

AN ABSTRACT OF THE THESIS OF

J. Scott Blackwood for the degree of Master of Science in Entomology presented on August 31, 2000. Title: Jerking Behavior Among Phytoseiid Mite Species (Acari: Phytoseiidae).

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Brian A. Croft

Jerking, which we defined as a pronounced and often repeated lunging of the entire body, was studied in larvae among seven species of phytoseiid mites, and in the nymphal stages of *Neoseiulus fallacis* (Garman). This behavior was observed in all active immature stages of *N. fallacis*, and in larvae of six of seven species studied. Jerking was usually triggered by direct contact with a conspecific predator or an active immature stage of two-spotted spider mite, *Tetranychus urticae* Koch. With *N. fallacis* larvae, jerking occurred occasionally without direct contact. Usually in these cases, jerking occurred in response to the nearby movement of a mite, and less frequently, no stimulus was observed. The larval jerking tendency, or the mean proportion of contacts resulting in larval jerking, of a species was significantly correlated with a tendency to congregate. Often in species with larvae having high jerking and congregating tendencies, grouped larvae repeatedly probed their immediate area and each other with their front legs. Species with larvae having higher mean jerking tendencies also had higher mean numbers of jerks per jerking response. There was no consistent trend among species in jerking tendencies of young, middle aged, and older larvae. Jerking appeared

to be a generalized response to any inter-individual contact, and not directed toward any specific individual. Larvae of *N. fallacis* had a higher tendency to jerk than conspecific protonymphs and deutonymphs, and had both the highest jerking and congregating tendencies among larvae of all species studied. An individual was more likely to jerk when approached by another mite than when it was the approaching member, and when observed in approaching *N. fallacis* larvae, jerking often appeared aggressive. Jerking *N. fallacis* larvae experienced fewer and shorter investigations, and fewer attacks from cannibalistic adult females than anesthetized larvae that were unable to jerk.

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Jerking Behavior Among Phytoseiid Mite Species (Acari: Phytoseiidae)

by

J. Scott Blackwood

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CONTRIBUTION OF AUTHORS

Dr. Brian A. Croft and Dr. Peter Schausberger assisted in the development of experimental designs, contributed viewpoints for the interpretation of results, and were involved in the writing of this manuscript. All work was performed in the laboratory of Dr. Brian A. Croft.

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Jerking Behavior Among Phytoseiid Mite Species (Acari: Phytoseiidae)

INTRODUCTION

Several species of phytoseiid mites are predators of phytophagous mites and insects. Many are successful biological control agents in diverse agroecosystems and serve as model animals in ecology and behavior (Walter and Proctor, 1999). Recently, considerable attention has been given to intra- and interspecific interactions among phytoseiid mites. Aspects such as cannibalism, intraguild predation, and spatial scale of aggregation were investigated (Croft and Croft, 1996; Croft *et al.*, 1996; Schausberger, 1998, 1999ab; Schausberger and Croft, 1999b, 2000a, b; Walzer and Schausberger, 1999a, b; Zhang and Croft, 1994, 1995; Zhang and Sanderson, 1993; Zhang *et al.*, 1992; Slone and Croft, 1998). Some studies reported that immature stages of several species exhibit a behavior termed “jerking” that appeared to be involved with intra- and/or interspecific interactions (Monetti and Croft, 1997b; Schausberger and Croft, 1999a; Zhang and Croft, 1995). Schausberger and Croft (1999a) described jerking as a “forward and backward lunging of the entire body without ambulatory movement” that occurred in response to contact with con- or hetero-specific individuals. These studies primarily focused on larvae, probably for several reasons: this life stage shows high variation among species in other behavioral traits such as activity, feeding, and interleaf movement (Schausberger and Croft, 1999a; Monetti and Croft, 1997b; Croft *et al.*, 1995; Zhang and Croft, 1994; Croft and Croft, 1993), and it is the life stage that is probably most susceptible to mortality due to predation (MacRae and Croft, 1993; Schausberger, 1997, 1999a; Yao and Chant, 1989; Zhang and Croft, 1995). Jerking has also been observed in

nymphs (Schausberger and Croft, 1999a). However, jerking in these life-stages has been given less attention. Despite the widespread occurrence of this behavior among phytoseiid mites, knowledge about the nature and adaptive purposes of jerking is vague and limited.

Suspected purposes for jerking have been proposed, all of which imply an intra- and/or interspecific communicative function. Proposed functions have included a signal involved in interspecific recognition (Monetti and Croft, 1997b; Zhang and Croft, 1995), a conspecific recognition signal involved in cannibalism deterrence (Zhang and Croft, 1995), a general avoidance response that might startle an intruder (Zhang and Croft, 1995; Schausberger and Croft, 1999a), and a mechanism for wafting infochemicals away from the body that may be more directly involved with intra- or interspecific communication (B.A. Croft, personal communication).

This study was initiated to investigate possible functions of jerking, and to describe the behavior and the contexts in which it occurs. We focused primarily on jerking in phytoseiid larvae, with the addition of some experiments involving protonymphs and deutonymphs of *Neoseiulus fallacis* (Garman). Tests were performed to answer the following questions: Do larvae of all species that exhibit the behavior have a similar tendency to jerk in contact situations with other individuals? Is the occurrence of jerking age-dependent within the larval stage? Does larval jerking predominantly occur in response to contact with specific individuals? In the process of investigating these aspects, observations prompted additional questions: Is jerking a type of communication that is responsive/defensive or initiative/offensive in nature? Are there relationships between jerking and any other behavioral tendencies among species? Is

jerking predominantly associated with a particular life stage(s)? Does larval jerking deter attack by cannibalistic adult females? These questions centered on possible functions of jerking, such as inter-individual spacing, energy conservation and avoidance (instead of moving away from an approaching individual), stage- or species-specific communication, mate identification, and cannibalism deterrence.

Jerking tendencies were compared among larvae of seven species of phytoseiid mites, i.e., *N. fallacis*, *Euseius finlandicus* (Oudemans), *Galendromus occidentalis* (Nesbitt), *Neoseiulus californicus* (McGregor), *Phytoseiulus macropilis* Banks, *Phytoseiulus persimilis* Athias-Henriot, and *Typhlodromus pyri* Scheuten. These species include representatives of all four life-style types as defined by McMurtry and Croft (1997) with a range of jerking tendencies (Schausberger and Croft, 1999a) and varying degrees of taxonomic relatedness. More detailed investigations were undertaken with larvae and nymphs of *N. fallacis*, a species that frequently exhibits jerking (Schausberger and Croft, 1999a).

MATERIALS AND METHODS

Phytoseiid adults were taken from laboratory-maintained colonies sustained on mixed life stages of *Tetranychus urticae* Koch prey and/or pollen of birch, *Betula pendula* Roth, and tulip *Tulipa gesnariana* L. *Tetranychus urticae* were obtained from a laboratory colony sustained on lima bean *Phaseolus lunatus* L. grown at $26 \pm 5^\circ\text{C}$, $70 \pm 10\%$ RH, 16:8h L:D photoperiod.

