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Predatory behaviors of *Neoseiulus californicus* and *Galendromus helveolus* (Acari: Phytoseiidae) attacking *Oligonychus perseae* (Acari: Tetranychidae)

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Abstract. Predatory behaviors of *Neoseiulus californicus* (McGregor) and *Galendromus helveolus* (Chant) attacking *Oligonychus perseae* Tuttle, Baker and Abbatiello on avocado leaves were videotaped and analyzed. Behaviors were recorded for "fresh" predators that were used $\leqslant$ 48 hr post receipt from a commercial insectary and "cold stored" predators that were maintained at 12°C for $\approx$ 14 days. Fresh and cold stored *G. helveolus* were observed to attack *O. perseae* only after invading webbed nests. Conversely, fresh and cold stored *N. californicus* employed three different modes of predatory attack: (1) intercepting and attacking migrant *O. perseae* outside of web nests; (2) attacking prey through nest webbing; or (3) invading and attacking *O. perseae* inside nests. Predatory efficacy of both *N. californicus* and *G. helveolus* was reduced following cold storage, as both species engaged in certain predatory behaviors less frequently in comparison to predators that were not stored at low temperatures. Our observed results for *N. californicus* and *G. helveolus* attacking *O. perseae* are interpreted in relation to the chaetotaxy hypothesis, which proposes that phytoseiid invasion efficiency and propensity of webbed nests is facilitated by dorsal setal lengths.

Introduction

Oligonychus perseae Tuttle, Baker and Abbatiello (Acari: Tetranychidae), first appeared in southern California, USA in 1990 (Bender 1993). This tetranychid pest feeds on the undersides of avocado leaves (*Persea americana* Miller), causing necrotic spots that are concentrated along midribs and veins (Aponte and McMurtry 1997). *Oligonychus perseae* adults aggregate and lay eggs within circular webbed nests (web nest subtype 'c' [Saitô (1983)]), which can provide protection against natural enemies, including phytoseiids that are hindered by webbing when attacking mites within nests. High densities of *O. perseae* (>500 mites per leaf) can cause defoliation and ensuing "flush" following leaf drop can provide ideal nutritive and oviposition resources for other pest species, such as *Scirtothrips perseae* Nakahara (Thysanoptera: Thripidae) (Hoddle et al. 1999). Defoliation also increases risk of sunburn to trees whose trunks and fruit are exposed after canopy thinning, and this damage can promote premature fruit drop and subsequent economic losses (Bender 1993).

Augmentative releases of both *G. helveolus* and *N. californicus* have demonstrated their potential to establish predators on avocado trees and control *O. perseae* in southern California ((Hoddle et al. 1999; Kerguelen and Hoddle 1999; Hoddle et al. 2000, unpubl. data)). However, the predatory behavior of *G. helveolus* and *N. californicus* towards *O. perseae* has not been investigated and analysis of the foraging behavior of these phytoseiids could significantly enhance our understanding of how these predators operate in the field.

Past behavioral studies have observed that tetranychid webs hinder some phytoseiid predators but not others (McMurtry et al. 1970; McMurtry 1982; Sabelis 1985). Varying attack rates by different species of phytoseiid towards nest dwelling tetranychids provided the foundation for the “chaetotaxy hypothesis” (Sabelis and Bakker 1992), which proposes that dorsal chaetotaxy is an indicator of how likely phytoseiids are to successfully invade tetranychid nests when foraging. Sabelis and Bakker (1992) proposed that the degree to which the phytoseiid is “protected” from webbing is a function of setal lengths on the middorsal and marginodorsal regions of the soma. The higher the protection index, the less hindered the phytoseiid will be by webbing as setae will hold webbing off the predator’s body, allowing it to invade tetranychid nests more readily. Theoretically, the most effective natural enemies of web nest inhabiting tetranychids will have the highest setal protection indices and effective control of these pests by phytoseiids with high dorsal indices should result because of successful nest invasion. While the setal protection indices for *N. californicus* and *G. helveolus* place them in the “no hinder” category (Sabelis and Bakker 1992), the lower setal protection index (SPI) values for *N. californicus* (middorsal protection index [MDPI] = 59; marginodorsal protection index [MGPI] = 78) suggest this species may be adversely affected to a greater extent by tetranychid webbing than *G. helveolus* (MDPI = 99; MGPI = 99).

