

Accepted Manuscript

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PII: S1049-9644(09)00149-2

DOI: [10.1016/j.biocontrol.2009.05.014](https://doi.org/10.1016/j.biocontrol.2009.05.014)

Reference: YBCON 2295

To appear in: *Biological Control*

Received Date: 5 January 2009

Revised Date: 18 May 2009

Accepted Date: 25 May 2009



Please cite this article as: Biddinger, D.J., Weber, D.C., Hull, L.A., Coccinellidae as predators of mites: Stethorini in biological control, *Biological Control* (2009), doi: [10.1016/j.biocontrol.2009.05.014](https://doi.org/10.1016/j.biocontrol.2009.05.014)

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1 For Submission to: *Biological Control*

2 Special Issue: "Trophic Ecology of Coccinellidae"

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5 **COCCINELLIDAE AS PREDATORS OF MITES: STETHORINI IN BIOLOGICAL CONTROL**

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15 **ABSTRACT.** The Stethorini are unique among the Coccinellidae in specializing on mites
16 (principally Tetranychidae) as prey. Consisting of 90 species in two genera, *Stethorus* and
17 *Parastethorus*, the tribe is practically cosmopolitan. The Stethorini are found in a diverse range
18 of habitats, including many agricultural systems such as pome and stone fruits, brambles, tree
19 nuts, citrus, avocados, bananas, papaya, palms, tea, cassava, maize, strawberries, vegetables,
20 and cotton, as well as ornamental plantings, grasslands, forests, and heathlands. Tetranychid
21 mite outbreaks became common in many agricultural systems only after World War II, when
22 widespread use of broad-spectrum insecticides increased. Stethorini were initially appreciated
23 only for their ability to suppress severe outbreaks of tetranychid populations. However, research
24 on their prey searching behaviors reveals that Stethorini use visual and olfactory stimuli to locate
25 small mite colonies in patchy distributions, and can be very effective in regulating their prey at
26 low densities. Moreover, acariphagous coccinellids colonize mite outbreaks earlier, and
27 consume more pest mites, than many other mite predators. Key to the use of coccinellids in
28 conservation biological control programs is the provision of overwintering habitats and refuges
29 from pesticides in and near cropland. When these conditions are fulfilled, Stethorini often play
30 important roles in maintaining suppression of tetranychid populations. Examples of successful
31 biological mite control with Stethorini include apple orchards in Pennsylvania, USA, and citrus
32 in Asia, and the unintended disruption of a tetranychid-based biological control program for the
33 invasive woody weed, gorse, in Australia and New Zealand. The systematics and taxonomy of
34 this group is challenging with many cryptic species, and molecular diagnostic tools are sorely
35 needed. How best to utilize their mite-suppressive potential in diverse settings requires better
36 knowledge of their requirements including utilization of alternative foods, refuges for dormancy
37 and from nonselective pesticides, and host-finding mechanisms.

38 **Key words:** Coccinellidae, *Stethorus*, Acari, acariphagous, tetranychid, spider mites

39

40 **1. Introduction**

41 The approximately 90 worldwide species of the tribe Stethorini Dobzhansky (genera
42 *Stethorus* Weise and *Parastethorus* Pang and Mao) are the only specialist mite predators in the
43 Coccinellidae. Most predaceous Coccinellidae are specialist aphid or scale feeders, but have a
44 wide range of accepted foods that they can utilize for various life processes (Obrycki et al., 2009;
45 Evans, 2009; Hodek and Honěk, 2009; Lundgren, 2009b; all in this issue). Entomophagous
46 coccinellid species (or genera) such as *Hippodamia convergens* Guerin-Meneville, *Coleomegilla*
47 *maculata* De Geer, *Harmonia axyridis* (Pallas), *Olla abdominalis* (Say), *Adalia*, *Eriopus*,
48 *Scymnus*, and *Psyllobora* feed on mites, but these prey are often suboptimal for reproduction
49 (Dean, 1957; McMurtry et al., 1970; Hodek and Honěk, 1996; Rondon et al., 2004), and these
50 taxa are not considered to be primary predators of mites (McMurtry et al., 1970; Hodek and
51 Honěk, 1996).

52 Within the Stethorini, adults and larvae of *Stethorus* and *Parastethorus* spp. are specialists on
53 spider mites (Tetranychidae) and the closely related Tenuipalpidae, which are known as false
54 spider mites or flat mites (Chazeau, 1985), both of which are important agricultural pests
55 worldwide. Many natural enemies within the Coleoptera, Dermaptera, Diptera, Hemiptera,
56 Neuroptera, and Thysanoptera feed on spider mites, but vary in their degree of adaptation to and
57 preferences for this prey and in their abilities to regulate pest mite populations (Helle and
58 Sabelis, 1985). Biological control of spider mites has centered on two groups of biological
59 control agents, the predatory mites in the family Phytoseiidae, and various species of Stethorini
60 (reviews by McMurtry et al., 1970; Helle and Sabelis, 1985; and McMurtry and Croft, 1997).

61 Our understanding of what constitutes an effective mite biological control agent has changed
62 considerably over the last 50 years. Early research focused on the abilities of acariphagous mites
63 and coccinellids to overcome spider mite outbreaks, and on the abilities of these predators to
64 develop resistance to pesticides applied to control primary pests in highly managed
65 agroecosystems such as apple and citrus. More recently, the potential of some phytoseiid
66 predators to regulate spider mites at low equilibrium densities has become more widely
67 appreciated (Croft, 1990; McMurtry and Croft, 1997; Biddinger and Hull, 2005).

68 Various species of Stethorini have received considerable attention over the last five decades
69 because of their potential as biological control agents of spider mites. At least 12 species of
70 Stethorini have been imported into the U.S. for this purpose (Gordon, 1985) and many more have
71 been purposefully redistributed throughout the world. Chazeau (1985) summarized information
72 on Stethorini general biology and reported that 40% of the 68 species attacked spider mites of
73 economic importance. This review summarizes disparate sources of information on *Stethorus*
74 across many different crops worldwide for the first time. We also examine the 40-year case
75 history of *Stethorus punctum punctum* (LeConte) as the key component of biological mite
76 control in Pennsylvania apple orchards, and the sustainability of using Stethorini as biological
77 control agents in the face of changing pesticide use patterns.

78

79 **2. Overview of Stethorini**

80 **2.1. Taxonomic status.** Earlier works placed *Stethorus sensu lato* in the tribe Scymnini, but
81 recent works placed it in the monogeneric tribe Stethorini Dobzhansky (Chazeau, 1985; Hodek
82 and Honěk, 1996; Giorgi et al., 2009, this volume). Stethorini are unique from all other
83 Scymninae by the convex anterior margin of the prosternum and the truncate clypeus near the

84 antennal bases (Gordon, 1985). Recently, Ślipiński (2007) raised the subgenus *Parastethorus*
85 Pang and Mao (Gordon and Chapin, 1983) to generic status, which this review reflects. Gordon
86 and Chapin (1983) had earlier placed the following species into what was then the subgenus
87 *Parastethorus*: *Stethorus tuncatus* Kapur from Malaysia, *S. gutierrezii* Chazeau from New
88 Hebrides, *S. nigripes* Kapur and *S. histrio* Chazeau from Australia. Five species from Asia are
89 now considered to be in *Parastethorus* as well: *S. dichiapiculus* Xiao, *S. guangxiensis* Pang and
90 Mao, *S. indira* Kapur, *S. malaicus* Xiao, and *S. yunnanensis* Pang and Mao (Yu, 1996).

91
92 **2.2. Morphology and life stages.** Almost all adults of *Stethorus* are small (1-1.5 mm),
93 pubescent, black with brown or yellow legs and antennae. The pubescence may be an adaptation
94 to aid foraging within the silken webbing of some tetranychids, a feature also seen in some
95 species of Phytoseiidae (Houck, 1985; McMurtry and Croft, 1997). Gender can be distinguished
96 by the small notch in the 8th sternite in male beetles (smooth in females) (McMurtry et al., 1974;
97 Biddinger, 1993). Species cannot be determined without examining the male genitalia; most
98 species cannot be determined in female specimens. The eggs are mostly white to creamy colored
99 elongated ellipsoids (a few species have pinkish or dark eggs) and are glued longitudinally along
100 the mid-veins of the undersides of the leaves. Larval color differs among species, and is often
101 useful in field identification (Khan et al., 2002; Muma, 1955b; Putman, 1955b; Pasqualini and
102 Antropoli, 1994; Pollock and Michels, 2002, 2003, 2007; Biddinger et al., 2008a, b). There are
103 generally four stadia. *Stethorini* larvae generally do not consume the entire mite as asserted by
104 Chazeau (1985); instead they pierce the mite eggs or active stages, repeatedly regurgitate and
105 imbibe the prey juices, leaving the crumpled exoskeleton (Cottier, 1934; Fleschner, 1950;
106 Collyer, 1953; Robinson, 1953; Putman, 1955a; Kaylani, 1967; Houck, 1991). Pupae are

107 uniformly dark brown or black, covered with numerous setae, and affixed to either side of the
108 leaves (Chazeau, 1985; Biddinger, 1993).

109 The cryptic nature of the adult species characteristics has undoubtedly led to species
110 misidentifications in the literature. Their superficial similarity to some species of *Delphastus*,
111 *Scymnus*, and *Telsimia* probably accounts for most reports of Stethorini feeding on scale or
112 aphids. The importance of this group in biological control in many crops throughout the world,
113 and the difficulties in separating species, make it an excellent candidate group for systematic
114 treatment as well as diagnostic taxonomy by molecular barcoding methods.