Immature phytoseiids used in experiments were obtained by placing 80-130 gravid adult females on either a tile or leaf arena bordered by moistened tissue paper. Excess prey and/or pollen were provided and the arena with mites was held at 20 to 25°C , 50 to 70% RH and 16:8 (L:D) photoperiod for 24 h. Eggs were collected and transferred to a separate arena until hatching.

Unless otherwise noted, all testing was performed in a standardized experimental setup, consisting of two bean leaves divided into ten 1.5cm^2 experimental chambers with strips of moist tissue paper. Five mobile immature and 20-25 eggs of *T. urticae*, and pollen when required for the species, were provided in each chamber and maintained throughout the experiments. The gender of phytoseiid subjects was not determined in experiments involving larvae and protonymphs due to an inability to differentiate at these stages. All adult and nymphal phytoseiids used were well fed prior to introductions to avoid cannibalism. Newly molted phytoseiid subjects were removed when observed.

Experiment 1. Larval Jerking and Group Formation.

For each of the seven phytoseiid species, six larvae of equal age (± 1.25 h) were placed in a standardized chamber with one conspecific adult female. Observations were made in each chamber for 4 min. every 5 h until at least three larvae molted to the protonymphal stage. This schedule, in addition to using similarly aged individuals, allowed the data to be classified according to 5h larval age classes, i.e., the average age of larvae for each observation period was classified as 0-5h, 5-10h, 10-15h, etc. This experiment was replicated 10 times for each species. The number of jerking events, the number of times larvae were touched by other individuals, the identity (stage and species) of the individuals involved in contact events, and the direction of contact (initiating or receiving) were recorded. From these data, mean jerking tendencies (proportions of contact events resulting in jerking) were calculated by taking the mean of all replicates for each species. Larval jerking tendencies among 5h age classes, contact individuals, and contact directions were calculated as the total number of jerking events over the total number of contact events for each of these categories. For ease of comparison among species having variable developmental times, jerking tendencies of 5h age classes for each species were condensed into average tendencies for young (first third of the larval stage), middle-aged (second third), and old larvae (last third) using weighted averages. Larvae of *N. fallacis* that were observed to jerk were reared to adulthood and their sex determined to test whether jerking occurs in both genders.

The number of individual “jerks” was also recorded for each jerking event. The median number of jerks per jerking event was calculated for each replicate, and the mean of all replicates was calculated to generate a mean statistic for each species. The median

statistic was used within replicates because all responses involving over 7 jerks were given the same value. This designation was necessary because some jerking events involved 30 or more jerks, particularly in species with higher jerking tendencies, which would have made simultaneous counting and observation of the other subjects by a single observer impossible.

Finally, the positions were sketched to show proximity of mites. Ambulatory activities were also recorded for each larva within each chamber prior to each observation period. We defined 'grouped' as positioned within four larval body lengths of another individual without persistent ambulatory movement. Lack of persistent ambulatory movement was used as the criterion to include larvae that were moving slightly in their immediate area, apparently probing to reconfirm the nearby presence of other individuals, but to exclude individuals that were ambulating within four larval body lengths of a conspecific by chance. The total proportion of larvae that were grouped in each age class was calculated for each species. The overall proportion that was grouped for each species was calculated by taking the mean of all replicates.

One-way analysis of variance (ANOVA) tests and multiple comparisons procedures were used to identify differences among species for mean jerking tendency, mean number of jerks per jerking response, and mean proportion grouped. Prior to all multiple comparisons, Levene's test (SPSS; Miller, 1986) for homogeneity of variance was performed to determine whether the assumption of equal variance among species was valid. When equal variance could be assumed, the LSD multiple comparisons procedure (SPSS; Sokal and Rohlf, 1995) was used to identify differences. If equal variance could not be assumed, the Games-Howell multiple comparisons procedure

(SPSS; Sokal and Rohlf, 1995) was used. This procedure is an approximate test of the equality of means using a studentized range and a standard error based on the average of the variances of the means (Sokal and Rohlf, 1995). Correlations between the mean jerking tendency and the mean number of jerks per jerking event and between the mean jerking tendency and the mean proportion of individuals that were grouped were tested among species with simple linear regressions. In all statistical tests, $p < 0.05$ was considered significant.

Experiment 2. Larvae, Protonymphs, and Eggs of *N. fallacis*: Jerking and Group Formation.

Two each of *N. fallacis* eggs, larvae, and protonymphs of similar age (± 1.25 h) were placed in a standardized chamber with one conspecific adult female. Jerking and group formation were recorded as above for both larvae and protonymphs. This experiment was replicated six times.

Experiment 3. Group Formation: Optimal Microhabitat vs. Inter-individual Attraction.

Six *N. fallacis* larvae were placed in each standardized chamber, as in experiment (1), but were then checked only once after 10-15h of age. The positions of the larvae were recorded with a sketch of their positions within the experimental chamber. The larvae were then removed and replaced with new larvae, and positions were again recorded. This was repeated in four different experimental chambers for a total of 22

trials. From these data it was possible to determine whether larvae were repeatedly forming groups in the same positions in each chamber.

Experiment 4. Jerking in Protonymphs and Deutonymphs of *N. fallacis*.

Standardized chambers were used with each of the following configurations: (a) six protonymphs (mixed age), one adult female, (b) six female deutonymphs (mixed age), one adult female, or (c) six female deutonymphs (mixed age), one adult male. Only female deutonymphs were used in part (b) because it is difficult to distinguish male deutonymphs from older protonymphs. Therefore, to be sure only deutonymphs were tested, only females (that could be identified with certainty as deutonymphs) were used. Observations were made during one 20 min. period for each of ten replicates, taken at least 30 min. after introduction to the chamber. In all configurations, all contact and jerking events were recorded as above. Phytoseiid males are known to exhibit tending behavior toward pre-reproductive deutonymphs (e.g. Monetti and Croft, 1997a). In configuration (c), deutonymphal jerking was monitored in relation to specific male tending behaviors: with the male being positioned nearby, touching, dorsal mounting, and in the mating position on the ventral side of the deutonymph. Mean jerking tendencies for the protonymphal and deutonymphal stages were calculated as the mean of all replicates in parts (a) and (b), respectively. Jerking tendencies were then compared among the life stages of *N. fallacis*, incorporating data from experiment (1), with a one-way ANOVA and LSD multiple comparisons procedure.

Experiment 5. Larval Jerking and Attack Success in *N. fallacis*.

Experimental chambers were again constructed on the ventral surface of bean leaves and bordered with moistened tissue paper. Chambers were 0.5 cm², and were exposed to 5 mobile immature *T. urticae* for approx. 6 - 8 hrs to provide some webbing. All *T. urticae* individuals were removed prior to introduction of phytoseiids. Three larvae were placed in each chamber with one conspecific adult female that had been deprived of food for 48h. Each group of three larvae was assigned to one of two treatments: anesthesia or control. Each treatment was replicated ten times.