Field trials have shown that *N. californicus* and *G. helveolus* both provide equal control of *O. perseae* on avocados in southern California and significantly reduced densities of this pest in comparison to untreated trees and trees sprayed with insecticides (Kerguelen and Hoddle 1999). *Neoseiulus californicus* is currently being recommended for use by growers because it is cheaper to purchase than *G. helveolus* (Hoddle et al. 2000, unpubl. data) and a mechanical dispenser has been developed to spray predators onto trees (Takano-Lee and Hoddle 2001). During the analysis of field samples taken from trees used in the above studies, we noticed that *G. helveolus* was invariably found inside *O. perseae* nests while *N. californicus* was most commonly found on leaves outside of nests (Hoddle, unpubl. data). The purpose of the work presented here was to quantify the predatory behavior of *N. californicus* and *G. helveolus* and to interpret field observations from biological control studies in terms of the setal protection hypothesis. We also sought to determine if predation behaviors and rates by *N. californicus* and *G. helveolus* were affected by long-term cool storage in comparison to predators that were not stored for long periods at low temperatures.

Materials and Methods

Source of phytoseiid predators and O. perseae

Neoseiulus californicus and *G. helveolus* were obtained from a commercial insectary (Biotactics, Perris California, USA). Phytoseiids were received in 45 ml plastic vials with enough *Tetranychus pacificus* McGregor (Acari: Tetranychidae) eggs to sustain predators for at least two days, and corn grits as a carrier to aid in the even dispersal of predators upon release. Phytoseiids were stored on ice packs and tested as either "fresh" (used within 2–3 days of receipt from the insectary) or "cold stored" (maintained in a cooler for approximately 14 days prior to behavioral analyses). Prior to testing, predators were removed from vials in which they were packaged and starved for 40–48 h. All predators were maintained at cool temperatures on ice packs in a cooler (12.4 ± 4.1 °C; 52.1 ± 9.0 % RH) except when videotaped. According to Auger et al. (1999), *N. californicus* movement should only be induced at temperatures greater than 12.7 °C. *Oligonychus perseae* infesting 'Hass' avocado leaves were obtained from a commercial orchard in Bonsall California, USA, and were the source of prey presented to predators in this study.

Filming predators searching in artificial arenas

Foraging activities of starved predators searching avocado leaves infested with *O. perseae* were videotaped. A video camera MTV-7366 (ScienceScope, Chino California, USA) was mounted on a dissecting microscope (Leica MZ12, Wetzler Germany). Adult phytoseiids were individually placed on avocado leaf arenas (2.0-cm diameter) containing motile *O. perseae* (3–18 [for fresh predators]; 2–21 [for cold stored predators]) and eggs (6–46 [for fresh predators]; 4–39 [for cold stored predators]). Leaf arenas with *O. perseae* were maintained on water-saturated foam pads in stainless steel pans at 25°C under long days (L:D 14:10) until use in videotaped behavior studies 7 days post set up. During this time period, *O. perseae* motile stages constructed web nests on individual leaf arenas and laid eggs within nests. At the time of videotaping of predator activity, each leaf arena had occupied webbed nests (2–13 [for fresh predators]; 3–22 [for cold stored predators]) containing eggs and motiles. Leaf arenas were peripherally ringed with Tanglefoot® (The Tanglefoot Company, Grand Rapids Michigan, USA) to prevent the escape of predators from leaf discs onto water-saturated foam pads. Predatory behavior of twelve "fresh" and twelve "cold stored" adult *N. californicus* and *G. helveolus* were videotaped. Observations and video recording of predatory behavior began immediately upon the introduction of a predator into the leaf arena containing *O. perseae* and foraging phytoseiids were videotaped for 60 min. If predators were engaged in prey attack at 60 min, then additional taping ensued until the attack behavior had been completed. Videotaped behaviors were categorized and time in behavior categories was quantified in seconds.