115
116 **2.3. Geographical Distribution.** Stethorini are present throughout the world in many
117 different climates ranging from tropical rainforests to temperate deciduous forests and plains to
118 colder northern regions of Europe, Canada and Russia (see map, Fig. 1, for distribution of
119 economically important species). *Stethorus punctillum* Weise has the largest distribution in the
120 group, ranging over most of temperate North America, Europe, and Asia. A major driving force
121 behind the current geographic distribution of Stethorini has been their intentional redistribution
122 by biological control scientists. For example, approximately 12 species (some of which were
123 never formally identified) were introduced into California from geographically diverse areas
124 such as Australia, China, Guatemala, India, Morocco, Pakistan, South Africa, and Turkey (Hall
125 and Fleschner, 1958; Gordon, 1982). Some of the earliest introductions occurred in Hawaii,
126 which apparently has no native species of Stethorini (Swezey, 1925; Fournier et al., 2002).
127 *Parastethorus nigripes* (Kapur) represents the most recent introduction of Stethorini in North
128 America (Gordon, 1993). This is an important predator of *Panonychus ulmi* (Koch) and
129 *Tetranychus urticae* Koch in Australia (Edwards and Hodgson, 1973; Field, 1979).

130 *Parastethorus nigripes* established itself in Texas corn where it consumes the Banks grass mite,
131 *Oligonychus pratensis* (Banks) (Pollock and Michels, 2002), but only after introductions into
132 California almonds failed (Hoy and Smith, 1982). The other recent addition to the North
133 American fauna is *P. histrio* (= *Stethorus histrio*), from the Mascarene Islands east of
134 Madagascar (Gordon and Anderson, 1979). It has since been found throughout Australia
135 (including Tasmania), New Caledonia and parts of South America. Aguilera P. (1987) surmised
136 it to be introduced accidentally into central Chile. Gordon and Chapin (1983) extended the range
137 north into the Yucatan (Mexico), but Pollock and Michels (2003) reported it for the first time in
138 the United States feeding on mites in corn, co-occurring with the native species *Stethorus caseyi*
139 Gordon and Chapin and *P. nigripes*. Pollock and Michels (2003) found *S. caseyi* to be relatively
140 scarce and speculated as to whether it had been displaced by these newly introduced species.

141 Additional introductions of Stethorini have likely established into new geographical ranges;
142 the number is unknown because many species can only be identified by taxonomic experts of the
143 group. The accidental introduction of *S. punctillum* from Europe into North America completely
144 displaced the native *S. punctum* from Ontario fruit orchards and other habitats over a 20 year
145 period (Putman, 1955a; Putman and Herne, 1966). In Québec, *S. punctillum* has been the only
146 species collected from raspberry and apple crops in the past 15 years (pers. comm. with Michèle
147 Roy, MAPAQ Laboratoire de Diagnostic en Phytoprotection).

148

149 **3. Behavior as predators**

150 **3.1. Prey searching behavior.** Many early studies of various species of Stethorini concluded
151 that they are “high density predators” unable to regulate spider mite populations at low densities
152 (Fleschner, 1950; Bailey and Caon, 1986; Tanigoshi and McMurtry, 1977). Congdon et al.

153 (1993) challenged this “high density predator” designation and asserted that high density spider
154 mite populations have become common only since the advent of synthetic insecticides (Huffaker
155 et al., 1970), and that the studies that support the “high density predator” status of Stethorini
156 ignored the spatial context of spider mite populations. While it is true that most Stethorini
157 species do not lay eggs until mite populations are relatively high in comparison to the low mite
158 levels maintained by some Phytoseiidae, the Stethorini have provided economically successful
159 regulation of pest mites in several cases. Reasons underlying these success stories include a) the
160 regulatory potential of the long-lived adults; b) the ability of adults to rapidly immigrate into
161 cropland; and c) the ability of non-pest tetranychid mite populations, non-tetranychid mites,
162 extrafloral nectaries, aphid honeydew, and pollen, to support populations of Stethorini before
163 pest mite populations reach outbreak proportions in crops. The importance of Stethorini species
164 worldwide as biological control agents is also suggested by the over 500 references found in the
165 course of this review.

166 Congdon et al. (1993) hypothesized that the active discovery of rare and very small prey
167 patches by adult Stethorini was a key element in their natural interactions with spider mites over
168 evolutionary time. Few, if any, predator eggs are laid until mite populations become high
169 enough to support the development of larvae, a common phenomenon in coccinellids (Seagraves,
170 2009, this issue). Then the impressive numerical response of Stethorini would reduce damaging
171 mite populations later in the season on crops which are often more tolerant of late season mite
172 injury. Pesticides applied for mite control frequently kill Stethorini, and so the natural low-
173 density interactions between predators and pests do not occur. Subsequently, spider mite
174 populations increase, and Stethorini immigrate in response to these ample mite populations.

175 Thus, there is the illusion that *Stethorini* function as “high density predators” within pesticide-
176 treated cropland.

177 Even when insecticides are applied to crops, *Stethorus* can quickly reduce mite populations
178 and may prevent economic injury. Adult *S. punctum* were able to find eight *P. ulmi*-infested
179 apple trees out of a 1-ha orchard, even though these infested trees had fewer than 1 mite/leaf
180 (Hull et al., 1977b). Similarly, *S. punctum* was able to find small patches of pest mites in
181 avocados, citrus, and raspberries (Congdon et al., 1993; McMurtry and Johnson, 1966; Haney et
182 al., 1987). Similar low-density detection of mite prey has also been demonstrated by *S. chengi* in
183 citrus orchards in China (Chen, 1993; Chen & Zhao, 1994). The cues that *Stethorini* adults
184 employ to find these small populations of mites are poorly understood, but some evidence points
185 to a combination of visual and olfactory cues. The detection of prey by the larval stages is
186 generally thought to be tactile with visual cues being non-existent (Fleshner, 1950; Putman,
187 1955a, b; McMurtry et al., 1970; Houck, 1985; Houck, 1986).

188
189 *3.1.1. Visual stimuli.* At least some species of *Stethorini* are visually attracted to white or
190 yellow colors. When spider mite populations are low, sticky traps can be more effective than
191 visual counts in monitoring *Stethorus* populations (Felland et al., 1995; Biddinger and Hull,
192 1996; Takahashi et al., 2001a; Roy et al., 2005). Readshaw (1975) used white sticky card traps to
193 monitor *Stethorini* populations in orchards early in the season. Felland et al. (1995) found that
194 yellow sticky card traps captured up to 15 times more *S. punctum* than white traps. Spider mite
195 feeding causes a yellowing (bronzing) of leaves, and like many other coccinellids (Seagraves,
196 2009, this issue), foraging *Stethorini* adults may use this color as an indication of prey. *Stethorus*

197 *punctum* is primarily diurnal (Hull et al., 1977b), which reinforces the hypothesis that vision is
198 an important foraging cue.

199
200 *3.1.2. Olfactory stimuli.* Prey-derived olfactory stimuli are another important cue for
201 foraging Stethorini adults. Colburn and Asquith (1970) examined the olfactory response of adult
202 *S. punctum* to *P. ulmi* under choice conditions. The beetles walked preferentially toward prey
203 versus the no-prey treatments in the presence and absence of apple foliage. Later work found
204 that *S. japonicus* and *S. punctillum* also are attracted to the volatiles of tetranychid-infested plants
205 (unpublished data cited in Takahashi et al., 2001b; Lentz et al., 2004). Lentz et al. (2004) went
206 on to show that at least some of the attractive volatiles were produced by infested cucumber and
207 bean plants.

208 There have been several efforts to identify the prey-associated chemistry that is attractive to
209 Stethorini. James (2003a) and James and Price (2004) found that *S. punctum* was attracted to
210 white traps baited with a synthetic herbivore-induced plant volatiles including methyl salicylate
211 and (Z)-3-hexenyl acetate under field conditions. More *S. punctum* were recovered from beating
212 samples in hop yards treated with time-release methyl salicylate, and the attraction of this and
213 other predators was observed to reduce *T. urticae* numbers dramatically in an unreplicated study.
214 Similar results were obtained with unbaited sticky cards in replicated vineyards treated with
215 time-release methyl salicylate. James (2005) also found cis-3-hexen-1-ol and benzaldehyde to
216 be attractive to *S. punctum* in additional field trials with multiple synthetic plant volatiles.

217 Although it is clear that olfactory cues are important in attracting foraging Stethorini,
218 beetles do not necessarily respond to specific olfactory stimuli under field conditions. For
219 example, *S. japonicus* was not significantly attracted to sticky traps with plant volatile blends in

220 a Japanese pear orchard, perhaps because high *Tetranychus kanzawai* Kishida populations may
221 have obscured the trap-associated volatile attractants (Takahashi et al., 2001a). In another study,
222 infested host odors or other plant cues (e.g., plant location or stature) may have inhibited the
223 attractiveness of mite-infested bean plants to *S. japonicus* (Takahashi et al., 2001b). Gillespie et
224 al. (1997) used potted bean plants infested with *T. urticae* to collect *S. punctillum* and several
225 other mite predators in several habitats in British Columbia, Canada, indicating perhaps that not
226 all Stethorini spp. are equally attracted to the same volatiles.

227

228 **3.2. Trophic Ecology and Life History Parameters.**

229 *3.2.1. Relative quality of mites as prey.* As shown in Table 1, Stethorini attack a large
230 number of tetranychid species on many different crops. Although it appears that most feed on
231 multiple tetranychid prey species, some species are more specialized than others and some
232 tetranychid prey are less suitable than others. For example, *S. punctillum* and *S. gilvifrons* do not
233 readily feed on or reproduce on the tetranychid mites of the genus *Bryobia* (Putman, 1955a;
234 Kaylani, 1967). Houck and Strauss (1985) found a weak, but consistent, feeding preference of *S.*
235 *punctum* for *T. urticae* over *P. ulmi*, but this preference was affected by preconditioning of the
236 predator for specific mite species, and preferences did not persist from larval to adult stages.

