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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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1 **Abstract**

2 The South American tomato leaf miner, *Tuta absoluta* Meyrick (Lepidoptera: Gelechiidae), is an
3 invasive Neotropical pest. After its first detection in Europe it rapidly invaded more than 30
4 Western Palaearctic countries becoming a serious agricultural threat to tomato production in both
5 protected and open field crops. Among the pest control tactics against exotic pests, biological
6 control using indigenous natural enemies is one of the most promising. Here, available data on the
7 Afro-Eurasian natural enemies of *T. absoluta* are compiled. Then, their potential for inclusion in
8 sustainable pest control packages is discussed providing relevant examples. Collections were
9 conducted in 12 countries, both in open field and protected susceptible crops, as well as in wild
10 flora and/or using infested sentinel plants. More than seventy arthropod species, 20% predators and
11 80% parasitoids, were recorded attacking the new pest so far. Among the recovered indigenous
12 natural enemies only few parasitoid species, namely some eulophid and braconid wasps, and
13 especially mirid predators have promising potential to be included in effective and environmentally-
14 friendly management strategies of the pest in the newly invaded areas. Finally, a brief outlook of the
15 future researches and applications of indigenous *T. absoluta* biological control agents is provided.

16

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

19

20 **Introduction**

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

37 In this framework, gaining knowledge on indigenous natural enemies that get adapted to the
38 new hosts and understanding their role in limiting the alien species is essential for establishing the
39 basis of suitable and sustainable control strategies of exotic pests. This applies also to one of the
40 latest invasive species arrived in the Western Palaearctic region: the South American tomato leaf
41 miner, *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae). This moth is a Neotropical species and
42 is considered a key pest of tomato in South America (Guedes and Picanço 2012; Luna et al. 2012)
43 where it remained confined until its first record in Western Palaearctic, in Spain in 2006 (Desneux

44 et al. 2010; Tropea Garzia et al. 2012). Afterwards, it rapidly spread throughout the Mediterranean
45 basin, in Europe, North Africa and Middle East (Desneux et al. 2011). *Tuta absoluta* is considered a
46 typical invasive species because of its capacity to develop very quickly on tomato cultivations and
47 to spread rapidly in new areas causing economically relevant damage (Desneux et al. 2010;
48 Caparros Megido et al. 2012).

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

56 On the other hand, various predators and parasitoids spontaneously attack *T. absoluta* in
57 tomato crops in Europe and in North Africa. Some of these, mainly native Miridae, have been
58 already employed in Integrated Pest Management (IPM) strategies (Castañé et al. 2011; Mollá et al.
59 2011; Cabello et al. 2012; Zappalà et al. 2012b; Chailleux et al. 2013a). However, several
60 screenings for effective natural enemy species in the invaded area are still ongoing (Chailleux et al.
61 2012; Gabarra et al. 2013). More than seventy species of generalist natural enemies have been
62 reported developing on *T. absoluta* in the Western Palaearctic region so far. These have been
63 sampled both on open field and protected susceptible crops as well as on wild flora and/or using
64 infested sentinel plants. Here we take into account all the available data, aiming at giving a
65 comprehensive picture of the composition of the species that spontaneously provide biological
66 control services and their current role in *T. absoluta* control programmes.

67

68

69 **Predators**

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

79 The most widely spread species are mirids belonging to the tribe Dicyphini, with
80 *Nesidiocoris tenuis* (Reuter) spontaneously recovered in eleven countries almost all year round both
81 in protected and open field tomato crops, and *Macrolophus pygmaeus* (Rambur) which was
82 observed preying on *T. absoluta* eggs and young instar larvae in three countries. Guenaoui et al.
83 (2011a) reported *M. caliginosus* Wagner as a predator of *T. absoluta* on tomato in Algeria.
84 However, considering the great number of misconceptions comprised in the classification history of
85 this species [= *M. melanotoma* (Costa)] and in agreement with the most recent taxonomical
86 reconsiderations (Martinez-Cascales et al. 2006; Castañé et al. 2013), also this record is likely to
87 refer to *M. pygmaeus*; therefore, it was included accordingly in table 1. Other four Dicyphini
88 species [*Dicyphus* sp., *D. errans* (Wolff), *D. maroccanus* Wagner and *D. tamanini* Wagner] were
89 sampled from infested tomato plants in Algeria, France, Italy and Spain (Table 1). Anthocorids
90 belonging to the *Orius* genus were found in open field and protected tomato crops infested by *T.*
91 *absoluta* in Jordan. Species of the *Nabis* genus were occasionally found in Iran and Spain. In
92 addition, lacewings belonging to the *Chrysoperla carnea* species group were found feeding on *T.*
93 *absoluta* in open field tomato and two species of predatory mites [*Amblyseius swirskii* Athias-

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

98

99

100 **Parasitoids**

101 A quite large number of parasitoid species (more than 50) was recorded developing on all the young
102 instars and eggs of the moth in the newly invaded areas (Table 2). Overall, the most abundant
103 parasitoid family was the Eulophidae one with 28 recovered species. *Neochrysocharis formosa*
104 (Westwood) [= *Closterocerus formosus* (Westwood)] was one of the most widely spread, being
105 found in four countries (Algeria, France, Italy, Spain). So far, this is the only species recorded on
106 *T. absoluta* both in Europe and in South America, where it was mentioned as a potential biocontrol
107 agent based on its wide host range (Noyes 2013) and presence in other crops, with parasitism rates
108 on *T. absoluta* ranging between 1.5 and 11.2% (Luna et al. 2011). *Closterocerus clarus* (Szelenyi)
109 was recovered on *T. absoluta* young larvae in Turkey. Six species belonging to the genus
110 *Necremnus* were found developing on *T. absoluta* in Algeria, Egypt, France, Italy, Spain and
111 Tunisia, including two entities that were identified as *N. sp. near artynes* and *N. sp. near tidius*.
112 *Necremnus artynes* was the most abundant species in Northwestern Algeria (Guenaoui et al.
113 2011b). Urbaneja et al. (2012) found *N. metalarius* (Walker), developing on *T. absoluta*-infested
114 tomato plants in Spain. However, the taxonomy of this genus is currently under revision, therefore
115 most of these records may need to be verified (Ferracini et al. 2012a; Zappalà et al. 2012a). Besides,
116 other aspects of their biology and ecology should be also further investigated. The ectoparasitoids
117 of Diptera, Lepidoptera and Coleoptera leafminer larvae, *Pnigalio incompletus* (Bouček) and *P.*
118 *cristatus* (Ratzeburg), often associated due to their shared hosts (Noyes 2013), emerged from *T.*

