

Intraspecific competition in immature *Amblyseius fallacis*, *Amblyseius andersoni*, *Typhlodromus occidentalis* and *Typhlodromus* *pyri* (Acari: Phytoseiidae)

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ABSTRACT

Intraspecific competition in immature *Amblyseius fallacis*, *Amblyseius andersoni*, *Typhlodromus occidentalis* and *Typhlodromus pyri* was examined in the laboratory using small cages at five different predator densities (two, four, eight, 16 and 32) in the absence and presence of prey (100 eggs of two-spotted spider mite, *Tetranychus urticae* (Koch), at $25 \pm 1^\circ\text{C}$, ~80% RH and 16L:8D photoperiod. In the absence of spider mite prey, some individuals of immature phytoseiids showed increased development and survival with increasing predator densities up to certain limits, but none survived to the adult stage, except for a single male each of *A. andersoni* and *A. fallacis* who completed development by cannibalizing on conspecifics at a density of 32 predators per cage. In the absence of spider mite prey, the mean immature survival time was independent of the initial predator density, but the variance of survival time increased with predator density. In the presence of prey, the proportion of immatures surviving to adulthood generally decreased with initial predator density and dropped sharply to almost none at the predator density of 32 for *A. fallacis*, eight for *A. andersoni*, 16 for *T. occidentalis* and four for *T. pyri*. The number of prey consumed per predator during the first day generally decreased with predator density in all four species, as prey available per predator decreased and the competition for food increased with predator density. Our data indicate that scramble competition is operating in these four species. Although cannibalism was occasionally observed, especially after the exhaustion of prey and in the generalist predators such as *A. andersoni*, the immatures of these phytoseiids were less influenced by the interference of conspecifics than by the increasing difficulty of finding food at high predator densities. The implications of this study for understanding phytoseiid population dynamics and their use in biological control are discussed.

Key words: Intraspecific competition, predation, cannibalism, Phytoseiidae, Tetranychidae.

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INTRODUCTION

The importance of some phytoseiid species in providing biological control of spider mites and other phytophagous arthropod pests has generated a large body of literature on their biology, ecology and use in pest control (Helle and Sabelis, 1985). Many studies on density-dependent processes of phytoseiids have emphasized functional and numerical responses of predators to prey density. Intraspecific density-dependent responses among phytoseiid predators are much less well known. Several studies have shown that density-dependent interactions among conspecific adults can affect the searching efficiency, oviposition rate and other aspects of the biology of some phytoseiid species (e.g. Kuchlein, 1966; Eveleigh and Chant, 1982; Sabelis, 1985, for a review). Intraspecific competition and cannibalism among immatures have not been investigated. Because of the clustering of eggs of many phytoseiid species and the low mobility of the immatures, intraspecific competition among phytoseiid immatures is expected to be high. Intraspecific competition among phytoseiid immatures may be especially intense when the parent generations have reduced food supplies to very low levels (Croft and MacRae, 1992a, b, 1993).

The importance of intraspecific competition in insect population regulation is well known (Nicholson, 1954); however, its role in regulation of phytoseiid population dynamics is largely undocumented. Sabelis and Lanne (1986) mentioned its possible roles in a paper dealing mainly with the effects of predator dispersal on the local and regional dynamics of predator-prey populations. The lack of knowledge about intraspecific competition in Phytoseiidae, in particular and in Acari, in general, greatly limits our understanding of its effects on the population dynamics of mites.

To our knowledge, intraspecific competition in mites has been studied only for one species, *Tyrophagus putrescentiae* (Schrank) (Santos, 1989). In this paper, we report on intraspecific competition and cannibalism in four phytoseiid species. This paper is part of a series of studies on the comparative biologies of immature *Amblyseius* (= *Neoseiulus*) *fallacis* (Garman), *Amblyseius andersoni* Chant, *Typhlodromus* (= *Metaseiulus*) *occidentalis* (Nesbitt) and *Typhlodromus pyri* Scheuten. These species are well-known biocontrol agents (Helle and Sabelis, 1985) and are also the major predators of phytophagous mites on various agricultural crops in Oregon (Hadam *et al.*, 1986; Strong and Croft, 1993). Several aspects of their biology, ecology and population dynamics have been studied, focusing on *T. pyri* and *T. occidentalis* (Croft, 1994; Dunley and Croft, 1990; Croft and MacRae, 1992a, b, 1993; MacRae and Croft, 1993; Croft *et al.*, 1990, 1992, 1993). Many of these studies have demonstrated the critical role that immature stages, especially larvae, may play as key links in insuring population survival at low prey densities. Croft *et al.* (1993) examined the effects of humidity on immature survival of the four species and discussed the implications for biological control of