237 Many prey change in their suitability for coccinellids as they age (Hodek and Honěk, 2009,
238 this issue), and mites are no exception. Stethorini adults and larvae often prefer mite eggs over
239 other pest life stages (Houck, 1991; Tanigoshi and McMurtry, 1977), but *S. madecassus*
240 preferred adult mites over eggs as prey (Chazeau, 1974b). Generally, eggs are the most
241 nutritious life stage of a prey item, largely because they contain less water (Lundgren, 2009a).
242 Also, the eggs may be less defended, more apparent to mobile adults, or more abundant than

243 other life stages. Most studies employ only a single life stage of mite prey (usually adult females
244 or eggs) when they determine the developmental rates of various Stethorini species, and do not
245 examine the nutritional values of the various prey stages or intraspecific competition between
246 predator stages. Houck (1991) speculated that varying the mite stages consumed by *S. punctum*
247 might prevent severe oscillations in both the predator and the prey populations. As with many
248 other coccinellids, Stethorini females often consume more prey than conspecific males (Hull et
249 al., 1977b; Chazeau, 1985).

250 Some Stethorini utilize non-tetranychid mites as alternative prey in times of starvation. Ullah
251 (2000) compared the suitability of the phytoseiid predatory mite, *Phytoseiulus persimilis* Athias-
252 Henriot, the eriophyid rust mite, *Auclops lycopersi* (Masse), the tenupalpid broad mite,
253 *Polyphagotarsonemus latus* (Banks), and the tetranychid spider mite, *T. urticae* as prey for
254 *Stethorus vagans* (Blackburn) adults. Mating and oviposition of fertile eggs was observed only
255 in *S. vagans* adults that were fed tetranychid or broad mites. However, mating, oviposition and
256 fecundity were much lower with the broad mite diet than with tetranychid prey. Rust mite, but
257 not phytoseiid mite, diets prolonged survival. Hull (pers. obs.) has observed *S. punctum*
258 commonly feeding on both the phytoseiid (most likely *Neoseiulus fallacis* (Garman)) and the
259 eriophyid mite, *Aculus schlechtendali* (Nalepa) early in the season when spider mite populations
260 were very low and the predators were pre-reproductive. Kaylani (1967) and Putman (1955a)
261 observed *Stethorus* spp. feeding on phytoseiids in the field, and Mathur (1969) observed adult *S.*
262 *gilvifrons* eating a predatory *Anystis* sp. (Acari: Anystidae).

263

264 3.2.2. *Non-mite foods of Stethorini.* Reports of Stethorini feeding on non-acarid prey and
265 non-prey foods challenge the assertion that all species feed and develop only on spider mites.

266 Al-Duhawi et al. (2006) found *S. gilvifrons* adults and larvae to be very efficient predators of all
267 stages of the *Bemisia tabaci* and, in laboratory trials, found the larvae completed their
268 development on this prey alone. Silva and Bonani (2008) reported *S. minutulus* Gordon and
269 Chapin feeding on the tobacco whitefly on cotton in Brazil as well. However, L.D. Silva (pers.
270 comm.) confirmed that the coccinellid found feeding on whiteflies was actually a species of
271 *Delphastus* (Sticholotidinae); some specimens of *S. minutulus* feeding on mites in the same
272 whitefly colony had been sent for identification by mistake. Mathur (1969) observed that
273 starving larval and adult *S. gilvifrons* ate *Macrosiphum* sp. (Hemiptera: Aphididae) “to a very
274 limited extent,” and Almatni and Khalil (2008) reported this species “fed occasionally” on
275 *Brachycaudus amygdalinus* (Schouteden)(Hemiptera: Aphididae). Masee (1940) noted *S.*
276 *punctillum* as a predator of *Phorodon humuli* (Schrank)(Hemiptera: Aphididae).

277 Numerous coccinellid species can utilize pollen, fungal spores, and nectar as alternative
278 food sources (Lundgren, 2009a, 2009b, this issue). Ullah (2000) found that addition of pollen or
279 honey to a water-only diet doubled the longevity of adult *S. vagans*, but beetles did not mate or
280 reproduce on either of these foods. Mathur (1969) found that *S. gilvifrons* consumed aphid
281 honeydew in the lab, and also stated that the larvae “remain adhere [*sic*] to the sticky secretion.”
282 Pemberton and Vandenberg (1993) reported that *Stethorus* spp. fed at *Prunus padus* L. foliar
283 extrafloral nectaries in South Korea, and Putman (1955a, 1963) found that *S. punctillum*, in the
284 absence of other food, would eat raisins, aphids, aphid honeydew, and peach leaf extrafloral
285 nectar. While all of these foods prolonged adult survival in *S. punctillum*, egg production was
286 greatly reduced or prevented (Putman, 1955a).

287

288 3.2.3 *Developmental and prey consumption rates.* Some attractive characteristics of
289 Stethorini for mite biological control are their prey consumption, longevity and high
290 reproductive capacity (Table 2). Each adult female may consume 30 to 60 mites per day. Total
291 fecundity ranges from 123 eggs in *S. tridens* (Fiaboe et al., 2007), 184 eggs in *S. madecassus*
292 (Chazeau, 1974a, b), 221 in *S. punctum* (Tanigoshi and McMurtry, 1977), 279 in *S. punctillum*
293 (Roy et al., 2003), to a high of 501 eggs in *S. japonicus* (Mori et al., 2005). Developmental times
294 for most species are approximately 17 d at 25°C from oviposition to adult eclosion (Fiaboe et al.,
295 2007; Mori et al., 2005; Putman, 1955a; Roy et al., 2002; Tanigoshi and McMurtry, 1977). The
296 number of Stethorini generations per year varies from 2 to 3 in temperate regions for *S.*
297 *punctillum* and *S. punctum* (Putman, 1955a; Colburn and Asquith, 1971) to more than 15 per
298 year for tropical species such as *S. siphonulus* and *S. pauperculus* (Puttaswamy and
299 Rangaswamy 1976; Puttaswamy and ChannaBasavanna 1977). Adult longevity is not known for
300 most species, but appears to be longer in temperate species which undergo diapause than in
301 tropical species, and is temperature dependent. Putman (1955a) found *S. punctillum* females in
302 Canada could commonly survive and lay eggs over multiple seasons under field conditions, with
303 an average longevity of over 400 days; males generally die sooner than females. Ullah (2000)
304 found adults of both sexes of *S. vagans* in Australia lived 126 days at 12°C compared to only 27
305 days at 30°C.

306 Since the developmental times differ little amongst species of Stethorini, the differences in
307 r_m -values between species are attributable to differences in reproductive rates (Mori et al., 2005)
308 (Table 2). At 24-25°C the r_m -values for *Stethorus* species range from 0.100 in *S. punctillum*
309 (Roy et al., 2003) to 0.160 in *S. loi* (Shih et al., 1991); a number of other species have been
310 evaluated and found to fall within this range (Chazeau, 1974a, b; Fiaboe et al., 2007; Mori et al.,

311 2005; Richardson, 1977; Tanigoshi and McMurtry, 1977). Sabelis (1985a, b, 1991) calculates
312 that the r_m -values for tetranychid mites range from 0.160 to 0.293 at around 25°C. This is
313 significantly higher than the values for Stethorini species listed in Table 2, but their functional
314 response to prey may still allow them to regulate pest populations.

315 Few studies have calculated the functional response of *Stethorus*. Houck (1991) examined
316 handling time as a component of the functional response of *S. punctum* to *T. urticae*, and found
317 that the handling time of starved beetles for each prey increased due to a greater extraction of
318 body fluids from individual prey. *Stethorus punctum* continued to feed even when satiated with
319 high prey densities and continued to pierce mites, initiate feeding, but then subsequently abandon
320 the prey with minimal extraction of bodily fluids in a classic Type 3 response. This type of
321 response has been observed in other systems as well (Hull et al. 1977a; Haji-Zadeh et al., 1993;
322 Peterson et al., 2000). Type 1 & 2 functional responses have been observed in other *Stethorus*
323 spp. (Hull et al. 1977a; Gotoh et al., 2004)

324
325 *3.2.4. Diapause and overwintering.* All Stethorini in temperate climates overwinter as adults,
326 with a reproductive diapause that is induced by short day lengths and cooler temperatures.
327 *Stethorus punctum* entered reproductive diapause at day lengths of 10 h or less and 21-22°C
328 (McMurtry et al., 1974). *Stethorus japonicus* was induced into reproductive diapause with day
329 lengths shorter than 13 h at 18°C (Mori et al., 2005). Species with large geographical ranges that
330 include both temperate and subtropical climates may hibernate in the colder area but not in the
331 warmer (Collyer, 1964; Kaylani, 1967). For example, *S. punctum* diapauses in Pennsylvania
332 (Colburn and Asquith, 1971; Colburn, 1971) and in Washington state (Horton et al., 2002), but is

333 active year round in southern California (McMurtry et al., 1970; 1974). Tropical species seldom
334 experience diapause (Chazeau, 1985; Hoy and Smith, 1982).

335 Several studies have shown that *S. punctillum* and *S. punctum* overwinter within fruit
336 orchards and the adjacent habitat. Putman (1955a) and Felland et al. (1995) determined that both
337 species moved into overwintering sites as early as mid-summer (July) and population densities
338 peaked in mid-autumn during apple leaf-fall. In Ontario, Putman (1955a) found that *S.*
339 *punctillum* only survived the winter in orchards if they were in contact with the soil, likely
340 because of the insulating effects of snow, whereas dead adults were often observed on the trunks
341 of peaches during the winter. This agrees with observations of *S. punctum* in Pennsylvania
342 orchards (Hull pers. obs.). Overwintering Stethorini are often found in aggregations near the
343 base of orchard trees, but this may be a function of increased survival in these protected areas
344 (Asquith and Hull, 1979; Colburn and Asquith, 1971; Felland and Hull, 1996; Readshaw, 1971).
345 Regardless of where they overwinter within a landscape, some North American *Stethorus* spp.
346 experience substantial mortality during the winter, with spring populations reported as 20 to 28%
347 of those found in the fall (Felland and Hull, 1996; Putman, 1955a). In areas where winters are
348 less severe, *Stethorus* may overwinter successfully in less protected sites. For example, *S.*
349 *punctum* commonly overwinter in cardboard bands wrapped around tree trunks in Washington
350 apple orchards (Horton et al., 2002), as does *S. punctillum* in Germany (Berker, 1958).