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

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

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

159 Two pteromalid species, *Halticoptera aenea* (Walker), *Pteromalus intermedius* (Walker) and
160 *Pteromalus semotus* (Walker), were found developing on the moth larvae in Italy, Turkey and Spain
161 respectively. Moreover, two species of chalcidid wasps, *Brachymeria secundaria* (Ruschka) and
162 *Hockeria unicolor* Walker, were associated with *T. absoluta* in Turkey. *Tuta absoluta* eggs were
163 parasitized spontaneously by *Trichogramma achaeae* Nagaraja & Nagarkatti in France, by
164 *Trichogramma bourarachae* Pintureau & Babault in Tunisia and by various other unidentified
165 *Trichogramma* species in Algeria, Egypt, France, Iran and Spain (Table 2). In South America more
166 than 12 species of Trichogrammatidae, four Encyrtidae and one Eupelmidae gen. sp. were reported
167 as *T. absoluta* egg parasitoids (Desneux et al. 2010). This higher richness may be due to climatic
168 factors as well as to a more intensive monitoring of egg parasitism in *T. absoluta* native region

169 where many biological control programs have been performed using egg parasitoids (Guedes and
170 Picanço 2012; Parra and Zucchi, 2004).

171

172 **Potential for use of indigenous natural enemies**

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

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

188 Beside the *environmental resistance* that all the recovered fortuitous natural enemies can
189 spontaneously offer in realistic field conditions, there are several approaches that can be artificially
190 implemented to enhance their role in regulating pest populations. Indeed, these indigenous natural
191 enemies can be *inoculated*, *augmented* and *conserved* in the cultivated environment. Inoculation of
192 mass reared *N. tenuis* has been successfully applied in tomato nurseries for the early installation of
193 the predator population in the young crop (Calvo et al. 2012), or directly in greenhouse with the

194 concomitant application of microbial pesticides (Desneux et al. 2010; Mollá et al. 2011). By
195 contrast, although this generalist predator, as well as *M. pygmaeus*, has been largely employed in
196 biological and integrated *T. absoluta* control programs with contrasting results (Arnó et al. 2009;
197 Abbes and Chermiti 2012; Nannini et al. 2012; Trottin-Caudal et al. 2012), it often prompts
198 insecticide applications at high densities due to damages caused to plants and fruits (e.g. Calvo et al.
199 2009; Arnó et al. 2010; Castañé et al. 2011). On the other hand, *M. pygmaeus* has been recently
200 proved not able to build up its populations when feeding only on this prey (Mollà et al. 2014). Thus,
201 higher levels of prey species diversity, such as the concomitant infestations of whiteflies (Bompard
202 et al. 2013), are required for effective inoculative applications of this predator species.

203 Commercially available *T. acheae* individuals are now used against *T. absoluta* by periodic
204 inundative releases (50 adults/m²) in commercial greenhouse successfully (Cabello et al. 2012;
205 Trottin-Caudal et al. 2012). Whereas, similar control levels can be achieved by combining lower
206 release rate of this egg parasitoid with mirid predators, i.e. *M. pygmaeus* and *N. tenuis* (Calvo et al.
207 2012; Chailleux et al. 2013a; 2013b). Fairly good control was obtained in Southern Spain with
208 multiple releases of *N. artynes*, although the reduction was not enough to limit fruit damage to the
209 level reached by *N. tenuis* when released in the nursery (Calvo et al. 2012; Urbaneja et al., 2012).

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

216

217

218 **Future outlooks**

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

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

242 In order to reduce the cost of multiple egg parasitoid releases (Cabello et al. 2012) and/or
243 plant damage of the released omnivorous predators (Castañé et al. 2011), further studies aimed at

244 setting economically sound mass rearing protocols of other indigenous natural enemies are to be
245 developed. This should be aimed at rearing entomophagous species having the least secondary
246 effects on the plants (phytophagy) as well as minimum potential for intraguild predation on other
247 beneficials present in the crop.

248 The overall increase of knowledge on the indigenous natural enemy complex would help all
249 habitat management strategies. These should be aimed at increasing the functional biodiversity
250 within the crop and within the farm, such as rational weed management for increasing food and
251 alternative preys/hosts for indigenous predators and parasitoids (Gardiner et al. 2009; Balzan and
252 Wäckers 2013; Tena et al. 2013). The increase in the abundance and diversity of the natural enemy
253 community could be also obtained through the use of the *banker plants* technique (Parolin et al.
254 2012a; 2012b). Actually, the first banker plant system was developed in greenhouse tomatoes using
255 tomato plants both as crop and banker plants (Stacey 1977). However, this made pest control harder
256 and resulted in reduced application of the technique by the growers. Since then this technique has
257 been successfully tested in tomato crops using non-crop banker plants for various pest-natural
258 enemies systems (Lambert et al. 2005; Xiao et al. 2011).

