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Natural enemies of the South American moth, *Tuta absoluta*, in Europe, North Africa and Middle-East, and their potential use in pest control strategies

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Abstract

The South American tomato leaf miner, *Tuta absoluta* Meyrick (Lepidoptera: Gelechiidae), is an invasive Neotropical pest. After its first detection in Europe it rapidly invaded more than 30 Western Palaearctic countries becoming a serious agricultural threat to tomato production in both protected and open field crops. Among the pest control tactics against exotic pests, biological control using indigenous natural enemies is one of the most promising. Here, available data on the Afro-Eurasian natural enemies of *T. absoluta* are compiled. Then, their potential for inclusion in sustainable pest control packages is discussed providing relevant examples. Collections were conducted in 12 countries, both in open field and protected susceptible crops, as well as in wild flora and/or using infested sentinel plants. More than seventy arthropod species, 20% predators and 80% parasitoids, were recorded attacking the new pest so far. Among the recovered indigenous natural enemies only few parasitoid species, namely some eulophid and braconid wasps, and especially mirid predators have promising potential to be included in effective and environmentally-friendly management strategies of the pest in the newly invaded areas. Finally, a brief outlook of the future researches and applications of indigenous *T. absoluta* biological control agents is provided.

Keywords: Biological control, Generalist predators, Integrated Pest Management, Invasive species, Parasitoid community, Western Palaearctic

Introduction

The composition of worldwide biotic communities has greatly changed in recent years due to the collapse of natural barriers to wild species movements mainly in relation to human activities (Liebhold and Tobin 2008). Among the newly-introduced insect species some can become invasive, with subsequent significant economic impacts. The success or failure of a biological invasion may depend on the species' life history parameters, on its response to climatic conditions, on the competition with native species and on the impact of natural enemies (Grabenweger et al. 2010). This last factor may be crucial in the invasion mechanism and the success of an invader, in terms of distribution and abundance, could be related to the absence or low efficacy of natural control in the new territories, as stated by the so called *Enemy Release Hypothesis* (Keane and Crawley 2002). Indeed, it is assumed that natural enemies in the newly invaded areas need time to get adapted and to control the exotic species effectively. This may be due to the fact that native antagonists need to adjust their behaviour and/or physiology to be able to successfully develop on the exotic prey/host. For these reasons natural enemy complexes on invaders may perform initially low percentage predation/parasitism (Cornell and Hawkins 1993). However, several examples of successful biological control using natural enemies that have not coevolved with the pest, the so called *New species association*, are also known (Hokkanen and Pimentel 1984; O'Connell et al. 2012).

In this framework, gaining knowledge on indigenous natural enemies that get adapted to the new hosts and understanding their role in limiting the alien species is essential for establishing the basis of suitable and sustainable control strategies of exotic pests. This applies also to one of the latest invasive species arrived in the Western Palaearctic region: the South American tomato leaf miner, *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae). This moth is a Neotropical species and is considered a key pest of tomato in South America (Guedes and Picanço 2012; Luna et al. 2012) where it remained confined until its first record in Western Palaearctic, in Spain in 2006 (Desneux et al. 2010; Tropea Garzia et al. 2012). Afterwards, it rapidly spread throughout the Mediterranean basin, in Europe, North Africa and Middle East (Desneux et al. 2011). *Tuta absoluta* is considered a typical invasive species because of its capacity to develop very quickly on tomato cultivations and to spread rapidly in new areas causing economically relevant damage (Desneux et al. 2010; Caparros Megido et al. 2012).

Although chemical control has been the first strategy adopted in the newly invaded areas, alternative control measures are being investigated (Cagnotti et al. 2012; Cocco et al. 2013) in compliance with the EU Directive on sustainable use of pesticides (Directive 2009/128/EC). In the case of *T. absoluta* the need for alternative control methods is strengthened by the development of resistance to insecticides by the pest (Haddi et al. 2012; Gontijo et al. 2013), as well as to the side effects of pesticides on beneficial arthropods (Arnó and Gabarra 2011; Biondi et al. 2012, 2013a; and see Desneux et al. 2007 for a thorough review).

On the other hand, various predators and parasitoids spontaneously attack *T. absoluta* in tomato crops in Europe and in North Africa. Some of these, mainly native Miridae, have been already employed in Integrated Pest Management (IPM) strategies (Castañé et al. 2011; Mollá et al. 2011; Cabello et al. 2012; Zappalà et al. 2012b; Chailleux et al. 2013a). However, several screenings for effective natural enemy species in the invaded area are still ongoing (Chailleux et al. 2012; Gabarra et al. 2013). More than seventy species of generalist natural enemies have been reported developing on *T. absoluta* in the Western Palaearctic region so far. These have been sampled both on open field and protected susceptible crops as well as on wild flora and/or using infested sentinel plants. Here we take into account all the available data, aiming at giving a comprehensive picture of the composition of the species that spontaneously provide biological control services and their current role in *T. absoluta* control programmes.