351 Spring emergence of *S. punctum* adults in Pennsylvania apple orchards over three seasons
352 was correlated with tree phenology, ground cover emergence traps, colored sticky card traps,
353 ambient temperatures, and degree day accumulations (Felland et al., 1995; Biddinger and Hull,
354 1996). Adults emerged from diapause at 100 and 300 degree days, base 5°C starting 1 March of
355 each year, with fifty percent emergence occurring at 210 DD_{5°C}. Emergence was 2, 47 and 96%

356 complete by the defined phenological stages of apple as half inch green, pink and petal fall
357 respectively, for the apple cultivar “Yorking.” Most adults emerged on days of average,
358 minimum, and maximum air temperatures of 15-20, 5-15, and 20-30°C, respectively.

359 3.2.5. *Natural enemies of Stethorini.* There is surprisingly little information available on the
360 natural enemies of Stethorini species despite numerous reports for other coccinellid species
361 (Riddick et al., 2009, this volume). A species of rickettsial disease (*Rickettsiella stethorae* Hall
362 and Badgley) from larvae in cultures of *Stethorus* nr. *punctum* from Morocco was described by
363 Hall and Badgley (1957). The disease spread rapidly to cultures of *S. punctum* from
364 Connecticut, *S. gilvifrons* from Hong Kong, *S. punctillum*, and *Stethorus* sp., possibly *S.*
365 *guatemalensis* = *S. granum* introduced from Guatemala (Hall and Fleschner, 1958). The disease
366 was not found in their prey (six-spotted mite, *Eotetranychus sexmaculatus* [Riley]). Among the
367 parasitic mites, the Laboulbeniales were found on several *S. punctillum* adults collected on
368 raspberry plants in Québec (Michèle Roy, MAPAQ Laboratoire de Diagnostic en
369 Phytoprotection, pers. comm.). We could find no records of parasitoids that attack Stethorini.

370 Cannibalism on preimaginal stages of *Stethorus* is also common (Cottier, 1934; Fleschner,
371 1950; Robinson, 1953; Chazeau, 1985). It does not appear to be an important cause of mortality
372 except during times of starvation (Collyer, 1953; Putman, 1955a; Kaylani, 1967; Mather, 1969)
373 or when larval densities become very high (Houck, 1991). Biddinger and Hull (pers. obs.)
374 believe the most significant predators to be the older instars of lacewings (*Chrysopa* spp.) and
375 other coccinellids. *Phidippus audax* (Hentz), a salticid commonly found in the tree canopy in the
376 late summer and fall, feeds on *Stethorus* larvae (Biddinger and Hull, pers. observ.). Rosenheim
377 et al. (2004a, b) found the tangle-nest spider, *Nesticodes rufipes* (Theridiidae), consumed larvae
378 of *S. siphonulus*, thereby disrupting biological control of the carmine spider mite, *Tetranychus*

379 *cinnabarinus*, on papaya in Hawaii. Putman (1955a) observed an unidentified species of
380 *Typhlodromus* feeding on the eggs of *S. punctillum* when confined. Haney et al. (1987) found
381 that *S. punctum* could regulate populations of citrus red mite in California citrus groves at low
382 levels, but in the presence of the Argentine ant, *Iridomyrmex humilis* (Mayr), mite populations
383 flared dramatically. They attributed this to active harassment of adult (and possibly immature
384 stages) *Stethorus* (also documented by Bartlett, 1963), which inhibited the feeding and numerical
385 response of the beetles.

386

387 **4. Conservation and value in biological control.**

388 The habitats of Stethorini are diverse, and include many agricultural systems such as tree and
389 small fruits, nuts, citrus, avocados, bananas, papaya, palms, tea, cassava, sugarcane, maize, and
390 various vegetables, as well as ornamental plantings, grasslands, forests, and heathlands. The
391 overview provided by Lo et al. (1989) of tetranychid predators in several crops in Taiwan is an
392 illustration of where acariphagous coccinellids often fit within natural enemy communities.
393 Typically coexisting with several phytoseiid mite predators, the staphylinid *Oligota* and green
394 lacewings (*Chrysopa*), *Stethorus loi* Sasaji is considered an important mite predator in citrus and
395 tea plantations, whereas in mulberry, strawberry, and pear, mite management practices focus
396 completely on phytoseiids. Citrus red mite (*Panonychus citri*) is preyed upon by a number of
397 Stethorini in Asia, frequently resulting in significant population suppression. For instance,
398 Huang et al. (1988) provide an account of inoculation of approximately 20 adult *Stethorus*
399 *siphonulus* per tree in six citrus orchards in southeastern China, resulting in reduction of *P. citri*
400 to below economic thresholds over the growing season, and drastic reduction in miticide input.

401 It is difficult to generalize which agroecosystems support Stethorini and/or phytoseiid mites
402 as effective tetranychid predators; this is likely a function of many factors such as pesticide use
403 history, crop phenology and characteristics, proximity to refugia for protection from climatic
404 extremes and agrochemicals, and experience and preference of pest management practitioners.
405 Globally, Stethorini perform best as biological control agents in low-input woody perennial
406 systems. Key to their optimal utilization as biological control agents are the provision of
407 sufficient overwintering habitats or other reservoirs for Stethorini in or near agroecosystems, and
408 their protection from particularly damaging pesticides. Under these circumstances, Stethorini are
409 often important contributors to the suppression of tetranychid populations. Examples are apple
410 orchards in Pennsylvania, USA, citrus and tea in East and South Asia, and in Australian and New
411 Zealand gorse (*Ulex europaeus* L. [Fabaceae]), where they suppressed a tetranychid biological
412 control for this invasive woody weed.

413

414 **4.1. Case studies of *Stethorus* in IPM systems.**

415 *4.1.1. Stethorus punctum in Pennsylvania orchards.* The best documented and most
416 successful biological control program incorporating Stethorini has been that of *S. punctum* in
417 apple and peach orchards of the eastern USA. Pennsylvania initiated a system for the biological
418 control of mites using *S. punctum* during the 1970s (reviewed in Asquith and Hull, 1979;
419 Chazeau, 1985; Croft, 1990; Hull and Beers, 1985; Tanigoshi et al., 1983). The program
420 reportedly reduced acaricide usage by 1000 metric tonnes of formulated product, realizing a
421 cumulative grower savings of US\$20 million over 25 years (Biddinger and Hull, 1996).

422 Key to the success of this program was early development of resistance by *S. punctum* to
423 organophosphate (OP) insecticides such as azinphosmethyl (Colburn and Asquith, 1973), and the

424 continuous use of this pesticide class in controlling susceptible primary pests (e.g., codling moth
425 and Oriental fruit moth) from the mid 1960s through the mid 1990s (Croft, 1990). The intense
426 selection pressure over decades of using multiple applications of the same insecticides per season
427 undoubtedly contributed to this resistance development, but another factor was a unique method
428 of application known as alternate row-middle spraying (Lewis and Hickey, 1964; Hull and
429 Beers, 1985). In the 1970s this became the preferred method of pesticide application by over
430 95% of mid-Atlantic fruit growers. Knight and Hull (1992 a, b) demonstrated that, using this
431 method, only ~20% dose of the pesticide is deposited on leaves or fruit on the opposite side of
432 the tree, leaving untreated refugia for *Stethorus*, even as new insecticides were employed, to
433 which the predator was not resistant (Hull et al., 1976; Hull and Beers, 1985; David, 1985;
434 Biddinger, 1993; Biddinger and Hull, 1996; Biddinger and Hull, 1999).

435 The usefulness of *Stethorus* was communicated directly to tree fruit growers through
436 insecticide and acaricide efficacy guides. A series of field studies and a computer simulation
437 model by Mowery et al. (1975) determined the expected efficacy of biological control of *P. ulmi*
438 based on visual predator and prey counts, information later incorporated into the Penn State
439 Apple Orchard Consultant program, one of the first IPM expert systems (Rajotte et al., 1987;
440 Travis et al., 1992). Pesticide recommendations focused not only on efficacy against primary
441 pests, but on use of products that *S. punctum* could tolerate: OPs and many acaricides (Biddinger
442 et al., 2008a). To protect *S. punctum*, pyrethroids, despite being inexpensive and effective on
443 many primary pests, were never recommended in Pennsylvania apples, and are rarely used there
444 after bloom (Hull and Knight, 1989; Hull and Starner, 1983; Hull et al., 1985ab). In contrast, in
445 Michigan and New York apples and in Pennsylvania peaches, *S. punctum* disappeared with
446 widespread adoption of pyrethroids in the late 1980s (Hull, pers. obs.).

447 The period of tetranychid mite control in Pennsylvania with *S. punctum* was characterized by
448 a lack of effective miticides. Starting in the mid 1990s, new miticide registrations offered more
449 effective, less expensive materials. Most growers abandoned recommended action thresholds for
450 *P. ulmi*, and miticide use increased dramatically. *Stethorus punctum* began to disappear from
451 apple orchards as lower populations of *P. ulmi* prevented predator reproduction. Of more lasting
452 impact however, was the development of OP resistance in the primary lepidopterous pests of
453 eastern apple orchards, which required adoption of new insecticide chemistries, some of which
454 were very toxic to *S. punctum*. These insecticides include the neonicotinoids, and several of the
455 insect growth regulators, which are toxic to various stages of *S. punctum* (Biddinger and Hull,
456 1993, 1996, 2005; Hull et al., 1991; Hull and Biddinger, 1991ab), in spite of being classified as
457 “reduced risk,” by the US EPA. James (2003b, 2004) reported similar effects on *S. punctum*
458 *picipes* in Washington hops. Many of these new insecticides have sublethal effects on pest
459 development and fecundity (Biddinger and Hull, 1999; Sun et al., 2000; Biddinger et al., 2006),
460 which have been demonstrated for *S. punctillum* through feeding on tetranychids on
461 imidacloprid-treated ornamental woody plants (Creary 2009).

