,b, 2005). In addition, several native species of *Eretmocerus* and *Encarsia* parasitize *B. tabaci* in Arizona and southern California (Hoelmer 1996; Gerling & Naranjo 1998; Naranjo et al. 2003), and at least two of the many exotic aphelinid parasitoids introduced into the southwestern USA over the past decade (Kirk & Lacey 1996; Hoelmer & Kirk 1999; Kirk et al. 2001) have become established in both Arizona and California (Goolsby et al. 2005; Naranjo, unpubl.).

Several studies have demonstrated trophic interactions between natural enemies attacking *B. tabaci*. Both Hoelmer et al. (1994) and Heinz et al. (1994) showed that while *Delphastus pusillus* (LeConte) consumed parasitized whitefly hosts containing younger stages of aphelinid parasitoids indiscriminately, it tended to avoid preying on hosts containing older parasitoid larvae and pupae, presumably because of hardening of the host cuticle and the introduction of air spaces around the parasitoid body that made it difficult for the beetles to access the parasitoid with their mouthparts. Likewise, Al-Zyoud and Sengonca (2004) and Fazal and Xiang (2004) found that two species of the coccinellid *Serangium* avoided preying on older aphelinid parasitoid larvae and pupae within *B. tabaci* hosts. Thus, depending on the timing of IGP there may be little potential impact on parasitism. *Chrysoperla carnea* (Stephens) readily preyed on *Encarsia transvena* (Timberlake) within whitefly hosts but parasitoid age was not specified (Kapadia & Puri 1990). Relatively few studies have examined the potential impact of IGP on biological control of *B. tabaci*. Heinz and Nelson (1996) investigated the impact of multiple natural enemies of *B. tabaci* on greenhouse poinsettias and found that *D. pusillus* alone or in combination with one or two

aphelinid parasitoid species resulted in greater pest suppression than either parasitoid alone or combined. Similarly, Hunter et al. (2002) showed that although the autoparasitoid *Encarsia sophia* (Girault & Dodd) affected densities of *Eretmocerus eremicus* Rose & Zolnerowich in field cages in cotton, it did not interfere with overall suppression of *B. tabaci*. Further studies are needed to establish the extent of IGP on parasitoids of *B. tabaci* and to understand how IGP might effect the estimation and impact of parasitism as a component of the biological control of this pest.

The objectives of this study were to determine the presence and extent of asymmetrical IGP on aphelinid parasitoids of *B. tabaci* by co-occurring generalist predators in the cotton system. A representative system consisting of three common generalist predators, *Geocoris punctipes* (Say), *Orius insidiosus* (Say) and *Hippodamia convergens* Guérin-Méneville, and a recently established exotic parasitoid species, *Eretmocerus* sp. nr. *emiratus*, was examined in laboratory studies. A series of free-choice and no-choice experiments were used to test the discrimination of predators feeding on parasitized and non-parasitized whitefly prey and measure attack rates on various types of prey. These results were then further used in sensitivity analyses to examine the potential consequences of IGP on both the estimation of marginal rates of parasitism in the field and on overall pest mortality based on extant field life table studies.

## Materials and methods

### *Insect and plant sources*

Adult *G. punctipes* and *O. insidiosus* were obtained from laboratory cultures reared on lepidopteran eggs (primarily *Pectinophora gossypiella* [Saunders]) and green beans. These are long-standing cultures that are augmented with field populations annually. Predators were reared in environmental chambers maintained at  $27 \pm 0.5^\circ\text{C}$ ,  $50 \pm 10\%$  RH with a 14:10 (L:D) photophase. *Hippodamia convergens* were collected from alfalfa and cotton fields in Maricopa, AZ and adults were held and fed *P. gossypiella* eggs and green beans for periods of a few days to 2 weeks prior to being used in experiments. Adult *B. tabaci* (biotype B) used to infest cotton plants were obtained from a greenhouse culture maintained on cotton plants that are augmented with field populations annually. *Eretmocerus* sp. nr. *emiratus* were supplied by USDA-APHIS, Mission Plant Protection Center, Mission, TX as pupae on hibiscus leaves.

Cotton, *Gossypium hirsutum* L. (cv. Deltapine 5415), plants were grown in greenhouses in commercial potting soil (Gardeners World, Phoenix, AZ) and fertilized weekly (Grow More<sup>®</sup>, Gardena, CA). Plants were maintained in an herbivore-free environment prior to infestation with *B. tabaci*.

To provide non-parasitized immature whiteflies for studies, cotton plants (six–eight leaf stage) were placed within whitefly colony cages for about 1 h to allow relatively light oviposition by adult females. After removing all adult whiteflies, these plants were then held in a separate, insect-free greenhouse to allow the eggs to hatch and mature to either the fourth instar to produce whitefly prey for experiments, or to the second–third instar to provide hosts for adult parasitoids. To produce parasitized whitefly nymphs, plants containing second–third stage nymphs were moved to another insect-free greenhouse. Small organandy leaf bags containing about five mating pairs of adult parasitoids were placed over leaves of these plants and allowed to forage and oviposit for 24 h. After removing the leaf bags and all the parasitoids, these exposed plants

were then held to allow parasitoid development. Parasitoid development is not apparent until the host reaches the fourth nymphal stage and so all immature parasitoids were presented to predators in fourth instar hosts.