Predators

Fifteen arthropod species were recorded preying on the South American tomato leafminer in the last few years in newly invaded Western Palaearctic countries (Table 1). They mainly belong to the order Hemiptera (ten species) and in particular to the families Miridae, Anthocoridae and Nabidae in descending order of species numbers. These predators include zoophytophagous bugs that usually colonize and establish in organic and IPM crops where they are also able to build up their populations before pest arrival, exploiting alternative preys, such as whiteflies, thrips, aphids, spider mites, leafminers as well as other Lepidoptera, and host plants (e.g. *Dittrichia viscosa* (L.) and *Solanum nigrum* (L.)) as alternative food sources (Perdikis et al. 2007; Desneux and O'Neil 2008; Ingegno et al. 2008).

The most widely spread species are mirids belonging to the tribe Dicyphini, with *Nesidiocoris tenuis* (Reuter) spontaneously recovered in eleven countries almost all year round both in protected and open field tomato crops, and *Macrolophus pygmaeus* (Rambur) which was observed preying on *T. absoluta* eggs and young instar larvae in three countries. Guenaoui et al. (2011a) reported *M. caliginosus* Wagner as a predator of *T. absoluta* on tomato in Algeria. However, considering the great number of misconceptions comprised in the classification history of this species [= *M. melanotoma* (Costa)] and in agreement with the most recent taxonomical reconsiderations (Martinez-Cascales et al. 2006; Castañé et al. 2013), also this record is likely to refer to *M. pygmaeus*; therefore, it was included accordingly in table 1. Other four Dicyphini species [*Dicyphus* sp., *D. errans* (Wolff), *D. maroccanus* Wagner and *D. tamanini* Wagner] were sampled from infested tomato plants in Algeria, France, Italy and Spain (Table 1). Anthocorids belonging to the *Orius* genus were found in open field and protected tomato crops infested by *T. absoluta* in Jordan. Species of the *Nabis* genus were occasionally found in Iran and Spain. In addition, lacewings belonging to the *Chrysoperla carnea* species group were found feeding on *T. absoluta* in open field tomato and two species of predatory mites [*Amblyseius swirskii* Athias-

Henriot and *A. cucumeris* (Oudemans)] were also reported from the moth eggs and first instar larvae in Spain. The ant *Tapinoma nigerrimum* (Nylander) (Hymenoptera: Formicidae) was found in Algeria preying on *T. absoluta* larvae. One unidentified species of Hymenoptera Sphecidae was recovered in Spain feeding on larval instars of the moth (Table 1).

Parasitoids

A quite large number of parasitoid species (more than 50) was recorded developing on all the young instars and eggs of the moth in the newly invaded areas (Table 2). Overall, the most abundant parasitoid family was the Eulophidae one with 28 recovered species. *Neochrysocharis formosa* (Westwood) [= *Closterocerus formosus* (Westwood)] was one of the most widely spread, being found in four countries (Algeria, France, Italy, Spain). So far, this is the only species recorded on *T. absoluta* both in Europe and in South America, where it was mentioned as a potential biocontrol agent based on its wide host range (Noyes 2013) and presence in other crops, with parasitism rates on *T. absoluta* ranging between 1.5 and 11.2% (Luna et al. 2011). *Closterocerus clarus* (Szelenyi) was recovered on *T. absoluta* young larvae in Turkey. Six species belonging to the genus *Necremnus* were found developing on *T. absoluta* in Algeria, Egypt, France, Italy, Spain and Tunisia, including two entities that were identified as *N.* sp. near *artynes* and *N.* sp. near *tidius*. *Necremnus artynes* was the most abundant species in Northwestern Algeria (Guenaoui et al. 2011b). Urbaneja et al. (2012) found *N. metalarus* (Walker), developing on *T. absoluta*-infested tomato plants in Spain. However, the taxonomy of this genus is currently under revision, therefore most of these records may need to be verified (Ferracini et al. 2012a; Zappalà et al. 2012a). Besides, other aspects of their biology and ecology should be also further investigated. The ectoparasitoids of Diptera, Lepidoptera and Coleoptera leafminer larvae, *Pnigalio incompletus* (Bouček) and *P. cristatus* (Ratzeburg), often associated due to their shared hosts (Noyes 2013), emerged from *T.*

