Effects of phytoseiid predators on the sex ratio of the spider mite *Panonychus ulmi*[1]

DAN L. JOHNSON[2]

Agriculture Canada Research Station, Lethbridge, Alta., Canada T1J 4B1

AND

HEATHER C. PROCTOR[3]

Department of Biological Sciences, University of Calgary, Calgary, Alta., Canada T2N 1N4

Received April 18, 1989

JOHNSON, D. L., and PROCTOR, H. C. 1991. Effects of phytoseiid predators on the sex ratio of the spider mite *Panonychus ulmi*. Can. J. Zool. **69**: 208–212.

The effect of predator presence on the adult sex ratio of a spider mite (*Panonychus ulmi*) was examined in a field experiment. Phytoseiid predators (chiefly *Typhlodromus occidentalis*) were removed from 32 trees harboring *P. ulmi* populations, and allowed to remain at natural levels on 32 other trees. Both total population density and proportion of males in the prey population were significantly higher in predator-free trees. Mechanisms that could explain the increase in the proportion of males are examined. The most probable is that greater male activity results in a higher encounter rate between predator and prey, and that subsequent higher male mortality when predators are present exaggerates the female-biased sex ratio. The theoretical effects of sex-biased predation on diplo-diploid and haplo-diploid organisms are discussed.

JOHNSON, D. L., et PROCTOR, H. C. 1991. Effects of phytoseiid predators on the sex ratio of the spider mite *Panonychus ulmi*. Can. J. Zool. **69** : 208–212.

Les effets de la présence d'un prédateur sur le rapport mâles:femmelles d'un tétranyque, *Panonychus ulmi*, ont été examinés au cours d'une expérience en nature. Les phytoseiidés prédateurs (surtout *Typhlodromus occidentalis*) ont été enlevés de 32 arbres comptant des populations de *P. ulmi*, et laissés dans 32 autres arbres. La densité totale des tétranyques et la proportion de mâles étaient significativement plus élevées dans les arbres sans prédateurs. Les facteurs qui peuvent expliquer l'augmentation de la proportion de mâles ont été examinés. L'hypothèse la plus probable est que normalement le nombre de rencontres entre prédateurs et proies est plus élevé dans le cas des mâles parce que ceux-ci sont plus actifs et leur taux de mortalité est donc plus élevé en présence des prédateurs, ce qui fait diminuer le rapport mâles:femmelles déjà faible. Les effets théoriques d'une prédation différentielle sur les mâles et les femelles chez des organismes diplo-diploïdes et des organismes haplo-diploïdes font l'objet d'une discussion.

[Traduit par la revue]

Introduction

The sex ratio of adult spider mites (Tetranychidae) is typically one male to three females (Wrensch 1985), but there are many factors that affect the degree of female bias. Foremost among these is fertilization status of the female; because tetranychids are haplo-diploid, unfertilized females produce entirely male (haploid) broods (Saitō 1987). Other factors that influence the relative numbers of male and female offspring are duration of copulation (Potter and Wrensch 1978; Helle and Pijnacker 1985), age of the female parent (Shih 1979), food quality during the ovipositional period (Young *et al.* 1986), and population density and temperature (Wrensch 1985).

Most studies of spider mite sex ratio have been conducted under laboratory or controlled greenhouse conditions. There have been no investigations of spider mite sex ratio in field situations under natural conditions of weather, dispersal, mating behavior, and predation. No study has examined the influence of predation by phytoseiid mites on the sex ratio of their prey, despite the importance of these predators in biological control (Sabelis 1985).

In this study we examined the impact of phytoseiid predators, chiefly *Typhlodromus occidentalis* Nesbitt and *Typhlodromus caudiglans* Schuster, on the sex ratio of the European red mite (or fruit tree red spider mite), *Panonychus ulmi* Koch, in an orchard environment.

