Population Interaction Between *Stethorus punctum picipes* (Coleoptera: Coccinellidae) and *Tetranychus urticae* (Acari: Tetranychidae) in Red Raspberries at Low Predator and Prey Densities

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ABSTRACT Previous studies concluded that species in the coccinellid genus *Stethorus* Weise, although obligate predators of tetranychid mites, exhibit a strong numerical response only to high population densities of their prey. The study reported here was conducted to test the hypothesis that in western Washington red raspberries, *Stethorus punctum picipes* Casey is capable of detecting and attacking spider mite populations of very low density which are distributed in small, widely scattered patches during the early part of the growing season. In addition to using conventional leaf sampling methods, *S. p. picipes* interactions with prey were examined by observing their response to prey patches introduced into the field from laboratory cultures. Our results indicate that *S. p. picipes* is active at low prey densities, although undetected by conventional sampling methods, and is capable of locating rare, small prey patches. This finding suggests that dispersal and searching ability, rather than numerical response are the key components of this prey–predator association.

KEY WORDS *Stethorus punctum picipes*, spider mites, raspberry

PREVIOUS STUDIES OF *Stethorus* Weise spp. concluded that increases in population density occur only after spider mite prey becomes abundant. In the field, *Stethorus punctum picipes* Casey did not reproduce rapidly until avocado brown mite densities reached 10 adult females per leaf (McMurtry & Johnson 1966, McMurtry 1985) and apparently emigrated when spider mites were extremely scarce (McMurtry et al. 1970). Bailey & Caon (1986) showed that population increases of *Stethorus nigripes* Kapur lagged behind those of twospotted spider mite in seed lucerne and concluded that this is a "high density predator." The same phrase was used for *S. p. picipes* based on insectary studies where it was ineffective in maintaining low spider mite densities (Tanigoshi & McMurtry 1977). In laboratory studies of life history parameters, the developmental period of *Stethorus* spp. was substantially longer than that of its prey, and oviposition occurred only when prey was abundant (Putman 1955, Tanigoshi & McMurtry 1977). Subsequently, the biology and biological control potential of *Stethorus* spp. has received relatively little attention.

However, other characteristics of *Stethorus* spp. suggest considerable biological control potential. They are voracious obligate spider mite predators which are long lived as adults (Putman 1955, Tanigoshi & McMurtry 1977). *Stethorus punctum punctum* (LeConte) in apple orchards appeared to be capable of effective dispersal and searching for limbs or trees with experimentally elevated spider mite densities (Hull et al. 1977). In both avocados and citrus in southern California, *S. p. picipes* located small patches of prey early in the season when spider mite densities were generally low (McMurtry & Johnson 1966, Haney et al. 1987).

Biological control of spider mites by *Stethorus* spp. has been suggested but not explained in terms of population interactions, in several studies. Readshaw (1971, 1975) reported that *S. nigripes* populations in Australian apple orchards were very low at low spider mite densities but appeared to be the major factor maintaining spider mite populations at low densities. Bailey & Caon (1986) concluded that *S. nigripes* contributed to the control of spider mites in seed lucerne in spite of the "high density" nature of their numerical response. *S. p. picipes* is apparently the most important factor in spider mite

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biological control in avocados (McMurtry & Johnson 1966) and citrus (Haney et al. 1987). In the study by Shanks et al. (1992), reduction in *S. p. picipes* populations appeared to be a primary factor in the development of spider mite outbreaks following multiple insecticide applications.

Because "high density" spider mite populations have become common only since the advent of synthetic pesticides (Huffaker et al. 1970), we hypothesized that *Stethorus* spp. normally interact with spider mite populations at low densities of both prey and predator, and that the discovery of rare and very small prey patches (one to several female mites and their offspring on a single leaf), by adult predators is the key element in the interaction. If this is true, then the effectiveness of *Stethorus* spp. as biological control agents may not be based primarily on a numerical response like that well documented for some phytoseiid predators (e.g. reviewed by Logan 1982, McMurtry 1982, Tanigoshi 1982). Rather, it may be the result of behavioral mechanisms such as area-restricted search (Kareiva & Odell 1987) or chemotaxis or both, which lead to aggregation of predators at prey patches.