absoluta larvae both in Italy and in Turkey. Wasps identified as *P. soemius* or belonging to *P. soemius* species complex were recovered in Italy and in Spain (Table 2). This is a Palaearctic complex of generalist parasitoids, with an intense predatory behaviour both as larva and adult (Bernardo et al. 2006). *Stenomesius* near *japonicus* was recovered in France and in the North East of Spain on *T. absoluta* 2nd and 3rd instar larvae and an unidentified species belonging to the same genus was found in Algeria. Two species belonging to the genus *Elasmus* were recorded on *T. absoluta*; one, which was not identified at the species level, was found in Italy while *Elasmus phthorimaeae* Ferrière was recorded in Eastern Spain (Table 2). Specimens of *Sympiesis* sp. near *flavopicta* and of *Hemiptarsenus ornatus* (Nees) emerged from larvae collected in open field tomato crops in Israel. Another *Hemiptarsenus* species, *H. zilahisebessi* Erdös, and *Diglyphus isaea* (Walker) were found in association with *T. absoluta* in Algeria. The larval parasitoid *Diglyphus crassinervis* Erdös was recorded on *T. absoluta* only in Spain. Specimens classified as belonging to the *Elachertus inunctus* species group emerged from artificially infested sentinel plants in Italy; wasps identified as *Baryscapus bruchophagi* (Gahan) were found in Turkey. Finally, five other eulophid species, not identified at the species level (*Chrysocharis* sp., *Cirrospilus* sp., *Diglyphus* sp., *Elachertus* sp. and *Sympiesis* sp.), were also found parasitizing spontaneously the new host (see Table 2 for details).

Almost 30% of the recovered species were Ichneumonoidea, more precisely six species belonged to the family Ichneumonidae and the remaining fourteen to the family Braconidae. Among the six ichneumonids, those belonging to the *Diadegma* genus [*Diadegma* sp., *D. ledicola* Horstmann and *D. pulchripes* (Kokujev)] were found parasitizing *T. absoluta* mature larvae and pupae in Italy. The other three ichneumonid wasps, *Hyposoter didymator* (Thunberg), *Temelucha anatolica* (Sedivy) and *Zoophthorus macrops* Bordera & Horstmann, were recorded only in one country, Algeria and Spain respectively, on unspecified host instar stage. Among braconid wasps, some species were found on wild flora, namely *Solanum nigrum*, i.e. *Agathis fuscipennis*

Zetterstedt, recovered in Italy, and *Apanteles* sp., *Chelonus* sp., *Choeras semele* (Nixon), *Dolichogenidea litae* (Nixon) and *Diolcogaster* sp., recorded in Spain (Table 2). *Bracon* species were already reported as *T. absoluta* parasitoids in the pest native areas (Desneux et al. 2010) and several species belonging to this genus were found developing on the exotic pest in the newly invaded areas. Some of these were found in various countries, such as *B. hebetor* Say, a worldwide distributed and very polyphagous species (Yu & van Achterberg, 2010), which was recovered on *T. absoluta* in Algeria, Israel, Italy and Turkey. The Palaearctic species *B. nigricans* (Szépligeti) was recorded parasitizing *T. absoluta* mature larvae in France, Israel (where it was reported as *B.* near *nigricans*), Italy, Jordan and Spain. Whereas, *B. osculator* (Nees) and *B. didemie* Beyarslan were found only in Italy and in Turkey, respectively. Two braconid wasps, not identified at the species level, *Agathis* sp. and *Bracon* sp., emerged from parasitized larvae collected in Italy and Tunisia. However, some of these records should be verified, evaluating the suitability of *T. absoluta* as host for the reported parasitoids. Indeed, many ichneumonid species are known to develop on noctuid tomato pests, therefore if sampling was not carefully conducted the record can be related to a co-infestation of the crop by *T. absoluta* and noctuids.

Two pteromalid species, *Halticoptera aenea* (Walker), *Pteromalus intermedius* (Walker) and *Pteromalus semotus* (Walker), were found developing on the moth larvae in Italy,Turkey and Spain respectively. Moreover, two species of chalcidid wasps, *Brachymeria secundaria* (Ruschka) and *Hockeria unicolor* Walker, were associated with *T. absoluta* in Turkey. *Tuta absoluta* eggs were parasitized spontaneously by *Trichogramma achaeae* Nagaraja & Nagarkatti in France, by *Trichogramma bourarachae* Pintureau & Babault in Tunisia and by various other unidentified *Trichogramma* species in Algeria, Egypt, France, Iran and Spain (Table 2). In South America more than 12 species of Trichogrammatidae, four Encyrtidae and one Eupelmidae gen. sp. were reported as *T. absoluta* egg parasitoids (Desneux et al. 2010). This higher richness may be due to climatic factors as well as to a more intensive monitoring of egg parasitism in *T. absoluta* native region where many biological control programs have been performed using egg parasitoids (Guedes and Picanço 2012; Parra and Zucchi, 2004).