Behavioral categories and data analysis

Preliminary observations indicated three primary modes of predatory attack by *N. californicus*. The first attack mode of "patrolling" (PG) was characterized by the attack of migrant *O. perseae* outside of web nests. The second method of attack, "nest penetration" (NP), was the attack and consumption of prey directly through webbing. The third mode of attack, "nest invasion" (NI), was forced entry into webbed nests through marginal edges followed by attack and consumption of *O. perseae* inside nests. *Galendromus helveolus* was observed to only engage in NI. A combined total of seven behavioral categories were observed for the two phytoseiid species, these being: (1) inspection (use of prolegs to investigate encountered items such as *O. perseae* motile stages, eggs, exuviae, etc.); (2) searching (walking about the leaf arena); (3) patrolling (attack behavior one); (4) nest penetration (attack behavior two); (5) nest invasion (attack behavior three); (6) grooming (use of prolegs to clean body while predator was stationary); and (7) resting (predator standing motionless).

A time budget was constructed from videotaped behaviors using the mean proportion of time spent by fresh and cold stored *G. helveolus* and *N. californicus* in each behavioral category. Predators were compared (by species and storage conditions) with respect to mean duration of a behavior and the mean proportion of time [arcsine (square-root) transformation] spent engaged within each behavioral category. Data were analyzed with a two-way ANOVA for species and storage effects at 0.05 level of significance, as well as interaction effects. Tukey's Studentized Range test was used for means separation at the 0.05 level.

Prey consumption

The number of eggs and motiles consumed by each phytoseiid species in each storage category was recorded and expressed as a proportion of the total. These data were arcsine (square-root) transformed before analysis with two-way ANOVA (species x storage category) at 0.05 level of significance. Mean time to consume *O. perseae* prey was also calculated and analyzed by a two-way ANOVA. Intraspecific differences for motile versus egg consumption rates of *O. perseae* were determined with Studentized t-tests at the 0.05 level of significance.

Ethogram construction

Behavioral pathways for fresh and cold stored *N. californicus* and *G. helveolus* were constructed by calculating the frequency and directional path of each observed behavior in general order of occurrence. Behaviors occurring less than 10 times in frequency were omitted from the ethogram, unless they occurred immediately prior to or after an attack behavior.

Table 1. Modes of phytoseiid predator attack.

Storage Treatment	Species	Attack Mode	Percentage Engaging in Activity	n =
Fresh	*Galendromus helveolus*	NI	100%	12
	Neoseiulus californicus	NI	17%	2
	Neoseiulus californicus	NI + PG	8.33%	1
	Neoseiulus californicus	NP	8.33%	1
	Neoseiulus californicus	NP + PG	8.33%	1
	Neoseiulus californicus	PG	58%	7
Cold storage	*Galendromus helveolus*	NI	100%	12
	Neoseiulus californicus	NI	25%	3
	Neoseiulus californicus	NI + NP	17%	2
	Neoseiulus californicus	NP	8%	1
	Neoseiulus californicus	NP + PG	8%	1
	Neoseiulus californicus	PG	42%	5

PG = Patrolling; NP = Nest Penetration; NI = Nest Invasion

Results

In all videotaped events, every observed fresh and cold stored *G. helveolus* (n = 24) attacked and consumed prey after entering nests (i.e., nest invasion). Fresh and stored *N. californicus* (n = 24) demonstrated all three predatory attack behaviors. For fresh *N. californicus*, NI, NP, and PG were recorded with 17% (n = 2), 8.3%, (n = 1) and 58% (n = 7) frequency, respectively, for predators exhibiting single attack behaviors. Multiple attack behaviors were utilized by two fresh *N. californicus*, combining either NI+P, or NP+P (Table 1). Cold stored *N. californicus* exhibited NI, NP, and PG attacks 25% (n = 3), 8% (n = 1), and 42% (n = 5) of the time, respectively for predators exhibiting single attack behaviors. Multiple attack behaviors NI+NP and NP+PG were exhibited in 17% (n = 2) and 8% (n = 1) of recorded attacks by cold stored *N. californicus* (Table 1).