462 Around 2005, biological mite control in Pennsylvania apple orchards shifted to the
463 conservation of the phytoseiid predatory mite, *Typhlodromus pyri* (Schueten) (Biddinger et al.,
464 2008b). *Typhlodromus pyri* can survive on alternative food sources such as rust mites, pollen or
465 fungi when tetranychid mite densities are very low and do not seasonally disperse from trees, as
466 do other phytoseiid predators such as *Neoseiulus fallacis* (Garman) (Nyrop et al. 1998).
467 Biological mite control with *T. pyri* in Pennsylvania apple orchards does not suffer from
468 temporal or spatial asynchrony such as that found in raspberries (Roy et al. 2005). *Stethorus*
469 *punctum* is now considered a backup option for mite control when *T. pyri* conservation fails due

470 to the use of toxic insecticides rather than a complement to phytoseiids. Currently, neither *S.*
471 *punctum* nor *T. pyri* are providing significant mite control in Pennsylvania peach orchards
472 because of the heavy dependency on pyrethroid applications for pest control (Hull and
473 Biddinger, pers. obs.).

474
475 *4.1.2. Pesticide impacts and resistance in other Stethorini species.* Nienstedt and Miles
476 (2008) have established a bioassay for pesticide toxicity for *S. punctillum*, including effects on
477 development and fecundity, and demonstrated its sensitivity using the insect growth regulators
478 fenoxycarb and methoxyfenoside. This species developed resistance to azinphosmethyl in Italian
479 apple orchards under very similar circumstances to that of *S. punctum* in USA (Pasqualini and
480 Malvolta, 1985; Croft, 1990). The value of this predator has also been reduced as alternative
481 insecticides have been adopted to control azinphosmethyl-resistant primary pests (Pasqualini and
482 Antropoli, 1994). Biological control of mites in Italy is now also more dependent on the
483 phytoseiid predatory mites. *T. pyri* and *Amblyseius andersoni* (Chant)(Pasqualini, pers. comm.).

484 McMurtry et al. (1970) reviewed the biology and ecology of several North American
485 *Stethorus* spp. and noted the impact of orchard spray practices on them. *Stethorus bifidus* Kapur
486 was the most important insect predator of mites in New Zealand apple orchards, but is
487 susceptible to organophosphate insecticides (Collyer, 1964, 1976). The use of alternate-row
488 middle applications of reduced rates of insecticides was not adopted in New Zealand orchards or
489 in other countries with native species of Stethorini; this may contribute to the absence of
490 insecticide resistance. The introduction of the synthetic pyrethroids into New Zealand apple
491 spray programs severely impacted Stethorini populations and fruit IPM now largely relies on the
492 introduced pyrethroid resistant phytoseiid, *T. pyri* (Croft, 1990, Marwick, 1988). In Australian

493 apple IPM programs several species of Stethorini were important in the 1960-70's, but are now
494 dependent on phytoseiid predators for biological mite control (Edwards and Hodgson, 1973;
495 Readshaw, 1975; Walters, 1974, 1976 a, b, c; Bower and Kaldor, 1980).

496 Álvarez-Alfageme et al. (2008) examined the effect of two different Cry1Ab expressing
497 transgenic maize cultivars with lepidoptera-specific Bt toxins. The two-spotted spider mite, *T.*
498 *urticae*, retains the Bt toxin but its predator, *S. punctillum*, degrades it without measureable
499 effects on fitness or performance. This is consistent with field results comparing Cry1Ab
500 expressing maize with its isogenic cultivar in Spain, showing no significant differences in
501 coccinellid numbers, which were predominantly *S. punctillum* (de la Poza et al., 2005). Güllü et
502 al. (2004) reported similar results with *S. gilvifrons* comparing Cry1AB expressing maize with
503 an isogenic cultivar in Turkey. To our knowledge no specific deleterious findings are available
504 regarding *Stethorus* and rootworm-targeted (Cry3) transgenic maize.

505

506 **4.2. Mass rearing.**

507 Early biological control researchers cavalierly pursued the introduction of many Stethorini
508 into new regions, and accompanying these classical biocontrol introductions, considerable effort
509 went into the development of mass production methods using natural diets of mites and factitious
510 prey or artificial diets. The mass production of Stethorini using prey requires a tremendous
511 supply of mites. Fleschner (1950) conservatively calculated that *S. picipes* each required 300
512 mites for development and oviposition. Several species of mites have been used to rear
513 *Stethorus* including *Eotetranychus sexmaculatus* (Riley), *Tetranychus pacificus* McGregor, *T.*
514 *cinnabarinus* (Boisduval) (Finney, 1953; Scriven and Fleschner, 1960; Scriven and McMurtry,
515 1971).

516 Some host plants may not be suitable for cultures of Stethorini because of hooked trichomes
517 that may kill or impede the movement of larvae and adults. For example, prey mites must be
518 brushed from lima or scarlet runner bean plants before offering them to Stethorini as food since
519 the hooked trichomes on these plants can tear the larval integument, and damage the posterior
520 integument during defecation or oviposition by adults (Putman, 1955a; Walters, 1974; Biddinger,
521 1993). The smooth-leaved fava bean (*Vicia faba*) proved more suitable for rearing *Stethorus*
522 directly on the plants (Putman, 1955a; Biddinger, 1993).

523 *Stethorus* can also be reared on alternative foods. Colburn (1971) determined that a modified
524 wheat germ diet with honey greatly increased adult *S. punctum* survival in the laboratory over a
525 two week period compared to sugar water alone. Smirnoff (1958) reared *S. punctillum* and 17
526 other coccinellids on a diet consisting of cane sugar, honey, agar and royal jelly. Given the
527 limited work done on these non-prey diets, it is difficult to make any firm conclusions as to their
528 value in the mass production of beetles.

529 Applied Bio-nomics near Victoria, British Columbia, Canada, is the commercial supplier of
530 *S. punctillum* for releases in the United States and Canada. The company recommends *S.*
531 *punctillum* for release against *T. urticae*, *P. ulmi*, the spruce spider mite *Oligonychus ununguis*
532 (Jacobi), and the Southern red mite *Oligonychus ilicis* (McGregor). Since the beetles are
533 expensive (US\$30-50 per 100 adults), they are sold only in modest numbers compared to
534 phytoseiid mite predators, particularly for interior landscapes, conservatories, and greenhouses
535 with ornamental and vegetable crops, as well as for occasional field use on small fruits and
536 ornamental shrubs (Raworth et al., 2002; Jan Dietrich, Rincon-Vitova Insectaries, and Brian
537 Spencer, Applied Bio-nomics Corporation, pers. comms. with D. Weber, both on 5 Dec. 2008).
538

539 **4.3. Research on releases in urban, greenhouse and interior environments.**

540 Several studies have focused on using *Stethorus* for controlling spider mites in greenhouse
541 crops. Raworth (2001) found that releases of *S. punctillum* established and reproduced in peppers
542 and cucumbers but not in tomatoes. This study underscores yet again that the prey's host plant
543 can inhibit predators. Rott and Ponsonby (2000) found in UK glasshouse vegetables, that
544 simultaneous releases of *Neoseiulus californicus*, *S. punctillum*, and *P. persimilis* controlled
545 spider mites better than did *P. persimilis* alone; no intraguild predation was noted, and predator
546 performance varied by crop type. Combined releases of phytoseiids and *S. punctillum* have
547 shown success in greenhouses, interiorscapes, and urban shade tree IPM programs in Europe
548 (Gorski and Fajfer, 2003; Jäckel et al., 2000, 2008; Pöhle et al., 2002). These efforts are testing
549 combinations of releases of phytoseiid mites with *S. punctillum* with habitat modifications, e.g.
550 on shade trees increasing ground residue and providing shelterbands for overwintering. Interior
551 environments with low humidity and artificial lighting pose special challenges that are difficult
552 to overcome (Pöhle et al., 2002). Ornamental pest management is also seen as a possible niche
553 for *S. punctillum* releases in Denmark (Svendsen and Hansen, 2002).

554 **4.4. Inhibition of gorse biocontrol.**

555 *Stethorini* may suppress desirable mites that are biological control agents of invasive weeds.
556 Gorse, *Ulex europaeus* L. (Fabaceae), is a thorny woody shrub native to Europe, which was
557 widely re-distributed throughout the world as a living hedge to confine livestock. This plant is
558 also appreciated for its value as browse for stock, and for its abundant yellow flowers. By the
559 early 20th century, the dangerously weedy nature of gorse was recognized in New Zealand,
560 southern Australia, Tasmania, Chile, northwestern USA and Hawaii. Beginning about 20 years
561

ago, efforts turned toward classical biological control using two foliage-feeding arthropods, the gorse spider mite, *Tetranychus lintearius* Dufour (of British and Iberian origin) and gorse thrips, *Sericothrips staphylinus* Haliday (of English origin). *Tetranychus lintearius* has been released in New Zealand, Australia, Chile, and in the USA (Washington, Oregon, California, and Hawaii).

Established gorse spider mite populations grow to spectacular numbers with webbing that envelops gorse plants. But several regions have seen steep population declines due to predation by Stethorini and phytoseiids. In New Zealand, the native *S. bifidus* and less commonly the exotic *P. persimilis* suppress gorse spider mite populations to the extent that “after several years populations decline rapidly, and never outbreak again” (Hill et al., 2000). Peterson et al. (2000) found that *S. bifidus* can regulate *T. lintearius*, based on its functional response in laboratory arenas.

In Australia, predation on gorse mite by the native *Parastethorus histrio* as well as by the exotic phytoseiid *P. persimilis*, was detected soon after initial releases in Tasmania and Victoria, where “it is expected that both predators will significantly restrict its impact” (Ireson et al., 2003; 2004). Davies et al. (2007) estimated that 36% reduction in gorse biomass occurred in Tasmanian plots, where both *Parastethorus histrio* and *Phytoseiulus persimilis* were common. Without these predators, they estimated a 44% biomass reduction would have occurred, and this magnitude of effect was considered important in the context of gorse competition with other plants.