Potential for use of indigenous natural enemies

Studies have been carried out under laboratory conditions to assess the suitability of *T. absoluta* for various predator and parasitoid species. The seminal studies of Urbaneja et al. (2009) and Arnó et al. (2009) reported that *N. tenuis* and *M. pygmaeus* adults do actively feed on eggs (up to ~60 day^{-1}) and young larvae (~2 day^{-1})of the moth. These results were confirmed in larger scales (greenhouse) experiments (Mollá et al. 2011 and Bompard et al. 2013 for *N. tenuis* and *M. pygmaeus*, respectively). Similar results were obtained in the laboratory by Guenaoui et al. (2011a) with *N. tenuis* and *M. caliginosus*, by Cabello et al. (2009) studying *N. pseudoferus ibericus*, by Arnò et al. (unpublished data) for the bugs *D. tamaninii*, *O. majusculus* and *O. laevigatus*, as well as by Ferracini et al. (2012b) for *D. errans*.

Other studies were aimed to assess the development of mirid species when feeding on the new prey (Mollà et al. 2014) and the biology and behaviour of parasitoid species on *T. absoluta*. In the case of parasitoids it clearly emerged that under laboratory conditions *N.* sp. near *artynes*, *N.* sp. near *tidius* and *B. nigricans* were able to reduce significantly *T. absoluta* populations not only owing to the parasitism activity but also thanks to a non reproductive host-killing activity, namely host feeding and host stinging behaviours (Ferracini et al. 2012a; Biondi et al. 2013c).

Beside the *environmental resistance* that all the recovered fortuitous natural enemies can spontaneously offer in realistic field conditions, there are several approaches that can be artificially implemented to enhance their role in regulating pest populations. Indeed, these indigenous natural enemies can be *inoculated, augmented* and *conserved* in the cultivated environment. Inoculation of mass reared *N. tenuis* has been successfully applied in tomato nurseries for the early installation of the predator population in the young crop (Calvo et al. 2012), or directly in greenhouse with the concomitant application of microbial pesticides (Desneux et al. 2010; Mollá et al. 2011). By contrast, although this generalist predator, as well as *M. pygmaeus*, has been largely employed in biological and integrated *T. absoluta* control programs with contrasting results (Arnó et al. 2009; Abbes and Chermiti 2012; Nannini et al. 2012; Trottin-Caudal et al. 2012), it often prompts insecticide applications at high densities due to damages caused to plants and fruits (e.g. Calvo et al. 2009; Arnó et al. 2010; Castañé et al. 2011). On the other hand, *M. pygmaeus* has been recently proved not able to build up its populations when feeding only on this prey (Mollà et al. 2014). Thus, higher levels of prey species diversity, such as the concomitant infestations of whiteflies (Bompard et al. 2013), are required for effective inoculative applications of this predator species.

Commercially available *T. acheae* individuals are now used against *T. absoluta* by periodic inundative releases (50 adults/m^2) in commercial greenhouse successfully (Cabello et al. 2012; Trottin-Caudal et al. 2012). Whereas, similar control levels can be achieved by combining lower release rate of this egg parasitoid with mirid predators, i.e. *M. pygmaeus* and *N. tenuis* (Calvo et al. 2012; Chailleux et al. 2013a; 2013b). Fairly good control was obtained in Southern Spain with multiple releases of *N. artynes*, although the reduction was not enough to limit fruit damage to the level reached by *N. tenuis* when released in the nursery (Calvo et al. 2012; Urbaneja et al., 2012).

Finally, the data so far obtained by laboratory bioassays, as well as through various researches conducted in open field and protected tomato crops in the Western Palaearctic area suggest that the potentially effective indigenous antagonist species in *T. absoluta* control are the predators *M. pygmaeus* and *N. tenuis*, as well as the parasitoids *T. acheae*, *N.* sp. near *artynes*, *N. formosa*, *S.* cf. *japonicus* and *B. nigricans*. The applications of these indigenous organisms, individually and in association, should be further increased via conservation and augmentation strategies.

Future outlooks

Several entomophagous species recovered on *T. absoluta*, such as *Dicyphus* spp., *Diadegma* spp., *Bracon* spp., *Necremnus* spp., *N. formosa*, have been recorded in the past as widely spread on tomato crops also in those countries where they were not yet found in association with *T. absoluta* (Kerzhner and Josifov 1999; Yu and Van Actherberg 2010; Noyes 2013). Thus, most likely these species will be found associated to *T. absoluta* in other countries very soon, as expected in Iran (Baniameri and Cheraghian 2012). For this reason, further surveys in areas with still few records of *T. absoluta* natural enemies are encouraged. On the other hand, all the records of *T. absoluta* predator species obtained so far derive from direct field observation and samplings, and from experimental laboratory bioassays, while no studies have been conducted using newly-developed analytical techniques, such as the predator gut content molecular analysis (King et al. 2008; Juen et al. 2012). Indeed, these tools may be very useful to get an exhaustive assessment of the arthropod fauna which actually preys on new invasive pests (Harwood et al. 2007).

