Intra- and interspecific predation on four life stage groups by the adult females of *Metaseiulus occidentalis, Typhlodromus pyri, Neoseiulus fallacis* and *Amblyseius andersoni*

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ABSTRACT

Do adult females of oligophagous species such as *Neoseiulus fallacis* (Garman) and *Metaseiulus occidentalis* (Nesbitt) show less intra- and interspecific predation on phytoseiids when other foods are scarce than polyphagous species such as *Amblyseius andersoni* Chant and *Typhlodromus pyri* Scheuten? We caged single adult females of each species without food with ten of their own eggs or larvae, with ten eggs or larvae of the other species or with ten nymphs or adult females of *M. occidentalis* (*T. pyri* for *M. occidentalis*). We assessed the ambulatory activity, survival time, egg levels and prey loss in each test. Polyphages (in particular *T. pyri*) lived longer than oligophages (in particular *N. fallacis*) without food. The small *T. pyri* detected its own stages and benefited most by feeding on small active stages of other species. *Amblyseius andersoni*, the largest mite, fed and gained the most of any species when held with nymphs and female adults. *Metaseiulus occidentalis* fed on eggs of all four species to enhance survival. The large hyperactive *N. fallacis* gained the least from these behaviours. Each mite seemed uniquely adapted to survive conditions of scarce prey and these behaviours may explain their roles in phytoseiid mite complexes. Overall, oligophagous adult females fed less and gained less by feeding on phytoseiids than did polyphagous adult females.

Key words: Intraspecific predation, interspecific predation, life stage

INTRODUCTION

Complexes of phytoseiid mites occur on many perennial crops in western Oregan, USA. We have been studying competition among *Typhlodromous pyri* Scheuten, *Metaseiulus occidentalis* (Nesbitt), and *Amblyseius andersoni* Chant on apple, *Neoseiulus fallacis* (Garman), *T. pyri*, *M. occidentalis* and *A. andersoni* on hops and *N. fallacis* and *M. occidentalis* on strawberry when prey mites are scarce (MacRae and Croft, 1993; Strong and Croft, 1993; Coop and Croft, 1995). These predators, either alone or as complexes, can given excellent

control of the pests *Tetranychus urticae* (Koch) or *Panonychus ulmi* Koch (Croft and MacRae, 1993; Croft, 1994).

After suppressing their preferred prey to low levels, the adult female phytoseiid (stage most likely to persist) has mechanisms for surviving competition (Polis and Meyers, 1989; Yao and Chant, 1989; Walde *et al.*, 1992). It may either stay and feed on foods such as pollen, it may feed on its own life stages or those of other phytoseiids, it may disperse elsewhere or it may enter diapause if conditions are favourable (Helle and Sabelis, 1984). Here we report on the intra- and interspecific predation by adult females on four life stage groups and the impacts on survival and oviposition. We compare the oligophagous *M. occidentalis* and *N. fallacis* with the polyphagous *T. pyri* and *A. andersoni* (Zhang and Croft, 1994).

METHODS

One problem in studying phytoseiid mites while they are starving is how to hold them. Any open system (leaf or arena) that uses water or a sticky substance for containment has high losses. A 2.5 cm cage (70 μm cell strainer, Benton Dickinson Co. Lincoln Park, NJ) that contains all phytoseiid life stages has been described earlier (Croft and Croft, 1993; Zhang and Croft, 1995). This cage can be loaded only once so the tests must be of short duration, but when pest mite levels decline rapidly only one generation of immature phytoseiids is left before the adult females disperse. Thus, the conditions simulated here may not be so unreal.

