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Review

Coccinellidae as predators of mites: Stethorini in biological control

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ABSTRACT

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

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1. Introduction

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

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

Our understanding of what constitutes an effective mite biological control agent has changed considerably over the last 50 years. Early research focused on the abilities of acariphagous mites and coccinellids to overcome spider mite outbreaks, and on the abilities of these predators to develop resistance to pesticides applied to control primary pests in highly managed agroecosystems such as

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apple and citrus. More recently, the potential of some phytoseiid predators to regulate spider mites at low equilibrium densities has become more widely appreciated (Croft, 1990; McMurtry and Croft, 1997; Biddinger and Hull, 2005).

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

2. Overview of Stethorini

2.1. Taxonomic status

Earlier works placed *Stethorus sensu lato* in the tribe Scymnini, but recent works placed it in the monogeneric tribe Stethorini Dobzhansky (Chazeau, 1985; Hodek and Honěk, 1996; Giorgi et al., 2009, this volume). Stethorini are unique from all other Scymninae by the convex anterior margin of the prosternum and the truncate clypeus near the antennal bases (Gordon, 1985). Recently, Ślipiński (2007) raised the subgenus *Parastethorus* Pang and Mao (Gordon and Chapin, 1983) to generic status, which this review reflects. Gordon and Chapin (1983) had earlier placed the following species into what was then the subgenus *Parastethorus*: *Stethorus tuncatus* Kapur from Malaysia, *S. gutierrezii* Chazeau from New Hebrides, *S. nigripes* Kapur and *S. histrio* Chazeau from Australia. Five species from Asia are now considered to be in *Parastethorus* as well: *S. dichiapiculus* Xiao, *S. guangxiensis* Pang and Mao, *S. indira* Kapur, *S. malaius* Xiao, and *S. yunnanensis* Pang and Mao (Yu, 1996).

2.2. Morphology and life stages

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

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

2.3. Geographical distribution

Stethorini are present throughout the world in many different climates ranging from tropical rainforests to temperate deciduous



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

forests and plains to colder northern regions of Europe, Canada, and Russia (see map, Fig. 1, for distribution of economically important species). *Stethorus punctillum* Weise has the largest distribution in the group, ranging over most of temperate North America, Europe, and Asia. A major driving force behind the current geographic distribution of Stethorini has been their intentional redistribution by biological control scientists. For example, approximately 12 species (some of which were never formally identified) were introduced into California from geographically diverse areas such as Australia, China, Guatemala, India, Morocco, Pakistan, South Africa, and Turkey (Hall and Fleschner, 1958; Gordon, 1982). Some of the earliest introductions occurred in Hawaii, which apparently has no native species of Stethorini (Swezey, 1925; Fournier et al., 2002). *Parastethorus nigripes* (Kapur) represents the most recent introduction of Stethorini in North America (Gordon, 1993). This is an important predator of *Panonychus ulmi* (Koch) and *Tetranychus urticae* Koch in Australia (Edwards and Hodgson, 1973; Field, 1979). *Parastethorus nigripes* established itself in Texas corn where it consumes the Banks grass mite, *Oligonychus pratensis* (Banks) (Pollock and Michels, 2002), but only after introductions into California almonds failed (Hoy and Smith, 1982). The other recent addition to the North American fauna is *P. histrio* (= *Stethorus histrio*), from the Mascarene Islands east of Madagascar (Gordon and Anderson, 1979). It has since been found throughout Australia (including Tasmania), New Caledonia and parts of South America. Aguilera (1987) surmised it to be introduced accidentally into central Chile. Gordon and Chapin (1983) extended the range north into the Yucatan (Mexico), but Pollock and Michels (2003) reported it for the first time in the United States feeding on mites in corn, co-occurring with *P. nigripes* and the native species *Stethorus caseyi* Gordon and Chapin. Pollock and Michels (2003) found *S. caseyi* to be relatively scarce and speculated as to whether it had been displaced by these newly introduced species.

Additional introductions of Stethorini have likely established into new geographical ranges; the number is unknown because many species can only be identified by taxonomic experts of the group. The accidental introduction of *S. punctillum* from Europe into North America completely displaced the native *S. punctum* from Ontario fruit orchards and other habitats over a 20 year period (Putman, 1955a; Putman and Herne, 1966). In Québec, *S. punctillum* has been the only species collected from raspberry and apple crops in the past 15 years (personal communication with Michèle Roy, MAPAQ Laboratoire de Diagnostic en Phytoprotection). In Pennsylvania orchards, however, the pesticide resistant *S. punctum* was only found in fruit orchards, but *S. punctillum* was prevalent in adjacent Christmas tree plantations (Wheeler et al. 1973, Hull, personal observation).

3. Behavior as predators

3.1. Prey searching behavior

Many early studies of various species of Stethorini concluded that they are “high density predators” unable to regulate spider mite populations at low densities (Fleschner, 1950; Bailey and Caon, 1986; Tanigoshi and McMurtry, 1977). Congdon et al. (1993) challenged this “high density predator” designation and asserted that high density spider mite populations have become common only since the advent of synthetic insecticides (Huffaker et al., 1970), and that the studies that support the “high density predator” status of Stethorini ignored the spatial context of spider mite populations. While it is true that most Stethorini species do not lay eggs until mite populations are relatively high in comparison to the low mite levels maintained by some Phytoseiidae, the

Stethorini have provided economically successful regulation of pest mites in several cases. Reasons underlying these success stories include (a) the regulatory potential of the long-lived adults; (b) the ability of adults to rapidly immigrate into cropland; and (c) the ability of non-pest tetranychid mite populations, non-tetranychid mites, extrafloral nectaries, aphid honeydew, and pollen, to support populations of Stethorini before pest mite populations reach outbreak proportions in crops. The importance of Stethorini species worldwide as biological control agents is also suggested by the over 500 references found in the course of this review.

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

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

3.1.1. Visual stimuli

At least some species of Stethorini are visually attracted to white or yellow colors. When spider mite populations are low, sticky traps can be more effective than visual counts in monitoring *Stethorus* populations (Felland et al., 1995; Biddinger and Hull, 1995; Takahashi et al., 2001a; Roy et al., 2005). Readshaw (1975) used white sticky card traps to monitor Stethorini populations in orchards early in the season. Felland et al. (1995) found that yellow sticky card traps captured up to 15 times more *S. punctum* than white traps. Spider mite feeding causes a yellowing (bronzing) of leaves, and like many other coccinellids (Seagraves, 2009, this issue), foraging Stethorini adults may use this color as an indication of prey. *Stethorus punctum* is primarily diurnal (Hull et al., 1977b), which reinforces the hypothesis that vision is an important foraging cue.