Table 2. Time budgets and durations of behaviors (±SEM) exhibited by N. californicus and G. helveolus before transformation. Letters denote group (species and storage conditions) differences ($p < 0.05$), as analyzed by a two-way ANOVA and means separation test. Numbers in parentheses denote total frequency of occurrence within the behavioral category. I = inspection, S = searching, PG = patrolling, NP = nest penetration, NI = nest invasion, G = grooming, and R = resting

	Neoseiulus californicus		*Galendromus helveolus*	
Behavior	FRESH (n = 12) Proportion	COLD (n = 12) Proportion	FRESH (n = 12) Proportion	COLD (n = 12) Proportion
I	0.02 ± 0.01^{a}	0.02 ± 0.01^{a}	0.02 ± 0.00^{a}	0.01 ± 0.00^{a}
S	0.57 ± 0.03^{a}	0.40 ± 0.04^{b}	0.23 ± 0.05^{c}	0.19 ± 0.03^{c}
PG	0.07 ± 0.02	0.15 ± 0.06	N/A	N/A
NP	0.01 ± 0.00	0.08 ± 0.05	N/A	N/A
NI	0.11 ± 0.05^{a}	0.11 ± 0.05^{a}	0.21 ± 0.04^{b}	0.23 ± 0.03^{ab}
G	0.18 ± 0.03^{a}	0.21 ± 0.03^{a}	0.12 ± 0.02^{a}	0.14 ± 0.02^{a}
R	0.04 ± 0.02^{a}	0.03 ± 0.01^{a}	0.43 ± 0.07^{b}	0.42 ± 0.04^{b}

	Neoseiulus californicus		*Galendromus helveolus*	
Behavior	FRESH Time (sec)	COLD Time (sec)	FRESH Time (sec)	COLD Time (sec)
I	12.11 ± 4.02^{a} (76)	11.71 ± 2.00^{a} (177)	6.01 ± 0.71^{a} (107)	7.05 ± 1.44^{a} (81)
S	24.12 ± 1.19^{a} (1028)	30.97 ± 7.31^{a} (749)	16.97 ± 0.88^{b} (601)	22.13 ± 27.40^{ab} (380)
PG	222.57 ± 56.40 (14)	667.40 ± 214.13 (10)	N/A	N/A
NP	125.00 ± 26.00 (2)	691.40 ± 425.07 (5)	N/A	N/A
NI	95.49 ± 29.86^{a} (49)	105.98 ± 32.03^{a} (48)	69.46 ± 9.40^{a} (130)	97.01 ± 20.93^{a} (104)
G	26.36 ± 1.99^{a} (293)	47.46 ± 5.29^{b} (199)	25.95 ± 1.81^{a} (206)	31.91 ± 3.24^{a} (191)
R	39.52 ± 6.07^{a} (44)	109.53 ± 14.68^{a} (45)	110.43 ± 18.05^{a} (167)	109.53 ± 14.68^{a} (168)

Behavior of fresh and cold stored Neoseiulus californicus.

Fresh and cold stored *N. californicus* spent the greatest proportion (± SEM) of their time searching at 57.2 ± 3.4% and 39.6 ± 4.3%, respectively. Grooming activity also occupied a large proportion of time for both fresh and cold stored *N. californicus* at 17.8 ± 2.8% and 21.1 ± 3.0%, respectively. Searching behavior occurred significantly more frequently than all other activities for fresh *N. californicus,*(F = 34.62, df = 6, 77, $p < 0.005$); similarly, searching activities significantly dominated the behaviors of cold stored *N. californicus*, except grooming (F = 10.75, df = 6, 77, $p < 0.005$). Compared to fresh *N. californicus*, cold stored *N. californicus* engaged more frequently in inspection behavior, but less frequently in searching, patrolling, and grooming activity (Table 2).

Behavior of fresh and cold stored Galendromus helveolus.

Resting activities for fresh and cold stored *G. helveolus* dominated recorded behaviors at 42.5 ± 7.3% and 42.1 ± 4.2%, respectively, followed by searching at 23.3 ± 4.8% and 19.3 ± 2.6%, respectively, and nest invasion at 20.6 ± 3.7% and 23.3 ± 2.9%, respectively (Table 2). The proportion of time spent invading nests was significantly less than the proportion of time resting for both fresh and cold stored *G. helveolus* (F = 15.29, df = 4, 55, $p < 0.005$) (Table 2).