259 To fully exploit this strategy for *T. absoluta* control, increasing knowledge on the prey/host
260 range of its generalist entomophagous species is crucial (Ingegno et al. 2011; Desneux et al. 2009a;
261 2012). Indeed, the potential applications to enhance the natural enemies populations in the crop
262 could be numerous. In our case, an example is the installation or conservation in the tomato crop of
263 *Parietaria officinalis* L. plants infested by *Cosmopterix pulchrimella* Chambers (Lepidoptera:
264 Cosmopterigidae), that is an alternative host of *N. artynes* (Ferracini et al. 2012a). Another source
265 of *T. absoluta* antagonists could be represented by the proximity of potato plants infested by the
266 potato tuber moth, *Phthorimaea operculella* (Zeller) (Lepidoptera: Gelechiidae), which is often
267 attacked both by the endoparasitoid *D. pulchripes* and by the ectoparasitoid *B. nigricans* (Yu and
268 Van Actherberg 2010). However, although increasing the “right diversity” (Landis et al. 2000) has

269 been proved to reduce pest pressure effectively and to enhance natural enemy activity,
270 *P. operculella* is a serious potato pest and this application should be carefully evaluated before
271 being implemented. An important role may be played also by *Dittrichia viscosa* which is already
272 reported as a refuge plant for several predatory bugs that do move to tomato crops providing
273 important biological control services (Perdikis et al. 2007; 2011). However, as recently highlighted
274 by Castañé et al. (2013) for *Macrolophus* spp., a clarification in the taxonomy of the species related
275 to tomato is strongly needed for effective applications.

276

277 **References**

- 278 Abbes K, Biondi A, Zappalà L, Chermiti B (2013) Fortuitous parasitoids of the invasive tomato
279 leafminer *Tuta absoluta* in Tunisia. *Phytoparasitica* (In press) DOI 10.1007/s12600-013-
280 0341-x
- 281 Abbes K, Chermiti B (2012) Failure of the biological control of *Tuta absoluta* using the predator
282 *Nesidiocoris tenuis* in a protected tomato crop: analysis of factors. *IOBC/WPRS Bull* 80:231-
283 236
- 284 Al-Jboory IJ, Katbeh-Bader A, Al-Zaidi S (2012) First observation and identification of some
285 natural enemies collected from heavily infested tomato by *Tuta absoluta* (Meyrick)
286 (Lepidoptera: Gelechiidae) in Jordan. *Middle East J Sci Res* 11:435-438
- 287 Arnó J, Castañé C, Riudavets J, Gabarra R (2010) Risk of damage to tomato crops by the generalist
288 zoophytophagous predator *Nesidiocoris tenuis* (Reuter) (Heteroptera: Miridae). *B Entomol*
289 *Res* 100:105-115.
- 290 Arnó J, Gabarra R (2011) Side effects of selected insecticides on the *Tuta absoluta* (Lepidoptera:
291 Gelechiidae) predators *Macrolophus pygmaeus* and *Nesidiocoris tenuis* (Hemiptera: Miridae).
292 *J Pest Sci* 84:513-520

293 Arnó J, Sorribas R, Prat M, Matas M, Pozo C, Rodríguez D, Garreta A, Gómez A, Gabarra R
294 (2009) *Tuta absoluta*, a new pest in IPM tomatoes in the northeast of Spain IOBC/WPRS Bull
295 49:203-208

296 Baniameri V, Cheraghian A (2012) The first report and control strategies of *Tuta absoluta* in Iran.
297 EPPO Bull 42:322-324

298 Balzan MV, Wäckers FL (2013) Flowers to selectively enhance the fitness of a host-feeding
299 parasitoid: Adult feeding by *Tuta absoluta* and its parasitoid *Necremnus artynes*. Biol Control
300 67:21-31

301 Bernardo U, Pedata PA, Viggiani G (2006) Life history of *Pnigalio soemius* (Walker) (Hymenoptera:
302 Eulophidae) and its impact on a leafminer host through parasitization, destructive host-feeding
303 and host-stinging behavior. Biol Control 37:98-107

304 Biondi A, Desneux N, Siscaro G, Zappalà L (2012) Using organic-certified rather than synthetic
305 pesticides may not be safer for biological control agents: selectivity and side effects of 14
306 pesticides on the predator *Orius laevigatus*. Chemosphere 87:803-812

307 Biondi A, Zappalà L, Stark JD, Desneux N (2013a) Do biopesticides affect the demographic traits
308 of a parasitoid wasp and its biocontrol services through sublethal effects? PlosOne (In press)
309 DOI: 10.1371/journal.pone.0076548

310 Biondi A, Chailleux A, Lambion J, Zappalà L, Desneux N (2013b) Indigenous natural enemies
311 attacking *Tuta absoluta* (Lepidoptera: Gelechiidae) in Southern France. Egypt J Biol Pest
312 Control 23:117-121

313 Biondi A, Desneux N, Amiens-Desneux E, Siscaro G, Zappalà L (2013c) Biology and developmental
314 strategies of the Palaearctic parasitoid *Bracon nigricans* on the Neotropical moth *Tuta absoluta*.
315 J Econ Entomol 106:1638-1647

316 Bompard A, Jaworski CC, Bearez P, Desneux N (2013) Sharing a predator: can an invasive alien
317 pest affect the predation on a local pest? Pop Ecol 55: 433-440.

