Phoretic Dispersal of Armored Scale Crawlers (Hemiptera: Diaspididae)

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ABSTRACT  Dispersal and colonization of new areas by armored scale insects (Hemiptera: Diaspididae) is achieved by mobile first-instar nymphs, called crawlers. Few studies have considered the actual mechanisms by which crawlers disperse, and although crawlers are capable of actively wandering over short distances (generally <1 m), their dispersal over longer distances has been thought to be wind-mediated. Here, we present evidence of a potentially more important means of dispersal over longer distances (>1 m). We first confirmed that crawlers of four species of Diaspididae [Abgrallaspis aguacatae Evans, Watson & Miller; Hemiberlesia lataniae (Signoret); Aspidiotus nerii Bouché; and Diaspidiotus perniciosus (Comstock)] have four hairs on the end of each of their legs and that each of these hairs ends in a suction cup-like structure, reminiscent of the attachment structures possessed by phoretic mites. In a controlled environment, using crawlers of A. nerii, we then showed that the crawlers use these structures to attach themselves to three different insect species [Musca domestica L., Cryptolaemus montrouzieri Mulsant and Linepithema humile (Mayr)] and can effectively be moved phoretically by these insects. Crawlers can remain attached to flying insects for considerable periods of time, suggesting that this may be an important means of dispersal for armored scale insects. The importance of phoresy for diaspidid dispersal in the field remains to be determined.

KEY WORDS Abgrallaspis aguacatae, Hemiberlesia lanatiae, Aspidiotus nerii, Diaspidiotus perniciosus, phoresy

Armored scale insect species (Hemiptera: Diaspididae) are numerous and include some of the most damaging and refractory pests of perennial crops (Beardsley and Gonzalez 1975, Kosztarab 1990, Miller and Davidson 1990, 2005). Although there are many examples in the literature documenting the colonization of new areas by species of armored scale insects (Miller et al. 2005), there is by comparison, very little information on the physical mechanisms by which these “sessile” creatures disperse. Biological dispersal is the movement and establishment of a species away from an existing population or away from the parent organism (Clobert et al. 2001). In armored scales, only the first-instar nymph, commonly referred to as a crawler, is capable of dispersing and colonizing a new area. After emerging from the egg (or the female in viviparous species), the crawlers are initially mobile, but once they locate a suitable spot to settle, they insert their mouthparts into the host plant, and the females at least, remain there for the rest of their lives: adult males are winged and fly in search of mating opportunities (Howell 1975), but they cannot establish new populations. Diaspidid crawlers will wander under their own power, but have small energy reserves, and can survive for only a short time before they need to settle and feed (Koteja 1985). Factors such as temperature, humidity, dustiness, host species, and population density (Greathead 1972, Willard 1973, Beardsley and Gonzalez 1975) affect the wandering speed and behavior of crawlers, but generally they are active for less than one day, will remain on the same plant on which they emerged, and will often settle within 1 m of their sessile mother (Clark et al. 1989, Willink and Moore 1988).

Active wandering may be good for dispersal over short distances, but for dispersal over longer distances, it has long been thought that armored scale crawlers primarily make use of air currents. Wind-borne dispersal of crawlers has been documented in several species, and it has been suggested that morphological characteristics, such as a flattened body and long filamentous caudal setae, reduce terminal velocity allowing the crawlers to stay airborne longer while drifting in the wind (Greathead 1990, Gullan and Kosztarab 1997, Bullock et al. 2002). Crawlers have been recorded as being carried for distances ranging from a few meters to several kilometers, and more rarely a few hundred kilometers (Greathead, 1972, 1990, Gullan and Kosztarab 1997). Furthermore, some Diaspididae display behaviors that seem to be adaptations for take-off in a wind stream. For example, the
crawlers of *Aulacaspis tegaleensis* (Zehntner) orient themselves downwind, standing on their hind legs with antennae and forelegs outstretched (Greathead 1990). However, other species such as California red scale, *Aonidiella aurantii* (Maskell), crawlers actually seem to resist dislodgement by the wind (Greathead 1990).