Methods

Description of the study site

The experiment was conducted in the east section of the Trout Creek entomology apple orchard, Agriculture Canada Research Station, Summerland, British Columbia, Canada. This section was isolated from nearby experimental and commercial orchards and had not received acaricidal or insecticidal sprays for several years. The grass between the trees was mowed regularly. The orchard was irrigated weekly by under-tree sprinklers.

Predator removal

Phytoseiid mites were selectively removed by applying the insecticide carbaryl. Although strains of carbaryl-resistant *T. occidentalis* have been produced for integrated pest management (Roush and Hoy 1980), natural populations of *T. occidentalis* and *T. caudiglans* are highly susceptible to carbamate insecticides. *Panonychus ulmi*, however, is little affected by carbaryl (van de Vrie *et al.* 1972). When phytoseiids are removed by spraying, tetranychid mortality is reduced and tetranychid densities increase (Herne and Putman 1966; Sanford 1967; Hoyt 1969; McMurtry *et al.* 1970).

Half of the 64 trees used in the experiment (located at positions chosen randomly within an 8 × 8 Latin square) were sprayed with carbaryl (Sevin® 50% wettable powder), applied in 11 L of water per tree at 1 g carbaryl/L. Half of the 64 apple trees were 'McIntosh' and half were 'Delicious,' and the carbaryl treatment was applied to 16 trees of each of the two cultivars. Before application of the carbaryl, all trees included in the experiment were pruned to a height of 2.5–3.0 m. The side branches were further pruned so that adjacent trees were separated by at least 0.5 m. Trees were isolated during spraying with tall plastic barriers to prevent drift of the carbaryl. The treatment was applied on the morning of 30 May 1982. Hoyt and Caltagirone (1971) reported that the effect of carbaryl on phytoseiids is lessened if low central areas of the trees do not receive sufficient pesticide. Therefore,

---

[1] Contribution No. 3878821.

[2] Author to whom all correspondence should be addressed.

[3] Present address: Department of Zoology, Erindale College, University of Toronto, Mississauga, Ont., Canada L5L 1C6.

the entire tree, including the trunk and bark, was soaked during application. The 32 trees in the control group were sprayed with water alone, because the force of spraying can knock mites off the leaves and affect future population density (Hudson and Beirne 1970). No other acaricides or insecticides were applied during this experiment. Other aspects of orchard management are detailed in Johnson and Wellington (1984).

Estimates of population density and sex ratio

Population density was estimated from counts of phytoseiid and tetranychid mites on leaves collected every 2 weeks, from 13 May to 1 October 1982. On each of the nine sampling dates, 10 leaves were collected from each of the 64 trees. No very young or very old leaves were taken. Each leaf was placed in a 15 cm diameter plastic Petri dish and transferred to cold storage (2–4°C) within 15 min of collection. Collection of the 640 leaves per sampling date was usually accomplished within 2 days.

In the laboratory, each leaf was examined with a binocular dissecting microscope and the species, number, sex, and stadium of each mite were recorded. Adult phytoseiids were mounted on permanent microscope slides for identification.

The effects of cultivar and the predator removal treatment were tested with analysis of variance for each species and sampling date.

Results

Efficacy of predator removal

Most of the 1745 phytoseiids counted during the study were *T. occidentalis*. *Typhlodromus caudiglans* made up a small proportion of the phytoseiids (<5%). This species composition agrees with previous investigations in British Columbia orchards (Anderson and Morgan 1958; Downing and Moilliet 1967, 1971). Because of the preponderance of *T. occidentalis* and of taxonomic problems associated with the immature stages, we analyzed the counts of postlarval *Typhlodromus* as a single group. *Typhlodromus caudiglans* and *T. occidentalis* are similar in size and behavior.

The effect of the treatment on phytoseiid mite abundance was tested with analysis of variance. On trees of both cultivars, the *Typhlodromus* species were almost completely eliminated by the carbaryl application (Fig. 1). The counts recorded during the 16 weeks following spray application show that the predator removal treatment remained successful: on 960 leaves collected from the sprayed trees during this period, only 21 phytoseiids were found, compared with 360 phytoseiids on 960 leaves from the unsprayed trees. The effects of apple tree cultivar, rows, columns, cultivar × treatment interactions, and covariance of the pretreatment population level were not significant on any date.