- 318 Boualem M, Allaoui H, Hamadi R, Medjahed M (2012) Biologie et complexe des ennemis naturels
319 de *Tuta absoluta* à Mostaganem (Algérie). EPPO Bull 42:268-274
- 320 Cabello T, Gallego JR, Fernandez-Maldonado FJ, Soler A, Beltran D, Parra A, Vila E (2009) The
321 damsel bug *Nabis pseudoferus* (Hem.: Nabidae) as a new biological control agent of the
322 South American Tomato Pinworm, *Tuta absoluta* (Lep.: Gelechiidae), in tomato crops of
323 Spain. IOBC/WPRS Bull 49:219-223
- 324 Cabello T, Gallego JR, Fernandez FJ, Gamez M, Vila E, Del Pino M, Hernandez E (2012)
325 Biological control strategies for the South American tomato moth (Lepidoptera: Gelechiidae)
326 in greenhouse tomatoes. J Econ Entomol 105:2085-2096
- 327 Cagnotti CL, Viscarret MM, Riquelme MB, Botto EN, Carabajal LZ, Segura DF, López SN (2012)
328 Effects of X-rays on *Tuta absoluta* for use in inherited sterility programmes. J Pest Sci
329 85:413-421
- 330 Calvo J, Blockmans K, Stansly PA, Urbaneja A (2009) Predation by *Nesidiocoris tenuis* on *Bemisia*
331 *tabaci* and injury to tomato. Biocontrol 54:237-246
- 332 Calvo FJ, Lorente MJ, Stansly PA, Belda JE (2012) Preplant release of *Nesidiocoris tenuis* and
333 supplementary tactics for control of *Tuta absoluta* and *Bemisa tabaci* in greenhouse tomato.
334 Entomol Exp Appl 143:111-119
- 335 Canale A, Benelli G (2012) Impact of mass-rearing on the host seeking behaviour and parasitism by
336 the fruit fly parasitoid *Psytalia concolor* (Szepligeti) (Hymenoptera: Braconidae). J Pest Sci
337 85: 65-74
- 338 Caparros Megido R, Haubruge E, Verheggen FG (2012) First evidence of deuterotokous
339 parthenogenesis in the tomato leafminer, *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae).
340 J Pest Sci 85:409-412

341 Castañé C, Agustí N, Arnó J, Gabarra R, Riudavets J, Comas J, Alomar O (2013) Taxonomic
342 identification of *Macrolophus pygmaeus* and *Macrolophus melanotoma* based on
343 morphometry and molecular markers. *B Entomol Res* 103: 204-215

344 Castañé C, Arnó J, Gabarra R, Alomar O (2011) Plant damage to vegetable crops by
345 zoophytophagous mirid predators. *Biol Control* 59:22–29

346 Chailleux A, Desneux N, Seguret N, Do Thi Khanh H, Maignet P, Tabone E (2012). Assessing
347 European egg parasitoids as a mean of controlling the invasive South American tomato
348 pinworm *Tuta absoluta*. *PLoS ONE* 7: e48068. doi:10.1371/journal.pone.0048068

349 Chailleux A, Biondi A, Han P, Tabone E, Desneux N (2013a) Suitability of the host-plant system
350 *Tuta absoluta*-tomato for *Trichogramma* parasitoids and insights for biological control. *J Econ*
351 *Entomol* (In press)

352 Chailleux A, Bearez P, Pizzol J, Amiens-Desneux E, Ramirez-Romero R, Desneux N (2013b)
353 Potential for combined use of parasitoids and generalist predators for biological control of the
354 key invasive tomato pest, *Tuta absoluta*. *J Pest Sci* 86: 533-541

355 Cicero L, Sivinski J, Aluja M (2012) Effect of host diet and adult parasitoid diet on egg load
356 dynamics and egg size of braconid parasitoids attacking *Anastrepha ludens*. *Physiol Entomol*
357 37:177-184

358 Cocco A, Deliperi S, Delrio G (2013) Control of *Tuta absoluta* (Meyrick) (Lepidoptera:
359 Gelechiidae) in greenhouse tomato crops using the mating disruption technique. *J Appl*
360 *Entomol* 137:16-28

361 Cornell HV, Hawkins BA (1993) Accumulation of native parasitoid species on introduced
362 herbivores: a comparison of hosts as natives and hosts as invaders. *Amer Natur* 141:847-865

363 Delvare G, Lacordaire AI, Ramel JM (2011) *Necremnus artynes* (Walker, 1839) (Eulophidae), a
364 potential beneficial for the biological control of *Tuta absoluta* (Meyrick).

365 EPPO/IOBC/NEPPO Joint International Symposium on Management of *Tuta absoluta*
366 (Tomato Borer), 16–18 November 2011, Agadir, Morocco. Book of abstract:73

367 Desneux N, Decourtye A, Delpuech JM (2007) The sublethal effects of pesticides on beneficial
368 arthropods. *Annu Rev Entomol* 52:81-106

369 Desneux N, O’Neil RJ (2008) Potential of an alternative prey to disrupt predation of the generalist
370 predator, *Orius insidiosus*, on the pest aphid, *Aphis glycines*, via short-term indirect interactions.
371 *B Entomol Res* 98:631-639

372 Desneux N, Barta RJ, Hoelmer KA, Hopper KR, Heimpel GE (2009a) Multifaceted determinants of
373 host specificity in an aphid parasitoid. *Oecologia* 160:387-398

374 Desneux N, Stary P, Delebecque CJ, Garipey TD, Barta RJ, Hoelmer KA, Heimpel GE (2009b)
375 Cryptic species of parasitoids attacking the Soybean Aphid (Hemiptera: Aphididae) in Asia:
376 *Binodoxys communis* and *Binodoxys koreanus* (Hymenoptera: Braconidae: Aphidiinae). *Ann*
377 *Entomol Soc Am* 102:925-936

378 Desneux N, Wajnberg E, Wyckhuys KAG, Burgio G, Arpaia S, Narvaez-Vasquez CA, Gonzalez-
379 Cabrera J, Catalan Ruescas D, Tabone E, Frandon J, Pizzol J, Poncet C, Cabello T, Urbaneja
380 A (2010) Biological invasion of European tomato crops by *Tuta absoluta*: ecology, history of
381 invasion and prospects for biological control. *J Pest Sci* 83:197-215

382 Desneux N, Luna MG, Guillemaud T, Urbaneja A (2011) The invasive South American tomato
383 pinworm, *Tuta absoluta*, continues to spread in Afro-Eurasia and beyond: the new threat to
384 tomato world production. *J Pest Sci* 84:403-408

385 Desneux N, Blahnik R, Delebecque CJ, Heimpel GE (2012) Host phylogeny and specialisation in
386 parasitoids. *Ecol Lett* 15: 453-460

387 Doğanlar M, Yiğit A (2011) Parasitoid complex of the Tomato Leaf Miner, *Tuta absoluta* (Meyrick
388 1917), (Lepidoptera: Gelechiidae) in Hatay, Turkey. *KSÜ Doğa Bil Derg* 14:28-37

