Chapter 15
Natural Enemies of *Bemisia tabaci*: Predators and Parasitoids

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Introduction

Arthropod parasitoids and predators are ubiquitous and operate continuously on all life stages of the whitefly, functioning as control factors in the process. The goal of biological control is to better exploit this behavior in order to more effectively manage pests and reduce insecticide use. Biological control of whiteflies and other pests has been pursued through observation and utilization of natural enemy activity (e.g., Albajes et al. 2003), through search for and introduction of natural enemies (e.g., Gould et al. 2008; Nomikou et al. 2001), or through analysis of existing agroecosystems, indicating which key factors control the pest (e.g., Albajes and Alomar 1999; Naranjo and Ellsworth 2005; Naranjo et al. Chapter 6). Implementation has resulted from habitat manipulation to favor or conserve existing species, introduction of new species, and mass rearing and release of both (Albajes et al. 2003; Gould et al. 2008; Nomikou et al. 2001; Naranjo et al. 2004b).

The choice of which natural enemy or combination to use, and whether to only conserve the existing complex or augment numbers or species is often complex. Decisions should be made only after analysis of the efficacy of present pest-enemy interactions, including specific observations and life-table analytical studies. For example, Naranjo et al. (2004a, 2009) have shown, using life table analysis, a marked influence of factors such as plant species upon effectiveness of the natural enemy complex in managing *B. tabaci*.

The driving force behind conducting biological studies on *B. tabaci* enemies is, in addition to overall scientific interest, the desire to improve pest control. This is reflected in both the organisms studied and the kinds of studies conducted. Predators that have proven to be readily exploitable for mass culture – and manipulation in greenhouse agriculture – have been used most often in mass rearing and behavior investigations following host plant and compatibility studies. Studies on parasitoids, of which only three species have been commercially employed so far, incorporate

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several additional well-known and "hopeful" species. These studies include additional basic behavioral observations disclosing why these species do not always provide adequate control. The present review deals mainly with predators currently being used for augmentative biological control of *B. tabaci* such as *Macrolophus caliginosus* Wagner, *Nesidiocoris tenuis* (Reuter) and *Amblyseius swirskii* Athias-Henriot, and the commercially utilized parasitoids *Eretmocerus mundus* Mercet, *Er. eremicus* Rose and Zolnerowich and *Encarsia formosa* Gahan. Updates are also included on more elaborate studies with several other species that could potentially serve as commercial control agents in the greenhouse and the field. Finally, indigenous predators and parasitoids are present and active in all agroecosystems, even if in low numbers. The assessment of their contribution to biological control, and their ensuing conservation will hopefully help to suppress pest populations.

We hope this review will provide practical information as well as contribute to understanding of some basic questions relating to biological control, such as the value of parasitoids vs. predators and specific vs. more generalist parasitoids. However, no universal conclusions should be drawn, because each group of organisms could be suitable for utilization under different specific conditions.

Predator Biology and Ecology

Recent efforts at identification, evaluation, and use of predators as biological control agents of *B. tabaci*, are summarized in this section as an update of the review published by Gerling et al. (2001). Table 15.1 compiles the new records of potential *B. tabaci* predators obtained since then, from two reviews covering China and the Neotropics as well as several other new publications (see references in Table 15.1). Of the more than 150 arthropod species currently described as *B. tabaci* predators, few have been studied in detail. Data on the biology and ecology of 7 newly recorded predator species – 2 Coccinelidae, 4 Heteroptera, and 1 Diptera – and 14 species already mentioned in Gerling et al. (2001) have been published from 2001 to the present, and are summarized in this section.

Coleoptera

Sixteen new coccinellid species have been reported to feed on *B. tabaci*, mostly from China and the Neotropics. However, most of the recent work has focused on two well-known whitefly predators: *Serangium parcesetosum* Sicard and *Delphastus catalinae* (Horn). In choice experiments, *S. parcesetosum* consumed very few red spider mites, thrips, aphids or leafminers when late 4th instar nymphs (= "pupae") of either *B. tabaci, Trialeurodes vaporariorum* (Westwood) and/or *Trialeurodes ricini* (Misra) were available. Among these whitefly species, *S. parcesetosum* consumed more *B. tabaci* than *T. vaporariorum* but not more than *T. ricini* (Al-Zyoud and Sengonca 2004; Al-Zyoud 2007). Most predator species – e.g., *D. catalinae*,

Table 15.1 Predators recorded for *B. tabaci* not included in Gerling et al. (2001). The predators are listed in the table with the name appearing in the original papers (except for misspellings). Vázquez (2002) lists known predators of *B. tabaci* in the Neotropical area from the primary literature. Ren et al. (2001) compiles new data of predators in China together with a review of previous literature (mostly in Chinese)

Taxa	References
Acari	
Phytoseidae	
Euseius ovalis (Evans)	Borah and Rai (1989) in Nomikou et al. (2001)
Araneae	
Araneidae	
Neoscona doenitzi (Bösenberg and Strand)	Zhang et al. (2007a)
Linyphiidae	
Erigonidium graminicolum (Sundevall)	Zhang et al. (2007a)
Thomisidae	
Misumenops celer (Hentz)	Hagler and Naranjo (2005)
Coleoptera	
Coccinellidae	
Axinoscymnus apioides Kutnetsov and Ren	Wang et al. (2006)
Axinoscymnus cardilobus (Ren and Pang)	Ren et al. (2001)
Clitostethus stenalis (Pang and Gordon)	Ren et al. (2001)
Coccidophilus sp.	Vázquez (2002)
Delphastus davidsoni Gordon	Vázquez (2002)
Harmonia axyridis (Pallas) (=*Leis axyridis*)	Zhang et al. (2007a)
Lemnia biplagiata (Swartz)	Ren et al. (2001)
Nephaspis hydra Gordon	Vázquez (2002)
Olla v-nigrum Casey	Vázquez (2002)
Phrynocaria congener (Billberg)	Ren et al. (2001)
Propylea japonica (Thunberg)	Zhang et al. (2007a)
Pullus ruficurdus Erichson	Vázquez (2002)
Scymnus hoffmanni Weise	Zhang et al. (2007a)
Serangium japonicum Chapin	Ren et al. (2001)
Serangium montazerii Fürsch	Vatansever et al. (2003)
Serangium n.np	Asiimwe et al. (2007a)
Stethorus minulatus Gordon and Chapin	Silva and Bonani (2008)
Nitidulidae	
Cybocephalus nipponicus Endrödy-Younga	Ren et al. (2001)
Diptera	
Hybotidae	
Drapetis nr. *divergens*	Butler and Henneberry (1993) in Hagler (2002)
Syrphidae	
Allograpta exotica (Wiedemann)	Vázquez (2002)
Ocyptamus mentor (Curran)	Vázquez (2002)
Toxomerus lacrymosus Bigot	Vázquez (2002)
Heteroptera	
Anthocoridae	
Orius laevigatus (Fieber)	Arnó et al. (2008)

Table 15.1 (continued)

Taxa	References
Orius majusculus (Reuter)	Arnó et al. (2008)
Orius niger Wolff	Bayhan et al. (2006)
Orius sauteri (Poppius)	Zhang et al. (2007a)
Orius similis Zheng	Ren et al. (2001)
Berytidae	
Aknysus sp.	Vázquez (2002)
Jalysus spinosus (Say)	Vázquez (2002)
Miridae	
Camptotylus reuteri Jacovlev	Jazzar and Hammad (2004)
Campylomma chinensis Schuh	Ren et al. (2001)
Cyrtopeltis notatus (Distant)	Vázquez (2002)
Pseudatomoscelis seriatus (Reuter)	Hagler and Naranjo (2005)
Spanagonicus albofasciatus (Reuter)	Hagler and Naranjo (2005)
Reduviidae	
Zelus renardii Kolenati	Hagler and Naranjo (1994)
Hymenoptera	
Vespidae	
Polistes panamensis Holmgren	Vázquez (2002)
Neuroptera	
Chrysopidae	
Ancylopteryx octopunctata Fabricius	Ren et al. (2001)
Ceraeochrysa claveri (Navás)	Vázquez (2002)
Chrysocerca formosana (Okamoto)	Ren et al. (2001)
Chrysopa pallens (Rambur)	Zhang et al. (2007a)
Chrysoperla nipponensis (=*Chrysopa sinica*)	Lin et al. (2006)
Chrysoperla defreitasi Brooks	Vázquez (2002)
Chrysopodes collaris (Schneider)	Vázquez (2002)

Nephaspis oculatus (Blatchley) and *Axinoscymnus cardilobus* (Ren and Pang) – consumed immature stages, especially eggs (Liu and Stansly 1999; Ren et al. 2002; Huang et al. 2006; Legaspi et al. 2006). *Hippodamia convergens* Guérin-Méneville fed preferentially on whitefly eggs and adults over nymphs (Hagler et al. 2004) while *S. parcesetosum* fed more on late instar nymphs compared to eggs of *B. tabaci* (Al-Zyoud and Sengonca 2004). In contrast, *Propylea japonica* (Thunberg) successfully completed its development when feeding on *B. tabaci* nymphs, but not on whitefly eggs (Zhang et al. 2007b).