pest mites on apple, cranberry, strawberry and hop. Croft and Croft (1993) studied the immature survival and feeding on various life stages of *Tetranychus urticae* (Koch). Zhang and Croft (1994) provided a more detailed analysis of the immature life histories of *A. fallacis*, *A. andersoni* and *T. pyri* and *T. occidentalis*, including their survival rates, developmental times, activity, feeding rates, body size and covariance between some traits. In this study, we examined the intraspecific competition in each of these four species in both the presence and absence of eggs of prey, the spider mite *T. urticae* (Koch).

MATERIALS AND METHODS

Maintenance of cultures

Lima bean (*Phaseolus lunatus* L.) was used as the host plant for rearing *T. urticae*. Plants were germinated and grown in plastic bags (30 cm wide opening) with approximately 5 cm growing medium at the bottom. The growing medium was a mixture of soil, peat moss, sand and pumice (1:1:1:2 parts respectively). A spider mite culture was maintained on bean plants in a walk-in growth chamber controlled at 25–27°C.

The colonies of *A. fallacis*, *A. andersoni* and *T. pyri* originated from mites collected from agricultural crops in the Willamette Valley, Oregon (Hadam *et al.*, 1986). A native strain of *T. occidentalis* came from commercial apple orchards in the Hood River Valley, Oregon (Croft *et al.*, 1990). Populations of all four species had been cultured in the laboratory for over 4 years prior to this study, but new mites from the field had been added to stocks annually. Colonies of all four species were reared on 12 × 12 cm black paper resting on water-saturated plastic foam in a stainless steel pan (20 × 20 cm) (McMurtry and Scriven, 1965) at 25 ± 5°C, 16L: 8 D photoperiod and 40–95% RH. Predators were fed mixed life stages of two-spotted spider mites brushed from infested bean leaves three times per week.

Experimental procedures

For each predator species, cohorts of eggs were obtained by transferring approximately 50 adult females to a new small arena 1 day before the experiment. The arena consisted of a tile square (approximately 50 cm²) surrounded by water-saturated cellucotton in a plastic box (11 × 11 cm). The water barrier prevented mites from escaping. Surplus spider mites were brushed onto the arena and cotton fibres were provided under cover glass slides for oviposition by female predators. The tile and the plastic box were placed in a plastic container (30 × 20 × 8 cm) with a saturated solution of NaCl, which provided a relative humidity of ~80% at 25°C. Predator eggs were harvested every 12 h and transferred to a new arena. Unfed larvae hatched during the following 12 h were transferred and used in the experiments.

The effects of the initial predator density on the development and survival of immatures of each of the four species were tested both in the presence and absence

of prey. Five initial predator densities were used; two, four, eight, 16 and 32 per unit. In the presence of prey, 100 eggs of *T. urticae* were provided at the start of the experiment (0–100 eggs are within the range of prey density in the field). There were three replicates for each treatment combination. Mites were confined with or without prey eggs in 2.5 cm diameter screen cages (Croft *et al.*, 1993). The top of the cage was glued to a glass microslide, through which direct observation could be made. Counts were made daily on predator larvae that moulted to protonymphs and the survival of later stages was monitored until all the immatures died or developed into adults. In treatments with prey eggs, the number of eggs consumed during the first day was also recorded. All cages were placed in humidity chambers (controlled at ~80% RH using saturated NaCl) in a growth chamber at $25 \pm 1^\circ\text{C}$ and 16L : 8D photoperiod.