3.1.2. Olfactory stimuli

Prey-derived olfactory stimuli are another important cue for foraging Stethorini adults. Colburn and Asquith (1970) examined the olfactory response of adult *S. punctum* to *P. ulmi* under choice conditions. The beetles walked preferentially toward prey versus the no-prey treatments in the presence and absence of apple foliage. Later work found that *S. japonicus* and *S. punctillum* also are attracted to the volatiles of tetranychid-infested plants

(unpublished data cited in Takahashi et al., 2001b; Lentz et al., 2004). Lentz et al. (2004) went on to show that at least some of the attractive volatiles were produced by infested cucumber and bean plants.

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

Although it is clear that olfactory cues are important in attracting foraging Stethorini, beetles do not necessarily respond to specific olfactory stimuli under field conditions. For example, *S. japonicus* was not significantly attracted to sticky traps with plant volatile blends in a Japanese pear orchard, perhaps because high *Tetranychus kanzawai* Kishida populations may have obscured the trap-associated volatile attractants (Takahashi et al., 2001a). In another study, infested host odors or other plant cues (e.g., plant location or stature) may have inhibited the attractiveness of mite-infested bean plants to *S. japonicus* (Takahashi et al., 2001b). Gillespie et al. (1997) used potted bean plants infested with *T. urticae* to collect *S. punctillum* and several other mite predators in several habitats in British Columbia, Canada, indicating perhaps that not all Stethorini spp. are equally attracted to the same volatiles.

3.2. Trophic ecology and life history parameters

3.2.1. Relative quality of mites as prey

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

Many prey change in their suitability for coccinellids as they age (Hodek and Honěk, 2009, this issue), and mites are no exception. Stethorini adults and larvae often prefer mite eggs over other pest life stages (Houck, 1991; Tanigoshi and McMurtry, 1977), but *S. madecassus* preferred adult mites over eggs as prey (Chazeau, 1974b). Generally, eggs are the most nutritious life stage of a prey item, largely because they contain less water (Lundgren, 2009a). Also, the eggs may be less defended, more apparent to mobile adults, or more abundant than other life stages. Most studies employ only a single life stage of mite prey (usually adult females or eggs) when they determine the developmental rates of various Stethorini species, and do not examine the nutritional values of the various prey stages or intraspecific competition between predator stages. Houck (1991) speculated that varying the mite stages consumed by *S. punctum* might prevent severe oscillations in both the predator and the prey populations. As with many other coccinellids, Stethorini females often consume more prey than conspecific males (Hull et al., 1977b; Chazeau, 1985).

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

3.2.2. Non-mite foods of Stethorini

Reports of Stethorini feeding on non-acarid prey and non-prey foods challenge the assertion that all species feed and develop only on spider mites. Al-Duhawi et al. (2006) found *S. gilvifrons* adults and larvae to be very efficient predators of all stages of the *Bemisia tabaci* (Gennadius) and, in laboratory trials, found the larvae completed their development on this prey alone. Silva and Bonani (2008) reported *S. minutulus* Gordon and Chapin feeding on the tobacco whitefly on cotton in Brazil as well. However, Silva (personal communication) confirmed that the coccinellid found feeding on whiteflies was actually a species of *Delphastus* (Sticholotidinae); some specimens of *S. minutulus* feeding on mites in the same whitefly colony had been sent for identification by mistake. Mathur (1969) observed that starving larval and adult *S. gilvifrons* ate *Macrosiphum* sp. (Hemiptera: Aphididae) “to a very limited extent,” and Almatni and Khalil (2008) reported this species “fed occasionally” on *Brachycaudus amygdalinus* (Schouteden) (Hemiptera: Aphididae). Masee (1940) noted *S. punctillum* as a predator of *Phorodon humuli* (Schrank) (Hemiptera: Aphididae).

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

3.2.3. Developmental and prey consumption rates

Some attractive characteristics of Stethorini for mite biological control are their prey consumption, longevity and high reproductive capacity (Table 2). Each adult female may consume 30–60 mites per day. Total fecundity ranges from 123 eggs in *S. tridens* (Fiaboe et al., 2007), 184 eggs in *S. madecassus* (Chazeau, 1974a, b), 221 in *S. punctum* (Tanigoshi and McMurtry, 1977), 279 in *S. punctillum* (Roy et al., 2003), to a high of 501 eggs in *S. japonicus* (Mori et al., 2005). Developmental times for most species are approximately 17 d at 25 °C from oviposition to adult eclosion (Fiaboe et al., 2007; Mori et al., 2005; Putman, 1955a; Roy et al.,