Preliminary testing indicated that 45 sec. exposure to ethyl ether anhydrous immobilized larvae for 20-35 min. Larvae receiving the anesthesia treatment were positioned in an enclosed acrylic glass chamber with a fine screen at the bottom. Approximately 10ml of ethyl ether anhydrous was poured into a 30ml vial, and the top of the vial was secured to the bottom of the chamber for 45 sec. The vial was then removed and larvae were transferred to the experimental chamber.

Observations were taken for 30 min. in each replicate, recording each contact event between the adult female and larvae. Whether the female proceeded with investigation, attack, or piercing, and when the female and/or larva turned away were recorded for each contact event. A 'contact event' was defined as any touching between a larva and a female, 'investigation' as the probing of a larva by the female pedipalps, 'attack' as the grasping of the larva with the first and/or second pair of legs while pushing the mouthparts toward the larva, and a 'pierce' as when the female stopped moving for at least 30 sec. holding a larva to her mouthparts following an attack. In addition, duration of investigation was timed with a stopwatch and recorded, and jerking that occurred in

response to any of the female behaviors was documented with the number of jerks per event. Average length of investigations, as well as the proportions of contact events resulting in each of the female behaviors were compared between treatments using a two-sample t-test and a 2 x 2 G-test for the independence of two proportions, respectively (Sokal and Rohlf, 1995).

RESULTS

Definition Revisal.

We propose a revisal of the former definition of jerking provided by Schausberger and Croft (1999a). They defined jerking as a “repeated forward and backward lunging without changing location”. We define jerking in a less restricted manner, as a pronounced and often repeated lunging of the entire body. Rationale for this revision is provided below.

Larval Jerking: General Observations (Experiment 1).

Jerking was observed in larvae of all species except *E. finlandicus* (Table 1), and it always occurred in response to contact with a con- or heterospecific individual. An exception was with *N. fallacis*, which occasionally jerked when an individual walked nearby without direct contact, and less frequently, with no obvious stimulus. *Neoseiulus fallacis* larvae exhibited the highest jerking tendency and number of jerks per jerking event among species. In general, among the six species having jerking larvae, those with higher larval jerking tendencies also tended to jerk more repeatedly per jerking event (Table 1, Fig. 1; $R^2 = 0.853$, $p = 0.009$, 5 d.f., simple linear regression of number of jerks per jerking response on jerking tendency). Sex determination of several *N. fallacis* individuals that jerked as larvae confirmed that both genders jerk in the larval stage.

Among species having larvae that exhibited the behavior, jerking usually occurred in a forward (pronounced) and backward (retraction) direction, although sometimes

jerking was too subtle to discern a clear direction of motion. *Galendromus occidentalis* larvae were unique in direction of motion by jerking the caudal end of their bodies to the side, and it appeared that contacts made to the rear of the body were more likely to provoke the behavior in larvae of this species. With *N. fallacis* and *G. occidentalis* larvae, conspecifics often grappled with one another 1st pair of legs to 1st pair of legs, and while *N. fallacis* larvae generally jerked repeatedly in such events, *G. occidentalis* larvae usually did not.

Table 1. Larval jerking and group forming tendencies of seven phytoseiid species.

Species	Jerking Tendency ^α	Proportion Grouped ^β	Number of Jerks
<i>N. fallacis</i>	55.02% a	50.28% a	6.0 a
<i>P. macropilis</i>	40.15% ab	48.28% a	3.1 b
<i>G. occidentalis</i>	20.14% b	45.48% a	1.7 c
<i>P. persimilis</i>	15.33% bc	37.82% ab	2.7 bc
<i>N. californicus</i>	11.90% bc	36.70% ab	1.5 c
<i>T. pyri</i>	2.50% c	17.24% ab	1.0 -
<i>E. finlandicus</i>	0.00% c	15.19% b	-

^α The mean proportion of contact events with other individuals resulting in larval jerking. Values followed by the same letter within a column are not significantly different at $P<0.05$ level (ANOVA, Games-Howell test).

^β The mean proportion of larvae grouped with larval conspecifics. Values followed by the same letter within a column are not significantly different at $P<0.05$ level (ANOVA, Games-Howell test).

^λ The mean number of jerks per larval jerking event. Values followed by the same letter within a column are not significantly different at $P<0.05$ level (ANOVA, LSD).

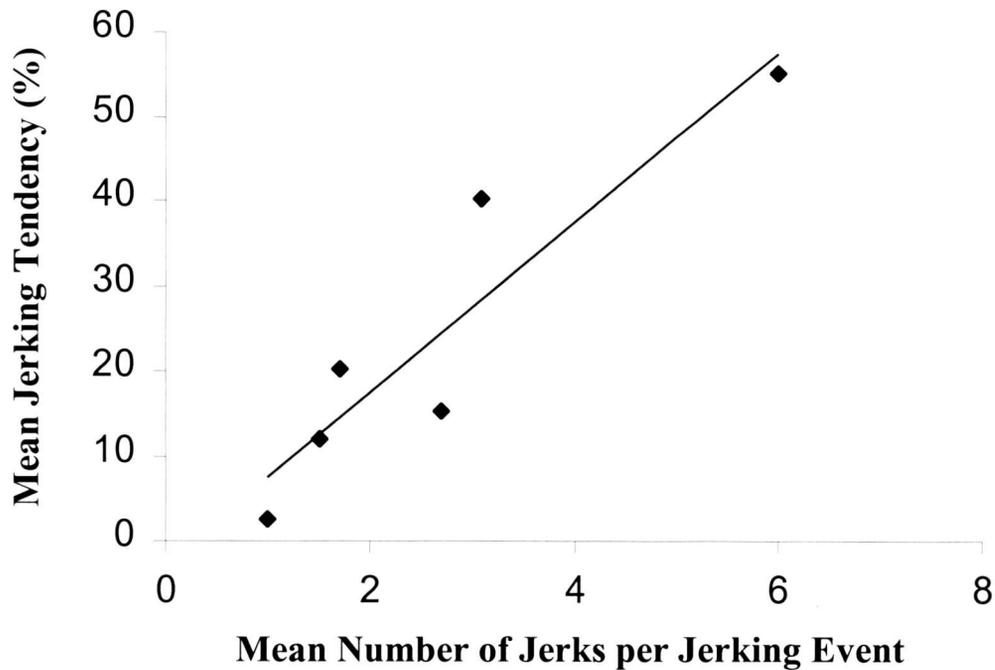


Figure 1. Simple linear regression of the mean number of jerks per larval jerking event on the mean proportion of contacts between individuals resulting in larval jerking for six phytoseiid species ($R^2=0.853$, $P=0.009$, 5 d.f.).

Larval Age, Contact Individuals, and Contact Direction (Experiments 1 and 2).

Trends of jerking with respect to larval age were variable among species, showing no consistent pattern (Fig. 2). Jerking tendencies in *N. fallacis* differed among contact events with conspecific protonymphs (experiment 2), adults, and larvae, and with mobile immature *T. urticae* (experiment 1) (Fig. 3). However, there was no evidence to suggest that larvae were predominantly jerking to any specific life stage, or that they had the ability to identify the other individual in contact events. Rather, differences among contact individuals were likely due to differences in the nature of contacts with the various individuals. In general, a more aggressive contact of longer duration was more effective in provoking a jerking response than a brief, subtle contact event. For instance,

protonymphs were relatively aggressive and persistent in contact events with larvae while well-fed adult females often only briefly and incidentally touched larvae while ambulating around the chamber.