In northwestern USA, *P. persimilis* has significantly reduced gorse mite colonies 3 to 4 years post-establishment (Pratt et al., 2003), and *S. punctillum* “has also caused severe declines” (Coombs et al., 2004), although the magnitude of the effect on the target weed is uncertain. The situation in Chile was more favorable for gorse mite populations, where, in spite of the presence

585 of *Parastethorus histrio* in Chile (Aguilera P., 1987), the native staphylinid predator *Oligota*
586 *centralis* (Solier) was the only gorse mite predator commonly found, and its impact on *T.*
587 *linterarius* was not strong (Norambuena et al., 2007).

588 Predation on gorse mite populations by Stethorini, which in at least two of the four regions
589 has had a major impact on this classical weed biocontrol effort, should not come as a surprise. In
590 fact, this so-called biotic resistance was observed in Europe by Schroeder and Zwölfer (1970) in
591 endemic gorse habitats, predicted by Ireson et al. (1999), and continues in the UK, where *S.*
592 *punctillum* and phytoseiid predators limit gorse mite outbreaks (e.g., Kirby, 2005).

593

594 **5. Conclusions and directions for future work.**

595 Stethorini occur in association with spider mites in a variety of habitats throughout much of
596 the world. Although considered specialist predators, many species function as ecological habitat
597 generalists, able to disperse to multiple plants and to feed on multiple mite species. We have
598 little understanding, however, of these beetles' interaction with their environment other than with
599 their essential prey mites. The clear contributions of Stethorini to population regulation of
600 herbivorous mites in less-disturbed systems (e.g., the disruption of tetranychid-based gorse
601 classical biological control) contrasts with numerous observations that the intense management
602 of cropland exacerbates mite outbreaks by disrupting natural predators. The current and potential
603 roles of Stethorini in biological control can be strengthened by targeting research at several key
604 knowledge gaps.

605 (1) The role of alternative foods is little known, but may play an important role in population
606 dynamics, diapause, and migration, as with other coccinellids (Lundgren 2009b, this issue).

607 Stethorini consume alternative non-tetranychid mite prey, extrafloral nectar and pollen. They are

608 sensitive to plant characteristics and thus cultivar choice and vegetational diversity may increase
609 or hinder their efficacy.

610 (2) The vision and olfaction of Stethorini are apparently acute, yet their role in prey location
611 remains poorly explored. Research to address the sensory contributions to their impressive
612 dispersal abilities, and to investigate their response to spatially dynamic prey, is likely to be
613 particularly fruitful. Related to this, the regulatory functional responses that appear to prevent
614 tetranychid outbreaks merit further attention.

615 (3) There is a strong need for systematics research on the group, and for molecular tools to
616 distinguish cryptic species. Stethorini introductions have been common (both accidental and
617 intentional) and careless, and non-target considerations (including the dissemination of
618 entomopathogens and displacement of native species) now dictate a more responsible course.
619 This history of redistribution and the likelihood of significant numbers of yet unnamed species
620 (particularly in Asia) compel the advancement of Stethorini systematics.

621 (4) Habitat management shows potential for increasing the impact of Stethorini on pest
622 populations. The broad prey and host plant ranges of many species make non-crop habitat
623 valuable sources for predators that can rapidly deploy to colonize and protect crops. These
624 refuges can assist overwintering success in temperate systems, and provide safe havens from
625 pesticides. In milder climates, perennial reservoirs may serve as refuges within diversified
626 annual plantings (e.g., the role of the perennial castor bean, common in Indian farmscapes, which
627 serves as a reservoir for *Stethorus gilvifrons* and *S. pauperculus* [Mathur, 1969; Puttaswamy and
628 ChannaBasavanna, 1977]). Use of chemical control, even pesticides that have novel selectivity
629 (e.g. insect growth regulators) or are organic-approved (e.g. elemental sulfur) can be very
630 harmful to Stethorini and other biological agents. These effects are often seen only after

631 registration and widespread use; the breadth of pre-release non-target screening should be
632 broadened (e.g. with method of Nienstedt and Miles, 2008) to include the Stethorini.

633 The full potential of Stethorini as predators of spider mites will only be realized when
634 cultural and chemical farm management practices are truly integrated with biological controls
635 based on farm-scale scientific experimentation. Where proper conditions have come together,
636 such as in Pennsylvania apple orchards, in Asian citrus and tea, and in several other tropical
637 systems, Stethorini play an important role -- sometimes the most important role -- in suppressing
638 tetranychid populations.

639

640 **Acknowledgments**

641 We are grateful to Jon Lundgren and Michèle Roy and to two anonymous reviewers, for helpful
642 comments on an earlier draft. Michael Athanas of IIBBL, Long Zhang of China Agricultural
643 University, Michèle Roy of MAPAQ Laboratoire de Diagnostic en Phytprotection, and the staff
644 of the National Agricultural Library, located a number of the publications consulted. Meiling Z.
645 Webb of IIBBL, Tina Trenczek of University of Giessen, Germany, Hazem Abdelnabby of
646 Benha University in Egypt, and Hossein Hosseini Moghadam of Gent University in Belgium,
647 provided very useful translations. Mention of any proprietary products does not constitute
648 endorsement by the USDA.

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Figure 1. Recorded geographic distribution of Stethorini on agricultural crops.
 *Denotes introduced or suspected introduced. See Table 1 and Kapur (1948).



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ACCEPTED

1268 Table 1. Stethorini as predators of tetranychid and tenuipalpid mites on various plant hosts. The
 1269 referenced publications describe the predator as preying on prey listed; records with "*Stethorus* sp." are
 1270 not listed.

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Predator and prey

Crop or plant

Region

Reference

Parastethorus guangxiensis (Pang & Mao)^a

Panonychus citri (McGregor)

China (Guangxi)

Citrus

Li et al. (1990)

Parastethorus gutierrezii (Chazeau)^a

Oligonychus sp.

New Hebrides

Coconut palm

Chazeau (1979)

Parastethorus histrio (Chazeau)^b

Brevipalpus chilensis Baker

Chile

Beans

Aguilera P.(1987)

Brevipalpus chilensis Baker

Chile

Grape

Prado (1991)

Eutetranychus orientalis (Klein)

India

Citrus

Dhoooria (1981)

Oligonychus thelytokus Gutierrez

New Caledonia

Lychee, Plumeria

Chazeau (1979)

Oligonychus vitis Zaher & Shehata

Chile

Table Grapes

Prado (1991)

Oligonychus yothersi (McGregor)

Chile

Avocado

Prado (1991)

Oligonychus sp.

Australia

Pine tree (*Pinus* sp.)

Houston (1980)

Panonychus citri (McGregor)

Chile

Citrus

Aguilera P.(1987)

Panonychus citri (McGregor)

Peru

Citrus

Guanilo and Martinez (2007)

Panonychus ulmi (Koch)

Chile

Apple

Aguilera P.(1987)

Tetranychus kanzawai Kishida

Australia

Bindweed (*Convolvulus* sp.)

Houston (1980)

Tetranychus lintearius Dufour

Australia

Gorse

Ireson et al. (2003)

Tetranychus neocaledonicus Andre

New Caledonia

Chazeau (1979)

Tetranychus urticae Koch

Reunion

Various vegetables

Chazeau et al. (1974)

Tetranychus urticae Koch

Australia

Papaya

Houston (1980)

Tetranychidae

Apple

New Zealand

Chazeau (1979)

1318	Tetranychidae	Maize, redbud tree (<i>Cercis</i>)
1319	USA (Texas)	Pollock & Michels (2003)
1320	<i>Parastethorus indira</i> (Kapur) ^a	
1321	Tetranychidae	Taro
1322	India	Kapur (1950)

1323 ***Parastethorus nigripes* (Kapur)^a**

1324	<i>Oligonychus pratensis</i> (Banks)	Corn
1325	USA (Texas, Oklahoma)	Pollock & Michels (2002)
1326	<i>Panonychus citri</i> (McGregor)	Citrus
1327	Australia	Beattie & Gellatley (1983)
1328	<i>Panonychus ulmi</i> (Koch) ^c	Apple
1329	Australia	Walters (1976a)
1330	<i>Tetranychus lambi</i> Pritchard & Baker ^c	Banana
1331	Australia	Houston (1980)
1332	<i>Tetranychus urticae</i> Koch	Apple
1333	Australia	Edwards & Hodgson (1973)
1334	<i>Tetranychus urticae</i> Koch ^c	Soya
1335	Australia	Houston (1980)
1336	<i>Tetranychus urticae</i> Koch	Alfalfa seed crop
1337	Australia	Bailey & Caon (1986)
1338	<i>Stethorus aethiops</i> Weise	
1339	<i>Mononychellus tanajoa</i> (Bondar) complex	Cassava
1340	Kenya	Yaseen et al. (1982)
1341	<i>Tetranychus lombardinii</i> Baker & Pritchard	Cassava
1342	Kenya	Yaseen et al. (1982)
1343	<i>Tetranychus neocaledonicus</i> Andre	Cassava
1344	Kenya	Yaseen et al. (1982)
1345	<i>Tetranychus urticae</i> Koch	Cassava
1346	Kenya	Yaseen et al. (1982)
1347	<i>Stethorus aptus</i> Kapur	
1348	<i>Panonychus citri</i> (McGregor)	Citrus
1349	China (Guangxi)	Li et al. (1990)
1350	<i>Stethorus bifidus</i> Kapur	
1351	<i>Bryobia</i> sp.	Apple
1352	New Zealand	McMurtry et al. (1970)
1353	<i>Panonychus ulmi</i> (Koch), <i>Tetranychus urticae</i> Koch	Apple, plum, pear
1354	New Zealand	Collyer (1964)
1355	<i>Tetranychus lambi</i> Pritchard & Baker	Apple
1356	New Zealand	McMurtry et al. (1970)
1357	<i>Tetranychus lintearius</i> Dufour	Gorse
1358	New Zealand	Peterson et al. (1994)
1359	<i>Tetranychus urticae</i> Koch	Raspberry
1360	New Zealand	Thomas & Burnip (1984);
1361	<i>Stethorus caseyi</i> Gordon & Chapin	
1362	<i>Oligonychus pratensis</i> (Banks)	Maize
1363	USA (Texas)	Pollock & Michels (2003)
1364	<i>Stethorus chengi</i> Sasaji	

