

Within- and Between-Plant Dispersal and Distributions of *Neoseiulus californicus* and *N. fallacis* (Acari: Phytoseiidae) in Simulated Bean and Apple Plant Systems

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ABSTRACT Intra- and interplant movement and dispersal of *Neoseiulus californicus* (McGregor) and *Neoseiulus fallacis* (Garman) were studied on both lima bean, *Phaseolus lunatus* L., and apple branch, *Malus pumila* Miller, plant systems that were seeded with excess (50-100 per leaf) numbers of the twospotted spider mite, *Tetranychus urticae* Koch. Individuals of either predator were selected randomly from colonies of well-fed, mixed-age adult females and moved to test plants. When tested separately in each plant system, *N. californicus* dispersed a greater distance from the point of release than *N. fallacis* at 1-8 d. A fan placed in front of bean plants containing *T. urticae* and near equal densities of both predaceous mites, provided continuous air (wind) to 3 isolated receiver units located 2.5, 5, and 7.5 m downwind. Receiver units consisted of continuous bean foliage with excess (50-100 per leaf) *T. urticae*, but no predators. Wind speeds at the source and each receiver unit averaged 2.2, 0.9, 0.4, and 0.03 m/s. As predators eliminated prey, *N. fallacis* dispersed earlier at higher prey densities and further downwind than *N. californicus*, but cumulative densities of each predator in all receiver units were alike after 20 d. Results of both within- and between-plant dispersal studies supported the hypothesis that *N. californicus* has dispersal traits more like those of a generalist predator of spider mites than does *N. fallacis*. Spatial patterns of dispersal and biological control of pest mites are discussed in relation to predation types within the Phytoseiidae.

KEY WORDS *Tetranychus urticae*, biological control, predation types, aerial dispersal

WE HAVE BEEN studying the life history and predation characteristics of *Neoseiulus californicus* (McGregor) and *Neoseiulus fallacis* (Garman) (Croft et al. 1998, Monetti and Croft 1997a, b) to classify them as selective (specialist) or generalist predators of spider mites (Tetranychidae). Criteria proposed by McMurtry and Croft (1997) have been used for making predation rating assessments. Recent studies have comparatively explored the life histories of these 2 predatory mites under similar experimental conditions: Monetti and Croft (1997a) determined that *N. californicus* and *N. fallacis* were separate species, although some mating occurred and a few haploid males were produced from the interspecific cross of female *N. californicus* × male *N. fallacis*. In feeding studies, *N. californicus* nymphs showed higher inter- and intraspecific predation on eggs than *N. fallacis*, but adult females showed no differences (Monetti and Croft 1997b, Croft et al. 1998). *N. fallacis* larvae fed more on *Tetranychus urticae* Koch and showed higher frequencies of ambulation than *N. californicus* larvae, but *N. californicus* larvae showed a greater tolerance for moderate humidities (Monetti and Croft 1997b). Among

food types (insects, mites, and pollen), *N. californicus* reproduced more on thrips, but *N. fallacis* reproduced more on a wider range of spider mites and other phytophagous mites; both survived and reproduced well on maize pollen (Croft et al. 1998). In earlier, unrelated studies, *N. fallacis* had higher reproduction rates and immatures showed less within-plant movement than did the immatures of the 2 generalist predators, *Typhlodromus pyri* Scheuten and *Amblyseius andersoni* Chant (Croft et al. 1995, Zhang and Croft 1995).

McMurtry and Croft (1997) suggested that *N. californicus* and *N. fallacis* are selective type II predators of spider mites and that they probably have similar tendencies to move within and between plants to find aggregated prey. However, to our knowledge, no detailed comparisons of their actual movement or dispersal attributes have been made in a common plant system. In this study, our primary objective was to determine if *N. californicus* moves or disperses to the same extent and in similar patterns as *N. fallacis*, both within and between plants. Ultimately, we want to integrate our findings with data for other traits that have been identified to characterize different phytoseiid predation types (Croft et al. 1998, McMurtry and Croft 1997).