The period over which carbaryl remains toxic to *Typhlodromus* is shorter than these results seem to indicate. Flaherty and Huffaker (1970) successfully reintroduced *T. occidentalis* to grapevines treated with carbaryl 1 to 2 months previously. In our experiment, immigration of *Typhlodromus* back onto the sprayed trees was evidently negligible.

On the 32 unsprayed trees, the phytoseiid populations exhibited slow growth after 10 June. Phytoseiid population density peaked in early August, at 0.51 mites per leaf (SEM = 0.05; n = 320) on 'McIntosh' and 1.1 leaf (SEM = 0.17; n = 320) on 'Delicious.'

Effects of phytoseiid removal on P. ulmi abundance

Based on stage-frequency observations, there were at least five complete *P. ulmi* generations during the sampling period. A total of 10 448 adult males and 23 553 adult females were counted on the 5760 leaves collected during the experiment.
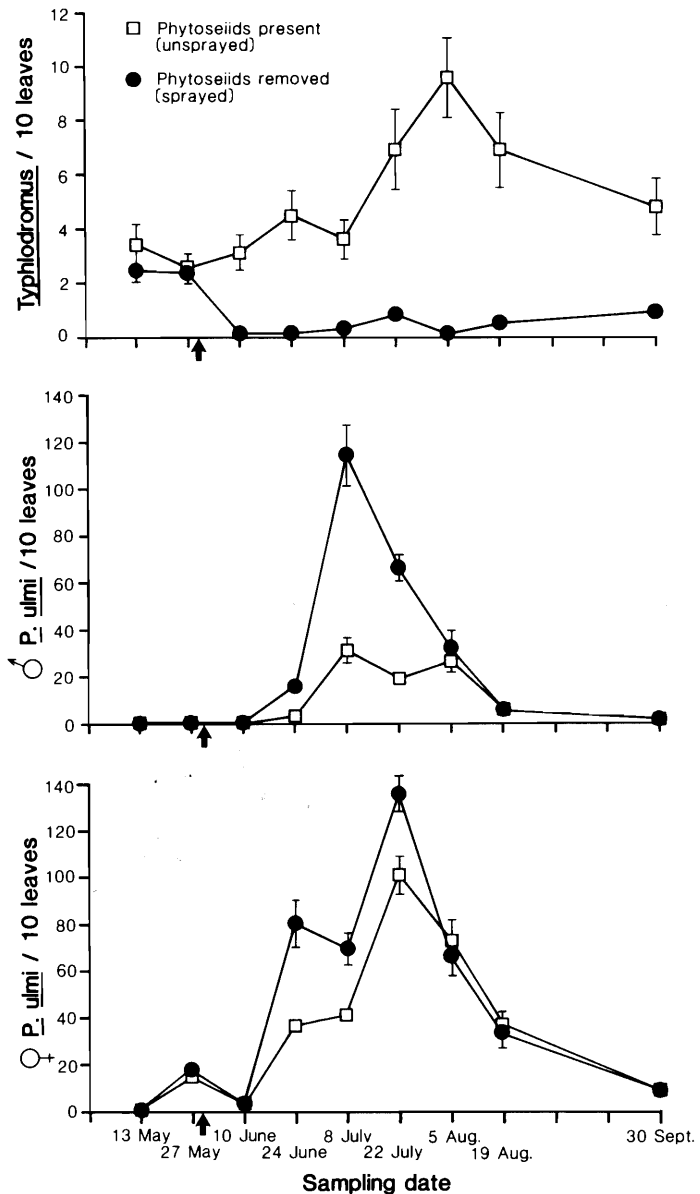

FIG. 1. Population density of the predator (*Typhlodromus*) and prey (adult *P. ulmi*). Means are from 32 trees (± SE). The predator removal treatment was applied on 30 May (arrow).