Table 1

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

Predator and prey	Crop or plant	Region	Reference
<i>Parastethorus guangxiensis</i> (Pang and Mao) ^a <i>Panonychus citri</i> (McGregor)	Citrus	China (Guangxi)	Li et al. (1990)
<i>Parastethorus gutierrezii</i> (Chazeau) ^a <i>Oligonychus</i> sp.	Coconut palm	New Hebrides	Chazeau (1979)
<i>Parastethorus histrio</i> (Chazeau) ^b <i>Brevipalpus chilensis</i> Baker <i>Brevipalpus chilensis</i> Baker <i>Eutetranychus orientalis</i> (Klein) <i>Oligonychus thelytokus</i> Gutierrez <i>Oligonychus vitis</i> Zaher and Shehata <i>Oligonychus yothersi</i> (McGregor) <i>Oligonychus</i> sp. <i>Panonychus citri</i> (McGregor) <i>Panonychus citri</i> (McGregor) <i>Panonychus ulmi</i> (Koch) <i>Tetranychus kanzawai</i> Kishida <i>Tetranychus lintearius</i> Dufour <i>Tetranychus neocaledonicus</i> Andre <i>Tetranychus urticae</i> Koch <i>Tetranychus urticae</i> Koch Tetranychidae Tetranychidae	Beans Grape Citrus Lychee, Plumeria Table Grapes Avocado Pine tree (<i>Pinus</i> sp.) Citrus Citrus Apple Bindweed (<i>Convolvulus</i> sp.) Gorse — Various vegetables Papaya Apple Maize, redbud tree (<i>Cercis</i>)	Chile Chile India New Caledonia Chile Chile Australia Chile Peru Chile Australia Australia New Caledonia Reunion Australia New Zealand USA (Texas)	Aguilera (1987) Prado (1991) Dhooria (1981) Chazeau (1979) Prado (1991) Prado (1991) Houston (1980) Aguilera (1987) Guanilo and Martínez (2007) Aguilera (1987) Houston (1980) Ireson et al. (2003) Chazeau (1979) Chazeau et al. (1974) Houston (1980) Chazeau (1979) Pollock and Michels (2003)
<i>Parastethorus indira</i> (Kapur) ^a Tetranychidae	Taro	India	Kapur (1950)
<i>Parastethorus nigripes</i> (Kapur) ^a <i>Oligonychus pratensis</i> (Banks) <i>Panonychus citri</i> (McGregor) <i>Panonychus ulmi</i> (Koch) ^c <i>Tetranychus lambi</i> Pritchard and Baker ^c <i>Tetranychus urticae</i> Koch <i>Tetranychus urticae</i> Koch ^c <i>Tetranychus urticae</i> Koch	Corn Citrus Apple Banana Apple Soya Alfalfa seed crop	USA (Texas, Oklahoma) Australia Australia Australia Australia Australia Australia	Pollock and Michels (2002) Beattie and Gellatley (1983) Walters (1976a) Houston (1980) Edwards and Hodgson (1973) Houston (1980) Bailey and Caon (1986)
<i>Stethorus aethiops</i> Weise <i>Mononychellus tanajoa</i> (Bondar) complex <i>Tetranychus lombardini</i> Baker and Pritchard <i>Tetranychus neocaledonicus</i> Andre <i>Tetranychus urticae</i> Koch	Cassava Cassava Cassava Cassava	Kenya Kenya Kenya Kenya	Yaseen et al. (1982) Yaseen et al. (1982) Yaseen et al. (1982) Yaseen et al. (1982)
<i>Stethorus aptus</i> Kapur <i>Panonychus citri</i> (McGregor)	Citrus	China (Guangxi)	Li et al. (1990)
<i>Stethorus bifidus</i> Kapur <i>Bryobia</i> sp. <i>Panonychus ulmi</i> (Koch), <i>Tetranychus urticae</i> Koch <i>Tetranychus lambi</i> Pritchard and Baker <i>Tetranychus lintearius</i> Dufour <i>Tetranychus urticae</i> Koch	Apple Apple, plum, pear Apple Gorse Rasperry	New Zealand New Zealand New Zealand New Zealand New Zealand	McMurtry et al. (1970) Collyer (1964) McMurtry et al. (1970) Peterson et al. (1994) Thomas and Burnip (1984), Charles et al. (1985)
<i>Stethorus caseyi</i> Gordon and Chapin <i>Oligonychus pratensis</i> (Banks)	Maize	USA (Texas)	Pollock and Michels (2003)
<i>Stethorus chengi</i> Sasaji <i>Panonychus citri</i> (McGregor) <i>Tetranychus urticae</i> Koch	Citrus Papaya	China Taiwan	Chen and Zhao (1994) Wen and Lee (1981)
<i>Stethorus comoriensis</i> Chazeau <i>Oligonychus coffeae</i> (Nietner) <i>Tetranychus neocaledonicus</i> Andre	Plumeria Breadfruit	Comoro Islands Comoro Islands	Chazeau (1971b) Chazeau (1971b)
<i>Stethorus darwini</i> (Brethes) ^d <i>Mononychellus caribbeanae</i> McG., <i>Mononychellus tanajoa</i> (Bondar) complex, various Tetranychidae <i>Panonychus ulmi</i> Koch <i>Tetranychus evansi</i> Baker and Pritchard	Cassava Apple Tomato	Guyana, Surinam Brazil Brazil	Yaseen et al. (1982) Lorenzato (1987) Paschoal (1970)
<i>Stethorus expectatus</i> Chazeau <i>Oligonychus</i> , <i>Panonychus</i> , <i>Schizotetranychus</i> spp. <i>Tetranychus fijiensis</i> Hirst <i>Tetranychus lambi</i> Pritchard and Baker	Various crops Coconut palm Cassava	New Guinea New Guinea New Guinea	Chazeau (1983) Chazeau (1983) Chazeau (1983)
<i>Stethorus exsultabilis</i> Chazeau <i>Oligonychus</i> , <i>Panonychus</i> , <i>Schizotetranychus</i> spp. <i>Tetranychus fijiensis</i> Hirst <i>Tetranychus lambi</i> Pritchard and Baker	Various crops Coconut palm Cassava	New Guinea New Guinea New Guinea	Chazeau (1983) Chazeau (1983) Chazeau (1983)

(continued on next page)

Table 1 (continued)