Although passive dispersal on the wind potentially allows diaspидid crawlers to move for considerable distances, it is likely to be a rather hap hazard method. It may be a suitable strategy for highly polyphagous species or for those that specialize on plants found in monocultures, but for species that specialize on particular host plants, especially if they are rare, passive wind-borne dispersal seems to carry a high risk of failure. Many small insect and mite species that face similar dispersal problems use a phenomenon known as phoresy to move from one host to another. Under phoresy one arthropod species with a low dispersal capability (passenger) attaches itself to a second arthropod species (vector) that is capable of dispersing over longer distances (Athias-Binche 1993, Palevsky et al. 2001, Grossman and Smith 2008). In general, the passenger is smaller than the vector, lacks effective independent dispersal structures, and just one life stage is phoretic (Selander 1985, Brown and Wilson 1992, Schwarz et al. 1996). Arthropods with phoretic relationships have morphological structures adapted for effective exploitation of the vector (e.g., modifications of the head and legs that enable grasping of the vector) (Selander 1985).

Although phoresy has not previously been reported in the English literature in armored scale insects (but see Marek 1952 for a reference in German), several other scale insect groups exhibit this behavior (Williams 1984). Crawlers of the mealybugs *Hippeococcus* spp. (Reyn 1954) and *Chaetococcus* spp. (Klein et al. 1992) reach new resource patches by hitchhiking on queen ants. Others, such as *Cystococcus* spp. crawlers, hitch a ride on conspecific winged adult males, dismounting and establishing on new plant hosts when the males find a receptive female (Gullan and Cockburn 1986). However, among arthropods, mites are known as masters in phoretic associations (Houck and O’Connor 1991, Houck 1994, Palevsky et al. 2001). Mites lack morphological adaptations for independent migration but exhibit a variety of attachment structures that enhance vector-boarding and phoretic dispersal (Moser and Cross 1975). Phoresy involves several classes of fixation principles that employ a variety of attachment structures: clamps, hooks, suckers and adhesive secretions (Gorb 2001). The clamp principle relies on the use of muscular force for holding onto a vector. The most common example is a hook attachment device consisting of a tarsal claw together with setae on legs. Larvae of meloid beetles use hook-like claws to attach to the body of their solitary bee vector (Selander 1985). The sucker principle relies on different pressures between the atmosphere and the suction cup structure and is good for attaching to smooth substrates. The function and specialization of the suction cups is dependent on their shape, flexibility, surface at the edge and the presence of muscles. Some suction cups produce fluids or liquid adhesive secretions to increase contact (Naldrett 1993, Gorb 2008). Various mite species have developed suction cups originating from a terminal leg structure called the empodium (Gorb 2001).

In a preliminary experiment to measure wind-dispersal of oleander scale, *Aspidiotus nerii* Bouché, crawlers, we found that very high wind speeds were required to dislodge crawlers from a surface (unpublished data). To determine how the crawlers could hang onto the surface despite these high wind speeds, we studied the leg morphology of crawlers of *A. nerii* and those of three more species of diaspидid scales (*Hemiberlesia lataniae* (Signoret); *Ahydrallaspis aquacatae* Evans, Watson & Miller; and *Diaspidiosus perniciosus* (Comstock)). For decades, it has been known that crawlers of almost all diaspидid species have a pair of ungual digitules (modified hairs) at the base of each tarsal claw, plus a pair of tarsal digitules at the apex of the tarsus. These digitules were thought primarily to help the crawlers remain attached to plants (Howell and Tippins 1975, Rosen 1990, Gullan and Kosztarab 1997). On closer inspection, under a scanning electron microscope, we found that the digitules on the legs of the crawlers resembled the structures found on the legs of phoretic mites. This led us to investigate the possibility that diaspидid crawlers could disperse by phoresy. Here, we report the results of lab experiments showing that armored scale crawlers will attach to other insect species and can subsequently be moved by a vector insect to a new resource patch.