#### *Free-choice experiments*

Experimental arenas consisted of organandy-vented Petri-dishes ( $15 \times 100$  mm diameter for *G. punctipes* and *H. convergens*;  $15 \times 60$  mm diameter for *O. insidiosus*) with a thin layer ( $\approx 5$  mm) of 1% agar poured in the bottom as a substrate to keep the leaf disks described below fresh. Leaves harvested from the greenhouse containing either fourth stage whitefly or parasitized fourth stage mummies were brought into the laboratory and small leaf disks (7 mm) containing a single prey item were cut from these leaves using a cork-borer. For experiments involving *G. punctipes* or *H. convergens*, a six by seven array of leaf disks (42 prey total) was established in the center of the Petri dish. This array presented a checker-board of parasitized and non-parasitized whitefly prey, i.e. every other prey item in either the  $x$  or  $y$  direction was a parasitized whitefly mummy. An ultra-fine, non-toxic pen (Sanford, Bellwood, IL) was used to place a small dot on the leaf disks containing parasitized mummies so that prey items could be accurately identified after exposure to predators. To control for the possibility of the ink affecting predator foraging behavior, parasitized or non-parasitized hosts were marked in alternate dishes throughout the course of the experiment. A similar set-up was used for *O. insidiosus* arenas except that a smaller Petri dish was used and only 16 total prey (eight whitefly, eight parasitoids) were presented, again in a checker-board pattern. Also, because this smaller predator had difficulty walking on the agar substrate, a moistened filter-paper disk was placed between the agar and the leaf disks.

Three different free-choice experiments were conducted with each predator species. First, predators were given a choice between early fourth instar nymphs and late larval stage parasitoids within host mummies (referred to hereafter as larval stage parasitoids). This stage of development is often referred to as the 'displaced-mycetome' stage of parasitism because the growth and movement of older parasitoid larva displaces the most obvious organs in the whitefly's body. Second, predators were given a choice between early fourth instar nymphs and pupal stage parasitoids. At this stage the parasitoid is clearly visible through the host cuticle. Third, predators were offered a choice between late fourth instar nymphs, sometimes referred to as the whitefly 'pupae', and pupal stage parasitoids. The latter choice was specifically offered to test the hypothesis that predators were using visual cues to locate and attack prey. Both pupal parasitoids and 'pupal' whiteflies have greater depth than early fourth instar whiteflies which are very flat and two-dimensional on the leaf surface (Gelman et al. 2002). Chronologically, parasitized fourth instar nymphs are older than non-parasitized nymphs because the parasitoid extends the developmental period of the nymph; however, both can be found on the same leaf in the field (unpublished data). Thus, these three comparisons represent the range of choices that foraging predators would likely encounter in the field.

After a 24-h prey starvation period (green beans provided for moisture) one adult female predator was introduced into the arena and allowed to forage for 24 h at  $27 \pm 0.5^\circ\text{C}$  and  $50 \pm 10\%$  RH with a 14:10 (L:D) photophase. For *G. punctipes* and *O. insidiosus* 5–10 days old adults were used; age was not controlled for field-collected *H. convergens*. Following exposure to predators, each prey in the arena was then

evaluated for predation. *Geocoris punctipes* and *O. insidiosus* are sucking predators, and predation was obvious because they would evacuate the contents of the whitefly or parasitoid leaving behind a deflated and transparent host or mummy cuticle. With the chewing predator *H. convergens* the prey item was simply missing. A total of 30–35 individual replicates of each prey contrast was conducted for each predator species but an individual test was counted only if more than two prey items were attacked.

#### No-choice experiments

The exact same methods as described above were used to estimate predator attack rates on one of four prey types; early fourth instar whitefly, 'pupal' stage whitefly, larval stage parasitoids and pupal stage parasitoids. For *G. punctipes* and *H. convergens* a total of 42 prey items of the same stage was offered; *O. insidiosus* was offered 16 total prey. A total of 20–25 individual replicates of each prey type was conducted for each predator species and as before an individual test was counted only if more than two prey items were attacked in order to generate comparable data to free-choice arenas.

#### Analyses

A preference index that takes into account the depletion of prey over time was used to assess predation on parasitized and non-parasitized whiteflies (Manly 1974; Chesson 1983). The index,  $\alpha$ , is given as

$$\alpha = \ln((n_{p0} - r_p)/n_{p0}) / [\ln((n_{p0} - r_p)/n_{p0}) + \ln((n_{w0} - r_w)/n_{w0})] \quad (1)$$

where,  $n_{p0}$  and  $n_{w0}$  are the numbers of parasitized and non-parasitized prey offered at the beginning of the experiment, and  $r_p$  and  $r_w$  are the numbers of parasitized and non-parasitized prey eaten over the 24-h assay period, respectively. The index returns a value between 0 and 1 with 0 indicating complete preference for non-parasitized prey and 1 indicating complete preference for parasitized prey. Manly (1974) showed that this estimator was asymptotically distributed as a normal random variate, and so a simple *t*-test was used to test the null hypothesis of no preference, i.e.  $\alpha = 0.5$ . One-way ANOVA was used to test for differences in predation rates on the four types of prey in no-choice studies and for differences in total predation rates in the three free-choice assays. The Tukey–Kramer HSD test was used to separate means (JMP, SAS Institute, Cary, NC).

Additional analyses were conducted to examine how the preference data might be used to improve the estimation of marginal rates of parasitism of *B. tabaci* from field life tables of this insect. Prior analyses (Naranjo & Ellsworth 2005) estimated marginal rates of parasitism ( $M_B$ ) from

$$M_B = d_B / (1 - d_A) \quad (2)$$

where  $d_B$  is the apparent or observed rate of parasitism and  $d_A$  is the sum of the apparent rates of mortality from all other relevant contemporaneous factors in the field (i.e. predation and dislodgement) (see Elkinton et al. 1992). This model assumes that parasitism will always be obscured by predation and dislodgement when these factors affect the same individual and that predation and dislodgement are non-discriminating, that is, predation or dislodgement of a parasitized or a non-parasitized whitefly is equally likely. If predators are instead discriminatory, preferring to attack either parasitized or non-parasitized whiteflies when given the choice, then different

formulae are needed for estimating marginal mortality rates due to parasitism. In this instance the following equations from Elkinton et al. (1992) would apply