Predator and prey	Crop or plant	Region	Reference
<i>Stethorus fenestralis</i> Houston			
<i>Tetranychus kanzawai</i> Kishida	Bindweed (<i>Convolvulus</i> sp.)	Australia	Houston (1980)
<i>Tetranychus lambi</i> Pritchard and Baker	Banana, papaya	Australia	Houston (1980)
<i>Tetranychus urticae</i> Koch	Papaya	Australia	Houston (1980)
<i>Stethorus fijiensis</i> Kapur			
Tetranychidae	—	Fiji	Swaine (1971)
<i>Stethorus fuerschii</i> Chazeau			
<i>Oligonychus chazeaui</i> Gutierrez	Palm tree	Madagascar	Chazeau (1971b)
<i>Tetranychus roseus</i> Gutierrez	Palm tree	Madagascar	Chazeau (1971b)
<i>Stethorus gilvifrons</i> (Mulsant)			
<i>Eutetranychus hirsti</i> Pritchard and Baker	—	Iran	Afshari et al. (2007)
<i>Eutetranychus orientalis</i> (Klein)	—	Iran	Afshari et al. (2007)
<i>Oligonychus afasiaticus</i> (McGregor)	—	Iran	Afshari et al. (2007)
<i>Oligonychus coffeae</i> (Nietner)	Tea	India	Sarmah and Bhattacharyya 2002.
<i>Oligonychus sacchari</i> (McGregor)	Sugarcane	Iran	Afshari (1999)
<i>Panonychus citri</i> (McGregor), <i>Eotetranychus</i> sp.	Orange, apple, rose	Philippines	Handoko (2004)
<i>Panonychus ulmi</i> Koch	Apple	Iran	Haji-Zadeh et al. (1993)
<i>Tetranychus turkestanii</i> Ugarov and Nikolski	Strawberry	Iran	Ahmed and Ahmed (1989)
<i>Tetranychus turkestanii</i> Ugarov and Nikolski	Various ornamentals	Iran	Sohrabi and Shishenbor (2007)
<i>Tetranychus urticae</i> Koch	Castor bean	India	Mathur (1969)
<i>Tetranychus urticae</i> Koch	Cucumbers, beans	Iran	Mehr-Khou et al. (2008)
Tetranychidae	Various crops	Lebanon	McMurtry et al. (1970)
<i>Stethorus griseus</i> Whitehead			
Tetranychidae	Apple	New Zealand	Chazeau (1979)
<i>Stethorus japonicus</i> Kamiya			
<i>Panonychus citri</i> (McGregor)	Citrus	Japan	McMurtry et al. (1970)
<i>Panonychus citri</i> (McGregor)	Mandarin orange	Japan	Tsuchiya (2005)
<i>Panonychus mori</i> Yokoyama	Japanese pear	Japan	Kishimoto and Adachi (2008)
<i>Tetranychus kanzawai</i> Kishida	Tea, hydrangea	Japan	Mori et al. (2005)
<i>Tetranychus urticae</i> Koch	Apple, citrus	Japan	Mori et al. (2005)
<i>Tetranychus urticae</i> Koch	Japanese pear	Japan	Kishimoto and Adachi (2008)
<i>Tetranychus viennensis</i> Zacher	Japanese pear	Japan	Kishimoto and Adachi (2008)
<i>Stethorus jejunus</i> Casey			
<i>Mononychellus tanajoa</i> (Bondar) complex	Cassava	Kenya	Yaseen et al. (1982)
<i>Tetranychus lombardini</i> Baker and Pritchard	Cassava	Kenya	Yaseen et al. (1982)
<i>Tetranychus neocaledonicus</i> Andre	Cassava	Kenya	Yaseen et al. (1982)
<i>Tetranychus urticae</i> Koch	Cassava	Kenya	Yaseen et al. (1982)
<i>Stethorus keralicus</i> Kapur			
<i>Raoiella indica</i> Hirst (Tenuipalpidae)	Areanut palm, coconut	India	Puttaswamy and Rangaswamy (1976)
<i>Stethorus loi</i> Sasaji			
<i>Panonychus citri</i> (McGregor)	Jujube	Taiwan	Wen et al. (1993)
<i>Tetranychus urticae</i> Koch	Papaya	Taiwan	Wen and Lee (1981)
Tetranychidae	Carambola	Taiwan	Chang and Leu (1986)
<i>Stethorus madecassus</i> Chazeau			
<i>Tetranychus neocaledonicus</i> Andre	Cotton	Madagascar	Chazeau (1971a)
<i>Tetranychus</i> spp., <i>Oligonychus</i> spp.	Various crops	Madagascar	Chazeau (1971a)
<i>Stethorus parcempunctatus</i> Puttarudrian and ChannaBasavanna			
<i>Raoiella indica</i> Hirst (Tenuipalpidae)	Coconut palm	India	Gupta (2001)
<i>Stethorus parapauerculus</i> Pang			
<i>Tetranychus piercei</i> McGregor	Banana	China (Hainan)	Chen et al. (2005)
<i>Tetranychus urticae</i> Koch	Cassava	China	Lin and Chen (1984)
<i>Stethorus pauperculus</i> Weise			
<i>Oligonychus indicus</i> (Hirst)	Sorghum	India	Kapur (1948)
<i>Oligonychus neocaledonicus</i> Andre	Papaya, castor bean, and Various crops	India	Puttaswamy and ChannaBasavanna (1977)
<i>Tetranychus ludeni</i> Zacher	Eggplant	India	Puttaswamy and ChannaBasavanna (1980)
<i>Tetranychus ludeni</i> Zacher	Waterhyacinth	India	Ansari and Pawar (1992)
<i>Stethorus punctillum</i> Weise			
<i>Eotetranychus buxi</i> (Garman)	Boxwood (<i>Buxus</i> sp.)	USA (Maryland)	Creary (2009)
<i>Eotetranychus carpini</i> (Oudemans)	Grapes	Italy	Laffi (1982)
<i>Eotetranychus tiliarium</i> Hermann	Linden trees (<i>Tilia</i> spp.)	Germany	Jäckel et al. (2000)
<i>Oligonychus afasiaticus</i> (McGregor)	Date palm	Algeria	Idder and Pintureau (2008)
<i>Oligonychus bicolor</i> (Banks)	Chestnut	Italy	Cinti et al. (1995)
<i>Oligonychus ununguis</i> (Jacobi)	Chinese Chestnut	Canada	Putman (1955a)
<i>Oligonychus ununguis</i> (Jacobi)	Pines, cedars and Arborvitae	USA (Pennsylvania)	Wheeler et al. (1973)
<i>Panonychus citri</i> (McGregor)	Citrus	China	Tian (1995)
<i>Panonychus ulmi</i> (Koch)	Fruit trees	Canada	Putman (1955a)
<i>Panonychus ulmi</i> (Koch)	Fruit trees	Europe	McMurtry et al. (1970)
<i>Panonychus ulmi</i> (Koch)	Apple	Italy	Pasqualini and Antropoli (1994)

Table 1 (continued)