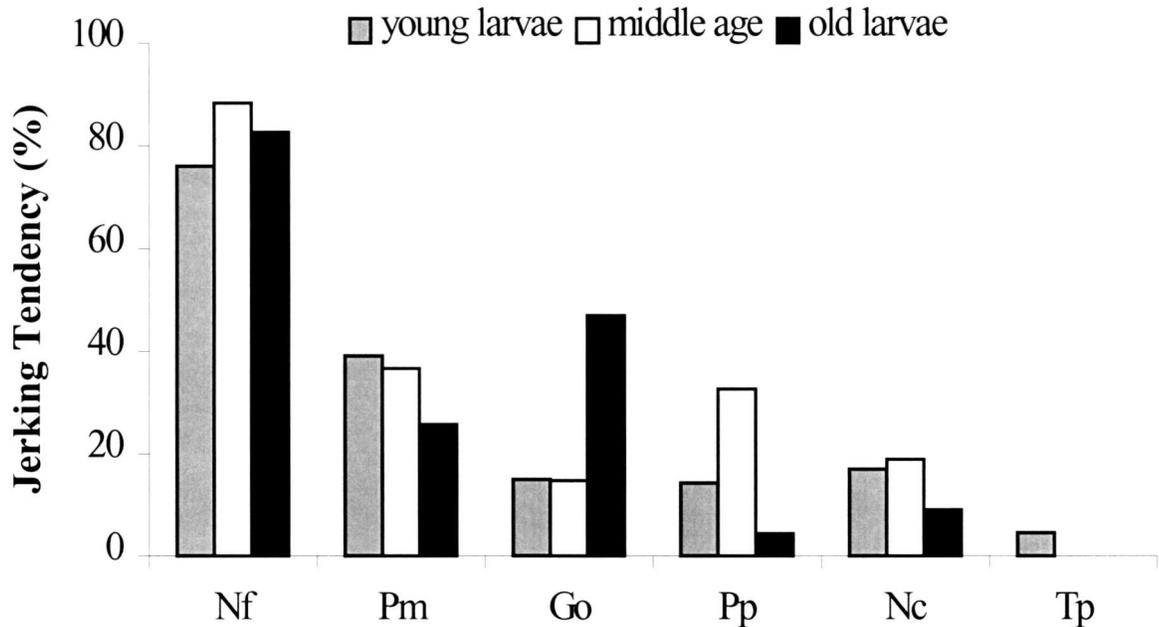


Figure 2. A comparison of the average proportion of contacts between individuals resulting in larval jerking in the first third, second third, and final third of the larval stage in six phytoseiid species.

Contact direction, or whether the larva initiated or received contact in a contact event, was influential in provoking a jerking response. Consistently among all immature stages of *N. fallacis*, jerking was less likely to occur in individuals that initiated contact and more likely to occur in approached individuals that received contact from other individuals (fig. 4). When jerking occurred in *N. fallacis* larvae that had initiated contact, jerking sometimes appeared aggressive.

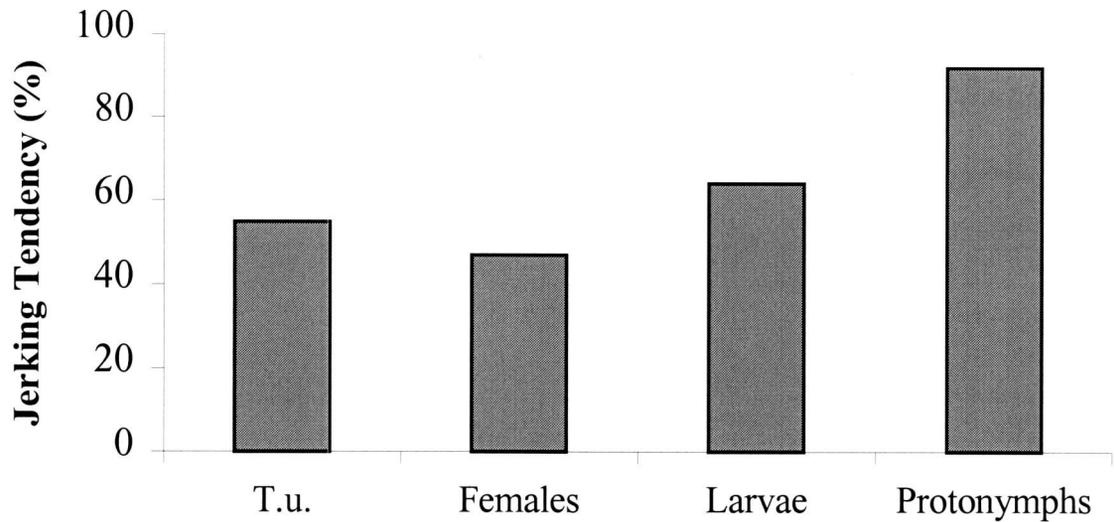


Figure 3. A comparison of the proportion of contacts resulting in jerking for *N. fallacis* larvae in contact events with mobile immature *T. urticae*, and with conspecific adult females, larvae, and protonymphs.

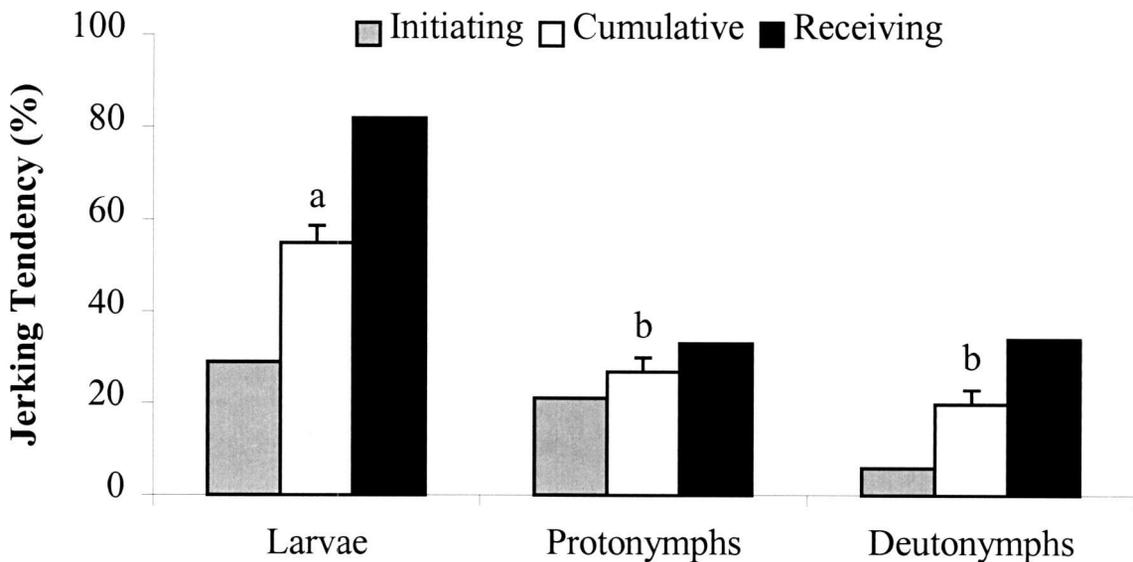


Figure 4. The mean proportion of contacts resulting in jerking for larvae, protonymphs, and deutonymphs of *N. fallacis* when initiating and receiving contact, and cumulatively (with standard errors) for each life stage. Cumulative jerking tendencies with the same letter above are not significantly different at the $P < 0.05$ level (ANOVA, LSD).