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Materials and Methods

Predator Source. Before mass rearing, *N. californicus* and *N. fallacis* were cultured (McMurtry and Scriven 1965) in the laboratory for 5 yr with field-collected predators added to the colonies annually. In all experiments, source populations of predators came from a mass rearing facility at Oregon State University: *N. californicus* and *N. fallacis* were produced in separate greenhouse rooms on lima beans, *Phaseolus lunatus* L., infested with *T. urticae* under conditions of 26:21 \pm 5°C (L:D), 75 \pm 10% RH, and a photoperiod of 16:8 (L:D) h (Strong and Croft 1995). All predators of both species were selected from populations of well-fed adult females (mixed ages) and individuals were transferred to experimental plant systems with a camel's-hair brush.

Within-Plant Movement: Small Simulated Plant System. To measure the movement of *N. californicus* and *N. fallacis* within a multistemmed, simulated plant system, a dense canopy of lima bean leaves covering a circular area of 0.3 m diameter (\pm 5 cm) was created from many individual stems. Vertical growth beyond the primary (unifoliolate) leaves was excised to create a 2-dimensional, single leaf layer surface. To make this simulated plant, a total of 55 \pm 3 seeds were planted in each of 10 polyethylene bags (30 cm diameter) that were filled with a potting mixture (Zhang and Croft 1994) of pumice, sand, peat moss, and soil (2:1:1:1). Seeds germinated in 1 wk, and 1 wk later each leaf on each plant was inoculated with 50–100 mixed life stages of *T. urticae*. Each simulated plant system was assigned randomly to a treatment and placed on 1 of 2 randomly assigned benches, 30 \pm 3 cm from other simulated plants in an environmental room at 26:21 \pm 10°C (L:D), photoperiod 16:8 (L:D) h, and 75 \pm 10% RH. Each bench was 1 by 3 m and served as an isolated container unit for bean plants with a 10 cm deep water moat between plants and any bench structures.

Predatory mites were added to each simulated plant 1 wk later. Treatments were 50 adult female predators of 1 species placed on a marked leaf at the center of each of 5 simulated plant replicates. Samples of 5 adjacent leaves were taken along 1 of 2 cardinal directions (either N–S or E–W) that were selected randomly each sample day. The median horizontal distance moved by predators on leaves located at positions 1–5 from the center was calculated along the transect of each replicate. While collecting samples, each leaf was excised from the plant and observed visually with an optical visor at 10 \times magnification and the number of adult females recorded. If immatures were to be counted, each leaf was marked and placed in a cooler chest for transport to the laboratory. Immatures were counted using a microscope (40 \times) within 1 h after they were sampled in the environmental room. Samples of adult females were taken on 3, 5, and 8 d after the initial transfer of female adults. Immatures were counted only on days 5 and 8. Each simulated plant

was sufficiently dense with bean leaves that vacant areas in the canopy were not created from destructive sampling.

Within-Plant Movement: Large Simulated Plant. During preliminary small plant tests, it was observed that *N. californicus* searched a greater distance over the surface of the simulated plant from the point of release than did *N. fallacis*, and it reached the outer boundaries of the plant system very quickly. Also, *N. fallacis* is known to be more sensitive to low humidity than *N. californicus* (Croft et al. 1993, Castagnoli and Simoni 1994, Monetti and Croft 1997b) and its apparent lower rate of movement within the small plants could have been an avoidance of the dryer conditions at the periphery. Thus, a 2nd, larger simulated plant test was used to give predators more space in which to move and to determine if reduced humidity from the release point outward was affecting predator movements. It was similar to the small plant test, except that 140 \pm 5 stems made up the foliage area of 0.66 m (\pm 5 cm) diameter, 100 predators of each species were released per replicate plant system (5 per species), sampling was at 1–4, 6, and 8 d after predator release, and 10 adjacent leaves per replicate were sampled along a randomly selected transect as described above. Immatures were sampled the same way as in the small simulated plant test, but on days 2, 4, 6, and 8.

Within-Plant Movement: Apple Branch System. To test whether plant species or orientation affected predator movement patterns, 10 Red Delicious apple, *Malus pumila* Miller, leaf branches of 1 m length (40 \pm 5 expanded leaves, 12.5 \pm 2 cm canopy diameter) were excised from a single apple tree on 15 July 1996. Each branch was individually held vertical in 1-gal plastic containers filled with nutrient solution (20:20:20%, N:P:K + micro nutrients), randomly assigned 1 of 2 treatments, and spaced 30 \pm 3 cm apart on a single bench. Replication, spider mite releases, and predator releases were as before (in bean test), except 50 predators of 1 species were released on the most basal apple leaf of each branch. Samples for adult females were as before except randomly selected leaves were observed (not removed) at every 10-cm vertical stem region of each branch (10 total leaves per branch were sampled), at 12, 24, 36, and 48 h after releasing predators.