The study reported here was carried out to examine the interaction between *S. p. picipes* and its spider mite prey, primarily *Tetranychus urticae* Koch, in red raspberries, investigating the following questions: is *S. p. picipes* active early in the season when spider mite density is typically very low (mean density less than one female per leaf)? Does *S. p. picipes* persist at very low prey densities? Do *S. p. picipes* adults effectively locate small, rare prey patches?

Materials and Methods

Field and Laboratory Techniques. *Stethorus punctum picipes* activity was studied using small patches of laboratory-reared spider mites referred to hereinafter as "trap colonies." These were deployed as follows: *T. urticae* was reared in the laboratory on bean plants of several varieties (lima, pinto, and red) and infested plants were transported to the field intact. One section of leaf, 1–6 cm^2, was cut and stapled to the upper surface of each selected mature raspberry leaf together with a small piece of fluorescent flagging tape. The excised bean leaf fragments desiccated and a variable number of spider mites migrated to the lower surface of the raspberry leaves, but the flagging tape remained highly visible. One week following placement, the trap colonies were carefully inspected for *S. p. picipes* adults, then excised and sealed individually in reclosable plastic bags. In the laboratory, a dissecting microscope was used to make counts of tetranychid females and *S. p. picipes* eggs, larvae, and adults. The presence or absence of tetranychid eggs and immature stages was also recorded for each leaf. Fifty trap colonies were placed in each field on each test date at approximately 10-m intervals, alternating between adjacent rows.

Spider mite and *S. p. picipes* density and dispersion were monitored using weekly or bimonthly samples of 50 mature leaves collected at random from the plants 0.8 to 1.8 m above the ground. Leaves were selected from fruiting canes (established the previous season) until those from the primocanes (current season's growth from roots) were well established. The switch from fruiting to primocane leaf samples occurred in mid- to late July, following the berry harvest and concurrent with early stages of senescence in fruiting cane foliage. Counts were made of *S. p. picipes* and spider mites as described for trap colonies.

Leaf samples and trap colony placements were random with respect to individual plants but were limited to the same rows within a given study year. The number of rows required varied from four to eight, depending on row length, and all study rows were at least the sixth from the field edge. The trap colony procedure was repeated, at 2, or 4-wk intervals, eight times for each field during the 1990 growing season, starting the week of 4–11 May and ending the week of 15–22 August. In 1991, it was repeated seven times starting the week of 27 April–4 May and ending the week of 19–26 August.

The studies were carried out in nine commercially productive red raspberry fields in western Washington state, five in Skagit (M, Y1, Y2, Y3, and S2), three in Pierce (S1, C, and R), and one in Snohomish County (B). Fields C, M, and S2a were studied in both 1990 and 1991. R, S1, and Y1 were studied only in 1990 and B, Y2, and Y3 only in 1991. An additional sampling site (S2b) in field S2 was added in 1991. Insecticide application practices varied among the fields, but the analysis of their effects on *S. p. picipes* is not included in this article.

Statistical Analyses. The spatial distribution of spider mites and *S. p. picipes* at low densities was expected to influence the interaction. To determine if spider mites or *S. p. picipes* or both were aggregated at low densities, all of the 50-leaf random samples with a mean of <1 female spider mite per leaf were pooled for each year and sorted into five patch size classes (0, 1, 2, 3, and >3 female mites per leaf). The distributions of spider mites among sampled leaves and *S. p. picipes* among spider mite patch size classes were compared with values predicted by null hypotheses of Poisson (random) distribution using a χ^2 goodness-of-fit test (CHISQ, Northwest Analyitical 1986).