389 El-Arnaouty A, Kortam MN (2012) First record of the Mired predatory species, *Nesidiocoris*
390 *tenuis* Reuter (Heteroptera: Miridae) on the Tomato Leafminer, *Tuta absoluta* (Meyrick)
391 (Lepidoptera: Gelechiidae) in Egypt. Egypt J Biol Pest Control 22:223-224

392 Ferracini C, Ingegno BL, Navone P, Ferrari E, Mosti M, Tavella L, Alma A (2012a) Adaptation of
393 indigenous larval parasitoids to *Tuta absoluta* (Lepidoptera: Gelechiidae) in Italy. J Econ
394 Entomol 105:1311-1319

395 Ferracini C, Ingegno BL, Mosti M, Navone P, Tavella L, Alma A (2012b) Promising native
396 candidates for biological control of *Tuta absoluta* in Italy. IOBC/WPRS Bull 80:51-55

397 Gabarra R, Arnó J (2010) Resultados de las experiencias de control biológico de la polilla del
398 tomate en cultivo de invernadero y aire libre en Cataluña. Phytoma-España 217:66-68

399 Gabarra R, Arnó J, Lara L, Verdú MJ, Ribes A, Beitia F, Urbaneja A, Téllez MM, Mollá O,
400 Riudavets J (2013) Native parasitoids associated with *Tuta absoluta* in the tomato production
401 areas of the Spanish Mediterranean Coast. Biocontrol (In press) DOI: 10.1007/s10526-013-
402 9545-8

403 Gardiner MM, Landis DA, Gratton C, Di Fonzo CD, O'Neal M, Chacon JM, Wayo MT, Schmidt MP,
404 Mueller EE, Heimpel GE (2009) Landscape diversity enhances biological control of an
405 introduced crop pest in the north-central USA. Ecol Appl 19:143-154

406 Gontijo LM, Nechols JR, Margolies DC, Cloyd RA (2012) Plant architecture and prey distribution
407 influence foraging behavior of the predatory mite *Phytoseiulus persimilis* (Acari:
408 Phytoseiidae). Exp Appl Acarol 56:23-32

409 Gontijo PC, Picanço MC, Pereira EJG, Martins JC, Chediak M, Guedes RNC (2013) Spatial and
410 temporal variation in the control failure likelihood of the tomato leaf miner, *Tuta absoluta*.
411 Ann Appl Biol 152:50-59

412 Gordh G, Bearsley JH (1999) Taxonomy and biological control. In: Bellows TS, Fischer TW (eds)
413 Handbook of Biological Control, Academic Press, San Diego, pp 45–56

414 Grabenweger G, Kehrli P, Zweimüller I, Augustin S, Avtzis N, Bacher S, Freise J, Girardo S,
415 Guichard S, Heitland W, Lethmayer C, Stolz M, Tomov R, Volter L, Kenis M (2010)
416 Temporal and spatial variations in the parasitoid complex of the horse chestnut leafminer
417 during its invasion of Europe. *Biol Invas* 12:2797-2813

418 Guedes RNC, Picanço MC (2012) The tomato borer *Tuta absoluta* in South America: pest status,
419 management and insecticide resistance. *EPPO Bull* 42:211-216

420 Guenaoui Y, Bensaad R, Ouezzani K (2011a). Importance of native polyphagous predators able to
421 prey on *Tuta absoluta* Meyrick (Lep: Gelechiidae) on tomato crops.
422 EPPO/IOBC/FAO/NEPPO joint international symposium on Management of *Tuta absoluta*
423 Agadir-Marocco, November 16-18, 2011. Book of abstract, 38.

424 Guenaoui Y, Bensaad R, Ouezzani K, Vercher R (2011b) Emerging opportunities to use native
425 entomophagous against *Tuta absoluta* Meyrick (Lepidoptera: Gelechiidae) infesting tomato in
426 unheated greenhouse in Northwestern Algeria. Between benefits and risks. 9^{eme} Conference
427 Internationale sur les Ravageurs en Agriculture, SupAgro, Montpellier, France, 25-27 October
428 2011:324-334

429 Haddi K, Berger M, Bielza P, Cifuentes D, Field LM, Gorman K, Rapisarda C, Williamson MS,
430 Bass C (2012) Identification of mutations associated with pyrethroid resistance in the voltage-
431 gated sodium channel of the tomato leaf miner (*Tuta absoluta*). *Insect Biochem Mol Biol*
432 42:506-513

433 Harwood JD, Desneux N, Yoo HJS, Rowley DL, Greenstone MH, Obrycki JJ, O'Neil RJ (2007)
434 Tracking the role of alternative prey in soybean aphid predation by *Orius insidiosus*: a
435 molecular approach. *Mol Ecol* 16:4390-4400

436 Heimpel GE, Antolin MF, Franqui RA, Strand MR (1997) Reproductive isolation and genetic
437 variation between two "strains" of *Bracon hebetor* (Hymenoptera: Braconidae). *Biol Control*
438 9:149-156

439 Hokkanen H, Pimentel D (1984) New approach for selecting biological-control agents. Can
440 Entomol 116:1109-1121

441 Ingegno BL, Goula M, Navone P, Tavella L (2008) Distribution and host plants of the genus
442 *Dicyphus* in the Alpine valleys of NW Italy. Bull Insectol 61:139-140

443 Ingegno BL, Pansa MG, Tavella L (2011) Plant preference in the zoophytophagous generalist
444 predator *Macrolophus pygmaeus* (Heteroptera: Miridae). Biol Control 58:174-181

445 Ingegno BL, Ferracini C, Gallinotti D, Alma A, Tavella L (2013) Evaluation of the effectiveness of
446 *Dicyphus errans* (Wolff) as predator of *Tuta absoluta* (Meyrick). Biol Control, (67):246-252

447 Juen A, Hogendoorn K, Ma G, Schmidt O, Keller M (2012) Analysing the diets of invertebrate
448 predators using terminal restriction fragments. J Pest Sci 85:89–100