Twenty adult females of each phytoseiid were randomly selected from a rearing unit and placed singly in cages either with no prey or with provisions of ten eggs or ten unfed larvae of their own species or of each other species. With nymphs or female adult prey, ten each of *M. occidentalis* (*T. pyri* for *M. occidentalis*) were placed with a single female adult. The predator species–prey species (stage) tests were replicated 20 times each. The tests were conducted consecutively among prey life stages (from no food to adult female prey), but simultaneously for all four predator species in a given treatment (all phytoseiids came from standard rearing units that had similar management conditions). The reasons for using only nymph or adult female *M. occidentalis* as prey were because they are small (Zhang and Croft, 1994) and easily captured by phytoseiids (Croft and Croft, 1996). Another reason was that it was impossible to hold ten *N. fallacis* or *A. andersoni* in open cells because of their activity levels. The feeding was standardized for the mites in the cages. Adult female predators were fed abundant prey 1 day before the tests were begun. With prey nymphs and adult females, only those that had fed within 3 h were provided (assessed by gut colouration). For nymphs and adults, a screen cage had to be cooled and held over ice until ten mites could be loaded. For the no food, egg or larval tests, only ice was used.

Mites in cages were held until death on 15 × 15 cm tile arenas in plastic boxes of 40 × 25 × 15 cm above a water–NaCl solution at 80% RH, 25 ± 1°C and 16 : 8 L : D photoperiod (Croft *et al.*, 1993). In assessments, each female adult was observed at the same time each day for survival, activity (ambulation, positive or negative), egg levels and prey loss. For egg levels, mites oviposited on cage walls, and provisioned eggs were placed on screens. Predation on eggs by adult females was a complication. We therefore used the egg levels to denote this factor. For prey loss, most (> 90%) was from predation, but some other types occurred at low levels.

In analysing the data, several questions were of primary interest.

(1) Does the survival time vary among predator species when they are unfed?
(2) Is the survival time increased when predators are held with their own stages or those of conspecifics?
(3) Does the survival time vary according to the life stage provided?
(4) Are the egg levels and prey loss affected by this predation?

To answer these questions, analyses of variance (three-way ANOVAs) were run for the dependent variables of (1) the survival time in hours, (2) the egg levels per adult female and (3) the prey loss per adult female. The independent variables of predator species, life stage (no prey, eggs or larvae) and prey species were included in each three-way ANOVA. Because of significant interactions in three-way ANOVAs, two-way ANOVAs were also run for all four prey groups for the effects of the predator × prey species interaction. To conduct mean difference tests, single-factor ANOVAs were run in two ways: (1) for each predator species × all prey species interactions within a prey life stage type and (2) for one prey species (and life stage type) × all predator species interaction. The means for the survival time, egg levels or prey loss were compared using Fisher's protected least significance difference (LSD) test (Petersen, 1985). The activity frequencies for the adult females in the treatment were compared by χ^2 tests after arc-sine transformation of data (Peterson, 1985).

RESULTS AND DISCUSSION

The ANOVAs (three-way) for the non-fed mites and egg and larval life stage tests (combined) showed significance for all the main and interaction effects for both the survival time and prey loss (Table 1). For egg levels, the main effects were significant for both the predator species and life stage type but not the prey species; only the predator × prey species interaction was significant.

The ANOVAs (two-way) for the predator species × prey species interaction in each of the four life stage groups had significant main effects on the survival at $p < 0.05$, except for prey species in the nymphal ($p = 0.576$) and adult female ($p = 0.356$) tests. Significant main effects for the egg levels were observed in all

TABLE 1

Three-way ANOVAs: impact of intra- and interspecific predation by adult female *M. occidentalis, N. fallacis, T. pyri* and *A. andersoni* on the survival time, egg levels and prey loss when held with no food, eggs and unfed larvae of four phytoseiid species