1365	<i>Panonychus citri</i> (McGregor)	Citrus	
1366	China	Chen & Zhao (1994)	
1367	<i>Tetranychus urticae</i> Koch	Papaya	
1368	Taiwan	Wen and Lee (1981)	
1369	<i>Stethorus comoriensis</i> Chazeau		
1370	<i>Oligonychus coffeae</i> (Nietner)	Plumeria	
1371	Comoro Islands	Chazeau (1971b)	
1372	<i>Tetranychus neocaledonicus</i> Andre	Breadfruit	
1373	Comoro Islands	Chazeau (1971b)	
1374	<i>Stethorus darwini</i> (Brethes) ^d		
1375	<i>Mononychellus caribbeanae</i> McG., <i>Mononychellus</i>	Cassava	
1376	Guyana, Surinam	Yaseen et al. (1982)	
1377	<i>tanajoa</i> (Bondar) complex, various Tetranychidae		
1378	<i>Panonychus ulmi</i> Koch	Apple	
1379	Brazil	Lorenzato (1987)	
1380	<i>Tetranychus evansi</i> Baker & Pritchard	Tomato	
1381	Brazil	Paschoal (1970)	
1382	<i>Stethorus exspectatus</i> Chazeau		
1383	<i>Oligonychus, Panonychus, Schizotetranychus</i> spp.	Various crops	
1384	New Guinea	Chazeau (1983)	
1385	<i>Tetranychus fijiensis</i> Hirst	Coconut palm	
1386	New Guinea	Chazeau (1983)	
1387	<i>Tetranychus lambi</i> Pritchard & Baker	Cassava	
1388	New Guinea	Chazeau (1983)	
1389	<i>Stethorus exsultabilis</i> Chazeau		
1390	<i>Oligonychus, Panonychus, Schizotetranychus</i> spp.	Various crops	
1391	New Guinea	Chazeau (1983)	
1392	<i>Tetranychus fijiensis</i> Hirst	Coconut palm	
1393	New Guinea	Chazeau (1983)	
1394	<i>Tetranychus lambi</i> Pritchard & Baker	Cassava	
1395	New Guinea	Chazeau (1983)	
1396	<i>Stethorus fenestralis</i> Houston		
1397	<i>Tetranychus kanzawai</i> Kishida	Bindweed (<i>Convolvulus</i> sp.)	
1398	Australia	Houston (1980)	
1399	<i>Tetranychus lambi</i> Pritchard & Baker	Banana, papaya	
1400	Australia	Houston (1980)	
1401	<i>Tetranychus urticae</i> Koch	Papaya	
1402	Australia	Houston (1980)	
1403	<i>Stethorus fijiensis</i> Kapur		
1404	Tetranychidae	---	Fiji
1405	<i>Stethorus fuerschi</i> Chazeau		
1406	<i>Oligonychus chazeaui</i> Gutierrez	Palm tree	
1407	Madagascar	Chazeau (1971b)	
1408	<i>Tetranychus roseus</i> Gutierrez	Palm tree	
1409	Madagascar	Chazeau (1971b)	
1410	<i>Stethorus gilvifrons</i> (Mulsant)		
1411	<i>Eutetranychus hirsti</i> Pritchard & Baker	---	Iran
1412	<i>Eutetranychus orientalis</i> (Klein)	---	Iran
1413	<i>Oligonychus afrasiaticus</i> (McGregor)	---	Iran
1414	<i>Oligonychus coffeae</i> (Nietner)	Tea	
1415	India	Sarmah & Bhattacharyya 2002.	

1416	<i>Oligonychus sacchari</i> (McGregor)	Sugarcane	Iran
1417	<i>Panonychus citri</i> (McGregor), <i>Eotetranychus</i> sp.	Orange, apple, rose	
1418	Philippines	Handoko (2004)	
1419	<i>Panonychus ulmi</i> Koch	Apple	Iran
1420	<i>Tetranychus turkestanii</i> Ugarov & Nikolski	Strawberry	Iran
1421	<i>Tetranychus turkestanii</i> Ugarov & Nikolski	Various ornamentals	Iran
1422	<i>Tetranychus urticae</i> Koch	Castor bean	
1423	India	Mathur (1969)	
1424	<i>Tetranychus urticae</i> Koch	Cucumbers, beans	Iran
1425	Tetranychidae	Various crops	
1426	Lebanon	McMurtry et al. (1970)	
1427	<i>Stethorus griseus</i> Whitehead		
1428	Tetranychidae	Apple	
1429	New Zealand	Chazeau (1979)	
1430	<i>Stethorus japonicus</i> Kamiya		
1431	<i>Panonychus citri</i> (McGregor)	Citrus	
1432	Japan	McMurtry et al. (1970)	
1433	<i>Panonychus citri</i> (McGregor)	Mandarin orange	
1434	Japan	Tsuchiya (2005)	
1435	<i>Panonychus mori</i> Yokoyama	Japanese pear	
1436	Japan	Kishimoto & Adachi (2008)	
1437	<i>Tetranychus kanzawai</i> Kishida	Tea, hydrangea	
1438	Japan	Mori et al. (2005)	
1439	<i>Tetranychus urticae</i> Koch	Apple, citrus	
1440	Japan	Mori et al. (2005)	
1441	<i>Tetranychus urticae</i> Koch	Japanese pear	
1442	Japan	Kishimoto & Adachi (2008)	
1443	<i>Tetranychus viennensis</i> Zacher	Japanese pear	
1444	Japan	Kishimoto & Adachi (2008)	
1445	<i>Stethorus jejunus</i> Casey		
1446	<i>Mononychellus tanajoa</i> (Bondar) complex	Cassava	
1447	Kenya	Yaseen et al. (1982)	
1448	<i>Tetranychus lombardii</i> Baker & Pritchard	Cassava	
1449	Kenya	Yaseen et al. (1982)	
1450	<i>Tetranychus neocaledonicus</i> Andre	Cassava	
1451	Kenya	Yaseen et al. (1982)	
1452	<i>Tetranychus urticae</i> Koch	Cassava	
1453	Kenya	Yaseen et al. (1982)	
1454	<i>Stethorus keralicus</i> Kapur		
1455	<i>Raoiella indica</i> Hirst (Tenuipalpidae)	Areanut palm, coconut	
1456	India	Puttaswamy &	
1457			
1458	<i>Stethorus loi</i> Sasaji		
1459	<i>Panonychus citri</i> (McGregor)	Jujube	
1460	Taiwan	Wen et al. (1993)	
1461	<i>Tetranychus urticae</i> Koch	Papaya	
1462	Taiwan	Wen and Lee (1981)	
1463	Tetranychidae	Carambola	
1464	Taiwan	Chang & Leu (1986)	
1465	<i>Stethorus madecassus</i> Chazeau		

1466	<i>Tetranychus neocaledonicus</i> Andre	Cotton
1467	Madagascar	Chazeau (1971a)
1468	<i>Tetranychus</i> spp., <i>Oligonychus</i> spp.	Various crops
1469	Madagascar	Chazeau (1971a)
1470	<i>Stethorus parcampunctatus</i> Puttarudrian & Channa	Basavanna
1471	<i>Raoiella indica</i> Hirst (Tenuipalpidae)	Coconut palm
1472	India	Gupta (2001)
1473	<i>Stethorus parapauperculus</i> Pang	
1474	<i>Tetranychus piercei</i> McGregor	Banana
1475	China (Hainan)	Chen et al. (2005)
1476	<i>Tetranychus urticae</i> Koch	Cassava
1477	China	Lin & Chen (1984)
1478	<i>Stethorus pauperculus</i> Weise	
1479	<i>Oligonychus indicus</i> (Hirst)	Sorghum
1480	India	Kapur (1948)
1481	<i>Oligonychus neocaledonicus</i> Andre	Papaya, castor bean, and
1482	India	Puttaswamy &
1483		Various crops
1484	<i>Tetranychus ludeni</i> Zacher	Eggplant
1485	India	Puttaswamy &
1486		
1487	<i>Tetranychus ludeni</i> Zacher	Waterhyacinth
1488	India	Ansari & Pawar (1992)
1489	<i>Stethorus punctillum</i> Weise	
1490	<i>Eotetranychus buxi</i> (Garman)	Boxwood (<i>Buxus</i> sp.)
1491	USA (Maryland)	Creary (2009)
1492	<i>Eotetranychus carpini</i> (Oudemans)	Grapes
1493	Italy	Laffi (1982)
1494	<i>Eotetranychus tiliarium</i> Hermann	Linden trees (<i>Tilia</i> spp.)
1495	Germany	Jäckel et al. (2000)
1496	<i>Oligonychus afrasiaticus</i> (McGregor)	Date palm
1497	Algeria	Idder & Pintureau (2008)
1498	<i>Oligonychus bicolor</i> (Banks)	Chestnut
1499	Italy	Cinti et al. (1995)
1500	<i>Oligonychus ununguis</i> (Jacobi)	Chinese Chestnut
1501	Canada	Putman (1955a)
1502	<i>Oligonychus ununguis</i> (Jacobi)	Various ornamental spruces,
1503	USA (Pennsylvania)	Wheeler et al. (1973)
1504		pinus, cedars & Arborvitae
1505	<i>Panonychus citri</i> (McGregor)	Citrus
1506	China	Tian (1995)
1507	<i>Panonychus ulmi</i> (Koch)	Fruit trees
1508	Canada	Putman (1955a)
1509	<i>Panonychus ulmi</i> (Koch)	Fruit trees
1510	Europe	McMurtry et al. (1970)
1511	<i>Panonychus ulmi</i> (Koch)	Apple
1512	Italy	Pasqualini & Antropoli (1994)
1513	<i>Tetranychus bioculatus</i> (Wood-Mason)	Marigold
1514	Bangladesh	Taleb & Sardar (2007)
1515	<i>Tetranychus cinnabarinus</i> (Boisduval)	Cotton, apple, watermelon
1516	Israel	Plaut (1965)