Establishment of female spider mites on trap colonies varied considerably, from 0 to >100 female mites per trap colony 1 wk following placement. To determine whether *S. p. picipes* was

Table 1. *Stethetherum p. picipes* frequency in trap colonies (percentage trap colonies with eggs or adults or both) and female spider mite frequency on random leaf samples (in parentheses) in western Washington red raspberry fields

Date	1990 Sites					
	C	M	S2a	R	S1	Y1
11 May	30 (0)	33 (86)	—	—	10 (33)	9 (0)
25 May	10 (2)	46 (52)	—	0 (0)	8 (12)	4 (2)
12 June	10 (2)	36 (100)	4 (0)	10 (2)	16 (40)	6 (0)
26 June	14 (4)	62 (94)	12 (2)	43 (0)	35 (50)	28 (0)
10 July	19 (20)	12 (82)	9 (2)	28 (0)	7 (18)	7 (4)
24 July	43 (10)	26 (98)	—	31 (18)	22 (36)	0 (14)
7 Aug.	54 (36)	50 (98)	0 (18)	19 (14)	34 (64)	4 (44)
22 Aug.	19 (58)	21 (58)	6 (30)	8 (66)	13 (48)	6 (84)

	1991 Sites						
	C	M	S2a	S2b	B	Y2	Y3
4 May	—	8 (0)	0 (4)	2 (20)	22 (0)	40 (0)	20 (0)
3 June	—	8 (2)	8 (2)	6 (16)	32 (0)	20 (2)	12 (2)
18 June	33 (4)	6 (0)	0 (22)	6 (26)	8 (0)	14 (0)	14 (2)
1 July	12 (2)	32 (18)	6 (40)	22 (34)	12 (0)	14 (4)	30 (2)
15 July	26 (6)	16 (20)	0 (52)	2 (80)	0 (0)	2 (16)	0 (20)
5 Aug.	26 (16)	2 (34)	0 (100)	0 (100)	3 (0)	2 (28)	2 (52)
25 Aug.	19 (38)	11 (100)	—	—	0 (2)	4 (92)	4 (96)

found more frequently on the more heavily infested trap colonies, 1990 trap colony data from all study sites were pooled, and the numbers of *S. p. picipes* eggs and adults per leaf in each of six female spider mite patch size categories (0–1, 2–5, 6–10, 11–20, 21–50, >50) were subjected to one way analysis of variance (ANOVA) (ANOVA1, Northwest Analytical 1986).

To evaluate the sensitivity of the two sampling methods to *S. p. picipes*, differences in the frequency of eggs and adults on trap colonies and randomly sampled leaves were analyzed using the Wilcoxon signed rank test (WILCOSR, Northwest Analytical 1986). Data from all fields were pooled for each year, and the analysis was carried out separately for each sampling date.

Results

S. p. picipes activity was detected early in the growing season or at low spider mite densities or both at all of the sites investigated in this study (Table 1). In 10 of the 13 fields (C, S2a, R, Y1 in 1990 and C, M, S2a, B, Y2, Y3 in 1991), spider mite frequency was low (<5%) in the random leaf samples through May and June, but *S. p. picipes* frequency on trap colonies at those sites ranged from 0 to 43%, averaging 14%. In fields M and S1 in 1990 and field S2b in 1991, spider mite frequencies in random leaf samples were higher (12–100%). At these sites, trap colony *S. p. picipes* frequencies ranged from 2 to 46%, averaging 24%. *S. p. picipes* was observed in a total of 78 of the 89 sets of 50 trap colonies. The number of female spider mites established in the trap colonies had no significant effect on the frequency of *S. p. picipes* eggs ($F = 1.93$; df = 5, 2060; $P > 0.05$) or adults ($F = 0.44$; df = 5, 2060; $P > 0.05$).

Three distinct temporal patterns of *S. p. picipes* activity were detected. First, adults appeared early in the season, even when spider mite prey was apparently scarce or absent. On 11 May 1990, *S. p. picipes* was found in trap colonies at all sampled sites (Table 1). On 4 May 1991, *S. p. picipes* was collected at five of the six sites at frequencies ranging from 2 to 40%, whereas the spider mite frequency in random leaf samples was 0% in all but two (Table 1).