Dependent variable/effects	df	MS	*F* ratio	*p* value
Survival time				
Predator species	3	332.42	110.45	0.0001
Life stage groups (LSG)	2	247.37	82.19	0.0001
Prey species	3	21.03	6.99	0.0001
Predator species × LSG	6	27.71	9.21	0.0001
Predator species × prey species	9	13.82	4.59	0.0001
Foods × prey species	6	9.69	3.22	0.0039
Predator species × LSG × prey species	18	10.40	3.45	0.0001
Error	912	3.10		
Eggs levels				
Predator species	3	61.14	107.87	0.0001
LSG	2	4.63	8.28	0.0003
Prey species	3	1.15	1.97	0.1172
Predator species × LSG	6	0.84	1.48	0.1828
Predator species × prey species	9	1.88	3.23	0.0005
Foods × prey species	6	0.55	0.98	0.4394
Predator species × LSG × prey species	18	0.58	1.02	0.4285
Error	912	0.57		
Prey loss				
Predator species	3	21.20	13.06	0.0001
LSG	2	6602.80	4065.59	0.0001
Prey species	3	29.37	18.08	0.0001
Predator species × LSG	6	10.84	6.67	0.0001
Predator species × prey species	9	29.61	18.23	0.0001
Foods × prey species	6	18.29	11.27	0.0001
Predator species × LSG × prey species	18	21.85	13.45	0.0001
Error	912	1.62		

LSG, Life stage group.

tests except for the prey species in the egg ($p = 0.227$), larval ($p = 0.331$) and nymphal ($p = 0.407$) tests. All the main effects for prey loss were significant ($p < 0.05$).

ANOVAs (one-way) for each predator species by all prey species interactions (in a life stage group) had significant p values (≤ 0.05) in eight of the eight tests for survival, six of the eight tests for the egg levels and eight of the eight tests for prey loss (Table 2); unfed controls were included in each life stage ANOVA for comparisons; letters after the means indicate that the ANOVA F values were significant, ($p < 0.05$). The ANOVA values for the single prey species by all predator species interaction within a life stage group were significant in all ten tests for either the survival time, egg level or prey loss (Table 2). The ANOVA

values for each predator species × nymphs or adult female prey interaction of *M. occidentalis* (and their own nymphs) were significant ($p < 0.05$) in two of the eight tests for survival, seven of the eight tests for the egg levels and eight of the eight tests for prey losses (Table 2). The ANOVA values for the nymphs or adult female prey of *M. occidentalis* or *T. pyri* (or their nymphs) with a single prey species × all predator species interaction were significant ($p < 0.05$) in five of the five tests for survival, four of the five tests for the egg levels and three of the five tests for prey losses (Table 2).

Survival time

With no prey (controls), *N. fallacis* and *M. occidentalis* died sooner than *A. andersoni* and *T. pyri* (Table 2). Survival was inversely related to the intrinsic rates of increase (*N. fallacis* > *M. occidentalis* > *A. andersoni* > *T. pyri*)(Croft *et al.*, 1995) and activity levels (*N. fallacis* > *M. occidentalis* = *T. pyri* > *A. andersoni*)(Croft and Croft, 1996; see below, Table 2).

With provisioned eggs, the survival times were extended beyond the controls for all the species except *N. fallacis* (Table 2). The survival time with eggs (provisioned for all species/control) was 1.85% for *T. pyri*, 1.57% for *M. occidentalis*, 1.51% for *A. andersoni* and only 1.03% for *N. fallacis*. Some females may have fed less on eggs than larvae that developed later. This was the case for *T. pyri* which prefers small active stages (Croft and Croft, 1993; Croft *et al.*, 1995). *Typhlodromus pyri*'s survival was shorter with its own versus other eggs (or larvae), which shows it can discriminate between them (MacRae and Croft, 1993; Croft *et al.*, 1996).

The survival time of the adults with larvae (all species) was increased over the controls for *T. pyri* (1.41%) and *M. occidentalis* (1.20%), but not *A. andersoni* (1.02%) or *N. fallacis* (1.03%) (Table 2). With the first three, the survival time was less with unfed larvae than eggs which reflects energy lost during larval development.