Coccinellids can perform well within greenhouse temperature ranges. *Serangium parcesetosum* completed nymphal development both at 18° and 30°C (Sengonca et al. 2004); *N. oculatus* completed development between 20–33°C (Ren et al. 2002); *D. catalinae* between 22–30°C (Legaspi et al. 2008); and *A. cardilobus* between 14–32°C (Huang et al. 2008). The estimated lower developmental threshold for the latter two species was 9–10°C. In contrast, longevity of *D. catalinae* when food was available was reduced from 174 days at 25°C to 16 days at either 5° or 35°C (Simmons and Legaspi 2004, 2007). No eggs hatched when maintained at 5°C, while 48% hatched at 15°C, although none of the resulting larvae reached the pupal stage. In a follow-up study, Simmons and Legaspi (2004) found that adults and pupae of *D. catalinae* survived 24 h at 5° and 35°C, but not temperatures below zero; egg-hatch was inversely related to duration of exposure to 5°C between 24 and 72 h and, in a field study, a few individuals were still able to survive during winter when temperatures dropped to –8°C. Moreover, a significant linear relationship of prey consumption enhancement with temperatures between 14 and 35°C could be demonstrated, although predation was similar at most of the temperatures. Simmons et al. (2008) determined a negative effect of low relative humidity on oviposition, egg hatching, and immature survival.

Heteroptera

Five new Anthocoridae, 2 Berytidae, 6 Miridae, and 1 Reduviidae species have been recorded as *B. tabaci* predators. Additionally, according to Perdikis et al. (2003) and Martínez-Cascales et al. (2006), most of the literature on *M. caliginosus* as a *B. tabaci* predator probably refers to *M. pygmaeus* (Rambur). However, we used the original name found in the references. Predatory Heteroptera colonize agroecosystems as diverse as greenhouses in the Mediterranean and cotton fields in the USA (Albajes and Alomar 1999; Naranjo 2001).

Polyphagy, which is well documented in Heteroptera, was confirmed in recent studies for *N. tenuis*. In laboratory experiments, it was able to complete nymphal development preying on a variety of arthropods including *B. tabaci*, *Ephestia kuehniella* Zeller, *Frankliniella occidentalis* (Pergande), or *Tetranychus urticae* Kock (Urbaneja et al. 2003).

Prey preference experiments have been conducted for the predators *M. caliginosus*, *Orius laevigatus* (Fieber), and *O. majusculus* (Reuter), which are often released in greenhouse crops (van Lenteren and Martin 1999; Castañé et al. 1999). *Macrolophus caliginosus* utilized *T. vaporariorum* rather than *B. tabaci* when similar stages of both whitefly species were offered (Bonato et al. 2006).

Even though the different species of *Orius* are considered to be mainly predators of thrips, field and laboratory studies show that they also prey readily and successfully on whiteflies. Both *O. laevigatus* and *O. majusculus* consumed all stages of *B. tabaci* and completed preimaginal development with high survival when fed exclusively on the whitefly in the laboratory. Both species preferred *F. occidentalis* over *B. tabaci*, but *O. majusculus* consumed more whiteflies than *O. laevigatus* in choice experiments (Arnó et al. 2008). Hagler and Naranjo (2005), who used immunological methods, found that more than 50% of the collected *Orius tristicolor* (White) individuals on cotton in Arizona had consumed eggs or adult females of *B. tabaci*. Likewise, Zhang et al. (2007a), who used molecular markers, determined that 67% of adults of *Orius sauteri* (Poppius) collected on cotton in China had consumed *B. tabaci*.

In laboratory assays, *M. caliginosus* fed preferably on older *B. tabaci* nymphs (Bonato et al. 2006), and *Lygus hesperus* Knight, an omnivore best known as a key pest of cotton and other crops, was observed feeding on whitefly nymphs more frequently than on eggs and adults combined (Hagler et al. 2004). In contrast, those same authors determined that adults of *O. tristicolor* and *Geocoris punctipes* (Say) preyed on *B. tabaci* adults more frequently than on eggs and nymphs combined.

Neuroptera

Seven new species of Neuroptera have been reported to prey on *B. tabaci*; some are considered important whitefly predators, especially in the neotropics (Vázquez 2002). Syed et al. (2005) determined that *B. tabaci* was better prey for *Chrysoperla carnea* (Stephens) than the cotton leafhopper *Amrasca devastans* (Distant), an important pest of cotton crops in Pakistan. Eggs and nymphs of *B. tabaci* were suitable prey for the development of *C. externa* (Hagen) and *Ceraeochrysa cincta* (Schneider) (Auad et al. 2001), although oviposition, fecundity and longevity of adults, egg and larval development, and egg viability were all influenced by the host plant (Silva et al. 2004a, b; Auad et al. 2005).

Diptera

Four new species of Diptera have been mentioned as preying on *B. tabaci*. These species include *Drapetis* nr. *divergens* Loew (Empididae), which have been observed in Arizona cotton fields feeding on adult whiteflies, whereas alternative prey and the habitat of the egg, larval and pupal stages of this species have not yet been described (Hagler 2002; Hagler and Naranjo 2005). More is known about *Coenosia attenuata* Stein (Muscidae) that is present in European vegetable and ornamental greenhouses (Kühne 1998; Rodríguez-Rodríguez et al. 1994; Gilioli et al. 2005; Téllez and Tapia 2005; Arnó et al. 2006a). The adults catch whiteflies, fungus gnats, leafminers, and other insects on the wing while larvae feed on soil organisms (Kühne 2000). Hagler (2002) reported a consumption rate of 1.9 *B. tabaci* adults per hour for *D.* nr. *divergens.* For *C. attenuata* adults, consumption depends on the prey species, with a maximum of up to 7 adults of *Drosophila melanogaster* Meigen in 12 h, or 7 adults of *Bradysia paupera* Tuomikoski per day (Kühne 2000; Gilioli et al. 2005). Larval and pupal development lasted between 22 and 30 days at 25°C (Moreschi and Süss 1998; Moreschi and Colombo 1999; Kühne 2000). Gilioli et al. (2005) demonstrated that *C. attenuata* adults are active over a range of temperatures between 12 and 36°C.

Acarina

Many phytoseiid mite species are polyphagous; with some known to effectively reduce *B. tabaci* populations on cotton and vegetable crops (Gerling et al. 2001). Developmental periods and oviposition rates of *Euseius scutalis* (Athias-Henriot) and *A. swirskii* were most favorable when they were feeding on *B. tabaci* compared to other prey (Nomikou et al. 2001). They fed mainly on whitefly eggs and crawlers, but rarely on later immature stages. Feeding on pollen and honeydew enhanced survival, development, and reproduction (Nomikou et al. 2002, 2003a). Both mite species were able to suppress *B. tabaci* populations on cucumber (Nomikou et al. 2001, 2002). Polyphagy and the ability to feed on alternative foods were found to promote persistence in the crop even if *B. tabaci* was scarce, enabling the inoculative release of mites before pest colonization (Nomikou et al. 2002, 2004; Messelink et al. 2006).