Between-Plant Movement. A greenhouse room (10 by 4 m) was modified to function like a wind tunnel by arranging 4 benches (1 by 3 m each) at 1 m height and 1.5 m apart. A fan next to an intake window (0.6 by 0.6 m) but in front of bench 1 produced continuous wind speeds that averaged 2.2, 0.9, 0.4, and 0.03 m/s over benches 1–4, respectively. Wind speeds were measured directly over the center of each bench with an anemometer. A screened window (1 by 2.2 m) 1 m downwind of bench 4 served as an outtake. A smoke bomb confirmed that minimal turbulence was produced as the air flowed across each bench with source and receiver plants in place. Contiguously arranged source plants, consisting of 325 bean stems per unit (6 units) on bench

1, had mixed populations of *T. urticae* at 14.6 ± 0.28 per stem and mixed *N. californicus* and *N. fallacis* at densities of 2.5 ± 0.49 and 1.7 ± 0.76 adult females per stem on day 1, respectively. Numbers of prey mites and adult female predators on bench 1 were estimated by taking random samples of 18 stems on days 1, 5, 10, and 19. Benches 2–4 were covered with a single layer of primary (unifoliolate) lima bean leaves (receiver plants) that had been inoculated with 50–100 *T. urticae* per leaf 1 wk earlier. Each bench contained a water moat similar to those used in within-plant studies. Predator samples were taken on each leaf on benches 2–4 at the same time, each day, for 20 d. Because of the potential for development of eggs from a few dispersing female predators that were not removed in sampling, receiver plants were replaced on day 10. All predator stages (mostly female adults) found on receiver plants were mounted on microscope slides and identified by the length of their prolateral and dorsocentral setae (Schuster and Pritchard 1963).

Statistical Analysis. Median distance moved by predatory mites in both bean (horizontal) and apple branch (vertical) systems were compared over time with repeated measures analysis of variance (ANOVA) (von Ende 1993). The Huynn-Feldt adjustment was used when the covariance matrix of the data did not meet the assumption of sphericity (SAS Institute 1992, von Ende 1993, Floyd 1996). Individual ANOVAs and Tukey honest significant difference tests were used to identify the days when median leaf positions were statistically different (<0.05) between species (SAS Institute 1992, von Ende 1993). Census data of predators that dispersed to leaves on benches 2–4 were compared graphically over time.

Results

Within-Plant Movement: Small Simulated Plant System. After transfer of predators to the single central leaf, *N. californicus* moved to the outer edges of the plant system by day 3 and the median distance moved by adult females was significantly greater than that of *N. fallacis* ($P = 0.008$; $df = 1, 8$; Fig. 1 a and b). The same trend was apparent on days 5 and 8, with *N. californicus* having a greater median distance moved than *N. fallacis* ($P = 0.025$ and 0.014 , respectively, $df = 1, 8$). Overall, the within-plant dispersal of *N. californicus* adult females during the entire 8-d experiment was significantly greater than that of *N. fallacis* (Table 1).

When combined, immature life stages demonstrated similar spatial and distributional differences as was seen for adult females (Table 1). For individual life stages, the median position of the larvae and deutonymphs of *N. californicus* was significantly greater than for those of *N. fallacis* on day 5 ($P = 0.035$ larvae; 0.007 deutonymphs; $df = 1, 8$) and day 8 ($P = 0.033$ larvae; 0.020 deutonymphs; $df = 1, 8$). The median distance position of protonymphs of *N. californicus* was not significantly greater ($P = 0.079$;