$$M_B = d_B / (1 - cM_A) \quad (3)$$

$$M_A = (b - (b^2 - 4cd_A)0.5) / 2c \quad (4)$$

$$b = c(d_A + d_B) + 1 - d_B \quad (5)$$

where  $M_B$ ,  $d_A$ , and  $d_B$  are as defined above,  $M_A$  is the marginal mortality rate for the competing factors, and  $c$  is an index that describes the outcome of competition between mortality factors. In Equation 2,  $c=1$  is implicit because factor  $A$  (e.g. predation) always wins any competition. However, in the case of discriminating predation  $c$  may take on values greater or less than 1. For the case outlined above, Elkinton et al. (1992) suggests that  $c$  can be estimated from the ratio of parasitized to non-parasitized hosts that are attacked by a predator. The variable  $c$  was estimated from each free-choice arena for each species, and along with field rates of  $d_A$ , and  $d_B$  from Naranjo and Ellsworth (2005), was used to solve Equations 3–5. The sensitivity of using Equations 3–5 with variable  $c$  rather than Equation 2 with  $c$  fixed at unity was then estimated by calculating the average per cent change in total generational mortality of 14 separate generations observed by Naranjo and Ellsworth (2005). To provide a more general assessment of the effect of predator preference on the estimation of marginal rates of parasitism, additional sensitivity analyses were performed based on two nominal levels of generational mortality (0.99 and 0.75) and three levels each of apparent parasitism and predation (0.10, 0.25, and 0.50) in a factorial arrangement. Equations 3–5 were used to estimate marginal rates of parasitism for a range of values of  $c$  (1–4) and sensitivity was again measured as the per cent change in total generational mortality from nominal values of 0.99 and 0.75. These levels of mortality represent the 90th and 10th percentiles from the life table studies of Naranjo and Ellsworth (2005). It should further be noted that the life table data used here were collected before the confirmed establishment of several exotic aphelinid parasitoids (Goolsby et al. 2005; Naranjo, unpubl.).

The marginal rate estimates the rate of mortality for a given factor as if it were the only factor operating. As such, the rate of intraguild predation can be inferred from the difference between marginal and apparent rates of parasitism where the latter measures the net level of parasitism after predation has occurred. The impact of IGP was then estimated for each predator species and prey contrast by calculating the average per cent change in total generational mortality of the 14 field cohorts noted above using marginal versus apparent rates of parasitism.

## Results

All three predator species displayed a significant ( $t > 5.8$ ,  $df \geq 24$ ,  $P < 0.01$ ) preference for parasitized hosts when given the choice between larval parasitoids and early fourth instar whitefly nymphs (Figure 1). Mean index values were 0.69, 0.78, and 0.74 for *G. punctipes*, *O. insidiosus* and *H. convergens*, respectively, and there were instances in which all three predators selectively consumed nothing but parasitized hosts. When offered a choice between pupal parasitoids and early fourth instar whitefly nymphs all three predators again displayed a significant ( $t > 3.9$ ,  $df \geq 24$ ,  $P < 0.01$ ) preference for parasitized hosts (Figure 2). Mean preference for pupal parasitoids was even stronger for *G. punctipes* (0.78) and *H. convergens* (0.89) compared with larval-stage parasitoids

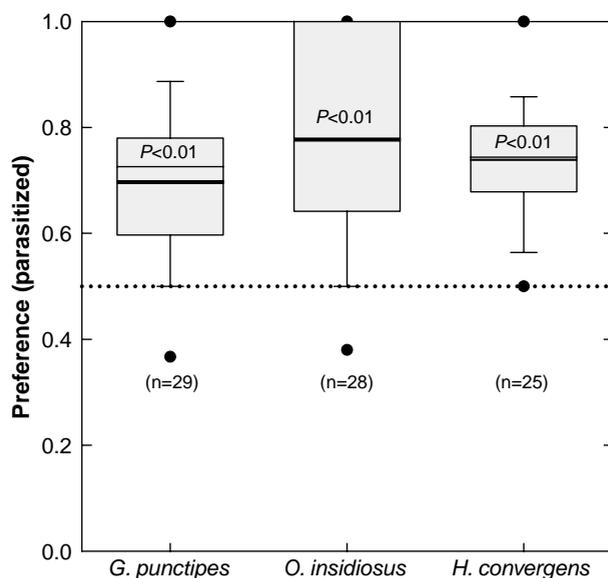


Figure 1. Box-plots of preference indices of three generalist predators when given a choice between an equal number of late larval-stage *E. sp. nr. emiratus* parasitoids (within *B. tabaci* mummies) and early fourth instar *B. tabaci* nymphs. The index (Equation 1) accounts for prey depletion over the assay period. *Geocoris punctipes*, *H. convergens* and *O. insidiosus* were presented with a total of 42, 42 and 16 prey items, respectively, and allowed to forage for 24 h at 27°C and 50% RH with a 14:10 (L:D) photophase. For box-plots the light and bold lines within the box represent the medium and mean, respectively, the box bounds the 25th and 75th percentiles, the whiskers denote the 10th and 90th percentiles and the points denote the range. The probability values denote testing of the null hypothesis (index = 0.5) of no preference (*t*-test).

and again there were instances for these two species when only parasitized hosts were consumed. Early fourth instar whitefly nymphs are very flat and almost translucent on the leaf surface (depth  $\approx 0.1$  mm, Gelman et al. 2002). In contrast, once the larval parasitoid is large enough to displace the host's mycetomes, the host begins to swell and become opaque. Thus, parasitized hosts may be more apparent to predators foraging on the leaf surface. This hypothesis was tested by presenting parasitized hosts along with late-stage fourth instar whitefly (this stage also swells and is opaque; depth  $> 0.27$  mm, Gelman et al. 2002). Both *G. punctipes* and *O. insidiosus* were non-discriminating in these arenas (mean  $\alpha \approx 0.50$ ,  $P > 0.94$ ), but *H. convergens* continued to display a significant ( $t = 3.3$ ,  $df = 26$ ,  $P < 0.01$ ), but slightly lower ( $\alpha = 0.68$ ), preference for parasitized hosts (Figure 3). Still, there were instances when this predator fed solely on parasitized hosts.