Nomikou et al. (2005) showed that naïve adults with no whitefly experience discriminated between infested and clean cucumber plants, and that they were more aggregated on whitefly-infested plants in comparison to uninfested ones. However, adult female *B. tabaci,* previously exposed to *A. swirskii*, avoided cucumber leaves inhabited by mites while accepting uninhabited leaves (Nomikou et al. 2003b). In addition, Meng et al. (2006) showed that *B. tabaci* adults avoided plants with mites feeding on whitefly, but not plants with mites feeding on pollen, even if they had previously fed on *B. tabaci*. Avoidance was less if the mites feeding on whitefly had previously fed on pollen, compared to mites that had always fed only on whitefly.

Parasitoid Biology and Ecology

This section summarizes recent efforts in identifying and studying parasitoids as biological control agents of *B. tabaci* since Gerling et al. (2001). Earlier data that had not been previously reviewed is also included.

Although individual parasitoid species might not act as key mortality factors, their effect can have an additive, decisive influence on whitefly-crop relationships. Described parasitoid species attacking *B. tabaci* include 46 *Encarsia*, 21 *Eretmocerus*, 3 *Amitus*, 1 *Neochrysocharis*, and 1 hyperparasitoid (*Signiphora*). An update to the former information concerning *Encarsia* and *Eretmocerus* is given in Tables 15.2 and 15.3. Recent work has added to the information on population dynamics, and the life history and utilization of some species, but most remain unstudied. Their use will require additional studies due to inherent differences in species bionomics, environmental conditions and cropping systems.

New records of parasitism incidence, rates of parasitism, new species, and new parasitoid locations appear continuously, primarily for the genera *Encarsia* (Evans 2007; Heraty et al. 2008) and *Eretmocerus* (Zolnerowich and Rose 2008) or both (Hernández-Suárez et al. 2003). Host ranges span from monophagy or narrow oligophagy as in *En. polaszeki* Evans to polyphagy as in *En. inaron* (Walker). Their use in biological control does not usually consider the degree of polyphagy, although Kirk et al. (2000) attributed host specificity to the decision to release the Spanish biotype of *Er. mundus* in Texas.

Recent geographical records include distribution of *En. inaron* in South America (Oliveira et al. 2003); *En. sophia* (Girault and Dodd) and *Er. mundus* in Uganda (Otim et al. 2005); two strains of *En. inaron* in Egypt (Abd-Rabou 2006); *En. desantisi* Viggiani, *En. nigricephala* Dozier, *En. pergandiella* Howard, and *Amitus* sp. in

Table 15.2 *Encarsia* species reported as parasitizing whtieflies of the genus *Bemisia* not included in Gerling et al. (2001)

Species	References	Remarks
accenta Schmidt and Naumann	Evans (2007)	*Bemisia* sp.
adusta Schmidt and Naumann	Evans (2007)	
aferi Schmidt and Polaszek	Heraty et al. (2007)	*Bemisia afer*
aleurothrixi Evans and Polaszek	Evans (2007)	
asterobemisiae Viggiani and Mazzone	Evans (2007)	
davidi Viggiani and Mazzone	Evans (2007)	
estrellae Manzari and Polaszek	Evans (2007)	
galilea Rivnay	Evans (2007)	*Bemisia afer*
insignis Schmidt and Polaszek	Heraty et al. (2007)	*Bemisia afer* group
levadicola Polaszek and Hernández	Evans (2007)	*Bemisia afer*
macoensis Abd-Rabou and Ghahari	Heraty et al. (2007)	
silvestrii Viggiani and Mazzone	Evans (2007)	*Bemisia* sp.
smithi (Silvestri)	Evans (2007)	
synaptocera Huang and Polaszek	Evans (2007)	
Encarsia sp.	Qiu et al. (2004a)	4 apparently new species

Nicaragua (Numes et al. 2006). Studies with *Encarsia* in Brazil revealed for the first time *En. aleurothrixi* Evans and Polaszek parasitizing *B. tabaci* (Oliveira et al. 2003).

Influences of plant species, location, seasons, and climate on parasitism rates and on the species complex of *B. tabaci* parasitoids in field crops were also demonstrated (e.g., López-Ávila et al. 2001; Ryckewaert and Alauzet 2002; Simmons et al. 2002; Vázquez 2002; Otoidobiga et al. 2004; Naranjo et al. 2004a; Sharma et al. 2004; Trujillo et al. 2004; Leite et al. 2005; Naranjo and Ellsworth 2005; Numes et al. 2006; Otim et al. 2006; Karut and Naranjo 2009).

Climatic differences influenced parasitism of *B. tabaci* on cassava in Uganda by *En. sophia* and *Er. mundus*, with the proportions of these two species varying at three different collecting sites (Otim et al. 2005). Possible influence on the existing parasitoid complex of *B. tabaci* by *En. sophia* was studied at three locations in the

Table 15.3 *Eretmocerus* species reported as parasitizing species of the genus *Bemisia* not included in Gerling et al. (2001)

Species	References	Remarks
aegypticus Evans and Abd-Rabou	Abd Rabou (2006)	
californicus Howard	Zolnerowich and Rose (2008)	
corni Haldeman (Maskell)	Zolnerowich and Rose (2008)	
diversiciliatus Silvestri	Zolnerowich and Rose (2008)	
haldemani Howard	Zolnerowich and Rose (2008)	
nikolskajae Myartseva	Abd Rabou (2006)	New association
roseni Gerling	Zolnerowich and Rose (2008)	"Non-*tabaci*" *Bemisia*
rui Zolnerowich and Rose	Zolnerowich and Rose (2008)	Monophagous
serius Silvestri	Zolnerowich and Rose (2008)	
Eretmocerus sp.	Qiu et al. (2004a)	Probably 2 new species

Caribbean Basin where *En. sophia* was first recorded in Guadeloupe in 1997 (Pavis et al. 2003).

Influence of the plant on the success of the parasitoid measured both as parasitoid immature survivorship and adult fitness is a continuing theme (Inbar and Gerling 2008). Reese (1994) estimated hatching rates of 80% on cabbage, but only 42% on tobacco for *En. sophia* (as *transvena*). Demographic parameters estimated for *Er. mundus* on pepper and tomato were similar (171.1 eggs/female) (Urbaneja et al. 2007), but fecundity on cotton was estimated at only 81.7 eggs/female at 25°C (Ghahari et al. 2005). Different experimental conditions, and possibly host and parasitoid biotypes, might explain these divergent results. Gerling et al. (2006) showed that size of emerging *Er. mundus* was not correlated with size of the whitefly host. Since parasitoid size is generally a fitness parameter, this result suggested that other features of the host plant species might be influential in determining parasitoid fitness.

Many of the life-history studies on longevity, fecundity, sex ratio, immature mortality and development involving different species have been conducted under different conditions. Although this renders them invalid for comparison among species and strains, resulting numerical values provide a general idea of the parasitoids' physiological capabilities and potential of performance under the specified conditions. Moreover, the IPM practitioner is able to find varied and useful data to aid in making decisions on his specific project. For example, although the rates of increase (r_m) of *B. tabaci* in 19 different cases at 25–26°C were 0.130 ± 0.01 (average ± SEM), those of the parasitoids varied under the same temperatures, but on different host plants as follows: *Encarsia lutea* (Masi) ($n=1$) 0.178, *En. bimaculata* (Heraty and Polaszek 2000) 0.163 ± 0.0165 ($n=5$) and *Er. mundus* 0.20 ± 0.016 ($n=5$). In order to facilitate these types of comparisons, life history parameters from the literature for *A. bennetti*, 6 species of *Encarsia* and 6 of *Eretmocerus* are summarized in Tables 15.4 and 15.5 and in the following text.

Encarsia

Encarsia females oviposit in any of the four whitefly nymphal instars but develop mainly in the fourth (e.g., *En. formosa*; Gelman et al. 2001) from which they emerge as adults. The first instar host nymph is the least suitable, resulting in highest parasitoid mortality and longest immature development. The third and early fourth instars are usually the most suitable for development (Gerling 1990). All *Encarsia* species – with the exception of *En. inaron* and the uniparental species – are autoparasitic, with males developing as parasitoids of other parasitoid immatures within the whitefly or occasionally other insects (Hunter and Woolley 2001). Four species attacking *B. tabaci* have been studied in recent years.