Interspecific behavioral comparisons

(1) *Inspection*. There were no significant differences for proportion of time engaged in inspection between *N. californicus* and *G. helveolus* and storage conditions, although the mean duration of time per inspection was $\approx$ 2x higher for fresh and cold stored *N. californicus* in comparison to *G. helveolus* (Table 2).

(2) *Searching*. Both a species effect (F = 47.10, df = 1, 44, $p < 0.005$) and storage effect (F = 6.43, df = 1, 44, $p = 0.015$) on proportion of time spent searching existed (Table 2). Searching times for fresh *N. californicus* were significantly greater than cold stored *N. californicus*, and fresh and cold stored *G. helveolus*. The mean proportion of time spent by cold stored *N. californicus* was also significantly different from either fresh or cold stored *G. helveolus*. There was both a species effect (F = 9.39, df = 1, 44, $p = 0.002$) and species∗storage interaction effect (F = 4.89, df = 1, 44, $p = 0.027$) for the mean duration of time spent searching (Table 2). Both fresh and cold stored *N. californicus* spent significantly longer periods of time searching than fresh *G. helveolus*.

(3) *Nest invasion*. Only a species effect (F = 14.66, df = 1, 44, $p < 0.005$) was observed. Cold stored *G. helveolus* spent significantly more time invading nests than fresh *N. californicus* or cold stored *N. californicus*.

(4) *Grooming*. A species effect (F = 6.44, df = 1, 44, $p = 0.015$), was observed, but no separation of means resulted. However, with regards to mean duration of time, there was both a species effect (F = 5.52, df = 1, 44, $p = 0.019$), and storage effect (F = 15.83, df = 1, 44, $p < 0.005$). Cold stored *N. californicus* groomed for significantly longer periods of time than fresh *N. californicus*, fresh *G. helveolus*, and cold stored *G. helveolus* (Table 2).

(5) *Resting*. There was a significant species effect for times spent resting (F = 93.80, df = 1, 44, $p < 0.005$). Both fresh and cold stored *N. californicus* rested for significantly smaller proportions of time than either fresh or cold stored *G. helveolus* (Table 2).

Prey consumption

Comparison of egg and motile consumption exhibited a species effect (F = 4.88, df = 1, 44, $p = 0.032$) and storage effect (F = 6.47, df = 1, 44, $p = 0.015$). Fresh *G. helveolus* consumed a significantly greater proportion of eggs and motiles than cold stored *N. californicus* (Table 3a). Fresh and cold stored *G. helveolus* and fresh *N.*

Table 3a. Prey consumption preferences (±SEM) by fresh and cold stored *Neoseiulus californicus* and *Galendromus helveolus* within a 60 min period [data before transformation]. Letters denote intergroup (species and storage conditions) differences ($p < 0.05$), as analyzed by a two-way ANOVA and means separation test. Numbers within parentheses denote total numbers of eggs or motiles consumed.

	Neoseiulus californicus		*Galendromus helveolus*	
	Fresh (n = 12)	Cold Stored (n = 12)	Fresh (n = 12)	Cold Stored (n = 12)
Eggs	0.625 ± 0.125^{ab} (13)	0.292 ± 0.130^{b} (10)	0.889 ± 0.085^{a} (28)	0.583 ± 0.149^{ab} (18)
Motiles	0.375 ± 0.125^{ab} (6)	0.708 ± 0.130^{b} (13)	0.111 ± 0.085^{a} (3)	0.417 ± 0.149^{ab} (7)

Table 3b. Prey consumption times (±SEM) (sec) by fresh and cold stored *Neoseiulus californicus* and *Galendromus helveolus* within a 60 min period. Letters denote intergroup (species and storage conditions) differences ($p < 0.05$), as analyzed by a two-way ANOVA and means separation test.

	Neoseiulus californicus		*Galendromus helveolus*	
	Fresh	Cold Stored	Fresh	Cold Stored
Eggs	239.62 ± 44.79^{a}	184.20 ± 34.61^{a}	169.86 ± 22.87^{a}	195.11 ± 25.86^{a}
Motiles	623.67 ± 131.41^{b}	898.77 ± 188.42^{b}	536.67 ± 126.42^{b}	558.71 ± 177.49^{b}

californicus displayed a preference for consuming *O. perseae* eggs over motiles. The most distinct prey preference was exhibited by fresh *G. helveolus*, which attacked eggs instead of motiles, 89% of the time.