**Materials and Methods**

**Source of Experimental Insects and General Bioassay Conditions.** For initial morphological examination, crawlers of three armed scale species were obtained. *H. lataniae* and *A. aquacatae* were collected from imported avocado fruit as part of another study (Morse et al. 2009). *D. perniciosus* was obtained from Kent Daane (University of California, Berkeley, CA) and *A. nerii* was obtained from Robert Luck (University of California, Riverside [UCR], CA). Subsequent bioassays concentrated on a single species, *A. nerii*, and active crawlers (>1 d old) were obtained daily from FAR, Inc. (Corona, CA). Potential vector insects were obtained from various sources. The predaceous beetles *Lindorus lophanthae* (Blaisdell) (Coleoptera: Coccinellidae) and *Cryptolaemus montrouzieri* Mult sant (Coleoptera: Coccinellidae) were purchased as adults from the Rincon-Vitova Insectaries, Inc. (Ventura, CA). *Musca domestica* L. (Diptera: Muscidae) and *Drosophila melanogaster* (Meigen) (Diptera: Drosophilidae) were obtained from the laboratories of Alec Gerry (UCR) and Len Nunney (UCR), respectively. Colonies of Argentine ants, *Linepithema humile* (Mayr), were obtained from Mike Rust (UCR). Ant colonies consisted of 10–20 queens, brood, and 2,000–5,000 workers and were maintained inside a plastic box (26.5 by 30 by 10 cm; Spectrum Containers, Inc., Evansville, IN). To prevent escape, the inner walls of
the colony box were coated with fluoropolymer resin (Choe and Rust 2006). All bioassays were done under general laboratory conditions (23 ± 4°C, 25–55% RH, and a photoperiod of 16:8 [L:D] h). The basic experimental design involved exposing crawlers of A. nerii to a potential insect vector species and allowing the vector insects to transport the crawlers to lemon fruits on which they could settle. Lemon fruits and leaves used in the bioassays were collected from pesticide free citrus orchards near the UCR campus.

**Leg Morphology of Diaspidid Crawlers.** The leg morphology of crawlers of *H. lataniae, A. aegacatae, D. perniciosus,* and *A. nerii* was investigated under a scanning electron microscope (SEM). Crawlers were euthanized in 70% ethanol and then transferred to 100% ethanol, which was subsequently replaced with two changes of HMDS (Heraty and Hawks 1998). Specimens were then removed from the HMDS and allowed to air dry, before being mounted on aluminum stubs with PELCO Tabs carbon conductive adhesive tabs (Ted Pella, Inc., Redding, CA), and coated with gold/palladium alloy and examined under a LYPH-Lock 4.5 freeze drying system (Cressington Scientific Instruments Ltd., Watford, United Kingdom). Specimens were examined under a Philips XL30-PEG SEM (FEI Co., Hillsboro, OR) at an accelerating voltage of 10–12 kV.

**Attachment of Diaspidid Crawlers to Beetles.** Adults of *C. montrouzieri* were exposed to crawlers of *A. nerii* for 20 min. Beetles with crawlers attached were fast-frozen on dry ice, and then moved to a prechilled freeze-drying vessel kept on dry ice to ensure its contents remained frozen. The vessel was then attached to a Lyph-Lock 4.5 freeze drying system (Labconco Corp., Kansas City, MO) and kept on dry ice until the freeze dryer reached the critical vacuum level. Specimens were lyophilized at −40°C and 14 μm of mercury for 24 h.

After freeze drying, the individual beetles were carefully adhered to aluminum stubs with PELCO Tabs. The adhesive tabs by themselves did not secure the beetles sufficiently, so ELECTRODAG 503 silver conductive paint (Ladd Research, Williston, VT) was added between the beetle and the stub to improve the physical and electrical contact. Specimens were then coated with gold/palladium alloy and examined under the SEM at an accelerating voltage of 10 kV.