When held with fed nymphs of *M. occidentalis* (*T. pyri* for *M. occidentalis*), the survival time was not much different from the controls (provisioned/control): *M. occidentalis* (0.95), *N. fallacis* (0.83) and *T. pyri* (0.96) and *A. andersoni* (1.09) (Table 2). It is likely that there are trade-offs between the benefits of predation versus the negative interference and greater activity when with the nymphs. These effects occurred with adult females (provision/control): *M. occidentalis* (0.83), *N. fallacis* (0.48), *T. pyri* (0.48) and *A. andersoni* (0.92) (Table 2). The largest mite, *A. andersoni*, had the least reduced survival time with this stage. Other tests have shown that *A. andersoni* more readily eats adult female *M. occidentalis* than do the other species (Croft and Croft, 1996).

Egg levels

The egg levels (reproduction minus predation) were different between species with no food: *N. fallacis* > *T. pyri* > *A. andersoni* > *M. occidentalis*. In all tests,

TABLE 2

Intra- and interspecific predation by adult females of *M. occidentalis, N. fallacis, T. pyri* and *A. andersoni* when held in screen cages with four life stage groups of phytoseiids

Predator Sp. Prey Sp.	Survival time(h)	Eggs female[b]	Activity frequency[b]	Prey loss per female[b]
Predator, female adult; prey life stage provided, Eggs[a]				
M.o. (uf)[c]	65[d] a[e] ab[f]	0.15 a[e] a[f]	0.54 NS[g]	0.0 a[e] NS
M.o.	109 c ab	0.05 a a	0.49	4.4 b a
N.f.	103 bc b	0.10 a a	0.68	4.8 b b
T.p.	84 b a	0.30 a a	0.64	5.8 c b
A.a.	113 c b	0.65 b a	0.61	4.5 b ab
N.f. (uf)	62 ab a	1.30 b d	0.81 NS	0.0 a
M.o.	80 c a	1.75 bc c	0.92	7.3 e b
N.f.	64 ab a	0.75 a bc	0.84	2.3 b a
T.p.	57 a a	1.80 c b	0.86	6.2 d bc
A.a.	55 a a	1.80 c b	0.79	5.1 c b
T.p. (uf)	89 a c	0.80 b c	0.60 NS	0.0 a
M.o.	182 c c	0.90 b b	0.70	4.8 d a
N.f.	134 b c	1.00 b c	0.65	6.3 e c
T.p.	121 ab b	0.60 a a	0.61	2.6 b a
A.a.	222 c c	1.00 b a	0.67	3.8 c a
A.a. (uf)	79 a bc	0.45 NS b	0.37 NS	0.0 a
M.o.	126 bc b	0.80 b	0.20	4.1 b a
N.f	108 b bc	0.35 ab	0.30	7.1 c c
T.p.	142 c b	0.60 a	0.52	7.6 c c
A.a.	101 b b	0.80 a	0.42	5.0 b ab
Predator, female adult; prey life stage provided; unfed larvae[a]				
M.o. (uf)	65 a ab	0.15 NS a	0.54 0.10	0.0 a NS
M.o.	60 a a	0.30 a	0.80	9.5 c a
N.f.	73 ab a	0.35 a	0.73	9.4 c a
T.p.	89 bc b	0.35 a	0.77	7.9 b a
A.a.	90 c a	0.20 a	0.83	8.0 b ab
N.f (uf)	62 a a	1.30 a d	0.81 NS	0.0 a
M.o.	73 b ab	1.65 ab c	0.89	9.0 d a
N.f.	56 a a	1.15 a bc	0.75	9.5 d a
T.p.	53 a a	2.20 b c	0.95	8.5 c a
A.a.	75 b a	1.85 b c	0.84	7.6 b a
T.p. (uf)	89 a c	0.80 a c	0.60 0.10	0.0. a
M.o.	118 bc c	1.20 b bc	0.76	10.0 c a
N.f.	136 cd b	1.20 b c	0.58	10.0 c a
T.p.	93 ab b	1.05 ab b	0.79	8.1 b a
A.a.	156 d b	0.95 ab b	0.81	8.2 b b

(*continued*)

TABLE 2 (Continued)