The abundance of all *P. ulmi* stages was strongly affected by phytoseiid removal (ANOVA; $P < 0.001$). In early July the sprayed trees had nearly four times as many active *P. ulmi* as were found on unsprayed trees. The sprayed trees had average densities of 129 active *P. ulmi* per leaf (SEM = 5.8; n = 320 leaves), resulting in significant chlorosis (Johnson 1983). Apple cultivar had a smaller but statistically significant effect; densities of all *P. ulmi* stages were about twice as high on 'Delicious' as on 'McIntosh' on most sampling dates (ANOVA; $P < 0.01$).

Effects of phytoseiid removal on P. ulmi sex ratio

The first *P. ulmi* generation was almost entirely female, suggesting that the specialized winter eggs produced in late fall are diploid.

The sex ratio of *P. ulmi* did not differ between the cultivars ($P > 0.1$) but was significantly altered after elimination of phytoseiids (ANOVA of proportion male, $P < 0.001$, 10 June–
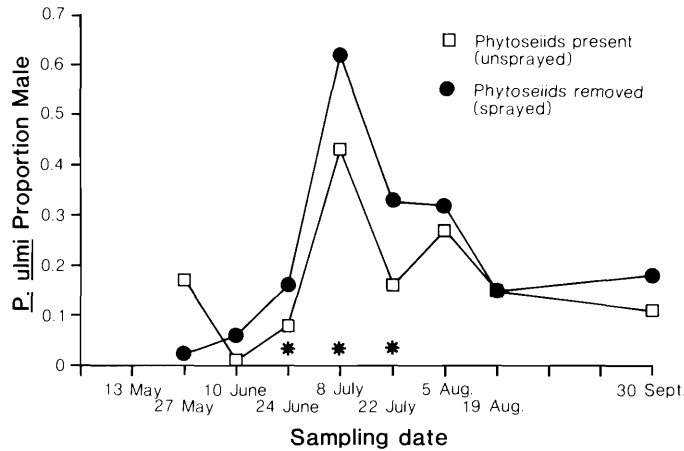
FIG. 2. The sex ratio (total males/total adults) of adult *P. ulmi* on treated and untreated trees. An asterisk indicates a significantly greater proportion of males.

22 July). The absence of predators was associated with a higher proportion of males (Fig. 2), indicating a differential effect of phytoseiid presence on male and female prey. The same result was apparent in per-tree and per-leaf analyses. Until late July, the leaves without phytoseiids had significantly higher proportions of males than did leaves with phytoseiids (Table 1). In total, the abundance of male *P. ulmi* on leaves of predator-free trees was 2.74 times as great as on leaves of the trees with natural phytoseiid populations intact, whereas the corresponding *P. ulmi* female abundance ratio was only 1.6.

Discussion

. Several hypotheses can be put forward to explain the observed sex ratio differences between the populations of *P. ulmi* on trees with and without predators. It is unlikely that the primary (fertilization) sex ratio is altered to favor males in the absence of predators. Young et al. (1986) found that when food quality was poor, as is likely to occur when predation pressure is low and population density high, female *Tetranychus urticae* Koch produced fewer sons than when high quality food was available. Predator presence in our experiment reduced overall population density (see Results) and by extension increased food quality; so, based on *T. urticae*'s response, one would expect any alteration of primary sex ratio by *P. ulmi* females to favor sons rather than reduce the proportion of male offspring.

It seems more likely that the sex ratio is altered in the adult stage. Male tetranychids could be subject to heavier predation than females because they are easier to handle, more palatable, or are encountered by the predator more often.

Adult males are smaller than females and may therefore be easier to subdue and manipulate. Although there have been several comparisons of the functional response of phytoseiid predators to different spider mite stages (eggs, larvae, protonymphs, and deutonymphs by Fernando and Hassell 1980; eggs and males by Sabelis 1985), there has been no comparison of predator preference when males and females are presented simultaneously.