1517	<i>Tetranychus mcdanieli</i> McGregor	Raspberry
1518	Canada	Roy et al. (2002)
1519	<i>Tetranychus shoenei</i> McGregor	Elm (<i>Ulmus americana</i>)
1520	USA (Maryland)	Creary (2009)
1521	<i>Tetranychus urticae</i> Koch	Beans
1522	Canada	Putman (1955a)
1523	<i>Tetranychus urticae</i> Koch	Sugar beets
1524	Israel	Plaut (1965)
1525	<i>Tetranychus urticae</i> Koch	Greenhouse crops
1526	Netherlands	McMurtry et al. (1970)
1527	<i>Tetranychus viennensis</i> Zacher	Apple & other fruits
1528	Turkey	Yigit & Uygun (1986)
1529	<i>Stethorus punctum picipes</i> Casey ^e	
1530	<i>Oligonychus punicae</i> (Hirst)	Avocado
1531	USA (California)	McMurtry et al. (1969)
1532	<i>Panonychus citri</i> (McGregor)	Citrus
1533	USA (California)	McMurtry et al. (1970)
1534	<i>Tetranychus tumidus</i> Banks	Banana
1535	Cuba	Perez et al. (2004)
1536	Tetranychidae	Walnuts, melon, apple
1537	USA	McMurtry et al. (1970)
1538	<i>Stethorus punctum punctum</i> (Leconte)	
1539	<i>Panonychus ulmi</i> (Koch) and other tetranychids	Fruit trees
1540	North America	McMurtry et al. (1970)
1541	<i>Tetranychus mcdanieli</i> McGregor	Fruit trees
1542	Canada	Robinson (1953)
1543	<i>Tetranychus pacificus</i> McGregor	Fruit trees
1544	Canada	Robinson (1953)
1545	<i>Stethorus siphonulus</i> Kapur	
1546	<i>Eutetranychus banksi</i> McGregor	Ornamentals
1547	Hawaii	Raros and Haramoto (1974)
1548	<i>Oligonychus exsicicator</i> (Zehntner)	Sugar cane
1549	Hawaii	Raros and Haramoto (1974)
1550	<i>Panonychus citri</i> (McGregor)	Citrus
1551	China (Fujian)	Huang et al. (1988)
1552	<i>Tetranychus cinnabarinus</i> (Boisduval)	Papaya
1553	Hawaii	Rosenheim et al. (2004b)
1554	<i>Tetranychus neocaledonicus</i> Andre	Custardapple (<i>Anona</i> sp.)
1555	French Polynesia	Chazeau (1979)
1556	<i>Tetranychus piercei</i> McGregor	Papaya
1557	China (Guangdong)	Lui & Lui (1986)
1558	<i>Tetranychus tumidus</i> Banks	Papaya
1559	Hawaii	Raros and Haramoto (1974)
1560	<i>Tetranychus urticae</i> Koch	Papaya
1561	Hawaii	Raros and Haramoto (1974)
1562	<i>Stethorus tridens</i> Gordon	
1563	<i>Panonychus citri</i> McGregor	Citrus
1564	Peru	Guanilo and Martinez (2007)
1565	<i>Tetranychus cinnabarinus</i> (Boisduval)	Cassava
1566	Colombia	Gordon (1982)

1567	<i>Tetranychus evansi</i> Baker & Pritchard	Tomato
1568	Brazil	Britto et al. (2009)
1569	<i>Tetranychus urticae</i> Koch	Cassava
1570	Colombia	Gordon (1982)
1571	Tetranychidae	Eggplant
1572	Colombia	Gordon (1982)
1573	<i>Stethorus utilis</i> Horn ^f	
1574	<i>Eotetranychus hicoriae</i> (McGregor)	Pecan
1575	USA (Southeast)	Tedders (1983)
1576	<i>Eotetranychus sexmaculatus</i> (Riley)	Citrus
1577	USA (Florida)	McMurtry et al. (1970)
1578	<i>Eutetranychus banksi</i> (McGregor)	Citrus
1579	USA (Texas)	McMurtry et al. (1970)
1580	<i>Mononychellus caribbeanae</i> (McGregor), <i>Mononychellus</i>	Cassava
1581	Colombia, Nicaragua,	Yaseen et al. (1982)
1582	<i>tanajoa</i> (Bondar) complex, various Tetranychidae	
1583	Trinidad	
1584	<i>Oligonychus pratensis</i> (Banks)	Sorghum
1585	USA (Texas)	Ehler (1974)
1586	<i>Tetranychus urticae</i> Koch, <i>Panonychus citri</i> (McGregor)	Citrus
1587	Cuba	Mora Morin (1991)
1588	Tetranychidae	Lychee
1589	USA (Florida)	Butcher (1951)
1590	<i>Stethorus vagans</i> (Blackburn)	
1591	<i>Bryobia praetiosa</i> Koch	Clover
1592	Australia (Tasmania)	Evans (1943)
1593	<i>Oligonychus exsicicator</i> (Zehntner)	Sugar cane
1594	USA (Hawaii)	Swezey (1923)
1595	<i>Oligonychus thelytokus</i> Gutierrez	Lychee
1596	New Caledonia	Chazeau (1979)
1597	<i>Oligonychus</i> sp.	Coconut palm
1598	New Caledonia	Chazeau (1979)
1599	<i>Oligonychus</i> sp.	Pine tree (<i>Pinus</i> sp.)
1600	Australia	Houston (1980)
1601	<i>Panonychus ulmi</i> (Koch)	Apple
1602	Australia	Walters (1976a)
1603	<i>Tetranychus lambi</i> Pritchard & Baker	Cassava
1604	New Caledonia	Chazeau (1979)
1605	<i>Tetranychus lambi</i> Pritchard & Baker	Papaya
1606	Australia	Houston (1980)
1607	<i>Tetranychus marianae</i> McGregor	Castor bean
1608	New Caledonia	Chazeau (1979)
1609	<i>Tetranychus marianae</i> McGregor	Ornamentals
1610	New Hebrides	Chazeau (1979)
1611	<i>Tetranychys neocaledonicus</i> Andre	Cassava
1612	New Caledonia	Chazeau (1979)
1613	<i>Tetranychus urticae</i> Koch	Vegetables
1614	New Caledonia	Chazeau (1979)
1615	<i>Tetranychus urticae</i> Koch	Soya and beans
1616	Australia	Houston (1980)
1617	<i>Stethorus vinsoni</i> Kapur	

1618 *Tetranychus evansi* Baker & Pritchard solanaceous plants
1619 Mauritius Mouitia (1958)

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1621 ^a Syn. : *Stethorus*, *Parastethorus* gen. nov. Ślipiński 2007.

1622 ^b Syn.: *Stethorus incompletus* Whitehead, *Stethorus histrio* Chazeau (Ślipiński 2007).

1623 ^c Reported as fed upon by Syn.: *Stethorus loxtoni* Britton & Lee

1624 ^d Syn.: *Stethorus ogloblini* Nunenmacher (Gordon 1982).

1625 ^e Syn. : *Stethorus picipes* Casey (Gordon 1985).

1626 ^f Syn. : *Stethorus atomus* Casey (Gordon 1985).

1627

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1628
1629 Table 2. Some biological parameters observed for six species of *Stethorus* predators of tetranychid mites
1630 (mean / range in italics)

1631				
1632				
1633	Predator:	<i>S. punctillum</i>	<i>S. punctum picipes</i>	<i>S.</i>
1634	<i>madecassus</i>	<i>S. tridens</i>	<i>S. japonicus</i>	<i>S. loi</i>
1635	Prey	Weise, on	Casey, on	
1636		Chazeau, on	Gordon, on	Kamija,
1637	on	Sasaji, on		
1638		<i>T. mcdanieli</i>	<i>O. punicae</i>	<i>T.</i>
1639	<i>neocaledonicus</i>	<i>T. evansi</i>	<i>T. urticae</i>	<i>T.</i>
1640	<i>kanzawai</i>			
1641		McGregor	(Hirst)	Andre
1642		Roy et al.	Tanigoshi and	
1643	Chazeau 1974a, b	Fiaboe et al. 2007	Mori et al. 2005;	Shih et
1644	al. 1991			
1645		2002, 2003	McMurtry 1977	
1646				
1647				
1648				
1649	Temperature (°C)	24/16-32	24.5/22-27	25/20-
1650	28.4	27/20-30	25/20-30	24
1651	Development time (days)	17/49-12	17/15.8-19	14/11-
1652	21	16/24-12	17/28-11	15.3
1653	Length of pre-oviposition period (days)	1.2/4.0-0.8	5.6/4-6	4.2/3-7
1654	Total progeny (eggs)	280/7-47	221/12-391	184/20-
1655	471	123	501/620-736	165
1656	Longevity of female (days)	70/112-19	90.0/75-243	
1657		43.6/10-134	72	69/128-
1658	66	48.4		
1659	$R_0/r_m/T^a$	-/0.100/	103.3/0.121/38.3	
1660		92.4/0.155/29.2	53/0.104/38	
1661		271/0.156/51.1	50/0.160/24.4	
1662	Prey consumed during development	239 ^b	361/325-379 ^c	
1663		491/303-754 ^d	184 ^c	--
1664	Prey consumed by ovipositing			
1665	females (mites per day)	66.3/52-87 ^b	35.9/32-44 ^e	
1666		46.8/11-80 ^e	67.8 ^c	294 ^f

1668 ^a R_0 = net production, r_m = intrinsic rate of natural increase per day; T = mean generation time (days)

1669 ^b Prey = various instars and adults

1670 ^c Prey = proto- and deutonymphs.

1671 ^d Prey = eggs only

1672 ^e Prey = adult females

1673 ^f Prey = eggs only, but averaged for only the first 20 days after adult female eclosion

1674 ^g Prey = deutonymphs only

1675 ^h Adult beetles, males and females, fed

1676

1677

1678