Intra- and interspecific predation by adult females of *M. occidentalis, N. fallacis, T. pyri* and *A. andersoni* when held in screen cages with four life stage groups of phytoseiids

Predator Sp. Prey Sp.	Survival time (h)	Eggs female[b]	Activity frequency[b]	Prey loss per female[b]
A.a. (uf)	79 a bc	0.45 NS b	0.37 0.000	0.0 a
M.o.	87 ab b	0.75 ab	0.60	10.0 c a
N.f.	68 a a	0.70 ab	0.42	10.0 c a
T.p.	66 a a	0.70 ab	0.83	10.0 c a
A.a.	101 b a	0.80 b	0.67	8.2 b b
Predator, female adult; prey life stage provided; fed nymphs[a]				
M.o. (uf)	65 NS ab	0.15 NS a	0.54 0.05	0.0 a NS
M.o.	68 ab	0.15 a	0.74	6.4 b a
T.p.	56 a	0.15 NS	0.81	7.6 c ab
N.f. (uf)	62 NS a	1.30 b d	0.81 NS	0.0 a
M.o.	49 a	0.20 a a	0.78	8.0 b b
N.f.	54 a	0.15 a	0.82	8.5 b b
T.p. (uf)	89 NS c	0.80 b c	0.60 0.10	0.0 a
M.o.	88 b	0.50 ab ab	0.84	9.3 c c
T.p.	82 b	0.40 a	0.78	7.1 b a
A.a. (uf)	79 NS bc	0.45 ab b	0.37 0.003	0.0 a
M.o.	88 b	0.65 b b	0.72	10.0 c c
A.a.	85 b	0.25 a	0.72	6.9 b a
Predator, female adult; prey life stage provided; female adults[a]				
M.o. (uf)	65 NS ab	0.15 a a	0.54 0.001	0.0 a NS
T.p.	54 bc	1.40 b b	0.94	2.4 b b
N.f. (uf)	62 b a	1.30 b d	0.81 NS	0.0 a
M.o.	30 a a	0.15 a a	1.00	1.5 b a
T.p. (uf)	89 b c	0.80 b c	0.60 0.003	0.0 a
M.o.	43 a ab	0.00 a a	0.97	3.0 b b
A.a. (uf)	79 NS bc	0.45 b b	0.37 0.000	0.0 a
M.o.	73 c	0.05 a a	0.97	6.0 b c

[a]Ten individuals per female adult phytoseiid were provided; fed nymphs were approx 50:50, protonymphs: deutonymphs. [b]Mean survival time, eggs per female before death, activity frequency for all observed times, number lost per female in first 24 h. [c]Treatment control of adult females mites held without food (uf = unfed); these data were used in ANOVA tests for each prey life stage for convenience in making comparisons. [d]Data for 20 single female adults in test with all prey stages. [e]Means in the first column followed by the same letter are not significantly different for that species of predator among prey species in that specific life stage group (no food, larvae, nymph or female adult) at $p \leq 0.05$; NS = not significant. [f]Mean in the second column followed by the same letter are not significantly different among species of predator for that specific prey species/life stage group, $p \leq 0.05$; NS = not significant. [g]Significance of χ^2 test that frequencies differ among treatments.

the egg levels for *M. occidentalis* were lowered by cannibalism. When prey rapidly become scarce and when cannibalism is accounted for, this mite usually lays approximately one egg per female (Croft *et al.*, 1995). The egg levels per female were higher than in the controls when eggs were provisioned in one or more tests for all species but *A. andersoni* (Table 2). Reduced new eggs were seen for *N. fallacis* and *T. pyri* when held with their own eggs, again indicating some discrimination. Sometimes the egg levels were greater for adult females that were held with unfed larvae versus those held with eggs (Table 2). This was because some adult females prefer these smaller active stages (*T. pyri*) (Croft and Croft, 1993; Croft *et al.*, 1996). As before (Croft *et al.*, 1995), the egg levels were usually much less in the tests with nymphs and adult females than with the smaller stages and sometimes less than with no prey (Table 2). This was because most phytoseiids do not readily feed on these larger phytoseiid life stages (*A. andersoni* is an exception; Croft and Croft, 1996). Another reason is because of egg cannibalism by provisioned nymphs or adult female *M. occidentalis* (Croft *et al.*, 1995, 1996). A reduction in eggs was not seen when ten *T. pyri* was added instead of *M. occidentalis* (Table 2). Ten added *T. pyri* probably added even more eggs for consumption by the one *M. occidentalis*. The benefits to *A. andersoni* (versus the others) from feeding on nymphs and adult females were not seen as added eggs (because of cannibalism by *M. occidentalis*; Croft *et al.*, 1995) but as a less reduced survival time (Table 2).