Larval Jerking and Group Formation (Experiments 1 and 2).

Larvae of species with higher jerking tendencies were more grouped on average than larvae of species with lower jerking tendencies (fig. 5; $R^2 = 0.966$, $p < 0.001$, 5 d.f., simple linear regression of the mean proportion grouped on log-scale jerking tendency for each species). However, any causal effects either of jerking on grouping or grouping on jerking could not be determined, given the observational nature of the experiment. In experiment (2), larvae also formed groups with conspecific protonymphs and eggs; 72.73% of all groups containing larvae also contained at least one protonymph, and 27.27% of all groups containing larvae contained at least one egg. In addition, adult females often oviposited near groups of immatures (in 5 out of 6 laid eggs). Detailed mapping of immature locations indicated that eggs were sometimes moved within the experimental chamber to positions near grouped immatures. In these cases, an egg appeared in a location where no egg was recorded in the previous observation. At the same time, an egg that was recorded in another location in the chamber was no longer found in that location. An alternate but less likely explanation is that one egg was consumed and another was laid between observations.

One-way ANOVA analyses and subsequent multiple comparisons procedures indicated significant differences among species with respect to jerking tendency ($F = 20.74$, $p < 0.001$, d.f. = 6, 63; Games-Howell), mean proportion grouped ($F = 5.76$, $p < 0.001$, d.f. = 6, 63; Games-Howell), and number of jerks per jerking event ($F = 20.61$, $p < 0.001$, d.f. = 4, 39; LSD) (Table 1). In the last case, larvae of *T. pyri* could not be considered in analysis because jerking occurred in only one replicate for that species.

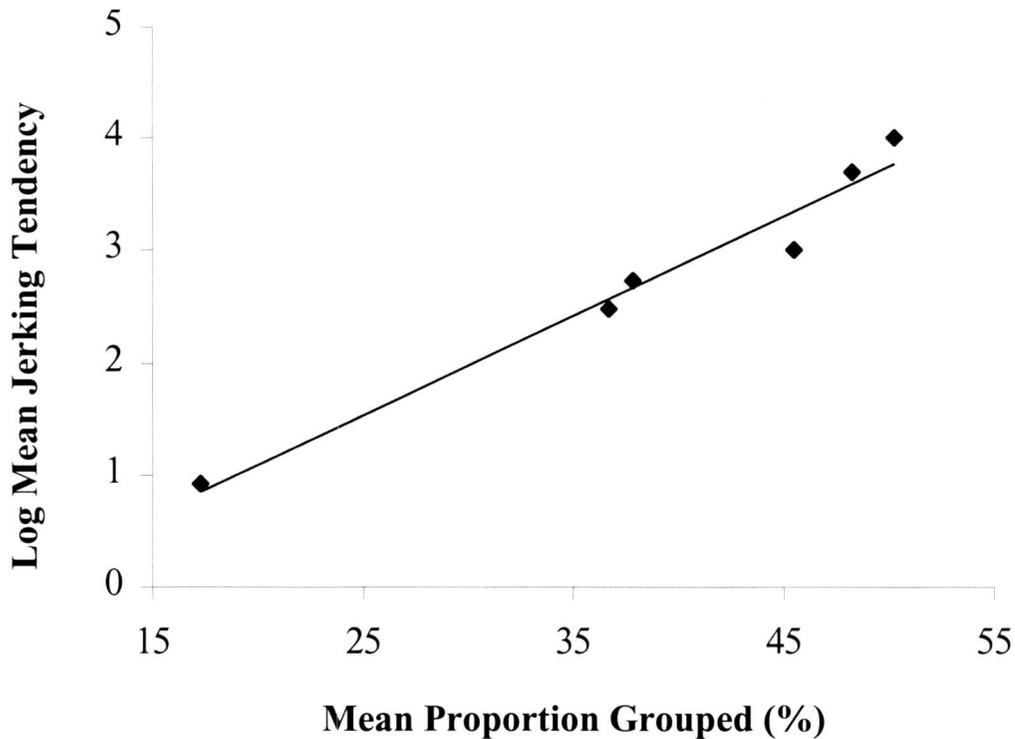


Figure 5. Simple linear regression of the mean proportion of larvae grouped with larval conspecifics on the mean proportion of contacts between individuals resulting in larval jerking (log scale) for six phytoseiid species ($R^2=0.966$, $P<0.001$, 5 d.f.).

Group Formation: Optimal Microhabitat vs. Inter-individual Attraction (Experiment 3).

Twenty-six groups of larvae formed at 25 different sites among four experimental chambers. In other words, only one larval group formed at a location that was occupied previously by a group. The positions of the groups were, however, generally located adjacent to leaf veins, indicating some microhabitat preference on individual leaves.

Jerking Among Life-stages of *N. fallacis* (Experiments 1 and 4).

Protonymphs had a slightly higher jerking tendency and more jerks per jerking event than deutonymphs, although the differences were statistically insignificant. Jerking tendencies of both of the nymphal stages (experiment 4) were significantly lower than the jerking tendency of larvae (experiment 1, $F = 30.84$, $p < 0.001$, d.f. = 2, 27; Fig. 4).

Nymphs usually jerked in a forward (pronounced) and backward (retraction) direction, although jerking was often too subtle to discern a clear direction of motion. Sometimes the pronounced motion was backward as opposed to forward, especially when contacted from the rear of the body. In other cases, jerking appeared dorso-ventral in motion.

Female deutonymphs had relatively high tendencies to jerk in contact events with adult males (experiment 4c, Table 2). In general, contacts made by males toward female deutonymphs were relatively aggressive and prolonged, which could be partly or entirely responsible for the observed high tendency. Jerking always occurred in cases where a male mounted a deutonymph dorsally and generally persisted until the male dismounted, sometimes lasting for several minutes. Mounted deutonymphs also sometimes walked slightly while jerking. In one case, before the male dismounted, a deutonymph stopped jerking after approximately 5 min. of continuous jerking by the deutonymph. This deutonymph then intermittently jerked and rested, with rest periods anywhere from several seconds to approximately 4 min. Only one jerking event occurred in the absence of immediate contact when the male was positioned nearby. In this case, the deutonymph was touched approximately 8 sec. previously by the male. Dorsal mounting occurred in 17.6 % of contact events, and of all dorsal mounting events, 18.8 % occurred in absence

of previous jerking. Males never proceeded to the mating position on the ventral side of the female deutonymph.