449 Karabuyuk F (2011) Determination of tomato leafminer [*Tuta absoluta* (Meyrick)] host, population
450 development with parasitoid and predators in the vegetable fields of the Eastern
451 Mediterranean. MSc Thesis, Natural and Applied Sciences Institute of Cukurova University,
452 Adana-Turkey, (in Turkish with English abstract)

453 Keane RM, Crawley MJ (2002) Exotic plant invasions and the enemy release hypothesis. Trends
454 Ecol Evol 17:164-170

455 Kerzhner IM, Josifov M (1999) Cimicomorpha II. Miridae. In: Catalogue of the Heteroptera of the
456 Palaearctic Region (Aukema B., Rieger C. eds.) 3:1-577

457 King RA, Read DS, Traugott M, Symondson WOC (2008) Molecular analysis of predation: a
458 review of best practice for DNA-based approaches. Mol Ecol 17: 947-963

459 Kolai N, Cherifa A, Berkani A, Saiah F, Badaoui M (2011) Observations on the biology of
460 *Necremnus artynes*; new parasitoids of *Tuta absoluta* in Mostaganem (Algeria).
461 EPPO/IOBC/NEPPO Joint International Symposium on Management of *Tuta absoluta*
462 (Tomato Borer), 16-18 November 2011, Agadir, Morocco.

- 463 Landis DA, Wratten SD, Gurr GM (2000) Habitat management to conserve natural enemies of
464 arthropod pests in agriculture. *Annu Rev Entomol* 45:175-201
- 465 Lambert L, Chouffot T, Tureotte G, Lemieux M, Moreau J (2005) Biological control of greenhouse
466 whitefly (*Trialeurodes vaporariorum*) on interplanted tomato crops with and without
467 supplemental lighting using *Dicyphus hesperus* (Quebec, Canada). *IOBC/WPRS Bull* 28:175-
468 178
- 469 Lara L, Aguilar R, Salvador E and Téllez MM (2010) Estudios de control biológico de la polilla del
470 tomate *Tuta absoluta* Meyrick (Lepidoptera; Gelechiidae) en cultivos hortícolas de
471 invernadero del Sureste Español. *Phytoma España* 221:39
- 472 Liebhold AM, Tobin PC (2008) Population ecology of insect invasions and their management.
473 *Annu Rev Entomol* 35:387-408
- 474 Loni A, Rossi E, Van Achterberg C (2011) First report of *Agathis fuscipennis* in Europe as
475 parasitoid of the tomato leafminer *Tuta absoluta*. *Bull Insectol* 64:115-117
- 476 Luna MG, Wada VI, La Salle J, Sánchez NE (2011) *Neochrysocharis formosa* (Westwood)
477 (Hymenoptera: Eulophidae), a newly recorded parasitoid of the Tomato Moth, *Tuta absoluta*
478 (Meyrick) (Lepidoptera: Gelechiidae), in Argentina. *Neotropic Entomol* 40:412-414
- 479 Luna MG, Sanchez NE, Pereyra PC, Nieves E, Savino V, Luft E, Virla E, Speranza S (2012)
480 Biological control of *Tuta absoluta* in Argentina and Italy: evaluation of indigenous insects as
481 natural enemies. *EPPPO Bull* 42:260-267
- 482 Madadi H, Parizi EM, Allahyari H, Enkegaard A (2011) Assessment of the biological control
483 capability of *Hippodamia variegata* (Col.: Coccinellidae) using functional response
484 experiments. *J Pest Sci* 84: 447-455
- 485 Martinez-Cascales JI, Cenis JL, Cassis G, Sanchez JA (2006) Species identity of *Macrolophus*
486 *melanotoma* (Costa 1853) and *Macrolophus pygmaeus* (Rambur 1839) (Insecta: Heteroptera:

487 Miridae) based on morphological and molecular data and bionomic implications. *Insect Syst*
488 *Evol* 37:385-404

489 Mollá O, Monton H, Beitia Crespo FJ, Urbaneja A (2008) La polilla del tomate *Tuta absoluta*
490 (Meyrick), una nueva plaga invasora. *Terralia* 69:36-42

491 Mollá O, Alonso M, Monton H, Beitia F, Verdù MJ, González-Cabrera J, Urbaneja A (2010)
492 Control Biológico de *Tuta absoluta*. Catalogación de enemigos naturales y potencial de los
493 miridos depredadores como agentes de control. *Phytoma Spain* 217:42-46

494 Mollá O, González-Cabrera J, Urbaneja A (2011) The combined use of *Bacillus thuringiensis* and
495 *Nesidiocoris tenuis* against the tomato borer *Tuta absoluta*. *Biocontrol* 56:883-891

496 Mollá O, Alonso-Valiente M, Biondi A, Urbaneja A (2014) A comparative life history study of two
497 mirid bugs preying on *Tuta absoluta* and *Ephestia kuehniella* eggs on tomato crops:
498 implications for biological control. *Biocontrol* (accepted pending revisions)

499 Nannini M, Atzori F, Murgia G, Pisci R, Sanna F (2012) Use of predatory mirids for control of the
500 tomato borer *Tuta absoluta* (Meyrick) in Sardinian greenhouse tomatoes. *EPPO Bull* 42:255-
501 259

502 Noyes JS (2013) Universal Chalcidoidea Database. World Wide Web electronic publication.
503 <http://www.nhm.ac.uk/chalcidoids>

504 O'Connell DM, Wratten SD, Pugh AR, Barnes AM (2012) 'New species association' biological
505 control? Two coccinellid species and an invasive psyllid pest in New Zealand. *Biol Control*
506 62:86-92

507 Parolin P, Bresch C, Poncet C, Desneux N (2012a) Functional characteristics of secondary plants
508 for increased pest management. *Intern J Pest Manag* 58:369-377