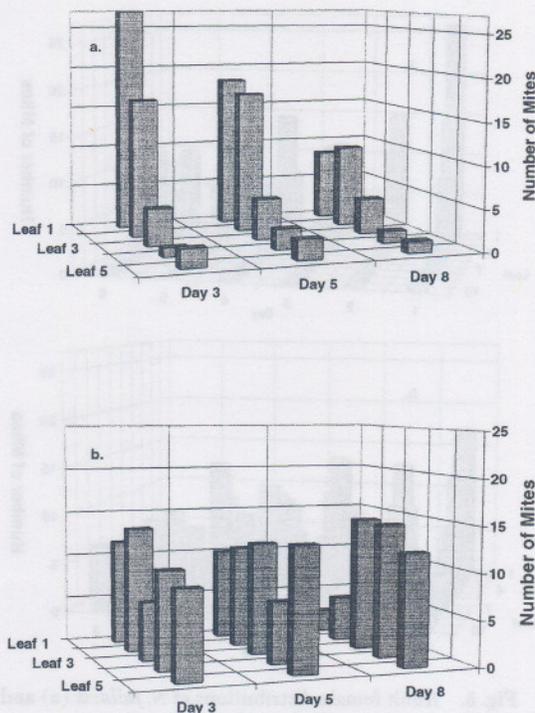


Fig. 1. Adult female distributions of *N. fallacis* (a) and *N. californicus* (b) in the small bean plant system.

$df = 1, 8$) than *N. fallacis* on day 5, but were significantly greater on day 8 (0.048 ; $df = 1, 8$).

Within-Plant Movement: Large Simulated Plant System. A few adult females of *N. californicus* dispersed to leaf 9 on the 1st d of the test but *N. fallacis* never reached beyond leaf 7 during 8 d (Fig. 2 a and b). The median distance moved by *N. californicus* on day 1, 4, and 6 was statistically greater than that of *N. fallacis* ($P = 0.015, 0.013, \text{ and } 0.002$, respectively; $df = 1, 8$). Data for days 2, 3, and 8 seemed to show similar differences (Fig. 2a–b) but, because of greater variation in the data, comparisons were not statistically significant. Again, over all dates, the trend was that adult females of *N. californicus* generally were found further from the point of release than were *N. fallacis* (Table 1).

Table 1. Repeated measures ANOVA of within-plant movement of *N. californicus* and *N. fallacis* adult females and immatures during all dates in 3 plant systems

Plant system	Life stage	Test duration, d	F	P
Bean small system	Adult females	8	22.41	0.0015
	Immatures	8	23.10	0.0001
Bean large system	Adult females	8	37.56	0.0003
	Immatures	8	8.72	0.0183
Apple branch system	Adult females	2	43.27	0.0002

$df = 1, 8$.

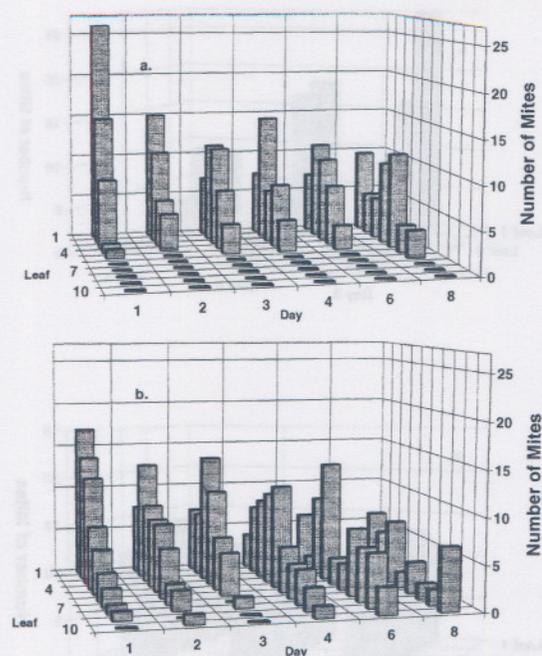


Fig. 2. Adult female distributions of *N. fallacis* (a) and *N. californicus* (b) in the large bean plant system.

Immature distributions (combined) again were similar to those of adult females in the large simulated plant system (Table 1). The median position or distance from the center of eggs and nymphs of *N. californicus* were significantly greater than those for *N. fallacis* over all days ($P = 0.012$ eggs; 0.005 protonymphs; 0.039 deutonymphs; $df = 1, 8$). Although slightly less significant, the same trend occurred with larvae ($P = 0.096$; $df = 1, 8$).