Encarsia formosa

This uniparental species has been studied extensively around the world as the most frequently used parasitoid against *T. vaporariorum* under greenhouse conditions

Table 15.4 Representative values of life history parameters measured for *Amitus bennetti* (*Ab*) and six most studied *Encarsia* species attacking *B. tabaci* at a temperature range of 25–30°C; *por.=porteri, per.=pergandiella*

	formosa strain		*bimaculata*					*sophia*		
Parameter	B	D	Mal	Fem	*lutea*	*per.*	*por.*	Mal	Fem	*Ab.*
Development (d)	14[a,m]	15[a]	12.7[b,c]	14[b,c]	11.9[d]	11.6[e]	18.9[f]	11[b,g]	12[h,b,g]	21.4[i]
Immature survival	0.875[j]							42–94%[h]		
Longevity (days)	50[a,m]	23[a]	5.4–8.4[c]		10.4[d]			11.3[**,g]		6.3[i]
Gen. time (days)	13[j]									
Day degrees (°C)			181.4[c]							
Fecundity (eggs/fem.)	141[j]		24.3[c]		32[d]			48.6[h,k]		78.8[i]
Sex ratio (f/m)								4.1–9.2[h,k,l]		
Day degrees			181.4 ± 2.4[c]							
Developmental. threshold (°C)			11.6 ± 0.31[c]							
Density dependence								At low density[k]		
Host killing/female								33.12[*,k]		
R_o 25°C			18.21[c]					15.5[**,k]		

*in addition to 48.6 eggs laid, during first 10 days of life
**outside temperature
[a] Qiu et al. (2004b)
[b] Antony et al. (2004)
[c] Qiu et al. (2006)
[d] Talebi et al. (2002)
[e] Liu and Stansly (1996)
[f] Viscarret and López (2004)
[g] Otim et al. (2008)
[h] Kapadia and Puri (1990)
[i] Joyce et al. (1999)
[j] Xu et al. (2003)
[k] Oster (1995)
[l] Reese (1994)
[m] Zhang et al. (2004)

(van Lenteren et al. 1996). Studies relating to *B. tabaci* became prevalent following outbreaks in European glasshouses (Drost et al. 1996) and include detailed examinations of its possible use in greenhouses. Although several strains of *En. formosa* have been found, their use for control of *B. tabaci* has yielded mixed results (Hoddle et al. 1997 and references therein).

Encarsia bimaculata

This is a recently described (Heraty and Polaszek 2000) dominant parasitoid of *B. tabaci* in India and China. Life history was investigated by Antony et al. (2004) and temperature responses were examined in detail by Qiu et al. (2006).

Table 15.5 Representative values of life history parameters measured for the six most studied *Eretmocerus* attacking *B. tabaci* at a temperature range of 25–30°C; *melanos=melanoscutum, queens=queenslandensis, nr. furu=nr. furuhashii, APF = Australian partenogenetic form*

	mundus					
Parameter	Biparental	APF	*eremicus* [a]	*melanos*	*queens*	*nr. furu* [a]
Development (days)	14.1[b–f]		23.1[g–j]	17[k]		15.9–17.1[l]
Longevity (days)	10.1[m,c–e]		22.7[g–i]	13.2[k]		6.5–8.1[l]
Fecundity (eggs/fem.)	171.1[m,d,e]	109.3[n]	28[g,j]	138[k]	106.4[n]	35.4–46.4[l]
Imm. Surv. (%)	75.5, 79.0[q]					57.4–73.2[l]
Sex ratio (f/m)	1.7[o,f]		1[p]			1.07–1.41[l]
R_o	51.0, 63.8[q]		9.7–47.0[j]			14.7–20.9[l]
r_m	0.219, 0.216[q]		0.115–0.212[j]			0.133–0.157[l]
Density dependence	At low density[o]					
Host killing/female	103.6[o]					

[a] Ranges obtained with different plant species under equal conditions
[b] Urbaneja and Stansly (2004)
[c] Talebi et al. (2002)
[d] Ghahari et al. (2005)
[e] Headrick et al. (1996)
[f] Kapadia and Puri (1990)
[g] Headrick et al. (1999)
[h] Greenberg et al. (2000)
[i] Qiu et al. (2004b)
[j] Powell and Bellows (1992)
[k] Liu (2007)
[l] Qiu et al. (2005)
[m] Urbaneja et al. (2007)
[n] DeBarro et al. (2000)
[o] Fried (1997)
[p] Hunter and Kelly (1998)
[q] Urbaneja et al. (2007). First value tomato, second value sweet pepper

Encarsia porteri (Mercet)

This South American species parasitizes *B. tabaci* on cotton, soybean and alfalfa in Argentina (Viscarret and López 2004), and has only been studied there.

Encarsia sophia (= *En. transvena* Timberlake)

This widespread species consists of at least two distinct populations or cryptic species (Giorgini and Baldanza 2004). Gould et al. (2008) reported the introduction of *En. sophia* from several countries as well as their release in the USA. Different performance levels against *B. tabaci* were found to be dependent on the geographic origin. It was considered ineffective in south Texas (Goolsby et al. 2005), while a strain from a desert region of Pakistan established effectively in the Imperial Valley and Arizona (Naranjo 2008; Roltsch et al. 2008). Studies on bionomics include published works by Oster (1995), Otim et al. (2008) and Reese (1994). These studies deal mainly with parasitoid behavior in relation to plant characteristics, density dependence, and sex ratios, and are discussed in the respective sections.

Other *Encarsia* species

Other species in the genus have been studied to a lesser degree. Albergaria et al. (2003) used life tables to show that an undetermined species of *Encarsia* in South America was the main mortality factor of the 4th instar whitfely. Rodríguez-Rodríguez et al. (1994) included *En. lutea* in their studies of parasitoids in greenhouse vegetable crops, while Liu and Stansly (1996) studied the bionomics of *En. pergandiella*.

Eretmocerus

All known *Eretmocerus* species oviposit under any of the four whitefly nymphal instars, but not under the pharate adults. The 1st instar larva penetrates into the host from underneath during the early 4th instar nymph (Gelman et al. 2005a). Second and 3rd instar nymphs are preferred for oviposition, and development is longer when the 1st instar nymph is attacked (Gerling 1966; Ghahari et al. 2005; Urbaneja and Stansly 2004). No differences were found in survivorship (85%) or offspring sex ratios (39.8%) for *Er. mundus* among progeny that developed from eggs laid under the different instars (Urbaneja and Stansly 2004). Unlike *Encarsia*, *Eretmocerus* are not autoparasitic. Most are biparental with a sex ratio that approximates 50%, while a few are uniparental, a condition that, at least sometimes is associated with infection by *Wolbachia*, e.g., *Er. mundus* (DeBarro et al. 2000).

Taxonomic identification of *Eretmocerus* species is difficult, resulting in probable misidentification and misrepresentations of host-parasitoid relationships (Zolnerowich and Rose 2008). Moreover, these authors indicate possible interbreeding of closely allied species introduced into the USA. The following species that attack *B. tabaci* have been studied and/or used in recent years.

Eretmocerus mundus

This species, in its biparental form, occurs widely as an indigenous species in the Mediterranean basin (Urbaneja et al. 2007), Uganda (Otim et al. 2005), Ethiopia and Zimbabwe (Gerling, personal observations), and Thailand (Kirk et al. 2000). In addition, an endemic "Australian parthenogenetic form" (APF) was reported by DeBarro et al. (2000). This suggests existence of extensive genetic variation, and multiple forms or strains in diverse geographical locations. *Er. mundus* was introduced into the USA (Gould et al. 2008) for *B. tabaci* control where it has become a dominant component of the *B. tabaci* parasitoid fauna along with other introduced *Eretmocerus* species (see below, Gould et al. 2008). Although its reported host range includes 12 different whitefly species (Zolnerowich and Rose 2008), attempts to rear it on *T. vaporariorum* have usually failed.

Eretmocerus eremicus (= *Er.* nr. *californicus*)

This species originated and is prevalent in the southwestern USA. Both it and *Er. mundus* were grouped in laboratory studies as having high reproductive rates over a short period compared to *En. formosa* which reproduced at a lower rate but over a more prolonged period (Qiu et al. 2004b). It is widely used to control *B. tabaci* and *T. vaporariorum* in greenhouses exploiting the fact that it parasitizes both whitefly species (Greenberg et al. 2000; Gerling et al. 2001). It was introduced into Spanish and other European greenhouses for control of the two whitefly species, although *Er. mundus* with its natural prevalence outdoors in Spain gave better results when only *B. tabaci* was present (Stansly et al. 2004).