Table 2. The mean proportion of contacts resulting in jerking and the mean number of jerks per jerking event for female deutonymphs of *N. fallacis* responding to conspecific male tending behaviors.

Male Behavior	Mean Jerking Tendency	Mean Number of Jerks
touching	51.4%	5.9
mounting	100.0%	>7.0
mating position	n/a	n/a

Larval Jerking and Attack Success in *N. fallacis* (Experiment 5).

Anesthetized larvae that were unable to jerk experienced higher investigation rates per contact event (G_{adj} (G adjusted with Williams' Correction) = 60.00, $p < 0.001$, d.f. = 1; χ^2 distribution), longer investigation periods ($t = 2.72$, $p < 0.010$, d.f. = 12), and higher attack rates per contact event ($G_{\text{adj}} = 19.05$, $p < 0.001$, d.f. = 1; χ^2 distribution) by adult females that were starved for 48 h (Table 3). The proportion of contacts resulting in piercing was also higher in anesthetized larvae, but with only marginal statistical significance ($G_{\text{adj}} = 3.27$, $0.05 < p < 0.10$, d.f. = 1; χ^2 distribution). In untreated larvae, jerking occurred in 70.7% of all contact events, much higher than the 46.6% recorded in experiment (1) for larvae in contact events with well-fed adult females. Jerking of larvae occurred just before all cases of attack by adult females, but once attacked, jerking never occurred. This is presumably due to the grasping of the larva by the adult female, which seemed to prohibit larval jerking movements.

Table 3. The behaviors of 48h starved adult females of *N. fallacis* when provided treated (unable to jerk) or untreated conspecific larvae.

Female Behavior	Treatment		P-value
	Anesthesia	Control	
Investigation ^α	57.5%	9.8%	<< 0.01
Attack ^α	17.8%	1.7%	<< 0.01
Pierce ^α	5.5%	1.2%	0.05 < p < 0.10
Mean Investigation Time ^β	3.4s	1.5s	< 0.01

^α The proportion of contact events between larvae and adult females of *N. fallacis* resulting in different female behaviors. P-values from 2 x 2 G-tests for the independence of two percentages (Sokal and Rohlf 1995).

^β The mean time spent by adult females investigating larvae per investigation event. P-value from a one-tailed, two-sample t-test (Sokal and Rohlf 1995).

DISCUSSION

The Schausberger and Croft (1999a) definition of jerking included two restrictions that were dropped. The direction of the motions was described as “forward and backward”, but the motion of *G. occidentalis* larvae involves a pronounced and often repeated lunging of the caudal end of the body to the side. This behavior is analogous to jerking in most respects. Second, the naming of this behavior in *G. occidentalis* as a “sidekick” is misleading, since kicking implies an action of the leg and not the body. Finally, although jerking most commonly occurred in a forward and backward motion among the other species, often jerking was too subtle to discern a clear direction of motion, especially among nymphs of *N. fallacis*. In some cases, the initial and pronounced motion was backward, perhaps better described as “backward and forward”. At other times, jerking motions appeared dorso-ventral. The former definition also included the restriction that no ambulatory movement occurred during jerking. However, *N. fallacis* deutonymphs mounted by males often walked slightly while jerking continuously. For this reason, this restriction was also dropped.

With the exception of *G. occidentalis*, our results support those of Schausberger and Croft (1999a) with respect to jerking tendencies among species. Their quantification of jerking was different than in this study, they measured the proportion of larvae exhibiting the behavior at discrete points in time. However, our quantification based on the proportion of contact events resulting in the behavior placed these seven species in a similar order, with *N. fallacis* having the highest jerking tendency, followed by *P. macropilis*, and with *E. finlandicus* lacking the behavior. Our results also confirm that

jerking occurs primarily in response to physical contact with con- and heterospecific individuals. In most cases where jerking occurred in the absence of direct contact, an individual was moving nearby. We suspect that spider mite webbing on leaf surfaces propagated vibrations caused by these movements, which were sensed by larvae a short distance away. Finally, the high tendency to form groups in larvae of *N. fallacis* found in the present study concurs with the observation reported in the former study.

Our results confirm the observation of Monetti and Croft (1997b) that jerking was more common in *N. fallacis* than in *N. californicus*. This further supports the conclusion that these are separate species.

No obvious correlations with other life history characteristics described in previous studies were found that might indicate an adaptive explanation for the behavior. A lack of correlation does not necessarily mean that similar factors are not involved in producing any two trends, however, and manipulative experimental work would be required to determine causation. With these limitations in mind, correlations were looked for only to develop hypotheses. There appeared to be no relationship between larval jerking and feeding requirements (non-feeding, facultative feeding, and obligatory feeding) or ambulatory activity (Schausberger and Croft, 1999a). *Neoseiulus fallacis* larvae are facultative feeders, *P. macropilis* larvae do not feed, and *E. finlandicus* larvae are obligate feeders. The remaining species, that are intermediate in jerking tendencies, include representatives of all three larval feeding types. Similarly, ambulatory activity showed no clear correlative trend.

Jerking does not appear to be related to life-style type as defined by McMurtry and Croft (1997). They classified phytoseiid species on a continuum of feeding

specialization ranging from type I to type IV, with type I specialists as selective predators of tetranychid mites and type IV generalists as pollen specialists that are not well adapted to feeding on tetranychids. From this perspective, *N. fallacis* was considered a type II specialist, *P. macropilis* a type I specialist, and *E. finlandicus* a type IV generalist, with the remaining four species studied here representing types I-III.

Behaviors similar to jerking have been observed in other arachnids, including spiders and scorpions. In these organisms, several types of vibratory communicative behaviors have been documented, many similar in description to phytoseiid jerking. Vibratory communication plays a role in courtship and reproductive isolation in the spider families Lycosidae (Aspey, 1976; Rovner, 1975), Dipluridae (Coyle, 1986), Ctenidae (Barth, 1993; Rovner and Barth, 1981), and Salticidae (Jackson, 1983), and in the scorpion families Scorpionidae (Alexander, 1957), Buthidae (Alexander, 1959), Diplocentridae (Rosin and Shulov, 1963), and Vaejovidae (Gaffin and Brownell, 1992). These signals can be transmitted directly, or indirectly through webbing, an individual plant, or via soil substrate. In the Salticidae, males only initiate vibratory courtship in the webs of conspecific females, and do not in webs of heterospecifics, presumably responding to chemical cues in the web. In the Ctenidae, females respond with vibratory signals with clear preference to conspecific males, and generally do not respond to congeneric heterospecifics. Among the spiders, vibratory communication is also involved in predation avoidance, mother-offspring communication, male-male competition, dominance, and maintenance of personal space (see Krafft, 1982 for a review). Among the scorpions, this type of behavior occurs exclusively in adult males and is predominantly involved in courtship with adult female conspecifics. Less

frequently, diplocentrid males exhibit the behavior to immature females, other males, heterospecific scorpions, and even to prey (Rosin and Shulov, 1963; see Polis and Sissom, 1990 for a review).