Predator and prey	Crop or plant	Region	Reference
<i>Tetranychus bioculatus</i> (Wood-Mason)	Marigold	Bangladesh	Taleb and Sardar (2007)
<i>Tetranychus cinnabarinus</i> (Boisduval)	Cotton, apple, watermelon	Israel	Plaut (1965)
<i>Tetranychus mcdanieli</i> McGregor	Raspberry	Canada	Roy et al. (2002)
<i>Tetranychus shoenei</i> McGregor	Elm (<i>Ulmus americana</i>)	USA (Maryland)	Creary (2009)
<i>Tetranychus urticae</i> Koch	Beans	Canada	Putman (1955a)
<i>Tetranychus urticae</i> Koch	Sugar beets	Israel	Plaut (1965)
<i>Tetranychus urticae</i> Koch	Greenhouse crops	The Netherlands	McMurtry et al. (1970)
<i>Tetranychus viennensis</i> Zacher	Apple and other fruits	Turkey	Yigit and Uygun (1986)
<i>Stethorus punctum picipes</i> Casey ^e			
<i>Oligonychus punicae</i> (Hirst)	Avocado	USA (California)	McMurtry et al. (1969)
<i>Panonychus citri</i> (McGregor)	Citrus	USA (California)	McMurtry et al. (1970)
<i>Tetranychus tumidus</i> Banks	Banana	Cuba	Perez et al. (2004)
Tetranychidae	Walnuts, melon, apple	USA	McMurtry et al. (1970)
<i>Stethorus punctum punctum</i> (LeConte)			
<i>Panonychus ulmi</i> (Koch) and other tetranychids	Fruit trees	North America	McMurtry et al. (1970)
<i>Tetranychus mcdanieli</i> McGregor	Fruit trees	Canada	Robinson (1953)
<i>Tetranychus pacificus</i> McGregor	Fruit trees	Canada	Robinson (1953)
<i>Stethorus siphonulus</i> Kapur			
<i>Eutetranychus banksi</i> McGregor	Ornamentals	Hawaii	Raros and Haramoto (1974)
<i>Oligonychus exsicicator</i> (Zehntner)	Sugar cane	Hawaii	Raros and Haramoto (1974)
<i>Panonychus citri</i> (McGregor)	Citrus	China (Fujian)	Huang et al. (1988)
<i>Tetranychus cinnabarinus</i> (Boisduval)	Papaya	Hawaii	Rosenheim et al. (2004b)
<i>Tetranychus neocaledonicus</i> Andre	Custardapple (<i>Anona</i> sp.)	French Polynesia	Chazeau (1979)
<i>Tetranychus piercei</i> McGregor	Papaya	China (Guangdong)	Lui and Lui (1986)
<i>Tetranychus tumidus</i> Banks	Papaya	Hawaii	Raros and Haramoto (1974)
<i>Tetranychus urticae</i> Koch	Papaya	Hawaii	Raros and Haramoto (1974)
<i>Stethorus tridens</i> Gordon			
<i>Panonychus citri</i> McGregor	Citrus	Peru	Guanilo and Martínez (2007)
<i>Tetranychus cinnabarinus</i> (Boisduval)	Cassava	Colombia	Gordon (1982)
<i>Tetranychus evansi</i> Baker and Pritchard	Tomato	Brazil	Britto et al. (2009)
<i>Tetranychus urticae</i> Koch	Cassava	Colombia	Gordon (1982)
Tetranychidae	Eggplant	Colombia	Gordon (1982)
<i>Stethorus utilis</i> Horn ^f			
<i>Eotetranychus hicolorae</i> (McGregor)	Pecan	USA (Southeast)	Tedders (1983)
<i>Eotetranychus sexmaculatus</i> (Riley)	Citrus	USA (Florida)	McMurtry et al. (1970)
<i>Eutetranychus banksi</i> (McGregor)	Citrus	USA (Texas)	McMurtry et al. (1970)
<i>Mononychellus caribbeanae</i> (McGregor), <i>Mononychellus tanajoa</i> (Bondar) complex, various Tetranychidae	Cassava	Colombia, Nicaragua, Trinidad	Yaseen et al. (1982)
<i>Oligonychus pratensis</i> (Banks)	Sorghum	USA (Texas)	Ehler (1974)
<i>Tetranychus urticae</i> Koch, <i>Panonychus citri</i> (McGregor)	Citrus	Cuba	Mora Morin (1991)
Tetranychidae	Lychee	USA (Florida)	Butcher (1951)
<i>Stethorus vagans</i> (Blackburn)			
<i>Bryobia praetiosa</i> Koch	Clover	Australia (Tasmania)	Evans (1943)
<i>Oligonychus exsicicator</i> (Zehntner)	Sugar cane	USA (Hawaii)	Swezey (1923)
<i>Oligonychus thelytokus</i> Gutierrez	Lychee	New Caledonia	Chazeau (1979)
<i>Oligonychus</i> sp.	Coconut palm	New Caledonia	Chazeau (1979)
<i>Oligonychus</i> sp.	Pine tree (<i>Pinus</i> sp.)	Australia	Houston (1980)
<i>Panonychus ulmi</i> (Koch)	Apple	Australia	Walters (1976a)
<i>Tetranychus lambi</i> Pritchard and Baker	Cassava	New Caledonia	Chazeau (1979)
<i>Tetranychus lambi</i> Pritchard and Baker	Papaya	Australia	Houston (1980)
<i>Tetranychus marianae</i> McGregor	Castor bean	New Caledonia	Chazeau (1979)
<i>Tetranychus marianae</i> McGregor	Ornamentals	New Hebrides	Chazeau (1979)
<i>Tetranychus neocaledonicus</i> Andre	Cassava	New Caledonia	Chazeau (1979)
<i>Tetranychus urticae</i> Koch	Vegetables	New Caledonia	Chazeau (1979)
<i>Tetranychus urticae</i> Koch	Soya and beans	Australia	Houston (1980)
<i>Stethorus vinsoni</i> Kapur			
<i>Tetranychus evansi</i> Baker and Pritchard	Solanaceous plants	Mauritius	Mouitia (1958)

^a Syn.: *Stethorus*, *Parastethorus* gen. nov. (Ślipiński, 2007).^b Syn.: *Stethorus incompletus* Whitehead, *Stethorus histrio* Chazeau (Ślipiński 2007).^c Reported as fed upon by Syn.: *Stethorus loxtoni* Britton and Lee.^d Syn.: *Stethorus ogloblini* Nunenmacher (Gordon, 1982).^e Syn.: *Stethorus picipes* Casey (Gordon, 1985).^f Syn.: *Stethorus atomus* Casey (Gordon, 1985).