Eretmocerus queenslandensis Naumann and Schmidt

This endemic Australian species was compared by DeBarro et al. (2000) with *Encarsia* spp. for efficiency on a number of host plants. Although the incidence of parasitism on *B. tabaci* by *Er. queenslandensis* was generally highest, it was outcompeted in the field by the uniparental (APF) *Er. mundus*.

Eretmocerus sp. nr. *furuhashii*

This species was studied by Qiu et al. (2004a) who showed that it accounted for 82% of total parasitism in China. This study also explored its biology, including development, survivorship, and reproduction on glabrous and non-glabrous host plants.

Eretmocerus emiratus Zolnerowich and Rose (Ethiopia)

Eretmocerus emiratus together with three additional species, *Er. melanoscutus* Zolnerowich and Rose, *Er. hayati* Zolnerowich and Rose, and *Er.* sp. nr. *emiratus* were introduced into the USA for biological control of *B. tabaci* (Zolnerowich and Rose 2008). All became established, with *Er. emiratus* from United Arab Emerits and *Er.* sp. nr. *emiratus* from Ethiopia becoming dominant in the desert regions of California and Arizona while *Er. hayati* from Pakistan dominated in south Texas (Gould et al. 2008) and surprisingly *Er. sp. nr. emiratus* from Sudan in Florida (P. Stansly, personal comm.).

Other *Eretmocerus* sp.

McCutcheon and Simmons (2001) reported studies on an undescribed species in the USA with rates of parasitism on *B. tabaci* ranging from 0 to 29% and an optimum temperature range of 25–35°C.

Behavior

Dispersal

When *Er. mundus* and *En. sophia* were released in cages with two whitefly-infested leaves, both remained searching for 24 h on the first found leaf ignoring the alternative leaf (Fried 1997; Oster 1995, respectively). Female *Er. eremicus* responded more readily to plant cues in flight cages than males. Females also flew longer than males and unmated females longer than mated females (Blackmer and Cross 2001; Bellamy and Byrne 2001). Both sexes sustained flight in excess of 60 min. Males dispersed in a manner consistent with a simple diffusion model while females engaged in wind-directed flight soon after leaving the release sites. The differential flight responses between sexes could relate to the females' drive to locate hosts for oviposition while the males must locate mates (Blackmer and Cross 2001).

Movement of feral populations of *Er. eremicus* and *Encarsia* spp. from overwintering *B. tabaci*-infested refuges in the desert agricultural region of southeastern California was examined by Pickett et al. (2004) using a rubidium chloride marking technique. They found that 15–63% of *Er. eremicus* caught in adjacent cotton and cantaloupe originated from expressly planted refuges. Between 40 and 75% of the aphelinids in the refuges were *Encarsia* spp., but 98% of the marked and captured parasitoids in the adjacent cotton and cantaloupe were *Eretmocerus* spp., perhaps indicating superior dispersal capability for the latter.

Functional Responses and Handling Times

Eretmocerus mundus showed positive functional responses – i.e., an increase in the percentage of hosts attacked per rising host density – on leaves with up to 35 hosts (Shimron 1991; Freid 1997). *Encarsia sophia* likewise showed a similar response within the range of 7–47 hosts/leaf, but not over the wider range of 7–365 hosts/leaf (Oster 1995). In both cases, parasitoid clutch size was used to explain these responses. Three species – *En. lutea*, *En. pergandiella*, and *Er. mundus* – fit the Holling Type II model when attacking nymphs of *B. tabaci* (Greenberg et al. 2001; Talebi et al. 2002). Temperature affected handling times, which were in the rank order: *En. pergandiella* > *Er. mundus* > *En. lutea*. Talebi et al. (2002) considered *En. lutea* more effective in controlling *B. tabaci* than *Er. mundus* because it had a relatively more favorable searching efficiency coefficient (1.825 at 25°C), as well as a favorable handling time coefficient (0.108 at 25°C).

Influence of Host Volatiles and Chemical Cues on Behaviour

Arrestment in response to host-emitted chemicals was host-density dependent for *Er. eremicus*, but not for *En. luteola* Howard (Shimron et al. 1992). Mandour et al. (2003) showed that females *En. bimaculata* spent most time searching in patches treated with water extracts of *B. tabaci* adults, nymphs, or exuviae followed by searching in patches treated with other extractants and finally untreated patches exhibiting both orthokinetic (random) and klinotaxic (directed) responses. In contrast, Siqueira and Farias (2003) found no response of naïve female *En. formosa* to volatiles from *B. tabaci* and tomato using a 4-port olfactometer.

Foraging on the Leaf

Van Lenteren et al. (1987) showed the significance of parasitoid behavior studies in explaining performance. Ardeh et al. (2005) observed that oviposition of *Er. mundus* and *Er. eremicus* accounted for the longest duration of all host-handling behaviors, and was greater for 3rd instar hosts than younger hosts. They showed that females accepted the first three nymphal stages for either egg laying or host feeding, in agreement with Akiva (2008) among others. Gelman et al. (2005b) showed that *Er. mundus* also accepted 4th instar whiteflies, but only at their early stage. Mendelbaum (2004) compared egg load and foraging of recently emerged females after 4 and 8 h of exposure to hosts. Females tended to switch more from oviposition to other activities at 8 h than at 4 h, and were also most active during morning hours irrespective of their egg load. She concluded that egg load, rather than experience, influenced oviposition rate changes with time. Fried (1997), studied behaviors over longer durations and showed that although oviposition of *Er. mundus* decreased with age (1–4 days), behavioral sequences did not change. Oster (1995) found that cotton leaf pubescence hampered *En. sophia* efficiency, and that behavior changed significantly with age. Young (1-day-old) females spent the entire observation hour on the leaf searching and parasitizing hosts, while 4-day-old females stung but never parasitized hosts during the second half hour of observation. Otim et al. (2008) found that minor differences in leaf pubescence did not influence parasitization by either *Er. mundus* or *En. sophia* on cassava.

Fewer studies have been conducted on other *B. tabaci* parasitoids. Responses of *En. luteola* did not depend on honeydew concentration (Shimron 1991). Foraging activity by *En. pergandiella* varied during the day and by leaf surface. Foraging activity peaked around mid-day; moreover, most adults (80%) searched on the abaxial leaf surface during that time (Simmons and McCutcheon 2001). Even though parasitoid abundance varied among 7 diverse crops, daily foraging activity was similar on the crops (Simmons et al. 2002).

Ovipositional Marking

Fried (1997) found that leg rubbing among naïve *Er. mundus* was performed on 43 (71%) of the 60 whitefly nymphs attacked. It was followed by whitefly emergence, death, or parasitoid emergence in 9, 23, and 67% of the 43 whitefly, respectively. Experienced females rubbed legs following all host encounters. The putative marking substance may be a C31 and/or C33 dimethylalkane which are major lipid components of hexane extracts from *Er. mundus* females (Buckner and Jones 2005). These compounds were detected in nymphs recently exposed to parasitoids, but not in control nymphs or in parasitized nymphs 10 d after exposure, indicating that the dimethylalkanes were probably transferred onto nymphal cuticles by the ovipositing *Er. mundus* females.

Host Feeding and Egg Production

Honeydew feeding can result in increased egg production even though the resulting eggs tend to be the lower quality hydropic (moisture absorbing) type (Burger 2002). Host feeding occurs in both *Encarsia* and *Eretmocerus* species and always causes the death of the host (Burger et al. 2005). *Encarsia* sting the host through the integument, while *Eretmocerus* penetrate the host through the vasiform oriface. This distinction correlates with the sharp-tipped ovipositor in *Encarsia* adapted to host piercing for oviposition vs. the blunt-ended *Eretmocerus* ovipositor used to slide the egg under the venter of the host (Gerling et al. 1998). Females of *En. formosa* and *Er. mundus* emerge with ready-to-lay eggs and are able to oviposit as soon as they emerge, but are clearly synovigenic. Given an average of 19.18 ± 0.6 eggs at emergence (Akiva 2008) and a lifetime egg production of 111.25 ± 27.81 eggs/female (Fried 1997), *Er. mundus* has an ovigenic index (OI) of 0.17 [OI= the proportion of the female's egg load at emergence to lifetime oviposition (Jervis et al. 2001)] as compared to 0.1 for *En. formosa* (Jervis et al. 2001). Akiva (2008) also showed that *Er. mundus* females continue to produce eggs and start to host-feed on their first post-emergence day, when their ovaries are still loaded with eggs, probably preparing nutrients for future egg development.