Second, adult *S. p. picipes* persisted through the early part of the growing season while spider mite frequency stayed below 5%. This pattern was observed at 8 of the 13 sites (Table 1). It was especially pronounced in field B (Fig. 1A), where *S. p. picipes* frequency in trap colonies was at least 8% until 1 July, even though no spider mites were collected in random leaf samples until August. Similarly, in field C (Fig. 1B), adult *S. p. picipes* frequency in trap colonies varied from 2 to 18% during the period 11 May through 26 June 1990 while spider mite density in leaf samples was only 0.02 females per leaf.

Third, *S. p. picipes* oviposition on trap colonies coincided with the appearance of spider mites in the random leaf samples. In field M (Fig. 1C and D), *S. p. picipes* adults were found on 4–10 % of the trap colonies early in both the 1990 and 1991 seasons, but trap colony oviposition frequency was higher in this field in 1990 when spider mite densities were one to two females per leaf, than in 1991 when the first detection of spider mites was delayed until 1 July. In field B (Fig. 1A), spider mites were not detected in random leaf samples until 26 August, and *S. p. picipes* eggs were not detected in trap colonies until 5 August, even though adult frequency was as high as 32% earlier in the season. In apparent

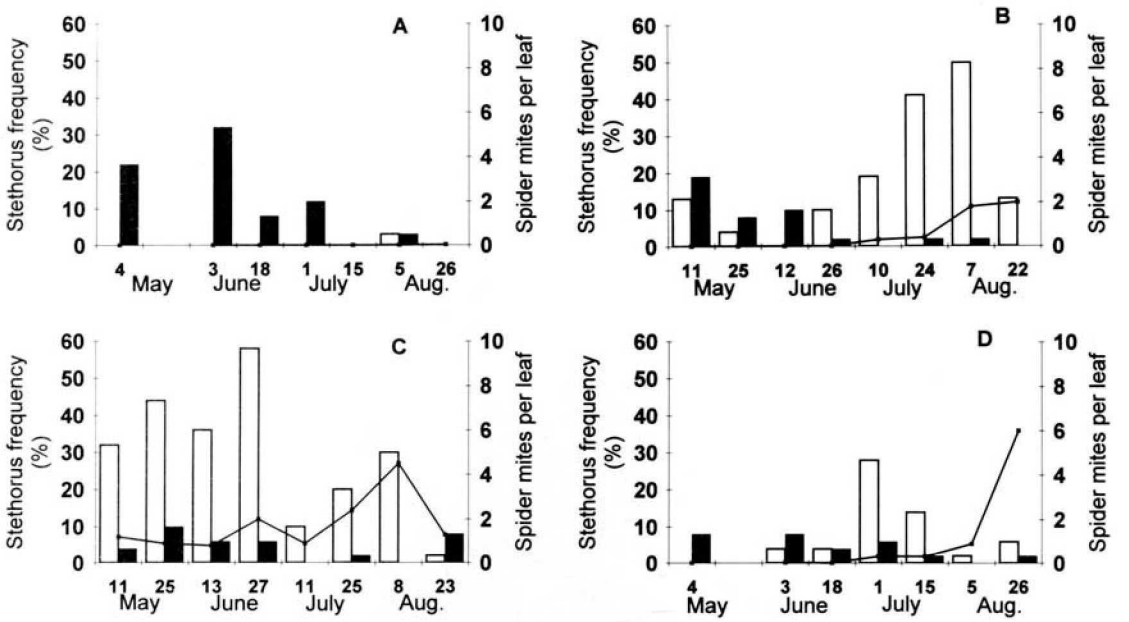

Fig. 1. Temporal trends in *S. p. picipes* adult (solid bar) and egg (open bar) frequency in trap colonies, and spider mite density (solid line) in random leaf samples in western Washington red raspberry. (A) Field B, 1991. (B) Field C, 1990. (C) Field M, 1990. (D) Field M, 1991.

contrast to this general pattern, *S. p. picipes* egg frequency on the first two sampling dates of 1990 in field C (Fig. 1B) was 13 and 4%, respectively, although spider mite frequency was 0 and 2% on the same dates. However, *S. p. picipes* egg frequency increased to ≈50% later in the season concurrent with an increase of spider mite density to two females per leaf.