Jerking and Chemical Communication.

The possibility remains that infochemical communication is associated with phytoseiid jerking. It has been shown that pheromones are involved in male tending of female deutonymphs (Rock *et al.*, 1976; Amano and Chant, 1978; Schulten, 1985), and pheromones and/or allelochemicals are suspected in con- and heterospecific prey discrimination in some species (Schausberger and Croft, 1999b). Johnstone (1997) outlined the components of an effective communicative signal as being conspicuous, stereotyped, and redundant, and having alerting mechanisms. Redundancy includes repetition and often involves multiple signals produced concurrently that may reinforce a message. Alerting mechanisms precede the rest of the signal and are highly detectable compared to the rest of the display. Jerking and/or chemical communication may play a role in some or all of these signal components. Jerking alone clearly satisfies the first three components, and may function alone as a communicative signal. However, if chemical communication is involved, the chemical message may represent the alerting component to the jerking signal. Conversely, jerking may represent the alerting component of the primary chemical signal. In the latter case, jerking may also function to waft infochemicals away from the body to the receiver. Another possibility is that chemical and jerking signals are produced concurrently to reinforce one another. Further testing is needed to uncover these potential phenomena.

Jerking in Phytoseiid Larvae.

The lack of a consistent trend among species of jerking through time in the larval stage contradicts our hypothesis that jerking serves as an alternate avoidance behavior just before molting, when energetic or physical constraints might constrain the ability to move away from an approaching individual. We initially considered this possibility because little to no ambulatory activity has been observed just prior to molting among all these species (Croft and Zhang, 1994; Schausberger and Croft, 1999a).

As previously mentioned, jerking in response to contact appears generalized, and the observed differences in jerking tendencies with different contact individuals were probably a result of the differing nature of contacts made by these different individuals. The overall higher tendency toward jerking when receiving contact as opposed to initiating contact in a contact event indicates a predominantly responsive and/or defensive nature of the behavior.

Jerking in larvae reduces the likelihood and duration of investigation by starved conspecific adult females. These results are consistent with the hypothesis that jerking may startle an intruder (Zhang and Croft, 1995; Schausberger and Croft, 1999a). Such effects may provide an adaptive benefit to the individual by reducing the probability of disease transmission. Poinar and Poinar (1998) pointed out that knowledge of diseases associated with mites is scarce, but bacteria, rickettsiae, fungi, Protozoa, viruses, and nematodes have been documented.

Larval jerking also reduces the chance of being attacked in contact events with cannibalistic adult females. Whether this is a product of species recognition and cannibalism avoidance or simply a product of a general deterrence effect of jerking

cannot be determined from these results. Future testing with heterospecific phytoseiids could reveal the mechanism behind this phenomenon. This result is consistent both with the hypothesis proposed by Zhang and Croft (1995) regarding the function of jerking in deterrence of cannibalism, and with the hypothesis that jerking may startle an intruder (Zhang and Croft, 1995; Schausberger and Croft, 1999a). In further support of these functions of jerking, Bakker and Sabelis (1989) performed a test similar to experiment (5) involving attack success of a phytoseiid predator (*Neoseiulus barkeri* Hughes) preying on thrips larvae (*Thrips tabaci* Lindeman). *Thrips tabaci* larvae exhibit an abdominal jerking behavior when threatened by an attacker. They found a significant increase in attack success of *N. barkeri* when thrips larvae were anesthetized and unable to jerk compared to when they were untreated.

The proportion of contact events resulting in piercing was not reduced in control larvae by a statistically significant margin in experiment (5). However, females attacking treated larvae appeared to have difficulty piercing due to the physical limpness and lack of resistance in these anesthetized individuals. An attacking female often pushed an anesthetized larva around the experimental chamber for an extended period, apparently lacking the resistance necessary to pierce the larva. Also, once attacked, untreated larvae were unable to jerk due to the grasping of the female. As a result, any comparison between treatments at this stage in the contact event would not show any effect of jerking.

We were concerned with possible confounding effects of the ether treatment, but several factors justified this method. First, it is unlikely that ether residues would be attractive to a predator. Since we found an increase in the probability of attack when

treated, we assume that any confounding effects involving chemical residues were minimal. A possible masking of predation deterrent pheromones by the ether raises a potential concern, however liquid ether has been used as a solvent for phytoseiid pheromones (Rock *et al.*, 1976), and therefore, this possibility seems unlikely. Another potential problem with the ether treatment is that treated larvae could not employ avoidance strategies, such as other forms of physical resistance or ambulating away, that a normal non-jerking larva could employ. However, since all individuals of *N. fallacis* have the potential to jerk, we could not simply compare jerking and non-jerking conspecifics. Also, comparing predation on larvae of different species with varying jerking tendencies was considered, but different species may be more or less attractive as prey for other reasons. Finally, there was no point in the recovery from anesthesia where larvae could walk normally while still unable to jerk. Larvae were observed to jerk in response to adult female contact as soon as they could walk. As a result, treated larvae had to be observed while totally immobilized.

Due to the ability of ether to dissolve pheromones, one possible problem is that the ether vapors may have absorbed and removed predation deterrent pheromones in treated larvae. Further testing of larvae immediately after recovery from the anesthesia could indicate whether or not this actually occurs. Assuming pheromone removal does not occur, results for recovered larvae would be similar to the results found with untreated larvae.

The results of experiment (5) indicate a reduced chance of attack on individuals that jerk when compared to non-jerking individuals of the same life-stage and species. However, previous studies on cannibalism and intraguild predation in phytoseiids provide

little evidence for reduced predation in species or life-stages with jerking larvae compared to species or life-stages with non-jerking larvae. Schausberger and Croft (2000a) found that adult females of *N. fallacis*, *N. californicus*, *T. pyri*, and *G. occidentalis*, species with jerking larvae, could discriminate con- and heterospecific larval prey and preferred the latter when given the choice. However, conspecific adult females when offered a heterospecific alternative also avoided non-jerking *E. finlandicus* larvae as prey, and no discrimination was found in *P. persimilis* or *P. macropilis*, species with jerking larvae. Croft *et al.* (1996) found that larvae of *N. fallacis* and *G. occidentalis* (with relatively strong jerking tendencies) were equally or more heavily preyed upon than larvae of *A. andersoni* and *T. pyri* (with lower jerking tendencies) (present study, Schausberger and Croft, 1999a) by adult females of all four species. Finally, *Kampimodromus aberrans* has been observed to frequently jerk as protonymphs but not as larvae (Schausberger and Croft, 1999a). Adult female *K. aberrans* discriminate between both larval and protonymphal con- and heterospecifics and prefer heterospecifics as prey (Schausberger, 1999b).