Estimated ratios of host feeding to oviposition are generally higher for *Encarsia* species: 20% for *En. formosa* (20%) vs. 7–9% in *Er. mundus* (van Lenteren et al. 1996; Urbaneja et al. 2007). Zang and Liu (2007) found that *En. sophia* exhibited superior host-feeding capacity ($\approx$ 3-fold) compared to *En. formosa* and *Er. melanoscutus.*

Natural Enemy Interaction

As with all types of organisms, interactions among and within natural enemy groups can run the gamut from mutually beneficial to mutually injurious. Internecine interactions among intraguild predators or parasitoids could conceivably reduce biotic mortality of target pests and thus the effectiveness of biological control. One objective of the biological control practitioner is to manage the agroecosystem in a way that minimizes such negative interactions. Therefore, understanding interrelationships among natural enemies is important for optimizing the effectiveness of biological control.

Intraguild Predation

The ladybeetle *S. parcesetosum* fed preferentially on unparasitized *B. tabaci* nymphs over nymphs parasitized by *En. formosa* 5 days earlier (Al-Zyoud and Sengonca 2004) or by *Er. mundus* 7 days after parasitoid oviposition (Al-Zyoud 2007).

Similarly, *S. japonicum* Chapin was capable of discriminating between whitefly nymphs containing advanced stages of parasitoids vs. unparasitized nymphs. However, no discrimination was observed against nymphs under which *Eretmocerus* sp. had oviposited 5 days previously. Consumption of parasitized nymphs subsequently decreased with parasitoid age (Sahar and Ren 2004). In choice experiments, adults and larvae of *D. catalinae* fed with equal frequency on nymphs parasitized by eggs or larvae of *En. sophia,* or unparasitized nymphs. However, parasitized hosts were rejected once they contained *En. sophia* pupae. Cage experiments showed a negative effect of this predator on the parasitoid populations and, consequently, the combined use of both natural enemies was not recommended (Zang and Liu 2007). Even worse, Naranjo (2007) showed that *H. convergens* was a discriminate predator of *Eretmocerus* immatures, preferring parasitized nymphs. Interactions among different predator species were observed by Al-Zyoud et al. (2005a). *Serengium parcesetosum* laid eggs in more protected portions of the leaf in the presence of *C. carnea*.

Naranjo (2007) examined predation of *G. punctipes* and *Orius insidiosus* (Say) on 4th instar *B. tabaci* nymphs, as well as nymphs parasitized by *Er.* sp. nr. *emiratus.* He found a significant preference for feeding on early 4th instar nymphs containing larval and pupal parasitoids, compared to unparasitized nymphs at that stage but not older 4th instars.

The predacious dipterans *C. attenuata* were compatible with *En. formosa* and the leaf miner parasitoid *Dacnusa sibirica* Telenga (Kühne 1998). However, Téllez and Tapia (2006) demonstrated that while *C. attenuata* adults did not feed on *O. laevigatus*, they did prey on the aphid parasitoid *Aphidius colemani* Viereck, the leafminer parasitoid *Diglyphus isaea* (Walker), the whitefly parasitoid *Er. mundus* and on the predator *N. tenuis.* The number of *A. colemani* and *D. isaea* attacked was higher when adults of *B. tabaci* were not present in the arena.

Parasitoid–Parasitoid Interactions

Some parasitoid interactions – such as competition, host feeding, multiparasitism and autoparasitism – are counterproductive to effective biological control. Indeed, theory predicts that host density is always lower when a primary parasitoid acts alone than when an autoparasitoid is also present (Briggs and Collier 2001). Invasion of *En. sophia* into *Er. mundus* cultures results in drastic reductions of the latter (Gerling unpublished data). Collier and Hunter (2001) reported that both *Er. eremicus* and *En. sophia* engaged in multiparasitism with no advantage conferred to either. They also found that *En. sophia* reduced progeny of *Er. eremicus* by host feeding, although conspecific host feeding was also observed so that the net effect could not be predicted.

A similar problem regarding host preference occurs with predicting effects of autoparasitism. At least one autoparasitic species – *En. pergandiella* – preferred to lay male-producing eggs in heterospecific over conspecific secondary hosts. This might be the cause for disruption of *En. formosa* activity in whitefly control by this species as reported from Spain (Gerling et al. 2001) and from Texas, although in the latter case, this was somewhat mitigated by the host species present (Bográn and Heinz 2002). Gerling and Rejouan (2004) found that younger pupae of *En. inaron, En. lutea*, and *En. sophia* were always more susceptible to host feeding or autoparasitism than older pupae, irrespective of melanization. The findings further defined the "window of opportunity" for male development described by Hunter and Kelly (1998) for *En. sophia*, and suggested an increasing probability with age of surviving competitive interactions among parasitoid pupae.

Entomopathogen-Parasitoid and Predator Interactions

Most studies indicate that entomopathogens and parasitoids are compatible for use in biological control of insect pests. For instance, when the mycoinsecticide *Beauveria bassiana* Strain GHA was used to control *B. tabaci* in commercial melons, mortality was inflicted from both fungi and parasitoids with minimal impact on the populations of *Er. mundus* (Jaronski et al. 1998). Applications of *Aschersonia* spp., *B. bassiana, Paecilomyces* spp., *Verticillium lecanii, Acremonium* sp., *Conidiobolus* spp., *Entomophthora* sp., and *Zoophthora radicans* were generally considered compatible with *Encarsia* and *Eretmocerus* spp. (Wang and Huang 2006). Likewise, BotaniGard® (a formulation of *B. bassiana*) had no adverse effects on *En. formosa* (Murphy et al. 1998). Other studies have demonstrated the compatibility of entomopathogens and parasitoids, including *Paecilomyces fumosoroseus*, *V. lecanii* and *B. bassiana* with *Encarsia* spp. (Scholz-Dobelin and Stockmann 2003), *V. lecanii* with *En. formosa* (Jazzar and Hammad 2004), *B. bassiana* JW-1 strain and Naturalis-L® (ATCC 74040 strain of *B. bassiana*) with *Encarsia* spp. and *Eretmocerus* spp. (Wright and Knauf 1994; Wright and Kennedy 1996). However, Shipp et al. (2003) found that *B. bassiana* might reduce efficacy of *En. formosa* and *Er. eremicus* and warned that caution should be taken when this fungus in applied.

Regarding entomophatogen-predator interaction, Wang et al. (2005) demonstrated that crude toxins of the entomopathogenic fungus *V. lecanii* decreased feeding capacity, especially of the larvae, and subsequently reduced fecundity and longevity of female *D. atalinae*.

Natural Enemy-Plant Interactions

Bemisia tabaci is very polyphaguous and its host plants can have a considerably marked influence on natural enemy activity (Inbar and Gerling 2008). Characteristics of host plants such as volatile emission, and especially leaf pubescence, may influence the behavior of coccinellid predators. Al-Zyoud et al. (2005b) found that the beetles preferred pubescent to glaborous host plants. They also found that larval development was shorter, mortality lower and longevity greater on cucumber compared to cotton. Liu (2005) found demographic parameters for *D. catalinae* on collards to be much more favorable than reported for other hosts, such as hibiscus, poinsettia, and tomato (Hoelmer et al. 1993; Heinz et al. 1994; Heinz and Zalom 1996, respectively), and suggested that the more glaborous nature of collard best explained such differences. Guershon and Gerling (2006) studied the foraging behavior of this predator by comparing the effect of adding artificial hairs to a glabrous cotton leaf and observed that leaf hairs hampered searching. Furthermore, after encountering and consuming a smooth *B. tabaci* nymph, beetles were more apt to reject setose nymphs such as found most often on hirsute hosts. Thus, whitefly nymph setosity may be a strategy to avoid predation. Conversely, Legaspi et al. (2006) found that *D. catalinae* predation rates over 24 h were not significantly higher on glabrous leaves of cowpea and collard than on tomentose leaves of cotton, hibiscus, and tomato. They suggested that factors like volatile secondary compounds, rather than leaf structure, might also be involved in host plant suitability.