Males are more active than females within trees and may have a higher probability of encounter with the predator, which would increase the predation rate (Sabelis 1981). We observed that male *P. ulmi* are more rapid in their movements than females. This greater degree of activity may lead to more contacts with the phytoseiid predator either because the males'

TABLE 1. Mean numbers of adult *P. ulmi* on apple leaves and sex ratio of prey as a function of phytoseiid presence

| | | Phytoseiid predators | |
	Parameter	Absent	Present (>1 per leaf)
13 May	N^a	29	12
	Female	1.10	1.25
	Male	0.69	0.43
	Sex ratio[b]	0.385	0.250
27 May	N	272	66
	Female	3.04	3.15
	Male	0.067	0.061
	Sex ratio	0.021	0.019
1 June	N	126	9
	Female	1.84	1.67
	Male	0.087	0.0
	Sex ratio	0.045	0.0
47 June	N	491	62
	Female	6.97	5.52
	Male	1.17	0.52
	Sex ratio	0.144	0.086
8 July	N	534	71
	Female	6.04	4.59
	Male	8.30	3.35
	Sex ratio	0.579	0.424
22 July	N	521	115
	Female	12.20	10.40
	Male	4.67	2.63
	Sex ratio	0.276	0.202
5 August	N	420	140
	Female	7.68	9.02
	Male	3.28	3.59
	Sex ratio	0.299	0.284
19 August	N	363	231
	Female	4.39	6.89
	Male	0.741	1.32
	Sex ratio	0.144	0.161
30 September	N	231	38
	Female	2.12	2.71
	Male	0.34	0.63
	Sex ratio	0.138	0.189

[a]N = sample size (number of leaves); only leaves with *P. ulmi* present were included.
[b]Sex ratio is calculated as the proportion of males (= total males/total adults) for a given treatment and date.

movements make them detectable at a greater distance than females or simply because of the greater probability of random encounter. The search and attack behavior of some phytoseiids is stimulated after they have touched moving prey (Takafuji and Chant 1976). Males may be less inclined than females to run away when contacted by a predator. Male tetranychids fight for the possession of females (Potter 1979); intrinsic aggression toward other active mites could stimulate attack by the contacted predator, or could result in a delayed escape response by the male prey.

In some cases, male tetranychids remain in the presence of predators, not through mistaken identification of their adversaries, but because they are defending their offspring. Saitô (1986) found that because of their greater aggression toward potential nest predators, male *Schizotetranychus celarius* (Banks) suffer greater mortality than do females. Although female *S. celarius*

TABLE 2. Predicted effects of sex-specific predation on tertiary (field) sex ratio, as a function of male ploidy

Ploidy of prey	Predation bias	Initial result of mortality	Effect on number of offspring	Effect on sex ratio
Diplo-diploid	Male ($2n$)	Fewer males, possibly a decrease in fertilization depending on the virility of males (assuming polygyny)	If a decrease in fertilization, then both male and female offspring reduced in number	No change
	Female ($2n$)	Fewer females, reduced total birth rate	Fewer offspring, both male and female offspring reduced in number	No change
Haplo-diploid	Male ($1n$)	Fewer males, possibly a decrease in fertilization depending on the virility of males (assuming polygyny)	If a decrease in fertilization, then fewer diploid (female) offspring	Becomes more male biased
	Female ($2n$)	Fewer females, but relatively more males per female, so increase in fertilizations	Fewer offspring overall, but more diploid (female) offspring	Becomes more female biased

mites pursue phytoseiid larvae, it is the males that attack and attempt to kill the predators (Yamamura 1987). However, *P. ulmi* neither lives communally, as does *S. celarius*, nor lays its eggs in a concentrated, defensible manner, so this hypothesis is unlikely to account for the effect of predators on *P. ulmi* males.