There were no significant differences between *N. californicus* and *G. helveolus* prey consumption times for either eggs or motiles (F = 0.82, df = 1, 65, $p = 0.37$ and F = 0.41, df = 1, 25, $p = 0.53$, respectively) or by storage condition (F = 0.22, df = 1, 65, $p = 0.64$ and F = 0.85, df = 1, 25, $p = 0.37$) (Table 3b). There was no significant level of species∗storage interaction for either eggs or motiles (F = 1.54, df = 1, 65, $p = 0.22$ and F = 0.30, df = 1, 25, $p = 0.59$; respectively). Consumption of motiles required a significantly longer period of time than consumption of eggs for fresh *G. helveolus* (t = −4.64, df = 29, $p < 0.005$), fresh *N. californicus* (t = −2.77, df = 17, $p = 0.03$), and cold stored *N. californicus* (t = −3.73, df = 21, $p = 0.003$). A difference was not observed for mean egg and motile consumption times by cold stored *G. helveolus* (t = −2.03, df = 23, $p = 0.09$) (Table 3b).

Ethogram construction

Behavioral pathways for both fresh and cold stored *N. californicus* (Figure 1) were initiated by searching. Searching by fresh *N. californicus* was interrupted by grooming (72.8%), inspection (17.3%), nest invasion (6.6%), or resting (3.3%). Inspection tended to lead to prey attack 48.8% of the time. The remaining 51.2% of behaviors originated as a searching behavior that only led to nest invasion. The ethogram of cold stored *N. californicus* was similar to that of fresh predators, with

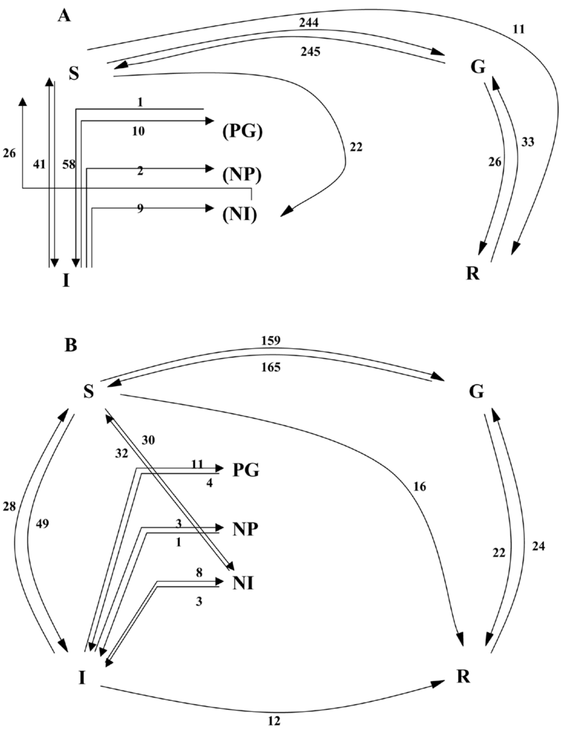

Figure 1. Ethogram of fresh (A) and cold stored (B) *Neoseiulus californicus*; I = inspection, S = searching, NI = nest invasion, G = grooming, and R = resting. Numbers on figure indicate frequency of occurrence. Behaviors occurring less than 10 times were omitted.

over 50% of inspection behaviors leading to predatory attack. Searching behavior was most commonly interrupted by grooming activity (63%).

For *G. helveolus*, searching initiated behavioral pathways for fresh and cold stored predators (Figure 2). Searching behavior of fresh *G. helveolus* was interrupted most commonly by inspection (34%), nest invasion (33%), or grooming (33%). Nest invasion attacks were most commonly initiated by searching behavior (71%) or by inspection (29%). Behavior of cold stored *G. helveolus* was similar to that of fresh *G. helveolus* and searching behavior was commonly interrupted by inspection (25%), nest invasion (24%), grooming (28%), or resting (22%).