Data analysis

The number and proportion of predatory mites that reached adulthood were calculated for each replicate. They were analysed by a three-factor ANOVA where species, predator density and the presence of prey were the three factors. Because patterns varied significantly among the species (as indicated by the significant three-way interaction), separate two-factor ANOVAs were performed for each species. The number of mites was log transformed and percentage data were arcsin square root-transformed before analyses to minimize error variance. For tests with prey, the per capita predation rates (prey eggs consumed per day per predator) were also calculated for each replicate. For tests without prey, the mean and variance (coefficient of variation, CV) of survival time were calculated for each replicate and were analysed using ANOVA. Immatures that reached adulthood are considered survivors in calculating the immature survival time. Both the mean and variance of survival time were log transformed before analyses.

All ANOVAs were performed using the program SuperANOVA (Abacus Concepts, Inc., Berkeley, CA, 1989). The significance level used in this study was set at 5%.

RESULTS

An analysis of variance including all four species revealed highly significant interactions between and among the independent variables (food, absence and presence, initial predator density of two, four, eight, 16 and 32 and predator species of *A. fallacis*, *A. andersoni*, *T. occidentalis* and *T. pyri*) in their effects on the proportion of predators that reached adulthood ($P < 0.0001$, Table 1, Fig. 1). This indicates that the effects of the presence of prey and predator density on the population of predators that reached adulthood differed significantly among the four species. Further analyses were therefore performed separately for each species (Table 1).

TABLE 1

Analysis of variance: effects of the absence and presence of *T. urticae* eggs and predator density (two, four, eight, 16 and 32) on the proportion of predators reached adulthood in *A. fallacis*, *A. andersoni*, *T. occidentalis* and *T. pyri*.

Effects	df	MS	F ratio	P-value
<i>All species</i>				
Food	1	10.774	608.941	0.0001
Density	4	1.478	83.514	0.0001
Species	3	1.098	62.059	0.0001
Food × density	4	1.574	88.962	0.0001
Food × species	3	1.077	60.864	0.0001
Density × species	12	0.143	8.103	0.0001
Food × density × species	12	0.147	8.282	0.0001
Error	80	0.018		
<i>A. fallacis</i>				
Food	1	7.659	328.853	0.0001
Density	4	0.361	15.502	0.0001
Food × density	4	0.434	18.629	0.0001
Error	20	0.023		
<i>A. andersoni</i>				
Food	1	0.943	43.649	0.0001
Density	4	0.375	17.370	0.0001
Food × Density	4	0.408	18.877	0.0001
Error	20	0.022		
<i>T. occidentalis</i>				
Food	1	5.074	955.695	0.0001
Density	4	0.843	158.749	0.0001
Food × density	4	0.843	158.749	0.0001
Error	20	0.005		
<i>T. pyri</i>				
Food	1	0.329	16.000	0.0001
Density	4	0.329	16.000	0.0001
Food × density	4	0.329	16.000	0.0001
Error	20	0.021		

The effects of predator density on the number of mites surviving to adulthood varied with the absence/presence of food in all four species (Table 1 and Fig. 1, left column). No mites survived to the adult stage in the absence of prey, except that a single male each of *A. andersoni* and *A. fallacis* completed development by cannibalizing on conspecifics at 32 predators per cage. In the presence of 100 spider mite eggs, the number of *A. fallacis* surviving to adulthood increased quickly with predator density of up to 16 predators per cage and then sharply decreased to almost none, the number of *A. andersoni* surviving to adulthood increased slightly with predator density until four predators per cage and then decreased to none, the number of *T. occidentalis* surviving to adulthood increased slowly with predator density until eight predators per cage and then decreased to almost none and most