Further applied aspects of the biology and ecology of the natural enemies species already identified as potential key natural enemies species should be further investigated. These are for example: their potential for mass rearing (Canale and Benelli 2012, Cicero et al. 2012), dispersal capacity (Tabone et al., 2012; Zappalà et al. 2012c), functional response to host densities (Madadi et al. 2011, Savino et al. 2012), foraging and host searching behaviours (Gontijo et al. 2012, Ramirez-Romero et al. 2012). This is particularly needed for those species groups with an uncertain taxonomy (namely *Necremnus*, *Bracon* and *Trichogramma* spp.), since different biological and ecological traits can be highlighted among different parasitoid cryptic species (Heimpel et al. 1997; Desneux et al. 2009b). Furthermore, in order to set up potential commercial mass rearing and/or to commercialize natural enemies throughout different countries, their taxonomy should be definitively clarified (Gordh and Bearsley, 1999; Stouthamer, 2008).

In order to reduce the cost of multiple egg parasitoid releases (Cabello et al. 2012) and/or plant damage of the released omnivorous predators (Castañé et al. 2011), further studies aimed at setting economically sound mass rearing protocols of other indigenous natural enemies are to be developed. This should be aimed at rearing entomophagous species having the least secondary effects on the plants (phytophagy) as well as minimum potential for intraguild predation on other beneficials present in the crop.

The overall increase of knowledge on the indigenous natural enemy complex would help all habitat management strategies. These should be aimed at increasing the functional biodiversity within the crop and within the farm, such as rational weed management for increasing food and alternative preys/hosts for indigenous predators and parasitoids (Gardiner et al. 2009; Balzan and Wäckers 2013; Tena et al. 2013). The increase in the abundance and diversity of the natural enemy community could be also obtained through the use of the *banker plants* technique (Parolin et al. 2012a; 2012b). Actually, the first banker plant system was developed in greenhouse tomatoes using tomato plants both as crop and banker plants (Stacey 1977). However, this made pest control harder and resulted in reduced application of the technique by the growers. Since then this technique has been successfully tested in tomato crops using non-crop banker plants for various pest-natural enemies systems (Lambert et al. 2005; Xiao et al. 2011).

To fully exploit this strategy for *T. absoluta* control, increasing knowledge on the prey/host range of its generalist entomophagous species is crucial (Ingegno et al. 2011; Desneux et al. 2009a; 2012). Indeed, the potential applications to enhance the natural enemies populations in the crop could be numerous. In our case, an example is the installation or conservation in the tomato crop of *Parietaria officinalis* L. plants infested by *Cosmopterix pulchrimella* Chambers (Lepidoptera: Cosmopterigidae), that is an alternative host of *N. artynes* (Ferracini et al. 2012a). Another source of *T. absoluta* antagonists could be represented by the proximity of potato plants infested by the potato tuber moth, *Phthorimaea operculella* (Zeller) (Lepidoptera: Gelechiidae), which is often attacked both by the endoparasitoid *D. pulchripes* and by the ectoparasitoid *B. nigricans* (Yu and Van Actherberg 2010). However, although increasing the “right diversity” (Landis et al. 2000) has been proved to reduce pest pressure effectively and to enhance natural enemy activity, *P. operculella* is a serious potato pest and this application should be carefully evaluated before being implemented. An important role may be played also by *Dittrichia viscosa* which is already reported as a refuge plant for several predatory bugs that do move to tomato crops providing important biological control services (Perdikis et al. 2007; 2011). However, as recently highlighted by Castañé et al. (2013) for *Macrolophus* spp., a clarification in the taxonomy of the species related to tomato is strongly needed for effective applications.

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Table 1. Predators observed feeding on *Tuta absoluta* in Western Palaearctic countries.