These patterns of discrimination abilities among species indicate that jerking is not required for species discrimination and that a high jerking tendency may not necessarily confer a survival advantage to an individual of a species when compared to an individual of a species with a lower tendency. However, these conclusions are limited in that they are drawn from observational trends. Not all traits of organisms are necessarily adaptive (Gould and Lewontin, 1979); for example, in *Phytoseiulus* species jerking may be vestigial. An investigation of systematic relationships within the Phytoseiidae could indicate possible evolutionary patterns in jerking among species. Another possibility is

that in *Phytoseiulus* species jerking may only effectively deter predation by other conspecific immatures. *Kampimodromus aberrans* may employ alternate predation avoidance behaviors as larvae and as protonymphs. Larvae of this species, that do not have to feed, are relatively inactive and often rest near structure (Schausberger and Croft, 1999a), possibly to hide from potential predators. Conversely, protonymphs must forage to survive (Schausberger, 1999a) and may then benefit from an alternate avoidance strategy such as jerking. Manipulative testing in these species could investigate such possibilities. Also, other factors are certainly involved in these trends, such as differences among species and among life-stages within species in pheromonal and/or allelochemical signals and in nutritional quality to the predator. Schausberger and Croft (2000b) found that generalists (that mostly discriminate between con- and heterospecific prey) received equal or greater nutritional benefits by preying upon heterospecifics vs. preying upon conspecifics, while specialists (that mostly do not discriminate between con- and heterospecific prey) received equal or greater nutrition by preying on conspecifics vs. preying on heterospecifics.

Jerking and Group Formation.

Turchin (1998) described two types of group forming behavior: aggregation and congregation. 'Aggregation' was defined as group formation where individuals are attracted to particular sites due to resource availability and/or microhabitat.

'Congregation' was defined as a type of aggregation that occurs as a result of behavioral responses to conspecific individuals, where individuals presumably derive some benefit

from the group association. Accordingly, the group formation of *N. fallacis* should be termed 'congregation'.

Potential adaptive advantages of group association have been investigated. Hamilton (1971), using a model of predator and prey behavior, determined that grouped individuals were more likely to avoid a predator, and that such avoidance could lead to evolution of group forming. Also, Brock and Riffenburg (1960) showed geometrically that the frequency of detection of prey by a predator reduces as an inverse function of the number of grouped prey. They also noted that nearly all species of fish that school are prey for a substantial portion of their life history, whereas non-schooling fish are generally climax species at the end of the food chain. Likewise, immature phytoseiids are highly susceptible to cannibalism and intraguild predation (e.g. Zhang and Croft, 1994, 1995). The exact cause of association between congregating and jerking among phytoseiids cannot be determined from these observational results. However, we propose two possibilities. First, jerking and congregation in concert may represent one of several possible strategies in predator avoidance. Congregation may decrease the likelihood of confrontation between a larva and a potential predator (Hamilton, 1971; Brock and Riffenburg, 1960). When confronted, jerking may deter a predator, even if only briefly, from proceeding with investigation or attack. If the predator returns to the location of this potential prey and other congregated individuals, chances are that the next confrontation will be with a different individual, yielding adaptive benefits for individuals that can momentarily deter a predator. Second, jerking may occur in congregative species only as a means to maintain personal space in commonly grouped individuals.

It is possible that species that do not jerk and congregate employ alternate strategies for predator avoidance, such as having fast ambulatory abilities or seeking cover. Non-jerking *Euseius* species, such as *E. finlandicus* and *E. hibisci*, have larvae that are very mobile and can ambulate considerably faster than other species (Schausberger and Croft, 1999a; Schausberger, 1997) which may preclude a need for other avoidance strategies. *Typhlodromus pyri* and *K. aberrans* that have larvae that do not jerk or that rarely jerk often seek physical structure and remain relatively inactive (Schausberger and Croft, 1999a; Croft and Croft, 1993). These characteristics, together with relatively small body size and the lack of a necessity to forage and feed in these species, may allow larvae to remain cryptic and thus minimize predator encounters (Croft *et al.*, 1999).

It has been documented that many phytoseiid species cluster their eggs (Zhang and Croft, 1995; Sabelis and Nagelkerke, 1988). The results of experiment (2) indicate that at least in *N. fallacis*, eggs may be preferentially laid and/or moved near conspecific immatures. Further study is needed to confirm that adult females move eggs, and to determine whether such clustering tendencies vary among species, possibly in a similar trend to the congregative tendencies of larvae. Also, discrimination in choosing oviposition sites based on the presence of con- and heterospecific immatures, and based on kin and non-kin relationships could be tested.

Jerking and Life-stages.

Jerking tendencies decrease through the active stages of *N. fallacis* development. Since larvae are likely the most susceptible stage to predation (MacRae and Croft, 1993;

Schausberger, 1997, 1999a; Yao and Chant, 1989; Zhang and Croft, 1995), this trend supports the notion that jerking may be primarily involved in predation deterrence.

Although deutonymphs had a relatively high tendency to jerk in contact events with adult males (comparable to the larval tendency), this could have been a consequence of the aggressive and persistent nature of contacts made by males toward female deutonymphs.

Whether this attraction to deutonymphs occurred in response to jerking in concert with pheromones, or in response to pheromones alone is unknown. Whether or not jerking is involved with pheromones in species recognition of females by males, signal recognition templates (for either type of signal) are at best poorly developed, at least in males of *N. fallacis* and *N. californicus*. In contrast with the keen species identification ability of some spiders (Barth, 1993; Jackson, 1983; Rovner and Barth, 1981), Monetti and Croft (1997b) found that males of these two phytoseiid species tend and mate freely with females of both species. Males of these and other phytoseiid species have even been observed to tend and mount protonymphal female and adult male conspecifics (personal observations).

Jerking has also been observed, although rarely, in adult female phytoseiids. Jerking was observed in the present study in one *P. macropilis* female, and on a few occasions in a species not included in this study, *Neoseiulus cucumeris* (Oudemans). Observations of jerking in *N. cucumeris* females were provoked by adult female conspecifics that were grouped close together and occasionally investigating each other with their mouthparts (personal observations). In the *P. macropilis* female, jerking occurred in response to contact made by an immature *T. urticae*. Jerking was not observed in adult males in this study.

The predominant appearance of jerking in sexually immature stages suggests another possible function: to signal to approaching males that successful mating cannot yet occur. In our observations, males never proceeded to the ventral mating position on jerking deutonymphs. Further observation is necessary to confirm this, and to determine the degree to which jerking occurs in sexually mature females prior to and after mating. Adult females of some phytoseiid species require multiple matings to maximize egg production while in other species one mating is sufficient (Schulten, 1985). Whether jerking in adult females corresponds to species-specific benefits involved with multiple matings also requires further investigation.

CONCLUSIONS

Our results indicate that the jerking behavior of phytoseiid mites may serve an avoidance function in response to contact with con- and hetero-specific individuals. Especially when combined with a tendency to congregate with conspecifics, deterrence of potential predators would have a significant impact on the ability of an individual to survive to adulthood, particularly in situations where non-phytoseiid food supplies have been depleted. It is as yet inconclusive whether jerking plays a role in pre-mating courtship and reproductive isolation. Further testing is needed to elucidate the possible connection between jerking and chemical communication, and the connection between jerking and congregation, to determine whether jerking reduces the attack success of heterospecific predators, and to further examine the potential role of jerking in phytoseiid courtship.

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