Within-Plant Movement: Apple Branch Systems. Individuals of *N. californicus* reached the terminal leaves of a 1-m plant system within 36 h (Fig. 3b); this was in contrast to *N. fallacis*, which did not reach the terminal leaves during 48 h. At each sample interval (12, 24, 36, and 48 h) the vertical median distance moved for *N. californicus* was significantly greater than for *N. fallacis* ($P = 0.039, 0.050, 0.020$, and 0.017, respectively; $df = 1, 8$). The overall distance moved by *N. californicus* during the entire 48-h experiment was greater than for *N. fallacis* (Table 1).

Between-Plant Movement. *N. fallacis* began to arrive at receiver plants considerably before *N. californicus* (Fig. 4a) and moved further away from the source plants or release site, which was just the opposite trend seen in within-plant movement studies. Sixteen *N. fallacis* females were collected from benches 2–4 on the 1st d of the experiment. *N. californicus* did not have 16 cumulative individuals that dispersed onto benches 2–4 until day 10 of the test. Over the first 10 d of the experiment, an average of 10 *N. fallacis* females dispersed to benches 2–4 as compared with only 2 *N. californicus* females. *N.*

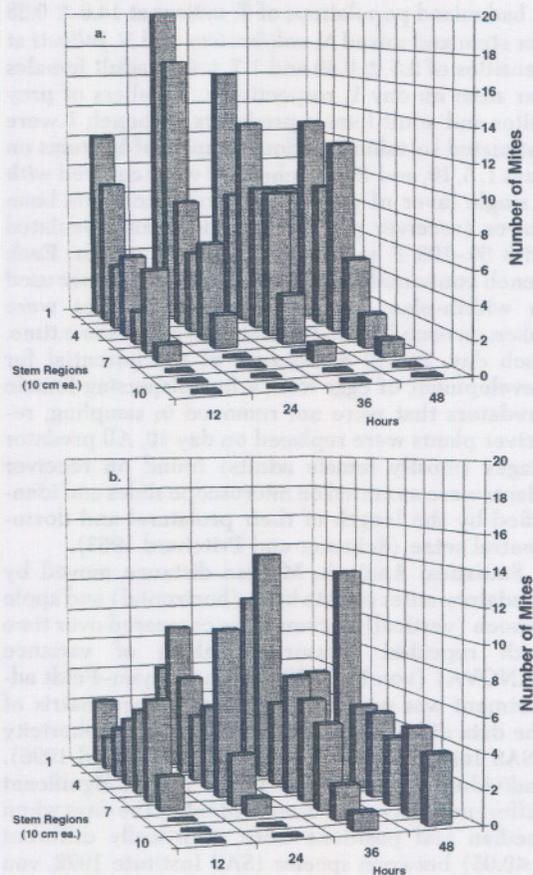


Fig. 3. Adult female distributions of *N. fallacis* (a) and *N. californicus* (b) in an apple branch system.

fallacis averaged 3 dispersed individuals per day over the last 10 d of the experiment as compared with 17 for *N. californicus*. *N. fallacis* also dispersed over a greater distance than did *N. californicus* (Fig. 4b–d). The percentage totals for *N. californicus* found on benches 2–4 were 81, 18, and 0%, respectively, whereas for *N. fallacis*, they were 47, 39, and 13%, respectively.

Discussion

In this study, within-plant dispersal of *N. californicus* was greater than that of *N. fallacis*, but *N. fallacis* moved sooner at low prey densities and dispersed a greater distance between plants. These differences led us to conclude that *N. californicus* had dispersal traits more like those of a generalist predator of spider mites than did *N. fallacis* (McMurtry and Croft 1997). A specialist predator of a highly aggregated spider mite such as *T. urticae* would likely remain aggregated on plants to exploit an ephemeral food resource, but it would also be adapted to rapidly finding new prey patches when local patches were depleted. In contrast, a generalist