2002; Tanigoshi and McMurtry, 1977). The number of Stethorini generations per year varies from 2 to 3 in temperate regions for *S. punctillum* and *S. punctum* (Putman, 1955a; Colburn and Asquith, 1971) to more than 15 per year for tropical species such as *S. siphonulus* and *S. pauperculus* (Puttaswamy and Rangaswamy, 1976; Puttaswamy and ChannaBasavanna 1977). Adult longevity is not

known for most species, but appears to be longer in temperate species which undergo diapause than in tropical species, and is temperature dependent. Putman (1955a) found *S. punctillum* females in Canada could commonly survive and lay eggs over multiple seasons under field conditions, with an average longevity of over 400 days; males generally die sooner than females. Ullah

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

Predator	<i>S. punctillum</i>	<i>S. punctum picipes</i>	<i>S. madecassus</i>	<i>S. tridens</i>	<i>S. japonicus</i>	<i>S. loi</i>
Prey	Weise, on <i>T. mcdanieli</i> McGregor Roy et al. (2002, 2003)	Casey, on <i>O. punicae</i> (Hirst) Tanigoshi and McMurtry 1977	Chazeau, on <i>T. neocaledonicus</i> Andre Chazeau (1974a,b)	Gordon, on <i>T. evansi</i> Baker and Pritchard Fiaboe et al. 2007	Kamija, on <i>T. urticae</i> Koch Mori et al. 2005; Gotoh et al. 2004	Sasaji, on <i>T. kanzawai</i> Kishida Shih et al. 1991
Temperature (°C)	24/16–32	24.5/22–27	25/20–28.4	27/20–30	25/20–30	24
Development time (days)	17/49–12	17/15.8–19	14/11–21	16/24–12	17/28–11	15.3
Length of pre-oviposition period (days)	1.2/4.0–0.8	5.6/4–6	4.2/3–7	10.3	4.7/7–13	4.1
Total progeny (eggs)	280/7–47	221/12–391	184/20–471	123	501/620–736	165
Longevity of female (days)	70/112–19	90.0/75–243	43.6/10–134	72	69/128–66	48.4
$R_0/r_m/T^a$	–/0.100/	103.3/0.121/38.3	92.4/0.155/29.2	53/0.104/38	271/0.156/51.1	50/0.160/24.4
Prey consumed during development	239 ^b	361/325–379 ^c	491/303–754 ^d	184 ^c	–	1,408 ^g
Prey consumed by ovipositing females (mites per day)	66.3/52–87 ^b	35.9/32–44 ^e	46.8/11–80 ^e	67.8 ^c	294 ^f	26.1 ^{g,h}

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

^b Prey, various instars and adults.

^c Prey, proto- and deutonymphs.

^d Prey, eggs only.

^e Prey, adult females.

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

^g Prey, deutonymphs only.

^h Adult beetles, males and females, fed.

(2000) found adults of both sexes of *S. vagans* in Australia lived 126 days at 12 °C compared to only 27 days at 30 °C.

Since the developmental times differ little among species of *Stethorini*, the differences in r_m -values between species are attributable to differences in reproductive rates (Mori et al., 2005) (Table 2). At 24–25 °C the r_m -values for *Stethorus* species range from 0.100 in *S. punctillum* (Roy et al., 2003) to 0.160 in *S. loi* (Shih et al., 1991); a number of other species have been evaluated and found to fall within this range (Chazeau, 1974a,b; Fiaboe et al., 2007; Mori et al., 2005; Richardson, 1977; Tanigoshi and McMurtry, 1977). Sabelis (1985a,b, 1991) calculates that the r_m -values for tetranychid mites range from 0.160 to 0.293 at around 25 °C. This is significantly higher than the values for *Stethorini* species listed in Table 2, but their functional response to prey may still allow them to regulate pest populations.

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

3.2.4. Diapause and overwintering

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

(McMurtry et al., 1970; 1974). Tropical species seldom experience diapause (Chazeau, 1985; Hoy and Smith, 1982).

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

Spring emergence of *S. punctum* adults in Pennsylvania apple orchards over three seasons was correlated with tree phenology, ground cover emergence traps, colored sticky card traps, ambient temperatures, and degree day accumulations (Felland et al., 1995; Biddinger and Hull, 1995). Adults emerged from diapause at 100 and 300 degree days, base 5 °C starting 1 March of each year, with fifty percent emergence occurring at 210 DD_{5°C}. Emergence was 2%, 47%, and 96% complete by the defined phenological stages of apple as half inch green, pink and petal fall, respectively, for the apple cultivar “Yorking.” Most adults emerged on days of average, minimum, and maximum air temperatures of 15–20, 5–15, and 20–30 °C, respectively.

3.2.5. Natural enemies of *Stethorini*

There is surprisingly little information available on the natural enemies of *Stethorini* species despite numerous reports for other

coccinellid species (Riddick et al., 2009, this volume). A species of rickettsial disease (*Rickettsiella stethorae* Hall and Badgley) from larvae in cultures of *Stethorus* nr. *punctum* from Morocco was described by Hall and Badgley (1957). The disease spread rapidly to cultures of *S. punctum* from Connecticut, *S. gilvifrons* from Hong Kong, *S. punctillum*, and *Stethorus* sp., possibly *S. guatemalensis* = *S. granum* introduced from Guatemala (Hall and Fleschner, 1958). The disease was not found in their prey (six-spotted mite, *Eotetranychus sexmaculatus* [Riley]). Among the parasitic mites, the Laboulbeniales were found on several *S. punctillum* adults collected on raspberry plants in Québec (Michèle Roy, MAPAQ Laboratoire de Diagnostic en Phytoprotection, pers. comm.). We could find no records of parasitoids that attack Stethorini.

Cannibalism on preimaginal stages of *Stethorus* is also common (Cottier, 1934; Fleschner, 1950; Robinson, 1953; Chazeau, 1985). It does not appear to be an important cause of mortality except during times of starvation (Collyer, 1953; Putman, 1955a; Kaylani, 1967; Mathur, 1969) or when larval densities become very high (Houck, 1991). Biddinger and Hull (personal observation) believe the most significant predators to be the older instars of lacewings (*Chrysopa* spp.) and other coccinellids. *Phidippus audax* (Hentz), a salticid commonly found in the tree canopy in the late summer and fall, feeds on *Stethorus* larvae (Biddinger and Hull, personal observation). Rosenheim et al. (2004a, b) found the tangle-nest spider, *Nesticodes rufipes* (Theridiidae), consumed larvae of *S. siphonulus*, thereby disrupting biological control of the carmine spider mite, *Tetranychus cinnabarinus*, on papaya in Hawaii. Putman (1955a) observed an unidentified species of *Typhlodromus* feeding on the eggs of *S. punctillum* when confined. Haney et al. (1987) found that *S. punctum* could regulate populations of citrus red mite in California citrus groves at low levels, but in the presence of the Argentine ant, *Iridomyrmex humilis* (Mayr), mite populations flared dramatically. They attributed this to active harassment of adult (and possibly immature stages) *Stethorus* (also documented by Bartlett, 1963), which inhibited the feeding and numerical response of the beetles.