Discussion

The predatory behaviors of fresh and cold stored *N. californicus* and *G. helveolus* differed significantly. The tri-modal predatory attack behaviors (prey were attacked outside of nests, through walls of nests, and after nests were invaded) demonstrated by *N. californicus* indicated that this phytoseiid will attack tetranychid prey inside and outside of protective webbed nests. These behaviors can be explained in terms

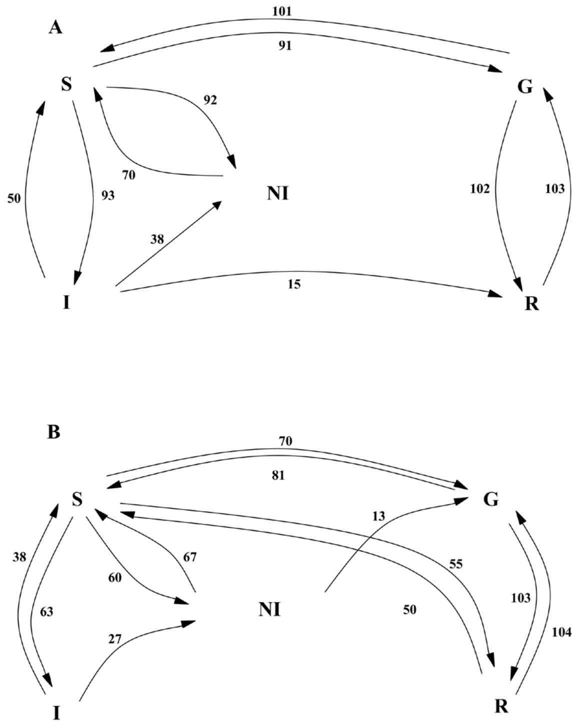

Figure 2. Ethogram of fresh (A) and cold stored (B) *Galendromus helveolus*; I = inspection, S = searching, PG = patrolling, NP = nest penetration, NI = nest invasion, G = grooming, and R = resting. Numbers on figure indicate frequency of occurrence. Behaviors occurring less than 10 times were omitted, unless they occurred immediately prior to or after an attack behavior.

of the setal protection hypothesis, as the setal characteristics of *N. californicus* classify it within the theoretical lower range of phytoseiids with dorsal setae facilitating successful nest invasion and subsequently the majority of attacks (67%, PG + NP) occurred outside of nests. In comparison, *G. helveolus* appears to be highly adapted to invading webbed tetranychid nests and was only observed attacking prey following successful nest invasion. The setal protection index value for *G. helveolus* is 67% (middorsal) and 27% (marginodorsal) higher than *N. californicus* (Sabelis and Bakker 1992) and, according to the chaetotaxy hypothesis, indicates a much higher predilection for nest invasion.

Theoretically, the less hindered a phytoseiid predator is by a tetranychid nest webbing, the more likely it is to be a successful predator of tetranychid species (Sabelis and Bakker 1992). *Galendromus helveolus* appears to have closely coevolved with web-producing tetranychid mites, since its only mode of attack was to invade nests, facilitated by nest wall ripping and forced entry activities. In addition, *G. helveolus* spent a 2-fold greater proportion of time invading nests than *N. californicus*. In contrast, *N. californicus* appears to act as a generalist tetranychid predator because it can initiate multiple attack behaviors. The behavior of *N. cali-*

fornicus suggests that it is opportunistic and capable of capturing several different types of prey as this predator has been reported attacking thrips (Sabelis and Van Rijn 1997) and other phytoseiids (Walzer and Schausberger 1999) in addition to tetranychid prey. In contrast, *G. helveolus* has only been reported attacking tetranychids. In the context of the chaetotaxy hypothesis, *G. helveolus* should be the more effective predator of tetranychids in webnests, rather than *N. californicus*. However, field trials with these predators for control of *O. perseae* have not distinguished differences in efficacy when *N. californicus* or *G. helveolus* were used alone or in combination (Kerguelen and Hoddle 1999).

Despite the lower setal protection of *N. californicus*, it still effectively reduces tetranychid populations on avocados through engaging in a combination of attack strategies that include nest invasion and attacks on prey outside of nests. Therefore, successful control of tetranychid populations in field situations is not necessarily contingent on setal morphology and attack behaviors may be more important for determining the potential efficacy of phytoseiids.