Order Family	Species	Known distribution[1]	*T. absoluta* instars	Country(ies)	Sampling method(s)	Season(s)	Reference(s)
Mesostigmata: Phytoseiidae	*Amblyseius swirskii* Athias - Henriot	Western Palaearctic	Eggs and L1	Spain	Protected crop (eggplant) sampling	Summer	Mollá et al. 2010
	Amblyseius cucumeris (Oudemans)	Cosmopolitan	Eggs and L1	Spain	Protected crop (eggplant) sampling	Summer	Mollá et al. 2010
Hemiptera: Miridae	*Dicyphus* sp.		Eggs and young larvae	France, Italy	Open field and protected crop sampling	Summer	Biondi et al. 2013b, Zappalà et al. unpublished data
	Dicyphus errans (Wolff)	Western Palaearctic	Eggs and L1	Algeria, Italy	Open field and protected crop sampling	Spring-autumn in the open field; all year round in greenhouses	Boualem et al. 2012, Ferracini et al. 2012b, Ingegno et al. 2013
	Dicyphus maroccanus Wagner	Mediterranean basin	Eggs and young larvae	Spain	Open field and protected crop sampling	Summer	Mollà et al. 2010
	Dicyphus tamaninii Wagner	Western Palaearctic	Eggs and young larvae	Algeria	Not specified	Not specified	Guenaoui et al. 2011a
	Macrolophus pygmaeus (Rambur)	Western Palaearctic	Eggs and young larvae	Algeria, France, Italy, Spain	Open field and protected crop sampling	Spring, summer, autumn	Arnò et al. 2009, Mollà et al. 2010, Guenaoui et al. 2011a, Boualem et al. 2012, Biondi et al. 2013b, Ingegno et al. 2013
	Nesidiocoris tenuis (=*Cyrtopeltis tenuis*) (Reuter)	Cosmopolitan	Eggs and young larvae	Algeria, Cyprus, Egypt, France, Jordan, Iran, Israel, Italy, Morocco, Spain, Turkey	Open field and protected crop sampling	Spring, summer, autumn, winter	Arnò et al. 2009, Guenaoui et al. 2011a, Karabuyuk, 2011, Rizzo et al. 2011, Al-Jboory et al. 2012, Boualem et al. 2012, El-Arnauty and Kortam 2012, Biondi et al. 2013b, R. Bouharroud pers. comm., Kiliç pers. comm., Martinou and Stavrinides unpublished data, Shaltiel-Harpaz and Gerling unpublished data
Hemiptera: Anthocoridae	*Orius* sp.		Not specified	Jordan	Open field and protected crop sampling	January-April	Al-Jboory et al. 2012
	Orius albidipennis (Reuter)	South Europe, North Africa and Asia	Not specified	Jordan	Open field and protected crop sampling	January-April	Al-Jboory et al. 2012
Hemiptera: Nabidae	*Nabis* sp.		Eggs and young larvae	Iran	Open field crop sampling	Summer	H. Madadi pers. comm.
	Nabis pseudoferus ibericus	Western Palaearctic	Not specified	Spain	Not specified	Not specified	Mollá et al. 2010
Neuroptera: Chrysopidae	*Chrysoperla carnea* species group		Not specified	Egypt	Open field crop sampling	Not specified	El-Arnauty unpublished data
Hymenoptera: Sphecidae	Undetermined species		Larvae	Spain	Not specified	Not specified	Mollá et al. 2008
Hymenoptera: Formicidae	*Tapinoma nigerrimum* (Nylander)	Western Palaearctic	Larvae	Algeria	Open field and protected crops	Summer	Guenaoui et al. 2011b

[1]Kerzhner and Josifov 1999

Table 2. Parasitoids recovered on *Tuta absoluta* in Western Palaearctic countries.

OrderFamily	Species	Known distribution[2]	T. absoluta instars	Country(ies)	Sampling method(s)	Season(s)	Reference(s)
Hymenoptera: Ichneumonidae	*Diadegma* sp.		Mature larvae-pupae	Italy	Open field crop sampling	Autumn	Zappalà et al. 2012a
	Diadegma ledicola Horstmann	Western Palaearctic	Mature larvae-pupae	Italy	Open field crop sampling	Summer, autumn	Ferracini et al. 2012a
	Diadegma pulchripes (Kokujev)	Palaearctic	Mature larvae-pupae	Italy	Open field (potato) crop sampling, sentinel infested plant	Summer, autumn	Zappalà et al. 2012a
	Hyposoter didymator (Thunberg)	Australasian, Western Palaearctic	Not specified	Algeria	Protected crop sampling	Spring	Boualem et al. 2012
	Temelucha anatolica (Sedivy)	Palaearctic	Not specified	Spain	Open field crop sampling	Not specified	Gabarra et al. 2013
	Zoophthorus macrops Bordera & Horstmann	Spain	Not specified	Spain	Open field crop sampling	Not specified	Gabarra et al. 2013
Hymenoptera: Braconidae	*Agathis* sp.		Larvae not specified	Italy	Open field crop sampling	Summer	Ferracini et al. 2012a
	Agathis fuscipennis Zetterstedt	Western Palaearctic		Italy	Open field sampling of infested *Solanum nigrum*	September - October	Loni et al. 2011
	Apanteles sp.		Not specified	Spain	*Solanum nigrum*	Not specified	Gabarra et al. 2013
	Bracon sp.		Mature larvae	Tunisia	Sentinel infested plants exposure	Spring, summer	Abbes et al. 2013
	Bracon (=*Habrobracon*) *didemie* Beyarslan	Turkey	Mature larvae	Turkey	Open field and protected crop sampling	Spring	Doganlar and Yigit 2011
	Bracon (=*Habrobracon*) *hebetor* Say	Cosmopolitan	Mature larvae	Algeria, Israel, Italy, Turkey	Open field and protected crop sampling	Spring, Summer	Doganlar and Yigit 2011, Ferracini et al. 2012a, Guenaoui and Dahliz unpublished data, Shaltiel-Harpaz and Gerling unpublished data
	Bracon (=*Habrobracon*) *nigricans* (=*concolorans, concolor, mongolicus*) Szépligeti	Palaearctic	Mature larvae	Egypt, France, Italy, Jordan, Spain	Open field and protected crop sampling, sentinel infested plants	Spring, Summer	Al-Jboory et al. 2012, Urbaneja et al. 2012, Zappalà et al. 2012, Biondi et al. 2013b, El-Arnaouty unpublished data
	Bracon (=*Habrobracon*) sp. near *nigricans*		Mature larvae	Israel, Spain	Open field crop sampling; sentinel infested plants	Spring, Summer	Gabarra and Arnò 2010, Gabarra et al. 2013, Shaltiel-Harpaz and Gerling unpublished data
	Bracon (=*Habrobracon*) *osculator* (Nees)	Palaearctic	Mature larvae	Italy	Open field and protected crop sampling, sentinel infested plants	Summer, autumn	Ferracini et al. 2012a, Zappalà et al. 2012
	Chelonus sp.		Not specified	Spain	*Solanum nigrum*	Not specified	Gabarra et al. 2013
	Choeras semele (Nixon)	Western Palaearctic	Not specified	Spain	*Solanum nigrum*	Not specified	Gabarra et al. 2013
	Cotesia sp.		Not specified	Spain	Open field crop	Not specified	Gabarra et al. 2013
	Diolcogaster sp.		Not specified	Spain	*Solanum nigrum*	Not specified	Gabarra et al. 2013
	Dolichogenidea litae (Nixon)	Western Palaearctic, Afrotropical	Not specified	Spain	Open field crop, sentinel infested plants	Not specified	Gabarra et al. 2013