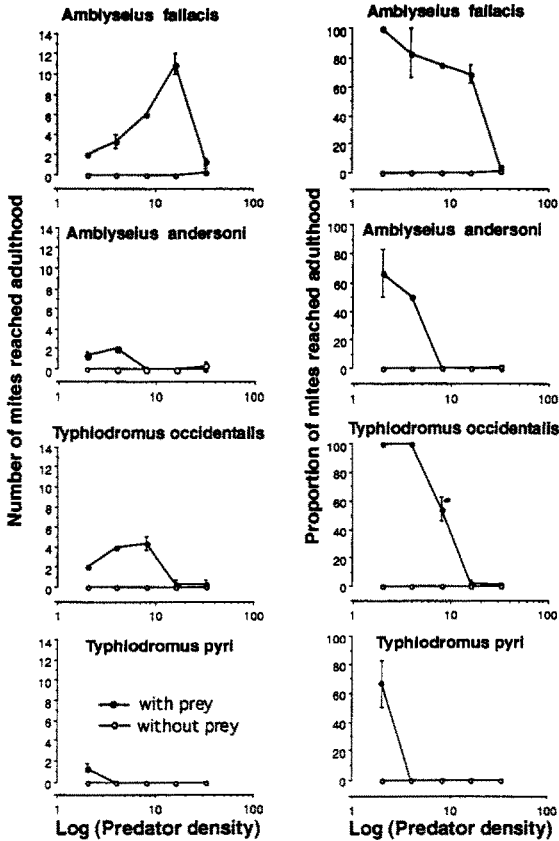


Fig. 1. The number and proportion of *A. fallacis*, *A. andersoni*, *T. occidentalis* and *T. pyri* that reached adulthood in relation to initial predator density in the absence or presence of prey (100 *T. urticae* eggs) at $25 \pm 1^\circ\text{C}$, $\sim 80\%$ RH and 16L : 8 D photoperiod. Bars represent mean standard errors.

T. pyri survived to the adult stage at two predators per cage but none completed development at higher predator densities (Fig. 1, left column).

The proportion of mites surviving to adulthood was plotted against predator density in Fig. 1 (right column) to show the intensity of intraspecific competition in the four species. At low predator densities, competition among immature *A. fallacis* increased only slowly with predator density, but at >16 predators per cage competition became so intense that almost none survived. There was severe competition among *A. andersoni* immatures at eight predators per cage and among *T. pyri* at four predators per cage. At four or fewer predators per cage, there was no competition among *T. occidentalis* immatures, but almost all died prematurely at 16–32 predators per cage.

TABLE 2

Analysis of variance: effects of predator density (two, four, eight, 16 and 32) on the mean and variance (CV) of immature survival time in *A. fallacis*, *A. andersoni*, *T. occidentalis* and *T. pyri*.

Effects	df	MS	F ratio	P-value
Mean survival time				
Species	3	0.180	34.002	0.0001
Density	4	0.004	0.810	0.5625
Species × Density	12	0.009	1.651	0.1161
Error	40	0.005		
Variance of survival time				
Species	3	0.0073	3.433	0.0261
Density	4	0.246	11.55	0.0001
Species × Density	12	0.032	1.505	0.1641
Error	40	0.021		

Immature development and the survival time also varied with the presence/absence of food and predator density (Figs 2 and 3). In the absence of prey (Fig. 2), the survival time of some immatures increased with increasing predator density. For example, at two to four predators per cage in the absence of food, larval *T. occidentalis* survived for only 2–3 days and none developed to protonymphs; one to three larvae completed development at higher predator densities by cannibalizing and/or scavenging and the survival time increased with predator density (Fig. 2). Similarly, at high predator densities in the presence of prey when the competition among the immature of *A. andersoni* and *T. pyri* was intense (Fig. 3), the survival time of some immatures increased with predator density because superior competitors were able to attack live conspecifics or to feed on newly dead mites.

An analysis of variance of the mean survival time and the variance (CV) of survival time in the absence of prey indicates that the mean survival time was in fact independent of predator density, but the variance of survival time decreased with predator density (Fig. 4). The mean survival times were lower in *T. occidentalis* than other species, because most *T. occidentalis* larvae died in the absence of prey.

The feeding rates per predator are shown in Fig. 5 for the four species. The number of prey consumed per predator generally decreased with predator density, as the number of prey available per predator decreased and competition increased with predator density. At the highest density (i.e. 32 predators per cage), over 80% of prey were consumed during the first day. At the lowest predator density (two predators per cage), the mean feeding rates during the first day varied considerably among the four species (Fig. 4): one *A. fallacis* or *T. occidentalis* consumed less than ten eggs (<20% of eggs available), whereas one *T. pyri* consumed over 20 eggs (~40% of eggs available) and one *A. andersoni* over 30 eggs (>60% of eggs available).