Many predatory Heteroptera also feed on plants and are referred to as *zoophytophagous*. In laboratory studies, *O. tristicolor* spent less time feeding on the plant and more on whitefly adults than *L. hesperus* (21 vs. 83% on plants and 79 vs. 17% on whiteflies, respectively). Other species spent an intermediate amount of their total feeding time feeding on plants (e.g., *G. punctipes* 66%) (Hagler et al. 2004). In some cases, phytophagy was found to injure the host plants, the level of damage being related to the abundance of arthropod prey. For example, *N. tenuis* caused significantly fewer necrotic rings on tomato when prey was available, both in laboratory and semi-field experiments (Arnó et al. 2006b; Sanchez 2008; Calvo et al. 2008).

Phytophagy enables longer survival and fecundity of predatory Heteroptera (Naranjo and Gibson 1996), but the more prey-dependent species require prey. A decrease in female survival and fertility of *M. caliginosus* was associated with decreasing whitefly availability on tomato and melon plants (Alomar et al. 2006). Poor predator establishment could be explained by low prey densities available on the crop. Jazzar and Hammad (2004) compared *B. tabaci* consumption rates by *Camptotylus reuteri* (Jakolev) and *M. caliginosus,* and concluded that *C. reuteri* was less dependent on *B. tabaci* densities than *M. caliginosus*. Urbaneja et al. (2005) demonstrated the inability of *N. tenuis* to survive on a strictly phytophagous diet and that it survived without prey longer on tomato than on pepper or eggplant.

Pavis et al. (2003) found that parasitoids were most diverse and efficient in controlling *B. tabaci* in Guadaloupe where crops were planted in small, diverse plots close to natural forest and only a few pesticides were used. Weeds favored the presence of parasitoids which reduced both the population of *B. tabaci* and the incidence of virus (Medina Balderas et al. 2002). Antony and Palaniswami (2002) reported that *Er. mundus* – which parasitized *B. tabaci* on sweetpotato – failed to develop on the population infesting cassava. Possibly, these effects were caused by genetic differences in the host population being expressed in distinct biotypes or cryptic species of *B. tabaci* known to colonize cassava (Burban et al. 1992; Legg 1996).

Low rates of parasitism have been associated with greater density and ridgidity of hairs on the leaves (Rajam et al. 1988). Oster (1995) reported a reduction in parasitism by *En. sophia* on pubescent cotton varieties and Gruenhagen and Perring (2001) observed less parasitism of whiteflies on plants bearing trichomes, although the incidence of parasitism was similar on a glabrous melon and its pubescent (with non-glandular trichomes) isoline. Headrick et al. (1996) and McAuslane et al. (2000) found higher rates of parasitization by *Eretmocerus* species on hirsute varieties of melon and soybean, respectively, indicating that some parasitoids could be more effective on certain hirsute plant leaves.

Responses of parasitoids to leaf pubescence may be influenced by other plant characteristics. For example, Gruenhagen and Perring (2001) believed parasitism of *B. tabaci* to be lower on velvet leaf, *Aboutilon theofrasti,* than on four other plant species, due to the exudate from glandular trichomes which entrapped the parasitoids, providing an enemy-free space for the pest. Wax is another leaf factor affecting parasitoid activity. Parasitism (primarily by *Eretmocerus* spp.) was elevated in field plots of reduced-wax collard as compared with the same genotype with normal wax (Jackson et al. 2000). Similarly, parasitism by *En. pergandiella* was elevated (4.5-fold) in the laboratory on reduced-wax collard compared with normal collard, but no effect was observed with *Eretmocerus* sp. (since described as *Er. rui* Zolnerowich and Rose) (McAuslane et al. 2000).

Relevance of Interactions Between Natural Mortality Factors to Biological Control

Naranjo (2007) using sensitivity analyses of field life table data, found only small negative effects of intraguild predation on mortality of *B. tabaci*. Hunter et al. (2002) observed that densities of *Er. eremicus* in cotton fields were higher in the absence of *En. sophia,* whereas *En. sophia* densities were unaffected by the presence of *Er. eremicus*, confirming laboratory results discussed above. However, releases of *Er. mundus* and *En. pergandiella* did not influence host suppression (Bográn and Heinz 2006). The two parasitoids were able to coexist for the duration of a field season when released simultaneously and at the same rate on *B. tabaci*-infested cotton plants in field cages. In contrast, releases of *En. formosa* together with *En. pergandiella* resulted in lower levels of host mortality than would be expected based on the observed mortality caused by individual parasitoid species (Bográn et al. 2002). Overall, the fact that one natural enemy could intervene with the controlling capacity of another – and that these effects could not be foreseen – must be considered and warrants more examination, especially under field conditions.

Utilization, Monitoring, and Assessing the Impact of Natural Enemies

Bemisia tabaci often reaches pestiferous levels in the absence of control measures. When biological control is employed as a corrective measure, effectiveness must be monitored in order to gauge future practices.

Utilization

Predators

Mirid bugs are widely used in the Mediterranean as biological control agents of whiteflies. *Macrolophus caliginosus* and *N. tenuis* commonly colonize in large numbers in both field crops and greenhouses where little or no broad-spectrum insecticides are used, providing not only efficient control of whitefly populations but also contributing to the control of other secondary pests (Alomar et al. 2002; Vacante and Benuzzi 2002; Nannini 2003; Arnó et al. 2005; Calvo et al. 2008; Sanchez 2008). In vegetable greenhouses, success in using mirids for biological control of *B. tabaci* includes the inoculative and augmentative release of *M. caliginosus* (Carboni et al. 2002; Vacante and Benuzzi 2002; Gabarra et al. 2003; Trottin-Caudal and Capy 2003), and *N. tenuis* (Calvo and Urbaneja 2004). Calvo et al. (2008) compared two different release rates of *N. tenuis* – 0.1 and 4 individuals/plant – in large exclusion cages and found significant reduction of the *B. tabaci* populations (> 90%) with both release rates. However, bug feeding can weaken the apex and arrest plant growth. Although often observed only at the end of the season and resulting in natural pruning of the plant (Sanchez et al. 2006; Arnó et al. 2006b), plant feeding by these mirids can produce flower abortion and yield losses (Sánchez and Lacasa 2008; Arnó et al. 2010). (See section on natural enemy plant interactions).

Bemisia tabaci populations increase quickly under warm conditions and the combined releases of *Er. mundus* and *M. caliginosus* often improves whitefly control. For example, the combined use of the parasitoid and predator provided better results than the use of any single natural enemy, especially in spring when whitefly populations were very high in an experimental tomato greenhouse, (Gabarra et al. 2006). Trottin-Caudal et al. (2006) observed improved control of *B. tabaci* when *M. caliginosus* was included with *Er. mundus* in heated greenhouses during winter tomato production.

The newest commercially available predator for whitefly control is *A. swirskii* and is used alone or in combination with *Er. mundus.* Releases of this predaceous mite have been widely used with remarkable success for *B. tabaci* control in sweet pepper greenhouses in Spain (Calvo and Belda 2006; Calvo et al. 2006), and in open field eggplant in Florida (see Stansly and Natwick Chapter 17).

In ornamentals, two coccinellid species controlled *B. tabaci* populations in large cage experiments. On hibiscus, *N. oculatus* effectively controlled the whitefly when a 1:4 predator: prey ratio was observed (Liu and Stansly 2005). Inoculative releases of *S. parcesetosum* also maintained whitefly populations at low levels during 10 weeks. Whitefly control was primarily due to prolonged adult survival and continuous feeding of adult beetles on the whiteflies (Ellis et al. 2001).