**Crawler Acquisition by Vector Insects From Lemons Infested With Crawler-Producing Scales.** Single species batches of the three potential vector insects (*M. domestica* [replicates = 6; total n = 210], *D. melanogaster* [replicates = 3; n = 150], or *L. lophanthea* [replicates = 3; n = 60]) were isolated with four *A. nerii*-infested lemons in a plastic container (20 by 20 by 7 cm) for 2–4 h. Lemons containing crawler-producing oleander scales were obtained from the lab of Robert Luck (UCR). The scales on these lemons were producing active crawlers with ~1,000 crawlers present per lemon. Vector insects were kept without food for at least 10 h before the experiment to increase their activity. After exposure to the crawlers, the vector insects were retrieved, cooled for several minutes in a freezer (−20°C), and the number of crawlers present on the body of each insect was determined.

**Crawler Short-Distance Dispersal Using Several Vector Insects.** Two experimental designs were used to investigate crawler dispersal on three different insect vectors. With *C. montrouzieri* and *M. domestica,* we used a slant-top sleeve cage with an organdy cloth back and glass top (dimensions: height in front, 33 cm; height in the back, 51 cm; depth, 48 cm; and width, 77 cm). The cage was divided in half (width wise) by a sheet of cardboard, leaving a narrow opening (averaging 3.5 cm) between the top of the wall and the glass lid. On one side of the cage, vector insects exposed to scale crawlers were released and on the other side, 10 lemons were placed on podiums (14.5 cm in height) to supply a substrate for crawlers to settle on. Vector insects (and crawlers) could move from one side of the cage to the other only by walking or flying through the narrow opening at the top of the dividing wall.

A plastic cylindrical vial (5.3 cm in diameter by 8.7 cm) containing either 100 adults of *C. montrouzieri* or 20–35 adults of *M. domestica,* plus crawlers of *A. nerii* at one of two densities (high density, 1.60 g or 7 × 10⁵ crawlers; or, low density, 0.01 g or ~4 × 10⁵ crawlers) was placed on one side of the cage and left undisturbed for 20–30 min to allow crawlers to attach to the vector insects. The lid of the vial was then removed to release the vector insects, and the vial with the remaining crawlers was removed from the cage. The release side of the cage was then covered with a black garbage bag to create dark conditions and induce movement of the vector insects to the side with the lemons. With *C. montrouzieri,* the experiment with the high crawler density was stopped after 4 h when we noticed the vector beetles starting to eat the crawlers that were settling on the lemons. Consequently, the low crawler density experiment was stopped after 20–30 min to avoid excessive predation. *M. domestica* did not feed on the scale crawlers, and experiments with that insect were allowed to run for 24 h at both crawler densities. At the end of the exposure time, the lemons were taken out of the cage and isolated in a separate plastic box. Scale presence and settlement on the lemons was then determined 48 h after the vector insects were initially released. As a control a vial containing 1.6 g crawlers was placed in the darkened release-side of the cage and left for 48 h to determine
whether the crawlers could settle on the lemons without the presence of vector insects.

For studies with Argentine ants, *L. humile*, we placed four glass jars (12 cm in height) upside down in a row inside a plastic window flower box (75 cm in length by 15 cm in width by 13 cm in height). On top of each glass jar a lemon was placed providing a settlement substrate for crawlers. Each lemon was connected to the next by a wooden popsicle sticks (10 cm in length) held in place with modeling clay. The first lemon also was connected by a popsicle stick to a plastic box containing an ant colony, and the last lemon, to a plastic box containing food for the ants and 1.6 g of crawlers of *A. nerii*. The internal walls of these two boxes were coated with fluoropolymer resin and the bottom of the window flower box was covered with ∼10 cm of soapy water to prevent the ants escaping. Thus, to forage for food from the colony box, the ants were forced to walk over each of the four lemons to a box containing both food and crawlers, and then return via the same route. The ants were allowed to forage for 18–22 h, and the numbers of scale crawlers present and settled on each lemon were determined 48 h after initial release of the ants. As a control, we used the same setup but without any ants (i.e., the phoretic vector) present, and we allowed the crawlers 48 h in which to disperse.