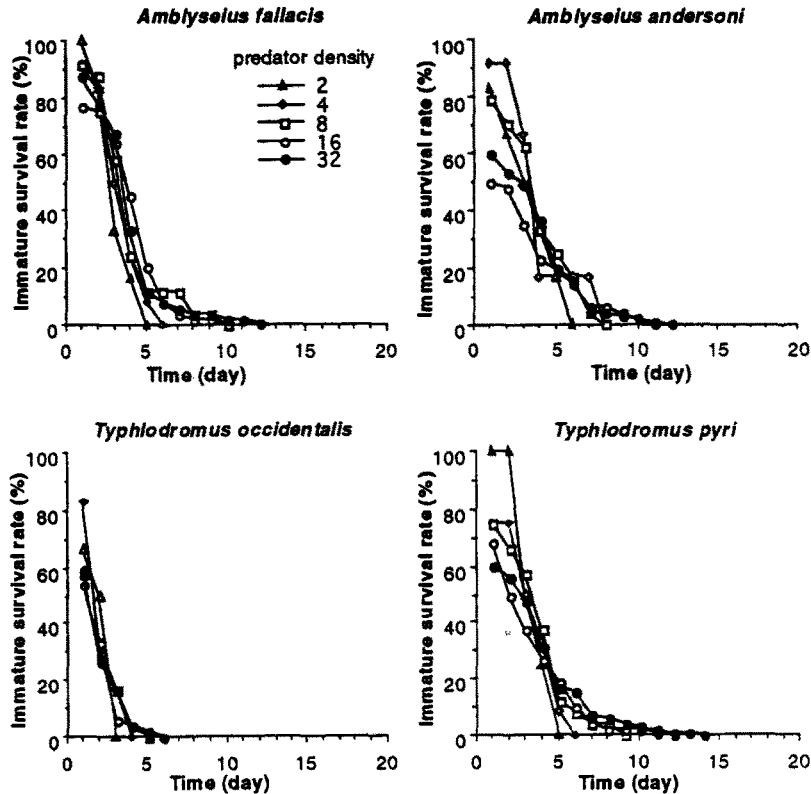


Fig. 2. Immature age-specific survivorship at different initial predator densities for *A. fallacis*, *A. andersoni*, *T. occidentalis* and *T. pyri* in the absence of prey at $25 \pm 1^\circ\text{C}$, $\sim 80\%$ RH and 16L:8D photoperiod.

DISCUSSION

Two main types of intraspecific competition are distinguished in the literature: contest competition and scramble competition (Nicholson, 1954). In contest competition, some individuals actively interfere with others and outcompete others; they get more food than the others who then die due to lack of food. Thus, some individuals may survive even at high predator densities and survival rates decrease smoothly with increasing predator density. In scramble competition, however, all individuals have equal access to the resource. At high predator densities, all individuals starve to death after the food is exhausted and survival rates drop drastically beyond a critical predator density. The only report on mite intraspecific competition (Santos, 1989) showed that scramble competition operates in the immatures of the acarid mite, *T. putrescentiae*.