There was no difference ( $P = 0.12$ ) in rates of consumption of parasitized or non-parasitized hosts by *G. punctipes* in no-choice arenas with an overall mean of 19.1 prey consumed in a 24-h period (Figure 4). Likewise, there was no significant difference in total prey consumption rates among the three types of free-choice arenas for this species with a mean of 18.7 prey consumed in 24 h (Figure 4). There also was no difference ( $P = 0.08$ ) in 24 h prey consumption rates among the four different prey types in no-choice arenas for *O. insidiosus*, where consumption rates averaged 5.9 (Figure 5). However, the total consumption of prey in free-choice arenas that presented larval parasitoids and late fourth instar whitefly nymphs was higher ( $F = 4.78$ ,  $df = 2, 79$ ,  $P = 0.01$ ) compared with the other two free-choice arenas. The

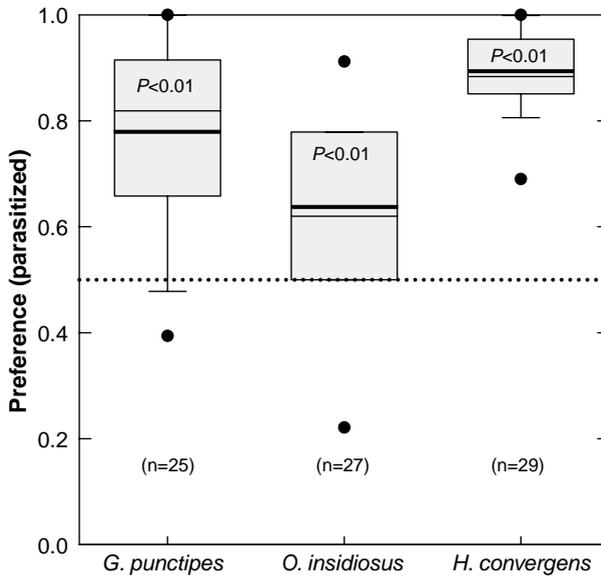


Figure 2. Preference indices of three generalist predators when given a choice between an equal number of pupal-stage *E. sp. nr. emiratus* parasitoids (within *B. tabaci* mummies) and early fourth instar *B. tabaci* nymphs. The index (Equation 1) accounts for prey depletion over the assay period. *Geocoris punctipes*, *H. convergens* and *O. insidiosus* were presented with a total of 42, 42 and 16 prey item, respectively, and allowed to forage for 24 h at 27°C and 50% RH with a 14:10 (L:D) photophase. For box-plots the light and bold lines within the box represent the medium and mean, respectively, the box bounds the 25th and 75th percentiles, the whiskers denote the 10th and 90th percentiles and the points denote the range. The probability values denote testing of the null hypothesis (index = 0.5) of no preference ( $t$ -test).

mean consumption rate over all free-choice arenas was 5.7 (Figure 5). *Hippodamia convergens* displayed a more variable response. Rates of prey consumption differed significantly ( $F = 11.1$ ,  $df = 3,82$ ,  $P < 0.01$ ) among the no-choice arenas, with the highest levels of consumption observed on pupal parasitoids and the lowest on early fourth instar whitefly nymphs (Figure 6). Mean consumption over all prey types was 17.1. There was no difference in total prey consumption rates (mean 16.9) between the three free-choice arenas ( $P = 0.97$ ).

Values for the preference variable  $c$ , which is the ratio of parasitized to non-parasitized prey consumed, varied widely over predator species and prey contrasts (Table I). Consistent with the preference index  $\alpha$ , this variable was close to unity when either *G. punctipes* or *O. insidiosus* were offered a choice of larval parasitoids and late fourth instar whitefly nymphs. In all other instances the value of  $c$  was greater than two. As a consequence, marginal mortality rates of parasitism that account for the obscuring effects of predation and the discriminatory behavior of the three predators in preferentially consuming parasitized hosts (Equations 3–5) led to higher estimates of parasitism than those based on non-discriminating predation (Equation 2, Table I). However, based on known, mean apparent rates of predation (0.274) and parasitism (0.046) on fourth instar whiteflies in the field (Naranjo & Ellsworth 2005), total generational mortality would be expected to change very little (0.021–1.126%) when accounting for predator preference in estimating marginal rates of parasitism.