Parasitoids

Although there are numerous cases of exotic whitefly infestations being completely controlled through introduction of exotic parasitoids, such has not been the case for

B. tabaci. The most extensive effort was initiated in the early 1990s with collections of parasitoids as well as entomopathogens and some predaceous coccinellids coordinated by the USDA-ARS European Biological Control Laboratory in Montpellier, France (Gould et al. 2008). From the worldwide explorations in 28 countries, 55 parasitoid cultures were established at the USDA-APHIS Quarantine Facility in Mission in Texas, where they were characterized taxonomically and through RAPD-PCR and their biological attributes studied (Goolsby et al. 2008). Promising candidates were mass reared and released in Texas, Arizona and California and to a lesser extent in Florida. The best-performing species or geographic populations in the desert Southwest were those that originated from similar climatic regions: the Arabian Peninsula, arid northeastern Africa (*Er. emiratus* and *Er.* sp. nr. *emiratus*), and hot, dry regions bordering the Mediterranean (*En. sophia*) (Hoelmer and Roltsch 2008), whereas *Er. hayati* from Pakistan came to dominate in the Rio Grande Valley of Texas (Ciomperlik and Goolsby 2008). The apparent exception to this pattern of geoclimatic matching was Florida where an as yet undescribed species from Sudan, also released as *Er.* sp. nr. *emiratus* is now dominant (P. Stansly unpublished data). Although *B. tabaci* continued as a pest in this region, the indigenous parasitoid fauna attacking it was largely replaced with more specific and efficient Old World species that provided more effective biological control.

Augmentative release of parasitoids for control of *B. tabaci* in greenhouses has been also been studied (e.g. Hoddle et al. 1998; Stansly et al. 2004, 2005) and has been a common practice in protected agriculture (greenhouses and plastic-covered annuals, Stansly et al. 2004, 2005). Several commercial companies are engaged in the mass rearing and use of *Er. eremicus* and *Er. mundus* for both vegetable and ornamental greenhouses. More details are given in Stansly and Natwick (Chapter 17).

Monitoring and Impact Assessment

This discussion is intended to complement the treatment of the methodology, application, and problem of monitoring and assessing natural enemy activity, provided by Naranjo (2001). Specific, organism-oriented work (predators and parasitoids) as well as general life table analyses are included.

Predators

Additional predators of *B. tabaci* have been identified using ELISA methods in the field to test for a whitefly-specific egg protein in captured predators (Hagler and Naranjo 2005). The ELISA system has also been used to evaluate and compare the feeding activity of the predator complex in cotton fields under different insecticide treatment regimes (Hagler and Naranjo 2005). These tests relied on a very specific antibody and therefore, only predation on eggs or gravid females could be assessed (Hagler et al. 1993) and activity of the predators such as *L. hesperus* that feed mainly on *B. tabaci* nymphs was underestimated (Hagler et al. 2004). ELISA tests have also been used to monitor intercrop movements of predators previously marked with specific IgG proteins (Hagler and Naranjo 2004). Overcoming the shortcomings of the stage-specific detection provided by ELISA, Zhang et al. (2007a, c) developed techniques to detect and quantify *B. tabaci* DNA within the predators' gut. They succeeded in identifying a number of new predator species of *B. tabaci* in China, and evaluating their importance in the cotton agroecosystem. Overall, specific difficulties arise when attempting to use serological or molecular marker techniques to quantify predation. Although the output of these techniques could be quantitative, actual estimation of prey consumed were complicated by uncontrolled factors such as prey size, metabolic differences among predator species, temperature, and digestion time since the last meal (Greenstone 1996; Naranjo and Hagler 1998; Agustí et al. 2000; Zhang et al. 2007c).

Parasitoids

Recent field work has been characterized by attempting to monitor adult parasitoids in addition to the relatively straight forward method of collecting whiteflies and examining them for parasitism. Otoidobiga et al. (2003) observed captures of 0.14–13 *Eretmocerus* sp. individuals per yellow sticky card as levels of parasitism varied between 36 and 87% over different seasons. They also monitored year-round whitefly infestations in overlapping cotton crops in Burkina Faso (Otoidobiga et al. 2004). Although parasitoid populations increased with host density, no density-dependent trend was observed. Hoelmer and Simmons (2008) showed that the lower surface of horizontally placed sticky traps captured more *Er. emiratus* than the upper surface, and that females were captured in greater numbers than males, but found no significant correlation between trap capture of parasitoids and the number of parasitized *B. tabaci* on leaf samples. The effectiveness of yellow sticky traps at different heights and in different seasons was monitored on the population dynamics of *B. tabaci* and its parasitoids on tomato (Qiu and Ren 2006).

A cup trap equipped with a 530 nm lime green light-emitting diode (LED) caught more adult whiteflies, but fewer *Er. eremicus*, *Er. mundus*, *Eretmocerus* sp. and *En. formosa* when compared to sticky traps (Nombela et al. 2003; Chu et al. 2003, 2004a; Simmons et al. 2004). Hagler et al. (2002) used an ELISA assay to detect a protein marker in a mark-release-recapture study on dispersal of *Er. erimicus*. Most of the 40% marked and recaptured parasitoids were males, although an equal proportion of each gender was released, indicating greater dispersal of males. Additional methods include the rubidium chloride marking technique that Pickett et al. (2004) used to examine the movement of feral populations of *Er. eremicus* and *Encarsia* spp. from overwintering *B. tabaci*-infested refuges into adjacent crops of cantaloupe and cotton in the desert agricultural region of southeastern California.

Life Table Studies

A more direct method for assessing and quantifying natural enemy effects is the use of life tables (see Naranjo et al. Chapter 6). In Arizona, cohort-based life table studies in cotton demonstrated that predation occurring during the 4th nymphal instar was the key factor affecting *B. tabaci* populations (Naranjo and Ellsworth 2005). These authors also found a relatively large portion of mortality due to dislodgement that they associated with chewing predation and weather events. Life table studies conducted in a variety of crops and weed hosts also pointed to the important contribution of natural enemy mortality to *B. tabaci* population dynamics over the entire year (Naranjo et al. 2004a).

In contrast to the Arizona desert situation, life table studies on cassava in Uganda (Asiimwe et al. 2007b) and on cotton in Turkey (Karut and Naranjo 2009) showed parasitism to be the main source of natural enemy-induced mortality. Sources and rates of mortality were discernable based on visible symptoms and the use of marginal mortality rates to correct for contemporaneious mortality events. Although reliable data on natural enemies were obtained, the relative importance of different mortality factors was not always apparent; furthermore, predation on adult whiteflies was not ascertained.

Conclusions

Bemisia tabaci-associated problems are here to stay and might even be increasing. However, the trend is toward greater use of non-insecticide based control methods including deployment of natural enemies (see also Antignus Chapter 13; Nombela and Muñiz Chapter 14). Here, we have updated the available information on the identity and use of natural enemies attacking *B. tabaci*. Numerous new species of predators and parasitoids have been found and studied. From these studies and the practical results of using natural enemies we can draw the following conclusions:

1. The identification of natural enemies and their quantitative role in the agroecosystem are important first steps. New horizons are being opened through the availability of new tools based on serological and molecular techniques, and time-tested methods such as life table analyses. These tools are continuously improving the ability to identify new natural enemies – especially predators – and to quantify their impact on the pest population. These techniques are providing a fuller picture of the role of natural enemies in suppression of *B. tabaci* in different agroecosystems.
2. Both predators and parasitoids are useful as control agents; however, each enemy has its' own specific conditions for optimal employment. Knowing these conditions is a prerequisite to their effective utilization as well as the inclusion of new organisms into our arsenal as was demonstrated in the case of *A. swirskii*. Moreover, the sensitivity to particular conditions such as plant species and pubescence can override other considerations: i.e. predators vs. parasitoids and host range of the natural enemy. The fact that most of the utilized predators are polyphagous, only *Er. mundus* among parasitoids can be considered truly monophagous, and that new natural enemies continue to be discovered and put to use, dictate that the search must continue.

3. Finally, testing and proving the quality and usefulness of natural enemies, especially parasitoids, has always been a weak point in their application. This is mostly due to the large number of organisms to be tested and complex tests required. Recently, it was demonstrated that a realitvely simple series of behavioral examinations and performance studies under field conditions can help in reducing the list of potential natural enemies. This may be done through utilizing a diagrammatic elimination scheme such as proposed by van Lenteren and Martin (1999) thus facilitating the introduction of new organisms for biological control.

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