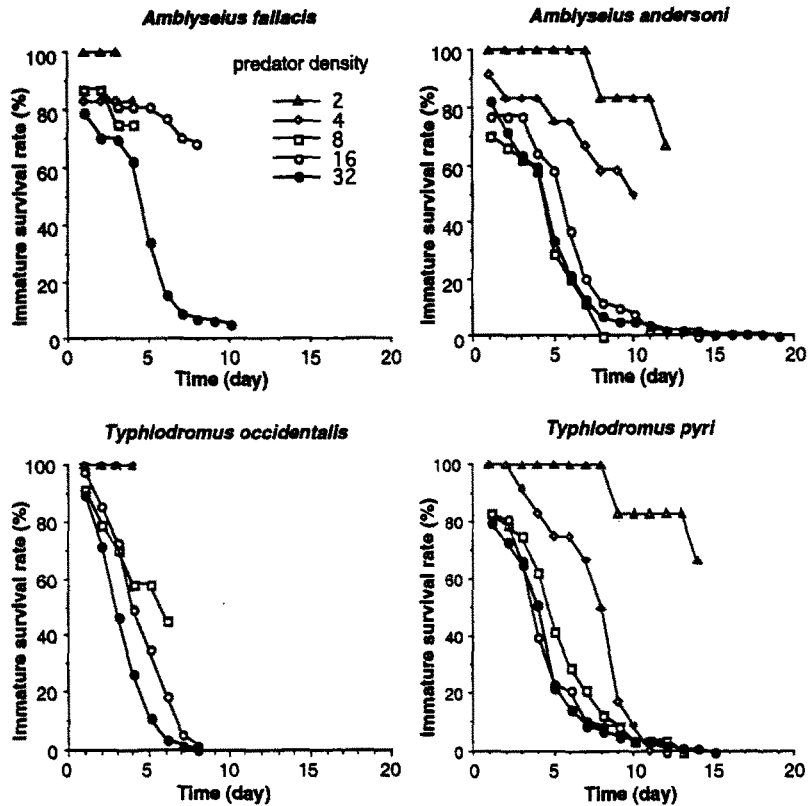


Fig. 3. Immature age-specific survivorship at different initial predator densities for *A. fallacis*, *A. andersoni*, *T. occidentalis* and *T. pyri* in the presence of prey (100 *T. urticae* eggs) at $25 \pm 1^\circ\text{C}$, $\sim 80\%$ RH and 16L : 8D photoperiod.

In this study, we have demonstrated intraspecific competition in immature *A. fallacis*, *A. andersoni*, *T. occidentalis* and *T. pyri*. The intraspecific competition in the four species may be generally characterized as of the scramble type, although weak contest and interference among conspecific individuals was observed in the two polyphagous predators (*A. andersoni* and *T. pyri*). In the absence of prey, we occasionally observed that some immatures could attack conspecifics. However, the success of such attacks was low. Immature phytoseiids were more likely to feed on dying or freshly dead conspecifics. In the presence of food, however, predators seemed to prefer prey (*T. urticae*) eggs to conspecifics. As a result, all prey were consumed before any predator could develop to adulthood when competition for food was intense. The population dynamical consequence of this type of scramble competition is likely to be that immature populations of these mites tend to go

extinct locally if no other density-dependent process is operating in the system.

In field situations, the immatures of generalist predators such as *A. andersoni* and *T. pyri* may feed on alternative prey and/or conspecifics for development and survival. These species may be able to persist even though they compete in a scramble fashion. In contrast, more specialized feeders such as *T. occidentalis* tend to become extinct faster. Dispersal is another mechanism by which some individuals may survive. Although little is known about the movement capacities and dispersal of immature phytoseiids, recent laboratory studies on their activity have shown that nymphal stages of *T. pyri* are very active and that they spend over 50% of the time walking (Z.-Q. Zhang and B.A. Croft, unpublished data). In studies of leaf residence time and interleaf movement of immatures of the four predator species held without prey (B.A. Croft, unpublished data), the immatures of *T. occidentalis* and *A. fallacis* were more prone to move than those of *T. pyri* and *A. andersoni*. However, successful immature dispersers may face the low probability of finding a mate.

The measurements of prey consumption showed that the two polyphagous predators (*A. andersoni* and *T. pyri*) attacked more prey per predators per day than the two oligophagous species (*T. occidentalis* and *A. fallacis*). As a result, fewer individuals of the polyphagous predators reached adulthood than the oligophagous species.