Various aspects of *G. helveolus* behavior suggested that this predator is specially adapted to a web nest invasion lifestyle. *Galendromus helveolus* spent significantly greater amounts of time resting than *N. californicus*. Resting activity by *G. helveolus* occurred primarily within nests upon cessation of feeding. We observed that *G. helveolus* became greatly distended after feeding and had difficulty exiting *O. perseae* nests and grooming was the predominant activity between these resting periods inside nests post-prey consumption. In addition, we observed that 16% of cases in which *G. helveolus* invaded a nest, *O. perseae* motiles fled the rest. High nest residency times by *G. helveolus* may increase opportunities to ambush motiles after they return to nests. Additionally, nest residency by *G. helveolus* may reduce risk of intraguild predation by naturally occurring mite predators on avocados such as *N. californicus* or *Euseius hibisci* Chant (Acari: Phytoseiidae) or *Stethorus* spp. (Coleoptera: Coccinellidae). Intraguild predation of phytoseiids within the avocado system by other phytoseiids or predaceous insects has not been studied. The possible occurrence of intraguild predation by tetranychid natural enemies in avocado cropping systems needs investigation, because augmentative releases of commercially-available predators will encounter naturally-occurring low density predator populations and these interactions could adversely affect the efficacy of biological control programs (Roseneheim 1998).

Galendromus helveolus tended to consume *O. perseae* eggs rather than motiles, suggesting that utilization of a nest invasion strategy may be beneficial for predators attacking sedentary and defenseless prey that are unable to abandon intact nests. The slower mobility of *G. helveolus* (in comparison to *N. californicus*) may also explain its tendency to consume eggs, as well as its inability to patrol for and successfully capture migrant tetranychids outside of nests.

In contrast to *G. helveolus*, *N. californicus* spent more of its time outside of nests searching. Consequently, our laboratory data support existing literature that the high activity levels of some *Neoseiulus* species probably enhances their utility as generalist biological control agents because of enhanced prey encounter rates (Raworth et al. 1994; Croft et al. 1995; Pratt et al. 1988; Greco et al. 1999). The high mobility of *N. californicus* on avocado leaves may result in higher encounter rates of occupied *O. perseae* nests and individual motile mites outside of nests. The ability of *N. californicus* to execute three different modes of predator attack reflects a flexibility of lifestyle that allows exploitation of tetranychid prey either within or outside of webbed nests.

As a byproduct of our behavioral assays, our data demonstrated that *N. californicus* and *G. helveolus* behaviors were both adversely affected after ≈14 days in cold storage in comparison to non-cold stored predators. Each of these two species, when stored at low temperatures, exhibited significantly increased behavioral times (except inspection and resting) in comparison to fresh predators when performing the same activity. In addition, searching and patrolling behaviors occurred at lesser frequencies. These two behaviors are important indicators of predator efficiency. The time budget for *G. helveolus* was less severely affected by storage conditions, but cold stored predators did engage in longer episodes of searching and attacking prey. Differences in duration of activity bouts were most likely due to decreased fitness, probably because of prolonged starvation at low temperatures. Cold storage conditions appear to significantly affect various aspects of phytoseiid behavior, and this emphasizes the importance of using and releasing natural enemies immediately after receipt from commercial insectaries to minimize impairment of field performance.

Prolonged storage of beneficial insects is an attractive concept for insectaries that must endure fluctuating market demands and seasonal abundances (Glenister and Hoffman 1998). However, there is evidence that extended cold storage can reduce *Amblyseius cucumeris* Oudemans (Acari: Tetranychidae) survivorship (Gillespie and Ramey 1988) and we have recorded impaired performance for *N. californicus* and *G. helveolus* in this study. Cold storage thresholds and durations will vary according to natural enemy species, and multiple cold storage facilities may be needed by commercial insectaries to store several product lines under optimal conditions if natural enemy quality is to be preserved. Commercial insectaries may need to consider incorporating behavioral measurements into product quality standards to determine if cold stored natural enemies have significantly altered behaviors and reproductive capacities that would result in the production of inferior biological control agents for sale (Burgio and Nicoli 1993; Whitaker-Deerberg et al. 1994; Bueno and Van Cleave 1997).

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