### Ability of Scale Crawlers to Remain Attached to *C. montrouzieri* During Flight

One hundred adults of *C. montrouzieri* were placed in a vial (12 by 11 cm) containing either 1.6 g (high density) or 0.01 g (low density) of crawlers of *A. nerii* and left undisturbed in the laboratory for 20–30 min to allow crawlers to attach to vectors. The container was then opened at one end of a room (2 m in width by 2 m in depth by 2.5 m in height). At the opposite end of the room was a single window (0.83 by 0.83 m) to which the beetles could fly. Fifty beetles were captured immediately after opening the container to determine the number of crawlers attached to the beetles before flight. The remaining 50 adults were captured after they had flown to the window, ∼20 min after release, and the number of crawlers on each beetle was determined. A second release was done in the same way except the beetles were captured from the window 1 h after release.

### Results

#### Leg Morphology of Diaspidid Crawlers

Scanning electron micrographs revealed that the crawlers of all four diaspidid species (*H. lataniae, A. aguacatae, D. perniciosus,* and *A. nerii*) possessed similar leg attachment devices: a well-developed single claw (ungula) and four digitules each ending in a suction cup-like structure (Figs. 1 and 2). We observed crawlers of *A. nerii* attached to the elytron of *C. montrouzieri* adults with a tarsal claw inserted under an edge of the individual imbricating reticulations of the cuticle and two
Crawler Acquisition by Vectors Insects. *C. montrouzieri* beetles walking over lemon leaves replete with 50–100 crawlers of *A. nerii* acquired passengers very quickly. The number of crawlers acquired by individual beetles did not differ significantly when the beetle was exposed to the crawlers for 1 min (mean ± SE = 1.20 ± 0.10) or 5 min (1.50 ± 0.13; Mann–Whitney U90.90 = 4489.5; P = 0.208). When exposed to lemons infested with crawler-producing scales, all three tested vectors were prone to acquiring crawlers, although the numbers acquired by the different vector species differed (*D. melanogaster*, mean ± SE = 0.11 ± 0.04; *L. lophanthae*, 0.60 ± 0.07; and *M. domestica*, 0.92 ± 0.11; Kruskal–Wallis H = 95.51, df = 2, P < 0.001).

Short-Distance Crawler Dispersal Using *C. montrouzieri* and *M. domestica* as Vectors. Movement of crawlers of *A. nerii* to the lemons was significantly increased by the presence of a vector insect (General Linear model: \( F_{1.10} = 9.02; P = 0.008 \)) and by an increase in the density of crawlers the vector insect was exposed to at the outset of the experiment (\( F_{1.10} = 25.23; P < 0.001 \)) (Fig. 3). Higher numbers of crawlers reached the 10 lemons in the presence of *C. montrouzieri* (high crawler density, mean ± SE = 275.40 ± 63.20; low crawler density, 24.00 ± 8.67) than *M. domestica* (high crawler density, 89.40 ± 10.50; low crawler density, 15.60 ± 2.77) (Fig. 3). In contrast, when no vector insect was present, over five attempts, a total of only three crawlers (mean ± SE = 0.6 ± 0.25) successfully reached the lemons (Fig. 3).