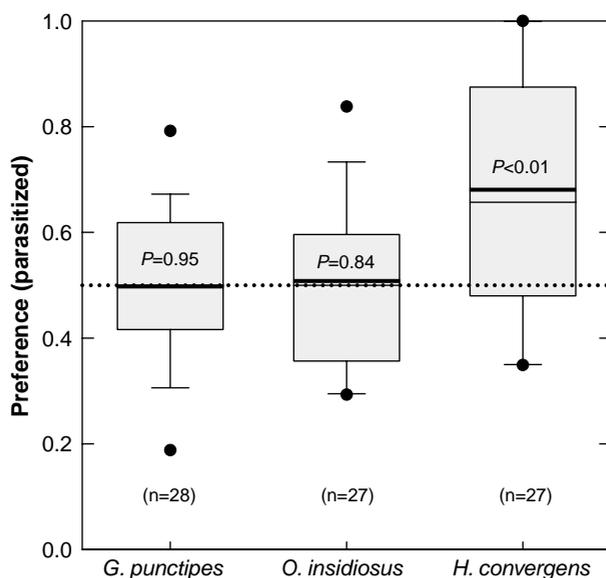


Figure 3. Preference indices of three generalist predators when given a choice between an equal number of late larval-stage *E. sp. nr. emiratus* parasitoids (within *B. tabaci* mummies) and late fourth instar *B. tabaci* nymphs ('pupae'). The index (Equation 1) accounts for prey depletion over the assay period. *Geocoris punctipes*, *H. convergens* and *O. insidiosus* were presented with a total of 42, 42 and 16 prey items, respectively, and allowed to forage for 24 h at 27°C and 50% RH with a 14:10 (L:D) photophase. For box-plots the light and bold lines within the box represent the median and mean, respectively, the box bounds the 25th and 75th percentiles, the whiskers denote the 10th and 90th percentiles and the points denote the range. The probability values denote testing of the null hypothesis (index = 0.5) of no preference (*t*-test).

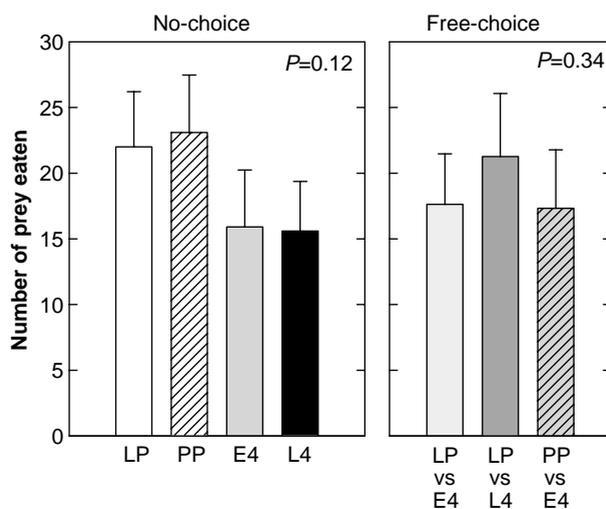


Figure 4. The total number of different types of prey consumed by *G. punctipes* in 24 h no-choice and free-choice assays at 27°C and 50% RH with a 14:10 (L:D) photophase. The probability values denote testing of the null hypothesis that all prey were consumed equally (one-way ANOVA). LP, larval parasitoid; PP, pupal parasitoid; E4, early fourth instar whitefly nymph; L4, late fourth instar whitefly nymph. Error bars represent 95% confidence intervals.

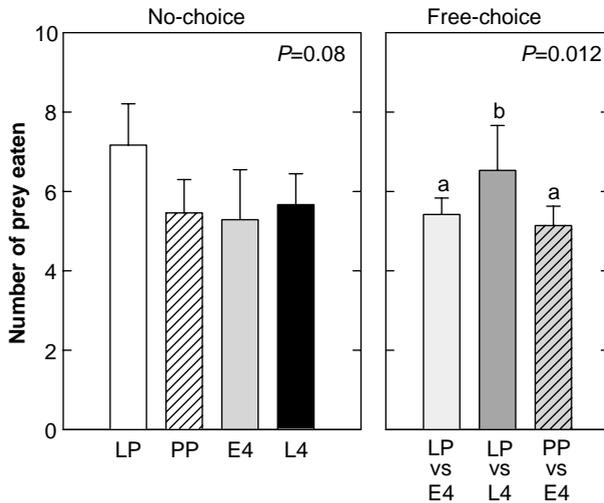


Figure 5. The total number of different types of prey consumed by *O. insidiosus* in 24 h no-choice and free-choice assays at 27°C and 50% RH with a 14:10 (L:D) photophase. The probability values denote testing of the null hypothesis that all prey were consumed equally (one-way ANOVA, Tukey–Kramer HSD for mean separation). LP, larval parasitoid; PP, pupal parasitoid; E4, early fourth instar whitefly nymph; L4, late fourth instar whitefly nymph. Error bars represent 95% confidence intervals.

Analyses to examine the more general effects of predator preference for parasitized prey over a range of total mortality, and apparent rates of parasitism and predation showed that estimates of generational mortality would again change very little (<0.5%) regardless of the levels of parasitism, predation or preference when overall

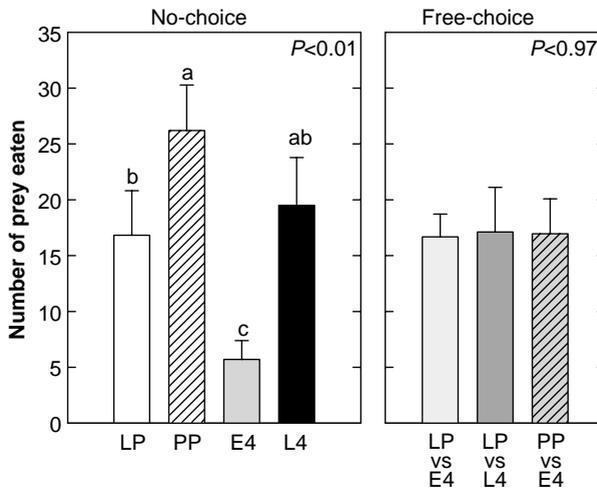


Figure 6. The total number of different types of prey consumed by *H. convergens* in 24 h no-choice and free-choice assays at 27°C and 50% RH with a 14:10 (L:D) photophase. The probability values denote testing of the null hypothesis that all prey were consumed equally (one-way ANOVA, Tukey–Kramer HSD for mean separation). LP, larval parasitoid; PP, pupal parasitoid; E4, early fourth instar whitefly nymph; L4, late fourth instar whitefly nymph. Error bars represent 95% confidence intervals.

Table I. Preference variables ( $c$ ) for estimating marginal rates of parasitism of *B. tabaci* under different prey choice circumstances, and implications of preference and intraguild predation.