The trap colony data discussed above suggested that *S. p. picipes* adults search very efficiently for rare prey patches at low prey densities. The subsequent analysis of *S. p. picipes* and spider mite distributions on leaves from random samples with a mean spider mite density of less than one female per leaf revealed two significant patterns. First, at these low densities, spider mites exhibited a strongly aggregated dispersion pattern (Fig. 2). The dispersion patterns from both years were significantly different from those expected from Poisson (random) distributions with the same means ($P < 0.001$).

Second, *S. p. picipes* was observed almost exclusively on these rare patches of prey (Fig. 2). The frequency of *S. p. picipes* on spider mite patches of 0, 1, 2, 3, and >3 females differed significantly ($P < 0.01$) from that expected under the null hypothesis of random distribution of *S. p. picipes*. *S. p. picipes* was also observed on a number of leaves where there were no female spider mites, but of these, 81% (in 1990) and 57% (in 1991) contained prey eggs or nymphal stages or both. Therefore, of the total number of *S. p. picipes* collected in random leaf samples when the mean spider mite density per leaf was <1.0, 94% (1990) and 83% (1991) were on leaves infested with spider mites. The substantial number of *S. p. picipes* on leaves with only immature stages of spider mites suggests that the absence of adult prey was caused by *S. p. picipes* feeding. Predation by *S. p. picipes* on adult spider mites was evidenced on many of these by characteristic remains of dead mites and *Stethorus* feces.

There was also an apparent trend of increased *S. p. picipes* frequency on prey patches of increasing size (Fig. 2), an observation which seems to contradict the trap colony data analysis showing no effect of patch size on the frequency of *S. p. picipes* attack. The contradiction is resolved, however, by considering the duration of patch establishment in the two cases. All trap colonies, regardless of prey number, were present for the same period of time. However in randomly sampled leaves, the number of mites in a patch would likely be correlated positively with the time elapsed since its establishment. Therefore, the relationship between patch size and *S. p. picipes* attack frequency shown in Fig. 2 is most likely the result of patch age and only coincidentally of its size.

Consistent with the results reported above, *S. p. picipes* was found with significantly greater frequency (Wilcoxon signed rank test, $P = 0.05$) on trap colony compared with randomly sampled leaves. This pattern held true throughout both seasons of the study, except on the last sample dates of both and on 10 July 1990, when spider

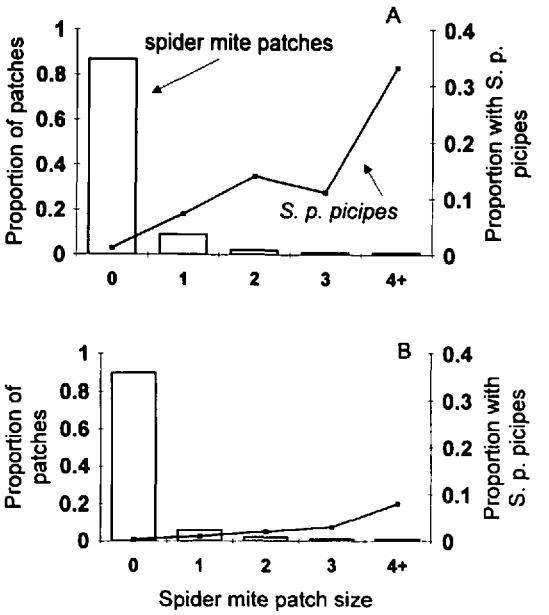

Fig. 2. Distribution of spider mite females and *S. p. picipes* adults and eggs on leaves from random samples with spider mite densities of less than one per leaf in western Washington red raspberry fields. (A) pooled data from 1990. (B) Pooled data from 1991.