509 Parolin P, Bresch C, Desneux N, Brun R, Bout A, Boll R, Poncet C (2012b) Secondary plants used
510 in biological control: A review. *Intern J Pest Manag* 58:91-100

- 511 Parra JRP, Zucchi RA (2004) *Trichogramma* in Brazil: feasibility of use after twenty years of
512 research. *Neotropical Entomology* 33(3):271-281
- 513 Perdikis D, Fantinou A, Lykouressis D (2011) Enhancing pest control in annual crops by
514 conservation of predatory Heteroptera. *Biol Control* 59:13-21
- 515 Perdikis D, Favas C, Lykouressis D, Fantinou A (2007) Ecological relationships between non-
516 cultivated plants and insect predators in agroecosystems: the case of *Dittrichia viscosa*
517 (Asteraceae) and *Macrolophus melanotoma* (Hemiptera: Miridae). *Acta Oecol* 31:299-306
- 518 Ramirez-Romero R, Sivinski J, Copeland CS, Aluja M (2012) Are individuals from thelytokous and
519 arrhenotokous populations equally adept as biocontrol agents? Orientation and host searching
520 behavior of a fruit fly parasitoid. *Biocontrol* 57:427-440
- 521 Riciputi C (2011) Pomodoro, contro la Tuta tre nuovi predatori naturali. *Culture Protette* 40:32-34
- 522 Rizzo MC, Margiotta V, Caleca V (2011) *Necremnus artynes* parassitoide di *Tuta absoluta* su
523 pomodoro, melanzana e *Solanum nigrum* in serra a conduzione biologica. Atti XXIII Congr
524 Naz Ital Entomol, 13-16 June 2011, Genova, Italy
- 525 Savino V, Coviella CE, Luna MG (2012) Reproductive biology and functional response of
526 *Dineulophus phtorimaeae*, a natural enemy of the tomato moth, *Tuta absoluta*. *J Insect Sci*
527 12: 153
- 528 Stacey DL (1977) Banker plant production of *Encarsia formosa* Gahan and its use in control of
529 glasshouse whitefly on tomatoes. *Plant Pathol* 26:63-66
- 530 Stouthamer R (2008) Molecular tools. In: van Driesche R, Hoddle M, Center T (eds) *Control of*
531 *pests and weeds by natural enemies: an introduction to biological control*, Blackwell
532 Publishing, pp 167–180
- 533 Tabone E, Bardon C, Desneux N (2012) Study of dispersal as a selection criterion for
534 Trichogrammatidae for biological control in cauliflower greenhouses. *Acta Hort* 927:227-235

- 535 Tena A, Pekas A, Wäckers K, Urbaneja A (2013) Energy reserves of parasitoids depend on
536 honeydew from non-hosts. *Ecol Entomol* 38: 278–289
- 537 Tropea Garzia G, Siscaro G, Biondi A, Zappalà L (2012) *Tuta absoluta*, an exotic invasive pest
538 from South America now in the EPPO region: biology, distribution and damage. *EPPO Bull*
539 42:205-210
- 540 Trottin-Caudal Y, Baffert V, Leyre JM, Hulas H (2012) Experimental studies on *Tuta absoluta*
541 (Meyrick) in protected tomato crops in France: biological control and integrated crop
542 protection. *EPPO Bull* 42:234-240
- 543 Urbaneja A, Montón H, Mollá O (2009) Suitability of the tomato borer *Tuta absoluta* as prey for
544 *Macrolophus caliginosus* and *Nesidiocoris tenuis*. *J Appl Entomol* 133:292-296
- 545 Urbaneja A, González-Cabrera J, Arnó J, Gabarra R (2012) Prospects for the biological control of
546 *Tuta absoluta* in tomatoes of the Mediterranean basin. *Pest Manag Sci* 68:1215-1222
- 547 Xiao Y, Chen J, Cantliffe D, Mckenzie C, Houben K, Osborne LS (2011) Establishment of papaya
548 banker plant system for parasitoid, *Encarsia sophia* (Hymenoptera: Aphelinidae) against
549 *Bemisia tabaci* (Hemiptera: Aleyrodidae) in greenhouse tomato production. *Biol Control*
550 58:239–247
- 551 Yu DSK, Van Achterberg C (2010) Taxapad Ichneumonoidea (May 2009 Version). In: *Species*
552 *2000 & Itis Catalogue Of Life: 2010 Annual Checklist* (Bisby FA, Roskov YR, Orrell TM,
553 Nicolson D, Paglinawan LE, Bailly N, Kirk PM, Bourgoin T, Baillargeon G, Eds). Dvd,
554 Species 2000, Reading, UK
- 555 Zappalà L, Bernardo U, Biondi A, Cocco A, Deliperi S, Delrio G, Giorgini M, Pedata PC,
556 Rapisarda C, Tropea Garzia G, Siscaro G (2012a) Recruitment of native parasitoids by the
557 exotic pest *Tuta absoluta* (Meyrick) in Southern Italy. *Bull Insectol* 65:51-61

558 Zappalà L, Siscaro G, Biondi A, Mollà O, González-Cabrera J, Urbaneja A (2012b) Efficacy of
559 sulphur on *Tuta absoluta* and its side effects on the predator *Nesidiocoris tenuis*. J Appl
560 Entomol 136:401-409

561 Zappalà L, Campolo O, Grande S, Saraceno F, Biondi A, Siscaro G, Palmeri V (2012c) Dispersal of
562 *Aphytis melinus* (Hymenoptera: Aphelinidae) after augmentative releases in citrus orchards.
563 Eur J Entomol 109: 561-568

564 Zouba A, Chermiti B, Kadri K, Fattouch S (2013) Molecular characterization of *Trichogramma*
565 *bourarachae* strains (Hymenoptera: Trichogrammatidae) from open field tomato crops in the
566 South West of Tunisia. Biomirror 4:13-19 www.bmjjournal.in BM/Vol.4/August 2013/bm-
567 1020310813