Hymenoptera: Chalcididae	*Brachymeria secundaria* (Ruschka)	Turkey	Larvae not specified	Turkey	Protected crop sampling	Spring	Doganlar and Yigit 2011
	Hockeria unicolor (Walker)	Turkey	Larvae not specified	Turkey, Spain	Protected crop sampling, sentinel infested plants	Spring	Doganlar and Yigit 2011, Gabarra et al. 2013
Hymenoptera: Eulophidae	*Baryscapus bruchophagi* (Gahan)	Turkey	Not specified	Turkey	Protected crop sampling	Spring	Doganlar and Yigit 2011
	Chrysocharis sp.		Larvae not specified		Protected crop sampling, sentinel infested plants	Spring, summer, autumn	Zappalà et al. 2012a
	Cirrospilus sp.		Larvae not specified	Algeria	Protected crop sampling	Spring	Guenaoui unpublished data
	Closterocerus clarus (Szelenyi)	Turkey	L1	Turkey	Protected crop sampling	Spring	Doganlar and Yigit 2011
	Diglyphus sp.		L2	Algeria	Protected crop sampling	Spring	Guenaoui unpublished data
	Diglyphus crassinervis Erdös	Palaearctic	Not specified	Spain	Open field crop sampling	Not specified	Gabarra et al. 2013
	Diglyphus isaea (Walker)	Australasian, Nearctic, Palaearctic, Oriental	Larvae not specified	Algeria, Spain	Protected crop sampling; uncultivated tomato; sentinel infested plants	Not specified	Boualem et al. 2012, Gabarra et al. 2013
	Elachertus sp.		Larvae not specified	Italy	Sentinel infested plants	Autumn	Zappalà et al. 2012a
	Elachertus inunctus species group		Larvae not specified	Italy	Sentinel infested plants	Spring	Zappalà et al. 2012a
	Elasmus sp.		Larvae not specified	Italy	Open field crop sampling, sentinel infested plants	Summer	Zappalà et al. 2012a
	Elasmus phthorimaeae Ferriere	Western Palaearctic	Not specified	Spain	Uncultivated tomato; *Solanum nigrum*	Not specified	Gabarra et al. 2013
	Hemiptarsenus ornatus (Nees)	Palaearctic, Oriental	Larvae not specified	Israel	Open field crop sampling	Not specified	Shaltiel-Harpaz and Gerling unpublished data
	Hemiptarsenus zilahisebessi Erdös	Palaearctic	L2	Algeria	Protected crop sampling	Not specified	Guenaoui et al. 2011b
	Necremnus sp.		Larvae not specified	Italy, Spain	Open field crop sampling; sentinel infested plants	Spring	Zappalà et al. 2012, Gabarra et al. 2013
	Necremnus artynes (Walker)	Palaearctic and Nearctic	L2-L3	Algeria, Egypt, Spain, France	Open field and protected crop (tomato, eggplant) sampling, *Solanum nigrum*, sentinel infested plants	Spring, summer	Gabarra and Arnò 2010, Mollà et al. 2010, Delvare et al. 2011, Guenaoui et al. 2011b, Kolai et al. 2011, Rizzo et al. 2011, Boualem et al. 2012, El-Arnauty unpublished data
	Necremnus near *artynes*		L1-L2-L3	Italy, France, Tunisia, Spain	Open field and protected crop (tomato, eggplant) sampling, sentinel infested plants, uncultivated tomato, *Solanum nigrum*	Spring, summer	Ferracini et al. 2012a, Zappalà et al. 2012a, Abbes et al. 2013, Biondi et al. 2013b, Gabarra et al. 2013
	Necremnus metalarus Walker	Western Palaearctic and Nearctic	L2-L3	Spain	Open field and protected crop sampling	Not specified	Urbaneja et al. 2012
	Necremnus tidius (Walker)	Palaearctic and Nearctic	Not specified	Italy	Not specified	Not specified	Riciputi 2011