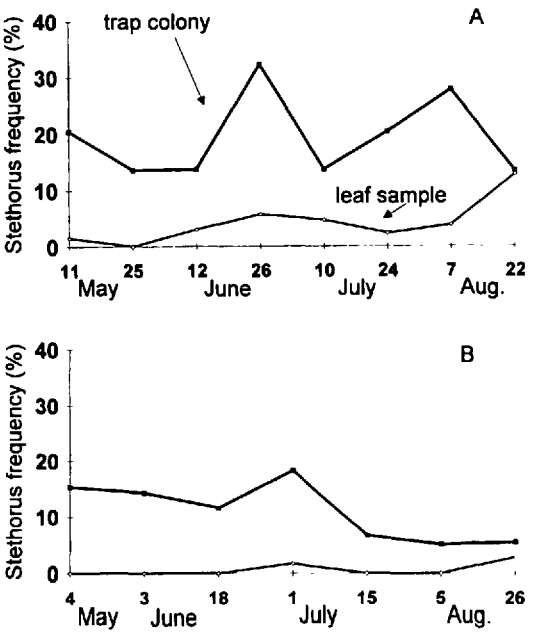

Fig. 3. Comparison of trap colony and random leaf sampling methods for detecting *S. p. picipes* activity in red raspberry fields. Pooled data from all fields. (A) 1990. (B) 1991.

mite densities were higher (Fig. 3). Hence, the most biologically meaningful trap colony measurements were those made at low spider mite densities.

Discussion

The trap colony technique used in this study revealed aspects of *S. p. picipes* biology which have gone undetected in previous studies. The depiction of *Stethorus* spp. as "high density predators" has relied almost exclusively on studies of random leaf samples. However, this investigation demonstrated that *S. p. picipes* is adapted to exploiting spider mite populations by actively locating rare patches of prey early in the season when both predator and prey populations are low. Although it is possible that the population biology of *Stethorus* spp. described here is unique to the red raspberry system, it is reasonable to infer that this predator has a greater effect than has previously been recognized on tetranychid populations in other systems as well.

Our study suggests that the early-season activity of *S. p. picipes* should be understood more as a spatial than as a numerical population phenomenon. This and previous studies suggest the following scenario: as spider mites emerge from overwintering sites and begin feeding on newly formed leaves, densities are low. At this time, *S. p. picipes* lays few eggs, but the adults are nevertheless locating small prey patches, perhaps even individual adult female spider mites. In addition to infrequently encountered prey, *Stethorus* spp. may also subsist on aphid honeydew or plant exudates (Putman 1955). As temperature, photoperiod, and the frequency and size of spider mite patches increase, *S. p. picipes* begins to oviposit, often among the spider mite eggs and immature stages left in the patch after the adults have been consumed. Not until the spider mite population becomes high enough to support the maturation of *S. p. picipes* larvae to adults does the *S. p. picipes* adult population begin to increase. Sustained high spider mite mortality resulting from the remarkably efficient searching and survival of *S. p. picipes* at low prey densities delays and reduces spider mite population increase.

The scenario might unfold differently in fields receiving insecticide applications that decimate *S. p. picipes* populations. Here, spider mite establishment is high, and small patches quickly expand to produce an outbreak. In these circumstances, *S. p. picipes* adults could subsequently disperse into a heavy infestation and attain their maximum reproductive rate, producing a large cohort of larvae and, within a few weeks, adults. If not disturbed by additional insecticides, an impressive numerical response by *S. p. picipes* might result, but as noted in many other studies, not usually in time to effect economically useful regulation of spider mite populations. The correlations between multiple insecticide applications and spider mite outbreaks, at least in the

study by Shanks et al. (1992) in red raspberries, appears to be accounted for by the elimination of *S. p. picipes*, especially during the early and middle parts of the season.

This study suggests an important role for *Stethorus* in the biological control of spider mites and raises important questions: what factors in addition to disruption by insecticides determine the level of *Stethorus* activity? Several possibilities are suggested by the patterns observed here, including overwintering survival as influenced by weather and cultural practices, *Stethorus*-spider mite interactions in the previous season, and proximity to predator reservoirs. Expanded study of the population biology and biological control potential of *Stethorus* spp. appears to be justified.

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