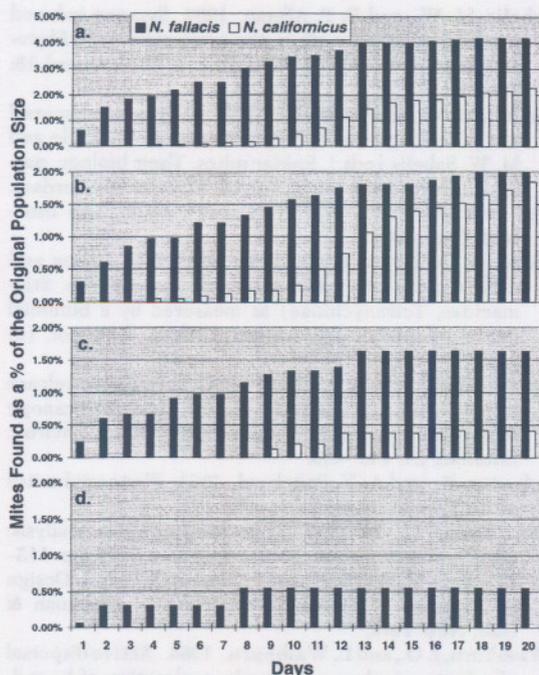


Fig. 4. Cumulative number of mites found in between-plant dispersal studies, (a) benches 2-4 cumulative, (b) bench 2, (c) bench 3, (d) bench 4.

predator of spider mites may move more widely on plants and disperse less from plant to plant because it can feed on other dispersed foods such as pollen and alternate prey and it is less dependent on finding highly dispersed and aggregated prey mites such as *T. urticae*.

These data also give perspective to the use of these predators for biological control. In a continuous plant system, as was represented by the simulated bean plant systems described herein, *N. fallacis* controlled or suppressed spider mites at the site of release and then moved, outward to the edge of the plant system (when there is one) (B.A.C., unpublished data). In contrast, *N. californicus* dispersed more throughout the plant system and reduced the entire spider mite population simultaneously at all locations. Because of these patterns, *N. fallacis* may appear to be better than *N. californicus* in controlling an aggregated spider mite (like *T. urticae*) depending on where one looks, how large sample sizes are, and how long samples are taken. However, both predaceous mites give similar levels of biological control with regard to timing, prey level, and predator production (B.A.C., unpublished data).

These differences in spatial patterns of dispersal may have relevance to predation efficiency and the effectiveness of either predator in controlling aggregated spider mites (e.g., *T. urticae*) versus more dispersed spider mites (e.g., *Panonychus ulmi* Koch) (Slone and Croft 1998). Both predators are often

associated with and can provide biological control of either of these spider mite types (Croft et al. 1998, McMurtry and Croft 1997). *N. californicus* appears to be more adapted to control prey that are less aggregated than *T. urticae*. This phytoseiid searches widely within-plant systems. Another attribute that seems relevant is that *N. fallacis* has higher rates of very local movement or ambulation in a prey patch or individual leaves, and has been referred to as being hyperactive when compared with other phytoseiids (Croft et al. 1996, Monetti and Croft 1997b). Although *N. fallacis* moved less often between prey patches, it seemed to be more active within a prey patch, turning rapidly and exploring the local universe as if it were monitoring its own progeny and prey levels before dispersing. In contrast, *N. californicus* moved more between local prey patches but showed less turning and local exploration. Just what purposes are served by these behaviors is unclear but they may influence the energy requirements and predation characteristics of these 2 species.

The differences seen in dispersal distances of *N. californicus* and *N. fallacis* (Fig. 4 b-d) are difficult to explain. One possibility is that *N. fallacis* dispersed more times, from one isolated receiver unit to another, to reach the most distant receiver plants on bench 4. However, this explanation is unlikely because there was an overabundance of prey in these studies and Croft et al. (1995) have reported that *N. fallacis* does not readily leave a prey patch. Another explanation may relate to dispersal behavior. Johnson and Croft (1976) described a stance or posturing behavior in *N. fallacis* that they associated with aerial dispersal; other reports suggested that this behavior may assist in dispersal, but is not a requisite (Washburn and Washburn 1984, Sabelis and Afman 1994). Similar behaviors have either not been seen or not studied in *N. californicus*. Just what role this posturing behavior might play in giving predators more lift or displacement by air currents is unknown. Also, the 2 phytoseiids may exhibit different behaviors during aerial transport such as withdrawing or extending their appendages (Sabelis and Dicke 1985). Another contributing factor may be related to the different morphologies of the 2 species, which in general are very similar. *N. fallacis* has longer dorsal setae than *N. californicus* (Schuster and Pritchard 1963, Croft et al. 1998), and this difference may affect their aerodynamics or buoyancy in the air. Unfortunately, little is known about the relationship between morphology and aerial dispersal of these mites or of small arthropods in general (Washburn and Washburn 1984).

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