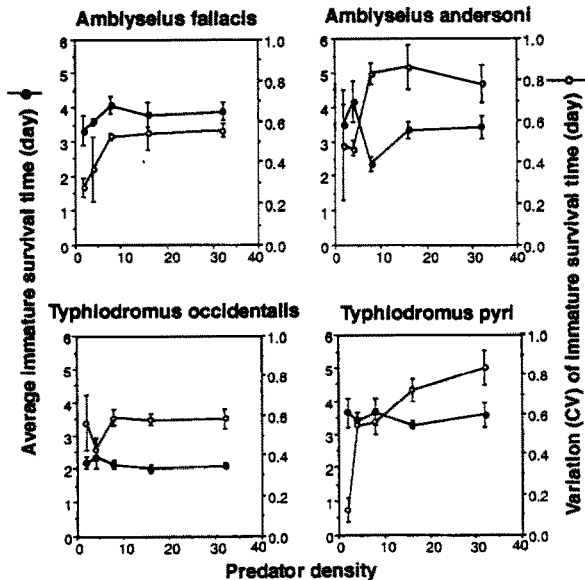


Fig. 4. Mean and variance (CV) of immature survival time in the absence of prey at different initial larval densities of *A. fallacis*, *A. andersoni*, *T. occidentalis* and *T. pyri* at $25 \pm 1^\circ\text{C}$, $\sim 80\%$ RH and 16L:8D photoperiod. Bars represent mean standard errors.

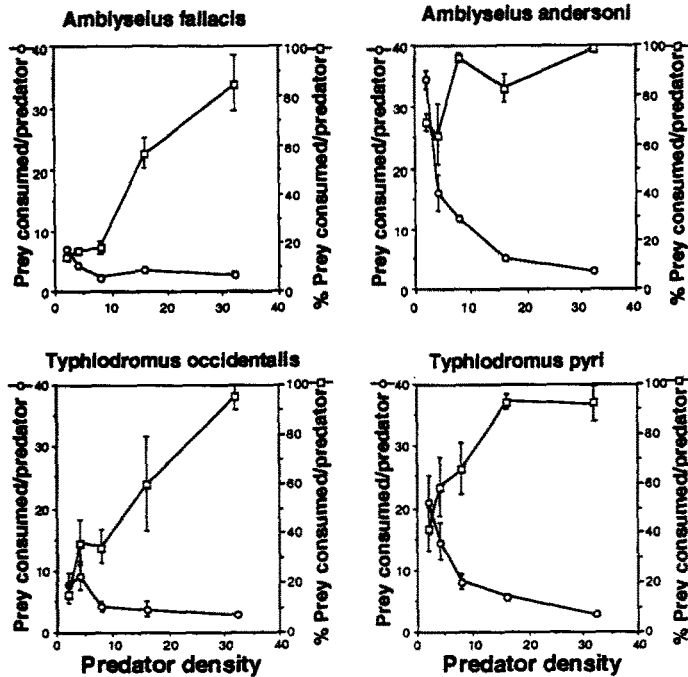


Fig. 5. Per capita predation rates of larvae/protonymphs of *A. fallacis*, *A. andersoni*, *T. occidentalis* and *T. pyri* in relation to predator density during the first day; 100 *T. urticae* eggs were provided at the start of the experiment. The left y-axis is the number of prey eggs consumed and the right y-axis is the proportion of prey eggs consumed. Bars represent standard errors.

A very interesting result from this study is that the mean survival time was independent of predator density, whereas the variance of survival time increased with predator density. The survival processes were different among treatments. These differences were revealed by the difference in variation in survival time rather than the mean survival time. The larger variance at higher predator densities indicates that some individuals could survive longer than others so that the chance of some individuals reaching adulthood was increased. This spread of risk at higher predator density increased the chances of persistence of local predator populations. It should be noted that, from a statistical standpoint, variation in survival time may increase with the number of predators used independent of any effect of density on survival.

The lack of strong contest competition among conspecific immatures may be associated with their defensive and recognition behaviour and the similar size among individuals. We frequently observed that two immatures rapidly bounced away from each other when they touched. We even observed that quiescent larvae of some species (e.g. *A. fallacis*) display characteristic jerky movements when approached by another mite. This behaviour could scare an intruder away. It might

be a form of intraspecific communication which would reduce the level of cannibalism. The similar size of immature conspecifics also makes it difficult for some individuals to outcompete others. For example, predator nymphs were more often observed to attack larvae or quiescent larvae than other nymphs. It is likely that predation among immature phytoseiids should be more common between different-sized conspecifics and between species of large and relatively small size. The latter type of interspecific predation among immatures of these four species will be reported in a future paper.

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