(Hymenoptera: Eulophidae)	*Necremnus* near *tidius*		L1-L2	Italy	Open field and protected crop sampling	Spring, summer	Ferracini et al. 2012a, Zappalà et al. 2012
	Neochrysocharis sp.			Algeria	Protected crop sampling	Spring	Boualem et al. 2012
	Neochrysocharis formosa (Westwood) (=*Closterocerus formosus*)	Cosmopolitan	L1-L2-L3	Algeria, France, Italy, Spain	Open field and protected crop sampling;sentinel infeted plants, *Solanum nigrum*	Spring, summer	Lara et al. 2010, Guenaoui et al. 2011b, Ferracini et al. 2012a, Zappalà et al. 2012, Biondi et al.2013b, Gabarra et al. 2013
	Pnigalio (=*Ratzeburgiola*) *cristatus* (Ratzeburg)	Palaearctic	L1-L2	Italy, Spain, Turkey	Open field and protected crop sampling, sentinel infested plant	Spring, summer, autumn	Doganlar and Yigit 2011, Ferracini et al. 2012a, Zappalà et al. 2012a, Gabarra et al. 2013
	Pnigalio sp. *soemius* complex		L1-L2	Italy	Open field and protected crop sampling	Summer, autumn	Ferracini et al. 2012a, Zappalà et al. 2012
	Pnigalio soemius (Walker)	Palaearctic, Oriental	Not specified	Spain	Open field crop sampling	Not specified	Gabarra et al. 2013
	Pnigalio incompletus (Boucek) (=*Ratzeburgiola incompleta*)	Western Palaearctic	Not specified	Italy, Turkey	Protected crop sampling	Spring	Doganlar and Yigit 2011, Zappalà et al. 2012a
	Stenomesius sp.		L2- L3	Algeria	Protected crop sampling	Spring	Guenaoui et al. 2011b
	Stenomesius sp. near *japonicus*		L2- L3	France, Spain	Open field and protected crop (tomato, eggplant) sampling, sentinel infested plant, *Solanum nigrum*	Spring, summer	Gabarra and Arnò 2010, Biondi et al. 2013b, Gabarra et al. 2013
	Sympiesis sp.		Not specified	Algeria, Italy	Protected crop sampling, sentinel infested plants	Spring	Boualem et al. 2012, Zappalà et al. 2012a
	Sympiesis sp. near *flavopicta*		Not specified	Israel	Open field crop sampling	Not specified	Shaltiel-Harpaz and Gerling unpublished data
Hymenoptera: Pteromalidae	*Halticoptera aenea* (Walker)	Nearctic, Palaearctic	Larvae not specified	Italy	Sentinel infested plants	Spring	Zappalà et al. 2012a
	Pteromalus intermedius (Walker)	Turkey	Larvae not specified	Turkey	Protected crop sampling	Spring	Doganlar and Yigit 2011
	Pteromalus semotus (Walker)	Palaearctic, Nearctic, Oriental, Australasian	Not specified	Spain	Sentinel infested plants	Not specified	Gabarra et al. 2013
Hymenoptera: Trichogrammatidae	*Trichogramma* spp.		Eggs	Algeria, Egypt, France, Iran, Spain	Protected crop sampling, sentinel infested plants	Spring, summer, autumn	Gabarra and Arnò 2010, Boualem et al. 2012, Zappalà et al. 2012a, Biondi et al.2013b, Gabarra et al. 2013, El-Arnaouty unpublished data, H. Madadi pers. comm.,
	Trichogramma achaeae Nagaraja & Nagarkatti	Nearctic, Neotropical, Oriental, Palaearctic	Eggs	France	Protected crop sampling	Summer	Biondi et al. 2013b
	Trichogramma bourarachae Pintureau & Babault	Western Palaearctic	Eggs	Tunisia	Open field crop sampling, sentinel infested plants	Spring	Zouba et al. 2013

[2]Yu and Van Actherberg 2010, Noyes 2013