	Marginal rate (parasitism) <sup>†</sup>				Rate of IGP <sup>†</sup>	Sensitivity to IGP (% change) <sup>§</sup>
	Mean $c$ <sup>*</sup>	Method 1	Method 2	Sensitivity <sup>‡</sup> (% change)		
<i>G. punctipes</i>						
LP vs. E4	2.13	0.063	0.097	0.351	0.051	0.517
PP vs. E4	2.68	0.063	0.119	0.578	0.073	0.741
LP vs. L4	1.09	0.063	0.065	0.021	0.019	0.193
<i>O. insidiosus</i>						
LP vs. E4	2.40	0.063	0.107	0.454	0.061	0.619
PP vs. E4	2.03	0.063	0.093	0.309	0.047	0.477
LP vs. L4	1.20	0.063	0.068	0.052	0.022	0.223
<i>H. convergens</i>						
LP vs. E4	2.21	0.063	0.100	0.382	0.054	0.548
PP vs. E4	4.11	0.063	0.172	1.126	0.126	1.278
LP vs. L4	2.60	0.063	0.115	0.537	0.069	0.700

LP, larval parasitoid; PP, pupal parasitoid; E4, early fourth instar whitefly nymph; L4, late fourth instar whitefly nymph. \*Ratio of parasitized to non-parasitized hosts attacked by predator;  $n = 25-29$ . <sup>†</sup>Marginal rate of parasitism calculated using mean apparent rates of parasitism (0.046) and predation (0.274) of fourth stage nymphs from Naranjo and Ellsworth (2005); Method 1 uses Equation 2 with  $c = 1$  implicit, Method 2 uses Equations 3–5 with  $c$  as indicated. <sup>‡</sup>Mean% change in total generational mortality from 14 cohorts observed in Naranjo and Ellsworth (2005) using Method 2 instead of Method 1 to estimate marginal mortality from parasitism. <sup>§</sup>Difference between the rate of apparent parasitism (mean = 0.046, Naranjo & Ellsworth 2005) and marginal parasitism estimated by Method 2. <sup>§</sup>Mean% change in total generational mortality from 14 cohorts observed in Naranjo and Ellsworth (2005) using apparent mortality rather than Method 2 to estimate marginal mortality from parasitism.

mortality is high (0.99; Figure 7A, C). However, when overall mortality is lower (0.75), the inclusion of predator preference in the estimation of marginal rates of parasitism leads to larger changes in generational mortality, especially at higher levels of preference, and apparent parasitism and predation (Figure 7B, D). Changes in generational mortality were most sensitive to changes in the rate of predation, with the largest changes in generational mortality ( $\approx 14\%$ ) associated with high levels of preference (4) and apparent predation (0.50) with parasitism fixed at a moderate level (0.25; Figure 7D).

The rate of IGP can be inferred from the difference between marginal and apparent rates of parasitism. The apparent rate of parasitism from life table studies averaged 0.046 (Naranjo & Ellsworth 2005) while the associated marginal rate varied from 0.065 to 0.172 (Table I) indicating rates of IGP ranging from 0.019 to 0.126, depending on predatory species and prey contrast, and averaging 0.058 over all contrasts. Still, based on observed generational mortality and average rates of apparent parasitism and predation from Naranjo and Ellsworth (2005), overall changes in generational mortality due to IGP would be expected to be small, ranging from 0.193 to 1.278% (Table I, last column). The median rate of generational mortality from the life table studies was  $\approx 0.94$ , so these results are consistent with hypothetical analyses above that indicated low sensitivity to apparent mortality rates and predator preference with high total mortality (Figure 7A, C).

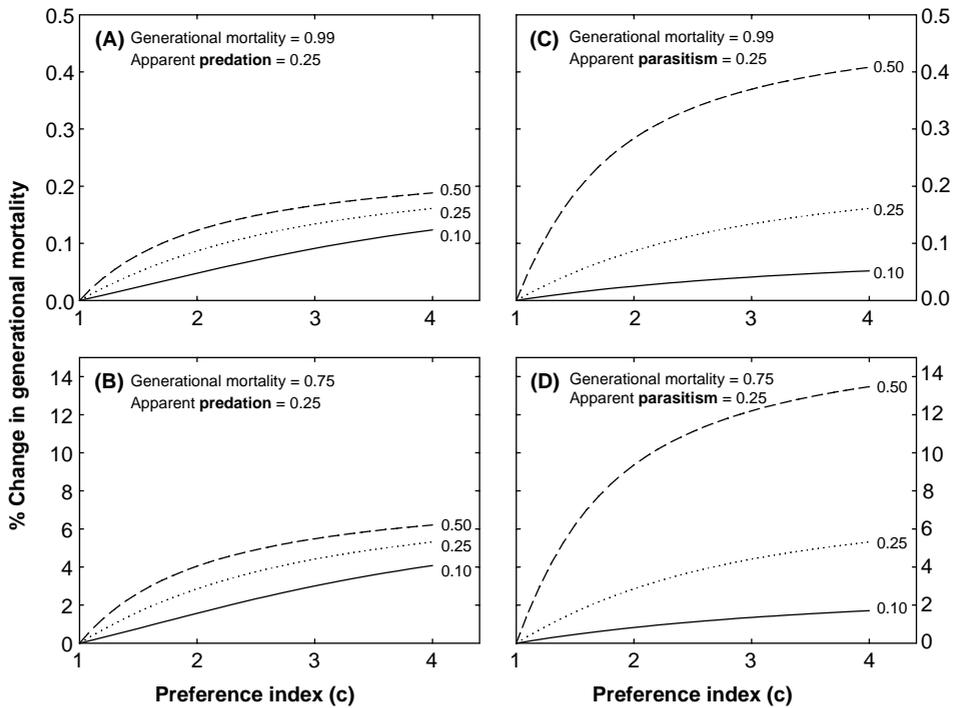


Figure 7. The influence of predator preference for parasitized prey on the estimation of total generational mortality for two nominal levels of mortality (0.75 and 0.99) and various levels of apparent parasitism and predation. The two panels on the left (A, B) present the effects of changing levels of parasitism (0.1, 0.25, 0.5) at a fixed (0.25) rate of predation; the panels on the right (C, D) present the effects of changing levels of predation (0.1, 0.25, 0.5) at a fixed (0.25) rate of parasitism. Note the  $y$ -axis scale change between upper and lower panels.