Short-Distance Crawler Dispersal Using Ants as Vectors. The presence of a foraging Argentine ant colony also significantly increased the dispersal of crawlers of *A. nerii* (General Linear model: \( F_{1.104} = 19.71, P < 0.001 \)) (Fig. 4). After 48 h, the number of settled crawlers was highest on the lemon nearest the food and crawler source (lemon 1; mean ± SE = 10.33 ± 2.85) but quickly declined on the subsequent lemons (i.e., with the distance from the crawler source: \( F_{3.104} = 8.38, P < 0.001 \)) (Fig. 4). In contrast, in the absence of ants over 13 replicates, only five crawlers made it to the first lemon, and none made it to lemons 2–4 (Fig. 4).

Ability of Scale Crawlers to Remain Attached to *C. montrouzieri* During Flight. Initial crawler density had a significant effect on the number of crawlers of *A. nerii* “picked up” by individuals of *C. montrouzieri* before release (high crawler density, mean ± SE = 84.14 ± 3.12; versus low crawler density, 30.11 ± 1.64; \( F_{1.394} = 158.73, P < 0.001 \)) (Fig. 5). The number of crawlers remaining attached declined over time (\( F_{3.394} = 314.29, P < 0.001 \)), but even 60 min after their release, individuals of *C. montrouzieri* were still carrying a substantial number of crawlers (6.32 ± 0.55 and 3.24 ± 0.27 in the high and low crawler density trials, respectively) (Fig. 5).

Discussion

Crawlers of all four diaspindid scale species showed the same morphological features at the tip of their legs,
density of 3.4 crawlers per cm², would pick up at least through an area harboring crawlers of increasing size of the vector: the larger βy vector number of crawlers that attached to a vector insect the area for 5 min. Unsurprisingly, we found that the one crawler in only one minute, although this number average, a single adult of number of them climbed onto the vector insect. On that when crawlers were exposed to vector insects, a attached by their suction cup to the elytron of a coc-cinellid beetle. In our attachment bioassays we found that when crawlers were exposed to vector insects, a number of them climbed onto the vector insect. On average, a single adult of C. montouzieri walking through an area harboring crawlers of A. nerii at a density of 3.4 crawlers per cm², would pick up at least one crawler in only one minute, although this number did not increase significantly if the beetle remained in the area for 5 min. Unsurprisingly, we found that the number of crawlers that attached to a vector insect increased with both increasing crawler density and increasing size of the vector: the larger fly vector M. domestica acquired more crawlers than D. melanogaster; and, although tested in different bioassays, the larger beetle vector C. montouzieri seemed to acquire more crawlers than L. lophan-thiae. In the next set of bioassays, we showed that these attached crawlers could be moved by the vector insect, at least over short distances in the laboratory, before settling on a suit-able substrate. A substantial number of crawlers set-tled on the lemons in the cage experiment for both M. domestica and C. montouzieri (Fig. 3). Argentine ants also were successful in transporting crawlers to the lemons (Fig. 4). This first group of bioassays did not necessarily require the crawlers to be strongly at-tached to the vector insect to be transported to a suitable substrate for crawler settlement, because that substrate was always <1 m away. However, the ex-periment with the C. montouzieri beetles in the small room showed that at least some crawlers were so well attached that they remained attached even after a flight of at least 2 m. Our experimental setup probably resulted in some of the beetles flying over even longer distances, either because they did not fly directly to the glass, and/or they did not stay there for the du-ra-tion of the study. However, 20 min after release, ≈30% of the original number of crawlers attached to the beetles exposed to the high crawler density re-mained attached, and after one hour, 8% of the original number were still attached (Fig. 5). We do not know if the crawlers were lost during the flight or if they disembarked after the beetles had landed on the win-dow. Nevertheless it is clear that once attached to a vector, a crawler can remain there for a considerable time and potentially be transported over a consider-able distance.