The simplest and most likely explanation is that greater male activity results in a higher encounter rate between predator and prey, and that the subsequent higher male mortality exaggerates the female-biased sex ratio. Although there are no other studies that show sexual bias in acarine predator–prey systems, research on other organisms provides examples for comparison. In a study of the mate-locating behavior of the tick-tock cicada, Gwynne (1987) found that male cicadas fell prey to web-building spiders more commonly than did females. Apparently, the males' active searching for sedentary females results in a greater encounter rate between males and webs. Encounter rates between predator and prey may increase not only because of greater prey activity but also because of greater detectability. Hairston *et al.* (1983) observed that the sex ratio of a copepod, *Diaptomus sanguineus* Forbes, became increasingly male biased over the summer. This bias was due to selective predation by fish on the more visible egg-bearing female copepods. In predator-exclusion experiments, these authors found that copepod populations inside fish-free enclosures had sex ratios near 1:1, while unprotected populations had ratios that reached almost 10 males to 1 female.

It is generally agreed that sex-specific mortality of offspring after the period of parental investment should not alter the primary sex ratio (Fisher 1930; Charnov 1982), but this does not necessarily hold for haplo-diploid organisms. Arrhenotokous animals such as spider mites may respond to sex-biased mortality in a manner totally different from that of diplo-diploid ones (Table 2). Because a shortage of males may result in fewer inseminations and hence fewer diploid (=female) offspring, male-biased predation could lead to the production of more males in the subsequent generation. Conversely, female-biased predation increases the probability of insemination (by increasing the number of males per female) and would therefore result in the production of more females. Thus, any alteration in tertiary sex ratio caused by predation would be ameliorated, if not self-corrected, by a subsequent alteration in the primary sex ratio. For the more usual case of diplo-diploid prey, there is no compensatory change in primary sex ratio.

Two areas of future investigation are suggested by this study. Laboratory studies of phytoseiid preference for male over female prey would be of practical as well as theoretical interest. Also, by subjecting laboratory populations of spider mites to different intensities of sex-biased mortality, one could test the predictions of subsequent changes in primary sex ratios that are listed in Table 2.

ANDERSON, N. H., and MORGAN, C. V. G. 1958. The role of *Typhlodromus* spp. in British Columbia apple orchards. Proc. Int. Congr. Entomol. (1956), **10**: 659–665.

CHARNOV, E. L. 1982. The theory of sex allocation. Princeton University Press, Princeton.

DOWNING, R. S., and MOILLIET, T. K. 1967. Relative densities of predaceous and phytophagous mites on three varieties of apple tree. Can. Entomol. **99**: 738–741.

——— 1971. Occurrence of phytoseiid mites (Acarina: Phytoseiidae) in apple orchards in south central British Columbia. J. Entomol. Soc. B.C. **68**: 33–36.

FERNANDO, M. H. J. P., and HASSELL, M. P. 1980. Predator-prey responses in an acarine system. Res. Popul. Ecol. **22**: 301–322.

FISHER, R. A. 1930. The genetical theory of natural selection. Clarendon Press, Oxford.

FLAHERTY, D. L., and HUFFAKER, C. B. 1970. Biological control of Pacific mites and Willamette mites in San Joaquin Valley vineyards. II. Influence of dispersion patterns of *Metaseiulus occidentalis*. Hilgardia, **40**: 309–330.

GWYNNE, D. T. 1987. Sex-biased predation and the risky mate-locating behavior of male tick-tock cicadas. Anim. Behav. **35**: 571–576.

HAIRSTON, N. G., JR., WALTON, W. E., and LI, K. T. 1983. The causes and consequences of sex-specific mortality in a freshwater copepod. Limnol. Oceanogr. **28**: 935–947.

HELLE, W., and PIJNACKER, L. P. 1985. Parthenogenesis, chromosomes and sex. *In* Spider mites: their biology, natural enemies and control. Vol. 1*a*. *Edited by* W. Helle and M. W. Sabelis. Elsevier/North Holland, New York. pp. 129–139.

HERNE, D. C., and PUTMAN, W. L. 1966. Toxicity of some pesticides to predacious arthropods in Ontario peach orchards. Can. Entomol. **98**: 936–942.

HOYT, S. C. 1969. Integrated chemical control of insects and biological control of mites on apple in Washington. J. Econ. Entomol. **62**: 74–86.