## Discussion

Intraguild predation on immature parasitoids has been demonstrated in a number of predator/parasitoid/prey systems (reviewed by Rosenheim et al. 1995; Brodeur & Rosenheim 2000) and so it is no surprise that all of the predators examined in this study readily preyed upon various stages of immature parasitoids within whitefly hosts even when given an alternative choice of non-parasitized prey. Many studies have documented that this asymmetrical IGP is either indiscriminant, with predators attacking and consuming parasitized and non-parasitized hosts in direct proportion to their abundance (e.g. Stark & Hopper 1988; Wells et al. 2001; Harvey & Eubanks 2005; McGregor & Gillespie 2005), or discriminant towards non-parasitized prey, especially as parasitoids age (Heinz et al. 1994; Hoelmer et al. 1994; Colfer & Rosenheim 2001; Al-Zyoud & Sengonca 2004; Fazal & Xiang 2004). However, when offered a choice of early fourth instar whitefly nymphs or whiteflies hosting either late larval or pupal stage parasitoids, all three predator species examined showed a strong preference for parasitized hosts. When offered a choice between late fourth instar whitefly nymphs and larval stage parasitoids *G. punctipes* and *O. insidiosus* became indiscriminant, but *H. convergens* continued to prefer parasitized prey. This general pattern for *H. convergens* was reinforced in no-choice experiments where the lowest

and highest consumption rates were for early fourth instar nymphs and pupal stage parasitoids, respectively.

Preferential predation on parasitized hosts is less common but has been observed in several systems (Tostowaryk 1971; Jones 1987; Meyhöfer & Klug 2002) and may be related to the differential distribution of parasitized and non-parasitized prey, nutritional aspects, or other behavioral factors. The behavioral shifts in *G. punctipes* and *O. insidiosus* are consistent with the hypothesis that parasitized prey are more apparent to predators searching on the leaf surface than early fourth instar nymphs. Parasitoid development causes the host to become opaque and swell slightly making it more obvious on the leaf surface compared with early fourth stage nymphs which are translucent and flat (Gelman et al. 2002). Late fourth instar nymphs also are more opaque and swollen, and thus, may be equally apparent to foraging predators as parasitized hosts. Why *H. convergens* consistently preferred parasitized hosts is unknown, but it did not appear to be associated with prey apparency. There may be a nutritional component that makes parasitized prey more acceptable, however, Roger et al. (2001) found that coccinellid larvae took longer to mature when feeding on cabbage looper eggs parasitized by *Trichogramma* compared with non-parasitized eggs. Additional study will be required to test whether nutritional aspects can explain the preference of *H. convergens* for parasitized prey.

The influence of prey distribution on the patterns of discrimination observed was not a factor in the experimental arenas and also is unlikely to play a role in the field. Distributions of whitefly nymphs on cotton plants in the field are stratified by age, with eggs and early instar nymphs found on leaves near the terminal growth and older stages found on progressively older leaves further down in the canopy (Naranjo & Flint 1994). Fourth instar nymphs and parasitized nymphs occupy the same general strata in the canopy, and it is common to see early and late fourth instar nymphs along with all stages of immature parasitoids interspersed on the same leaf. This occurs because there is some overlap of cohorts on a given leaf and because parasitoid development extends the presence of host nymphs which do not show signs of parasitism until later stages of parasitoid development (unpublished data). Thus, the free-choice arenas used here are representative of what foraging predators would encounter on individual leaves in the field.

Intraguild predation on aphelinid parasitoids attacking whiteflies has not been extensively studied. Most studies have examined small coccinellid predators (*Delphastus* and *Serangium*) and have shown that predation on young parasitoids is indiscriminant, but that because of physical factors associated with parasitoid development, older larval and pupal parasitoids are avoided by these beetles (Heinz et al. 1994; Hoelmer et al. 1994; Al-Zyoud & Sengonca 2004; Fazal & Xiang 2004). The mirid predator *Dicyphus hesperus* Knight, similar in size to *G. punctipes*, was found to be an indiscriminant IG predator of *Encarsia formosa* Gahan pupae in greenhouse whiteflies (McGregor & Gillespie 2005) and this behavior was not altered by parasitoid age (Labbe et al. 2006). No effect of parasitoid age was observed here either, because all three predators readily attacked both larval and pupal stage parasitoids. *Geocoris punctipes* and *O. insidiosus* are sucking predators, and there appears to be no physical limitation preventing them from penetrating and digesting the contents of either whitefly nymphs or parasitoids within the host cuticle. Likewise, *H. convergens* is a medium-sized coccinellid beetle whose mouthparts are capable of

penetrating and devouring whitefly nymphs as well as larval and pupal parasitoids within the host cuticle.