Activity frequency

With no prey, there were differences in the activity frequency of the adult females (Table 2); it was most for *N. fallacis* and least for *A. andersoni*. The levels were not different between the egg tests or controls of any species (Table 2), but with larvae, the adult females were more active (*A. andersoni*, $p < 0.000$ and *T. pyri* and *M. occidentalis*, $p = 0.01$), probably because of interference. As in the controls, the activity levels for *N. fallacis* with the larvae were high. The activity levels with provisioned nymphs and female adults were more different from the controls than with larvae for three of the four species (not *N. fallacis*); significance levels were greater for added females than for nymphs. Again, this was because of interference. Overall, there was a clear trend of increasing activity with increasing life stage size and the greatest change occurred between the egg and larval stage treatments.

Prey loss

Prey losses were greatest for the larvae followed by the nymphs, eggs and adult females (Table 2). Within the egg treatments, prey losses were least within species for *N. fallacis* and *T. pyri* (Table 2). There were 2-fold greater losses with unfed larvae versus the eggs and less intraspecifically for *A. andersoni* and *T. pyri*. A smaller prey loss within species occurred for two of the four cases with nymphs (not *N. fallacis* and *M. occidentalis*). The prey loss of 6.0 for *A. andersoni* when with ten adult females of *M. occidentalis* was twice that of any

other species and indicative of a favourable prey stage as was seen in survival and oviposition data.

Relevance to field studies

Adult female phytoseiids do not feed as much on their immatures in nature as was seen here, but these behaviours do affect their survival (Croft and MacRae, 1992, 1993; Croft, 1994). For example, *M. occidentalis* responds well to pest mite outbreaks, but it lays any remaining eggs rapidly when prey become scarce and feeds on them and eggs of any other phytoseiid. These behaviours enhance survival, but only briefly because it feeds less on the active stages of phytoseiids. These behaviours may enhance dispersal (Dunley and Croft, 1990).

The short survival time of *N. fallacis* when held without prey and its low tendency to prey on phytoseiids (especially its own), make it very prey dependent. It feeds little on other foods, except pollen (Helle and Sabelis, 1984) and disperses away rapidly (Coop and Croft, 1995; Strong and Croft, 1995). Its hyperactivity is puzzling. It aggregates with *T. urticae* but moves widely on plants (Croft *et al.*, 1996). Other than to disperse, *N. fallacis* seem to have few means to survive conditions of low prey density.

Typhlodromus pyri's strategy is different. It lives long without food, prefers small active phytoseiid life stages and feeds less on its own. It regulates pest mites well and does not disperse as widely as do some species (Dunley and Croft, 1990). While its small size would seemly make it a susceptible prey, it has evolved evasive behaviours to avoid macropredation (Croft and Croft, 1996).

The polyphagous, *A. andersoni* has many similar traits as has *T. pyri*, but it is less averse to prey on its own. Its large size and activity do not allow it to survive as long without food, but it is less likely to be eaten by macropredators (Croft and Croft, 1996). It eats large phytoseiid stages (Croft and Croft, 1996) and small insects (Croft, 1994) and it more readily disperses between plants (Dunley and Croft, 1990; Croft, 1994; Croft and Croft, 1996).

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