HOYT, S. C., and CALTAGIRONE, L. E. 1971. The developing programs of integrated control of pests of apples in Washington and peaches in California. *In* Biological control. *Edited by* C. B. Huffaker. Plenum Press, New York. pp. 395–421.

HUDSON, W. B., and BEIRNE, B. P. 1970. Effects of sprinkler irrigation on McDaniel and European red mites in apple orchards. J. Entomol. Soc. B.C. **67**: 8–13.

JOHNSON, D. L. 1983. On the relationship between the European red mite and apple leaf chlorophyll. J. Entomol. Soc. B.C. **80**: 42–45.

JOHNSON, D. L., and WELLINGTON, W. G. 1984. Simulation of the interactions of predatory *Typhlodromus* mites with the European red mite, *Panonychus ulmi* (Koch). Res. Popul. Ecol. **26**: 30–50.

MCMURTRY, J. A., HUFFAKER, C. B., and VAN DE VRIE, M. 1970. Ecology of tetranychid mites and their natural enemies: a review. I. Tetranychid enemies: their biological characters and the impact of spray practices. Hilgardia, **40**: 331–390.

POTTER, D. A. 1979. Reproductive behavior and sexual selection in tetranychine mites. *In* Recent advances in acarology. I. *Edited by* J. G. Rodriguez. Academic Press, New York. pp. 137–145.

POTTER, D. A., and WRENSCH, D. L. 1978. Interrupted matings and the effectiveness of second inseminations in the two-spotted spider mite. Ann. Entomol. Soc. Am. **71**: 882–885.

ROUSH, R. T., and HOY, M. A. 1980. Selection improves Sevin resistance in spider mite predator. Calif. Agric. **34**: 11–14.

SABELIS, M. W. 1981. Biological control of two-spotted spider mites using phytoseiid predators. Part I. Modelling the predator-prey interaction at the individual level. PUDOC, Wageningen. Agric. Res. Rep. No. 910.

―――― 1985. Predation on spider mites. *In* Spider mites: their biology, natural enemies, and control. Vol. 1a. *Edited by* W. Helle and M. W. Sabelis. Elsevier/North Holland, New York. pp. 1103–129.

SAITŌ, Y. 1986. Prey kills predators: counter-attack success of a spider mite against its specific phytoseiid predator. Exp. Appl. Acarol. **2**: 47–62.

―――― 1987. Extraordinary effects of fertilization status on the reproduction of an arrhenotokous and sub-social spider mite (Acari: Tetranychidaè). Res. Popul. Ecol. **29**: 57–71.

SANFORD, K. H. 1967. The influence of spray programs on the fauna of apple orchards in Nova Scotia. XVII. Effects on some predacious mites. Can. Entomol. **99**: 197–201.

SHIH, C. T. 1979. The influences of age of female *Tetranychus kanzawai* on sex ratio and life cycle of its progeny. *In* Recent advances in acarology. I. *Edited by* J. G. Rodriguez. Academic Press, New York. pp. 511–517.

TAKAFUJI, A., and CHANT, D. A. 1976. Comparative studies of two species of predacious phytoseiid mites (Acarina: Phytoseiidae), with special reference to their responses to the density of their prey. Res. Popul. Ecol. **17**: 255–310.

VAN DE VRIE, M., MCMURTRY, J. A., and HUFFAKER, C. B. 1972. Ecology of tetranychid mites and their natural enemies: a review. III. Biology, ecology, pest status, and host plant relations of tetranychids. Hilgardia, **41**: 343–432.

WRENSCH, D. L. 1985. Reproductive parameters. *In* Spider mites: their biology, natural enemies and control. Vol. 1a. *Edited by* W. Helle and M. W. Sabelis. Elsevier/North Holland, New York. pp. 165–170.

YAMAMURA, N. 1987. Biparental defense in a subsocial spider mite. TREE, **2**: 361–362.

YOUNG, S. S. Y., WRENSCH, D. L., and KONGCHUENSIN, M. 1986. Control of sex ratio by female spider mites. Entomol. Exp. Appl. **40**: 53–60