In most of these experiments, we used high numbers of crawlers to allow the crawlers to attach themselves to the vector insects. It is unlikely that in the field such high densities are often found. However, it is clear that the crawlers do not have too much trouble attaching themselves to other insects and that they can remain attached to these vectors even during flight. How commonly the crawlers attach themselves in the field remains to be established. All insects used in our tests seemed to end up with at least some crawlers attached to them. This may either be the result of the high crawler densities that we applied or may indicate that the crawlers do not have a preference for a particular vector. Although the phoretic relationships in mites are often specific, i.e., a particular phoretic mite spe-cies will only be found on a particular vector, there are also mite species that do not seem to be vector specific at all. For example, the species Histio-gaster arbo-signis Woodring (Acarina: Acaridae) has been found to use >40 vector species belonging to three insect orders (O’Connor 1990); Carpoglyphus lactis (L.) (Acarina: Carpoglyphidae), has been found on the head and tongues of at least nine species of nymphalid butter-flies (Treat 1975).

It is interesting to note that the behavior of crawlers thought to be associated with take-off in the wind resembles the behavior associated with mounting on a vector insect in some phoretic mites. Binns (1979) describes the perching behavior of Scutacarus baculi-tarus Mahunka (Acarina: Scutacaridae) mites used to make contact with their phoretic vector, a phorid fly. The mites will stand up straight on their hind legs (fourth legs) with their anterior legs held out. The mites reacted very rapidly, and attached themselves to the structure touching their legs. In observations by Binns (1979) they attached themselves to a fungal hypha that was used to elicit the response. A similar behavior is thought to be associated with aerial dis-persal in the coccid scale Pulvinaria mesembryanthem-i (Vallot) (Hemiptera: Coccidae) and Pulcinaria delotti Gill (Hemiptera: Coccidae) (Washburn and Washburn 1984). They describe the behavior as follows: “Some crawlers lifted both the pro- and meso-thoracic legs, supporting themselves only on the metathoracic legs. In this standing posture the longi-tudinal axis of the crawler body was 45° to 90° to the
substrate, and this posture was held until they were blown from the arena.” We observed a similar posture taken by the oleander scale crawlers when they were walking around on a glass microscope slide (R.S., unpublished data).

Our study shows that other insects can transport crawlers from one place to another where they dismount and successfully establish on a new substrate. This transport can take place if the vector insect only walks but also if flight is involved. Our results with oleander scale crawlers indicate that—at least for this species—many different vector insects can provide transport. Although phoretic transport of crawlers has been shown in other scale insect species, we found only a single report in the literature where diaspidid scale crawlers were shown to be transported and this involved crawlers of the San Jose scale, *Diaspidiotus perniciosus* (Comstock), being transported by different ant species (Marek 1952). This reference is not widely cited in the English literature but was cited by Beardsley and Gonzalez (1975), stating that “A report (Marek 1952) that San Jose scale crawlers fasten themselves to legs and other parts of ants, and are transported in a phoretic manner, needs to be confirmed.”

Given that most armored scale species have relatively low lifetime fecundity, in retrospect it seems obvious that wind dispersal is likely not the only means of scales settling on new host plants. Koteja (1990) noted that “Total fecundity is low in the Diaspididae. Most species produce 50–150 offspring”. With this low fecundity and no evidence that wind dispersal is directed, the chance of a monophagous crawler landing on a suitable host plant is low. One exception to this is the scale *A. tegalensis*, which is found on sugarcane and produces 700–800 progeny (Greathead 1972). We believe it is not a coincidence that wind dispersal has been shown to be an important method by which this species disperses (Greathead 1972, 1975, 1990).

Crawlers obviously can be dispersed by wind. Our initial attempts at trying to study wind dispersal of oleander scale crawler were similar to observations by Willard (1973), with California red scale, *Aonidiella aurantii* by Willard (1973), with California red scale, *oleander scale crawlers* were similar to observations of *D. perniciosus*; Alex Gery for *M. domestica*; Len Nunney for *D. melanogaster*; Michael Rust for *L. humile*; and Lindsay Robinson, Alan Urean, and Pamela Watkins for technical assistance. This work was supported in part by grants to R.S. and J.G.M. from the California Avocado Commission.

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