4. Conservation and value in biological control

The habitats of Stethorini are diverse, and include many agricultural systems such as tree and small fruits, nuts, citrus, avocados, bananas, papaya, palms, tea, cassava, sugarcane, maize, and various vegetables, as well as ornamental plantings, grasslands, forests, and heathlands. The overview provided by Lo et al. (1990) of tetranychid predators in several crops in Taiwan is an illustration of where acariphagous coccinellids often fit within natural enemy communities. Typically coexisting with several phytoseiid mite predators, the staphylinid *Oligota* and green lacewings (*Chrysopa*), *Stethorus loi* Sasaji is considered an important mite predator in citrus and tea plantations, whereas in mulberry, strawberry, and pear, mite management practices focus completely on phytoseiids. Citrus red mite (*Panonychus citri*) is preyed upon by a number of Stethorini in Asia, frequently resulting in significant population suppression. For instance, Huang et al. (1988) provide an account of inoculation of approximately 20 adult *S. siphonulus* per tree in six citrus orchards in southeastern China, resulting in reduction of *P. citri* to below economic thresholds over the growing season, and drastic reduction in miticide input.

It is difficult to generalize which agroecosystems support Stethorini and/or phytoseiid mites as effective tetranychid predators; this is likely a function of many factors such as pesticide use history, crop phenology and characteristics, proximity to refugia for protection from climatic extremes and agrochemicals, and experience and preference of pest management practitioners. Globally, Stethorini perform best as biological control agents in

low-input woody perennial systems. Key to their optimal utilization as biological control agents are the provision of sufficient overwintering habitats or other reservoirs for Stethorini in or near agroecosystems, and their protection from particularly damaging pesticides. Under these circumstances, Stethorini are often important contributors to the suppression of tetranychid populations. Examples are apple orchards in Pennsylvania, USA, citrus and tea in East and South Asia, and in Australian and New Zealand gorse (*Ulex europaeus* L. [Fabaceae]), where they suppressed a tetranychid biological control agent for this invasive woody weed.

4.1. Case studies of Stethorini in IPM systems

4.1.1. *Stethorus punctum* in Pennsylvania orchards

The best documented and most successful biological control program incorporating Stethorini has been that of *S. punctum* in apple and peach orchards of the eastern USA. Pennsylvania initiated a system for the biological control of mites using *S. punctum* during the 1970s (reviewed in Asquith and Hull, 1979; Chazeau, 1985; Croft, 1990; Hull and Beers, 1985; Tanigoshi et al., 1983). The program reportedly reduced acaricide usage by 1000 metric tonnes of formulated product, realizing a cumulative grower savings of US\$20 million over 25 years (Biddinger and Hull, 1995).

Key to the success of this program was early development of resistance by *S. punctum* to organophosphate (OP) insecticides such as azinphosmethyl (Colburn and Asquith, 1973), and the continuous use of this pesticide class in controlling susceptible primary pests (e.g., codling moth and Oriental fruit moth) from the mid 1960s through the mid 1990s (Croft, 1990). The intense selection pressure over decades of using multiple applications of the same insecticides per season undoubtedly contributed to this resistance development, but another factor was a unique method of application known as alternate row-middle spraying (Lewis and Hickey, 1964; Hull and Beers, 1985). In the 1970s this became the preferred method of pesticide application by over 95% of mid-Atlantic fruit growers. Knight and Hull (1992a,b) demonstrated that, using this method, only ~20% dose of the pesticide is deposited on leaves or fruit on the opposite side of the tree, leaving untreated refugia for *Stethorus*, even as new insecticides were employed, to which the predator was not resistant (Hull et al., 1976; Hull and Beers, 1985; David, 1985; Biddinger, 1993; Biddinger and Hull, 1995; Biddinger and Hull, 1999).

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

The period of tetranychid mite control in Pennsylvania with *S. punctum* was characterized by a lack of effective miticides. Starting in the mid 1990s, new miticide registrations offered more effective, less expensive materials. Most growers abandoned recommended action thresholds for *P. ulmi*, and miticide use increased dramatically. *Stethorus punctum* began to disappear from apple orchards

as lower populations of *P. ulmi* prevented predator reproduction. Of more lasting impact however, was the development of OP resistance in the primary lepidopterous pests of eastern apple orchards, which required adoption of new insecticide chemistries, some of which were very toxic to *S. punctum*. These insecticides include the neonicotinoids, and several of the insect growth regulators, which are toxic to various stages of *S. punctum* (Biddinger and Hull, 1993, 1995, 2005; Hull et al., 1991; Hull and Biddinger, 1991a,b), in spite of being classified as “reduced risk,” by the US EPA. James (2003b, 2004) reported similar effects on *S. punctum picipes* in Washington hops. Many of these new insecticides have sublethal effects on pest development and fecundity (Biddinger and Hull, 1999; Sun et al., 2000; Biddinger et al., 2006), which have been demonstrated for *S. punctillum* through feeding on tetranychids on imidacloprid-treated ornamental woody plants (Creary 2009).

Around 2005, biological mite control in Pennsylvania apple orchards shifted to the conservation of the phytoseiid predatory mite, *Typhlodromus pyri* (Schueten) (Biddinger et al., 2008b). *T. pyri* can survive on alternative food sources such as rust mites, pollen or fungi when tetranychid mite densities are very low and do not seasonally disperse from trees, as do other phytoseiid predators such as *Neoseiulus fallacis* (Garman) (Nyrop et al. 1998). Biological mite control with *T. pyri* in Pennsylvania apple orchards does not suffer from temporal or spatial asynchrony such as that found in raspberries (Roy et al. 2005). *Stethorus punctum* is now considered a backup option for mite control when *T. pyri* conservation fails due to the use of toxic insecticides rather than a complement to phytoseiids. Currently, neither *S. punctum* nor *T. pyri* are providing significant mite control in Pennsylvania peach orchards because of the heavy dependency on pyrethroid applications for pest control (Hull and Biddinger, personal observation).

4.1.2. Pesticide impacts and resistance in other *Stethorini* species

Nienstedt and Miles (2008) have established a bioassay for pesticide toxicity for *S. punctillum*, including effects on development and fecundity, and demonstrated its sensitivity using the insect growth regulators fenoxycarb and methoxyfenozide. This species developed resistance to azinphosmethyl in Italian apple orchards under very similar circumstances to that of *S. punctum* in USA (Pasqualini and Malavolta, 1985; Croft, 1990). The value of this predator has also been reduced as alternative insecticides have been adopted to control azinphosmethyl-resistant primary pests (Pasqualini and Antropoli, 1994). Biological control of mites in Italy is now also more dependent on the phytoseiid predatory mites. *T. pyri* and *Amblyseius andersoni* (Chant) (Pasqualini, personal communication).