There have been few studies quantifying rates of predation on *B. tabaci* by individual predator species and none that have measured predation on fourth stage nymphs by any of the predators examined here. The two larger predators, *G. punctipes* and *H. convergens* averaged about 17–19 fourth stage nymphs daily at about 27°C, whether parasitized or not. The smaller *O. insidiosus* averaged about six per day. *G. punctipes* was able to consume a maximum of about 35 adult *B. tabaci* in 24 h (Cohen & Byrne 1992) and Hagler et al. (2004) showed that *H. convergens*, *G. punctipes* and *O. tristicolor* (Say) consumed about 6, 1 and 0.5 mixed-stage nymphs per hour, respectively, in observational studies. In cotton fields, fourth stage nymphs incur the highest levels of mortality of any developmental stage and most of this mortality is due to predation (Naranjo & Ellsworth 2005). In unmanaged cotton fields, densities on leaves would be equivalent or higher than those presented in experimental arenas here over extended portions of the season. Thus, the rates measured here might be useful in developing predictive models of predation for these common predator species.

Intraguild predation is generally considered to be detrimental to biological control because it interferes with the ability of natural enemies, particularly parasitoids, to exert their potential suppressive effects on pest populations (e.g. Press et al. 1974; Snyder & Ives 2001; Kaplan & Eubanks 2002). However, generalizations are difficult because there also are instances in which the addition of an IG predator may have no effect on pest suppression (e.g. Harvey & Eubanks 2005) or may even enhance overall biological control (Roland 1990; Heinz & Nelson 1996; Colfer & Rosenheim 2001). The results of laboratory studies here were extrapolated to the field using life table data collected in Arizona cotton fields (Naranjo & Ellsworth 2005) as a means of estimating the potential effect of IGP on both the measurement of parasitism and its impact in pest population suppression. At least three mortality factors (predation, dislodgement, unknown) operate in every nymphal stage of *B. tabaci*, and it is difficult or impossible to measure most of them, including parasitism, directly in the field (Naranjo & Ellsworth 2005). Instead, the accurate estimation of most mortality factors requires mathematical techniques and an understanding of competing forces to calculate marginal attack rates, which provide an estimate of a given mortality factor as if it were the only one operating on the stage in question (Elkinton et al. 1992). The marginal rate of parasitism must take into account the competing effects of predation and dislodgement. Because of the discriminate nature of IGP discovered in this system, a modified method might be needed to accurately estimate marginal rates of parasitism. However, based on known levels of apparent parasitism in the field, analyses here demonstrated that accounting for prey preference may not have a meaningful effect on the estimation of marginal parasitism. Based on three representative predators and a variety of possible two prey choices, analyses suggest that marginal parasitism changed very little, and more importantly, this change, in turn, had very minor effects on the estimation of generational mortality at representative levels of total mortality. Although this study has not exhaustively examined all potential predators and their IGP behavior relative to immature parasitoids, the low average level of apparent parasitism in Arizona cotton fields (4.6%) makes it unlikely that accounting for preference in life table analysis would be justified relative to the cost of collecting such information for all IG predators or the

resolution such adjustments would ultimately provide. However, the life table data used here was collected prior to the establishment of several species of exotic aphelinids (Goolsby et al. 2005; Naranjo, unpubl.) and these recent introductions may lead to higher rates of parasitism. In addition higher levels of apparent parasitism are typically observed in southern California (Roltsch, pers. comm.). Further sensitivity analyses suggested that at lower levels of total mortality and higher rates of either parasitism or predation, changes in estimated generational mortality may be greater, especially when predator preference for parasitized prey is high (see Figure 7). The effect was greatest when predation and preference was relatively high while parasitism remained moderate. This follows directly from the increased probability of predators obscuring parasitism in this situation leading to higher rates of marginal parasitism. Thus, there may be circumstances when predator preference for parasitized prey should be accounted for in life table analyses and this will depend on the levels and sources of mortality.

Another feature of calculating marginal parasitism is that the precise level of IGP can be estimated as the difference between apparent and marginal mortality, with the latter taking into account the competing effect of predation on parasitized nymphs. The rate of IGP was estimated to range from 0.019 to 0.126 depending on predatory species and prey contrast. Overall, the rate of IGP was relatively small (mean = 0.058 over all contrasts), and more importantly, it had only minor effects on the estimation of total generational mortality of *B. tabaci* which is a more meaningful measure of pest suppression than parasitism per se. Nonetheless, this IGP also represents additional mortality in parasitoid populations, and even though the rate was relatively low, it could have subtle negative effects on parasitoid dynamics and abundance over multiple generations. Overall, an accurate assessment of whether mortality imposed by IGP will have longer term consequences on pest and parasitoid dynamics must await more detailed and longer-term field experiments, including life tables studies on parasitoid populations, that examine effects of IGP on the population growth of parasitoids and their suppressive effects on pest populations (see Briggs & Borer 2005). The analyses here provide working hypotheses upon which future understanding can be advanced.

### Acknowledgements

I thank Bill Roltsch (California Department of Food & Agriculture), Jay Rosenheim (University of California, Davis, CA) and two anonymous reviewers for helpful comments on earlier drafts of this manuscript. I also thank Rebecca Burke, Kim Beimfohr and Gregory Owens for expert technical assistance.

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### ERRATUM

Online Publication Date: 01 January 2007

To cite this Article: (2007) 'ERRATUM', Biocontrol Science and Technology, 17:7, 771

To link to this article: DOI: 10.1080/09583150701566134

URL: <http://dx.doi.org/10.1080/09583150701566134>

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## ERRATUM

Intraguild predation on *Eretmocerus* sp. nr. *emiratus*, a parasitoid of *Bemisia tabaci*, by three generalist predators with implications for estimating the level and impact of parasitism by Steven E. Naranjo, published in 17(5/6) 2007, pp. 605–622.

Equations 1 and 4 should read as follows:

$$\alpha = \ln((n_{p0} - r_p)/n_{p0}) / [\ln((n_{p0} - r_p)/n_{p0}) + \ln((n_{w0} - r_w)/n_{w0})] \quad (1)$$

$$M_A = (b - (b^2 - 4cd_A)^{0.5}) / 2c \quad (4)$$