568

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

Order Family	Species	Known distribution ¹	<i>T. absoluta</i> instars	Country(ies)	Sampling method(s)	Season(s)	Reference(s)
Mesostigmata: Phytoseiidae	<i>Amblyseius swirskii</i> Athias - Henriot	Western Palaearctic	Eggs and L1	Spain	Protected crop (eggplant) sampling	Summer	Mollá et al. 2010
	<i>Amblyseius cucumeris</i> (Oudemans)	Cosmopolitan	Eggs and L1	Spain	Protected crop (eggplant) sampling	Summer	Mollá et al. 2010
Hemiptera: Miridae	<i>Dicyphus</i> sp.		Eggs and young larvae	France, Italy	Open field and protected crop sampling	Summer	Biondi et al. 2013b, Zappalà et al. unpublished data
	<i>Dicyphus errans</i> (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
	<i>Dicyphus maroccanus</i> Wagner	Mediterranean basin	Eggs and young larvae	Spain	Open field and protected crop sampling	Summer	Mollá et al. 2010
	<i>Dicyphus tamaninii</i> Wagner	Western Palaearctic	Eggs and young larvae	Algeria	Not specified	Not specified	Guenaoui et al. 2011a
	<i>Macrolophus pygmaeus</i> (Rambur)	Western Palaearctic	Eggs and young larvae	Algeria, France, Italy, Spain	Open field and protected crop sampling	Spring, summer, autumn	Arnò et al. 2009, Mollá et al. 2010, Guenaoui et al. 2011a, Boualem et al. 2012, Biondi et al. 2013b, Ingegno et al. 2013
	<i>Nesidiocoris tenuis</i> (= <i>Cyrtopeltis tenuis</i>) (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	<i>Orius</i> sp.		Not specified	Jordan	Open field and protected crop sampling	January-April	Al-Jboory et al. 2012
	<i>Orius albidipennis</i> (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	<i>Nabis</i> sp.		Eggs and young larvae	Iran	Open field crop sampling	Summer	H. Madadi pers. comm.
	<i>Nabis pseudoferus ibericus</i>	Western Palaearctic	Not specified	Spain	Not specified	Not specified	Mollá et al. 2010
Neuroptera: Chrysopidae	<i>Chrysoperla carnea</i> 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	<i>Tapinoma nigerrimum</i> (Nylander)	Western Palaearctic	Larvae	Algeria	Open field and protected crops	Summer	Guenaoui et al. 2011b

570 ¹Kerzhner and Josifov 1999

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

573

Order/Family	Species	Known distribution ²	T. absoluta instars	Country(ies)	Sampling method(s)	Season(s)	Reference(s)
Hymenoptera: Ichneumonidae	<i>Diadegma</i> sp.		Mature larvae-pupae	Italy	Open field crop sampling	Autumn	Zappalà et al. 2012a
	<i>Diadegma ledicola</i> Horstmann	Western Palaearctic	Mature larvae-pupae	Italy	Open field crop sampling	Summer, autumn	Ferracini et al. 2012a
	<i>Diadegma pulchripes</i> (Kokujev)	Palaearctic	Mature larvae-pupae	Italy	Open field (potato) crop sampling, sentinel infested plant	Summer, autumn	Zappalà et al. 2012a
	<i>Hyposoter didymator</i> (Thunberg)	Australasian, Western Palaearctic	Not specified	Algeria	Protected crop sampling	Spring	Boualem et al. 2012
	<i>Temelucha anatolica</i> (Sedivy)	Palaearctic	Not specified	Spain	Open field crop sampling	Not specified	Gabarra et al. 2013
	<i>Zoophthorus macrops</i> Bordera & Horstmann	Spain	Not specified	Spain	Open field crop sampling	Not specified	Gabarra et al. 2013
Hymenoptera: Braconidae	<i>Agathis</i> sp.		Larvae not specified	Italy	Open field crop sampling	Summer	Ferracini et al. 2012a
	<i>Agathis fuscipennis</i> Zetterstedt	Western Palaearctic		Italy	Open field sampling of infested <i>Solanum nigrum</i>	September - October	Loni et al. 2011
	<i>Apanteles</i> sp.		Not specified	Spain	<i>Solanum nigrum</i>	Not specified	Gabarra et al. 2013
	<i>Bracon</i> sp.		Mature larvae	Tunisia	Sentinel infested plants exposure	Spring, summer	Abbes et al. 2013
	<i>Bracon</i> (= <i>Habrobracon</i>) <i>didemie</i> Beyarslan	Turkey	Mature larvae	Turkey	Open field and protected crop sampling	Spring	Doganlar and Yigit 2011
	<i>Bracon</i> (= <i>Habrobracon</i>) <i>hebetor</i> 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
	<i>Bracon</i> (= <i>Habrobracon</i>) <i>nigricans</i> (= <i>concolorans</i> , <i>concolor</i> , <i>mongolicus</i>) 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
	<i>Bracon</i> (= <i>Habrobracon</i>) sp. near <i>nigricans</i>		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
	<i>Bracon</i> (= <i>Habrobracon</i>) <i>osculator</i> (Nees)	Palaearctic	Mature larvae	Italy	Open field and protected crop sampling, sentinel infested plants	Summer, autumn	Ferracini et al. 2012a, Zappalà et al. 2012
	<i>Chelonus</i> sp.		Not specified	Spain	<i>Solanum nigrum</i>	Not specified	Gabarra et al. 2013
	<i>Choeras semele</i> (Nixon)	Western Palaearctic	Not specified	Spain	<i>Solanum nigrum</i>	Not specified	Gabarra et al. 2013
	<i>Cotesia</i> sp.		Not specified	Spain	Open field crop	Not specified	Gabarra et al. 2013
	<i>Diolcogaster</i> sp.		Not specified	Spain	<i>Solanum nigrum</i>	Not specified	Gabarra et al. 2013
	<i>Dolichogenidea litae</i> (Nixon)	Western Palaearctic, Afrotropical	Not specified	Spain	Open field crop, sentinel infested plants	Not specified	Gabarra et al. 2013

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

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