McMurtry et al. (1970) reviewed the biology and ecology of several North American *Stethorus* spp. and noted the impact of orchard spray practices on them. *Stethorus bifidus* Kapur was the most important insect predator of mites in New Zealand apple orchards, but is susceptible to organophosphate insecticides (Collyer, 1964, 1976). The use of alternate row-middle applications of reduced rates of insecticides was not adopted in New Zealand orchards or in other countries with native species of *Stethorini*; this may contribute to the absence of insecticide resistance. The introduction of the synthetic pyrethroids into New Zealand apple spray programs severely impacted *Stethorini* populations and fruit IPM now largely relies on the introduced pyrethroid resistant phytoseiid, *T. pyri* (Croft, 1990; Marwick, 1988). In Australian apple IPM programs several species of *Stethorini* were important in the 1960–1970s, but are now dependent on phytoseiid predators for biological mite control (Edwards and Hodgson, 1973; Readshaw, 1975; Walters, 1974; Walters, 1976a,b,c; Bower and Kaldor, 1980).

Álvarez-Alfageme et al. (2008) examined the effect of two different Cry1Ab expressing transgenic maize cultivars with lepidoptera-specific Bt toxins. The two-spotted spider mite, *T. urticae*,

retains the Bt toxin but its predator, *S. punctillum*, degrades it without measurable effects on fitness or performance. This is consistent with field results comparing Cry1Ab expressing maize with its isogenic cultivar in Spain, showing no significant differences in coccinellid numbers, which were predominantly *S. punctillum* (de la Poza et al., 2005). Güllü et al. (2004) reported similar results with *S. gilvifrons* comparing Cry1AB expressing maize with an isogenic cultivar in Turkey. To our knowledge no specific deleterious findings are available regarding *Stethorus* and rootworm-targeted (Cry3) transgenic maize.

4.2. Mass rearing

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

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

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

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

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

Several studies have focused on using *Stethorini* for controlling spider mites in greenhouse crops. Raworth (2001) found that releases of *S. punctillum* established and reproduced in peppers and cucumbers but not in tomatoes. This study underscores yet again that the prey's host plant can inhibit predators. Rott and Ponsonby (2000) found in UK glasshouse vegetables, that simultaneous re-

leases of *Neoseiulus californicus*, *S. punctillum*, and *P. persimilis* controlled spider mites better than did *P. persimilis* alone; no intraguild predation was noted, and predator performance varied by crop type. Combined releases of phytoseiids and *S. punctillum* have shown success in greenhouses, interiorscapes, and urban shade tree IPM programs in Europe (Gorski and Fajfer, 2003; Jäckel et al., 2000, 2008; Pöhle et al., 2002). These efforts are testing combinations of releases of phytoseiid mites with *S. punctillum* with habitat modifications, e.g., on shade trees increasing ground residue and providing shelterbands for overwintering. Interior environments with low humidity and artificial lighting pose special challenges that are difficult to overcome (Pöhle et al., 2002). Ornamental pest management is also seen as a possible niche for *S. punctillum* releases in Denmark (Svendsen and Hansen, 2002).

4.4. Inhibition of gorse biocontrol

Stethorini may suppress desirable mites that are biological control agents of invasive weeds. Gorse, *Ulex europaeus* L. (Fabaceae), is a thorny woody shrub native to Europe, which was widely redistributed throughout the world as a living hedge to confine livestock. This plant is also appreciated for its value as browse for live-stock, and for its abundant yellow flowers. By the early 20th century, the dangerously weedy nature of gorse was recognized in New Zealand, southern Australia, Tasmania, Chile, northwestern USA and Hawaii. Beginning about 20 years 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). *T. 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 a 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 3–4 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 of *P. histrio* in Chile (Aguilera, 1987), the native staphylinid predator *Oligota centralis* (Solier) was the only gorse mite predator commonly found, and its impact on *T. lintearius* was not strong (Norambuena et al., 2007).

Predation on gorse mite populations by Stethorini, which in at least two of the four regions has had a major impact on this classical weed biocontrol effort, should not come as a surprise. In fact, this so-called biotic resistance was observed in Europe by Schroe-

der and Zwölfer (1970) in endemic gorse habitats, predicted by Ireson et al. (1999), and continues in the UK, where *S. punctillum* and phytoseiid predators limit gorse mite outbreaks (e.g., Kirby, 2005).

5. Conclusions and directions for future work

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

(1) The role of alternative foods is little known, but may play an important role in population dynamics, diapause, and migration, as with other coccinellids (Lundgren, 2009b, this issue). Stethorini consume alternative non-tetranychid mite prey, extrafloral nectar and pollen. They are sensitive to plant characteristics and thus cultivar choice and vegetational diversity may increase or hinder their efficacy.

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

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

(4) Habitat management shows potential for increasing the impact of Stethorini on pest populations. The broad prey and host plant ranges of many species make non-crop habitat valuable sources for predators that can rapidly deploy to colonize and protect crops. These refuges can assist overwintering success in temperate systems, and provide safe havens from pesticides. In milder climates, perennial reservoirs may serve as refuges within diversified annual plantings (e.g., the role of the perennial castor bean, common in Indian farmscapes, which serves as a reservoir for *S. gilvifrons* and *S. pauperculus* [Mathur, 1969; Puttaswamy and ChannaBasavanna, 1977]). Use of chemical control, even pesticides that have novel selectivity (e.g., insect growth regulators) or are organic-approved (e.g., elemental sulfur) can be very harmful to Stethorini and other biological agents. These effects are often seen only after registration and widespread use; the breadth of pre-release non-target screening should be broadened (e.g., with method of Nienstedt and Miles, 2008) to include the Stethorini.

The full potential of Stethorini as predators of spider mites will only be realized when cultural and chemical farm management practices are truly integrated with biological controls based on farm-scale scientific experimentation. Where proper conditions have come together, such as in Pennsylvania apple orchards, in

Asian citrus and tea, and in several other tropical systems, Stethorini play an important role—sometimes the most important role—in suppressing tetranychid populations.

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