

ABIOTIC AND BIOTIC PEST REFUGES HAMPER BIOLOGICAL CONTROL OF MEALYBUGS IN CALIFORNIA VINEYARDS

K.M. Daane,¹ R. Malakar-Kuenen,¹ M. Guillén,² W.J. Bentley³,
M. Bianchi,⁴ and D. González,²

¹ Division of Insect Biology, University of California,
Berkeley, California, U.S.A.

² Department of Entomology, University of California,
Riverside, California, U.S.A.

³ University of California Statewide IPM Program, Kearney Agricultural Center,
Parlier, California, U.S.A.

⁴ University of California Cooperative Extension,
San Luis Obispo, California, U.S.A.

INTRODUCTION

Four mealybug species cause economic damage in California vineyards. These are the grape mealybug, *Pseudococcus maritimus* (Ehrhorn); obscure mealybug, *Pseudococcus viburni* (Signoret); longtailed mealybug, *Pseudococcus longispinus* (Targioni-Tozzeti); and vine mealybug, *Planococcus ficus* (Signoret) (Godfrey *et al.*, 2002). The grape, obscure, and longtailed mealybugs belong to the *Pseudococcus maritimus-malacearum* complex—a taxonomically close group of mealybugs (Wilkey and McKenzie, 1961). However, while the origins of the grape and longtailed mealybugs are believed to be in North America, the ancestral lines of the obscure mealybug are unclear. Regardless, these three species have been known as pests in North America for nearly 100 years. The vine mealybug, in contrast, was first identified in California in the Coachella Valley in the early 1990s (Gill, 1994). It has since spread into California's San Joaquin Valley and central coast regions, with new infestations reported each year.

The four species are similar in appearance; however, mealybugs in the *P. maritimus-malacearum* complex have longer caudal filaments than vine mealybug (Godfrey *et al.*, 2002). There are also some biological differences that change the level of economic damage and the effectiveness of biological control agents. For example, mealybugs in the *P. maritimus-malacearum* complex can feed on the vine's fruit, trunk, canes, or leaves (Geiger and Daane, 2001). The vine mealybug feeds on these same plant parts and also on the vine roots, where it finds some protection from temperature extremes and parasitoids (Malakar-Kuenen *et al.*, 2001). All four species excrete honeydew as they feed, which promotes sooty mold fungi (Flaherty *et al.*, 1992) and lowers grape bunch quality (Geiger *et al.*, 2001). However, the vine mealybug excretes far more honeydew per individual than the three species in the *P. maritimus-malacearum* complex. Also, vine mealybug can have four to six generations per year (Malakar-Kuenen, 2001), nearly twice as many as the grape mealybug (Geiger and Daane, 2001), which increases its potential for rapid increase and economic damage.

A number of predators have been recorded attacking mealybugs in California. This group includes lady beetles (*Cryptolaemus montrouzieri* Mulsant, *Hyperaspis* sp. and *Scymnus* sp.), green lacewings (*Chrysopa oculata* Say, *Chrysopa nigricornis* Burmeister, *Chrysopa coloradensis* Banks, *Chrysoperla comanche* Banks and *Chrysoperla carnea* [Stephens]), brown lacewings (*Hemerobius californicus* Banks), and a cecidomyiid fly (*Dicrodiplosis californica* Felt) (Daane *et al.*, 1996; Geiger and Daane, 2001). Spiders are the most abundant insect predators in California vineyards (Costello and Daane, 1999); however, their role in mealybug control is unknown. While many of these predators are present in vineyards, their ability to provide mealybug control (unless mass-released) has not been demonstrated.

Most successful mealybug biological control programs have used encyrtid parasitoids. Indeed, both the grape and longtailed mealybugs have long been reported to be primarily controlled by a complex of encyrtids. For example, Clausen (1924) recorded more than 80% parasitism of grape mealybug in the San Joaquin Valley; five species were reported, with *Zarhopalus corvinus* (Girault) being the dominant parasitoid. Recent surveys showed that the two dominant species are *Acerophagus notativentris* (Girault) and *Pseudaphycus angelicus* (Howard) (Daane et al., 1996, Geiger and Daane, 2001). In contrast, no parasitoids were reared from thousands of obscure mealybugs collected from central coast vineyards between 1992 and 1994 (Daane, unpub.). Similarly, initial surveys showed low parasitism levels of the vine mealybug in the Coachella Valley (González, unpub.).

Here, we discuss the effectiveness of recent classical biological control efforts against the obscure and vine mealybugs. In 1996, two parasitoids of the obscure mealybug, *Pseudaphycus flavidulus* (Brethes) and *Leptomastix* nr sp. *epona*, were imported into California, cleared through quarantine, and released into central coast vineyards between 1997 and 1999. Recoveries of both species were made during the release period. In a separate program, coordinated by D. González, parasitoids were imported for vine mealybug control (González, 1998). Five parasitoid species were imported, including *Anagyrus pseudococci* (Girault) and *Leptomastidea abnormis* (Girault). These last two species appeared to be the most effective and were the ones released in the Coachella Valley (both parasitoid species were already present in California but the imported material is considered to be better adapted to desert conditions, González, unpub.).

For both the obscure and vine mealybug programs, the low levels of parasitism observed were attributed, in part, to ant interference. Ants collecting honeydew from homopterans have long been known to interfere with parasitoid activity (e.g., Bartlett, 1961; Traniello, 1989). Here, we compare parasitoid effectiveness in projects against the obscure mealybug (central coast) and vine mealybug (Coachella Valley and San Joaquin Valley). We discuss the different regional influences caused by different ant species and mealybug biology. Finally, we discuss the importance host refuge size (from parasitoids) and the role ants might play as a “biological force” in the expansion of host refuges.

MATERIAL AND METHODS

Field Sites

Obscure mealybug. In 1999, two vineyards were used to determine (1) the establishment and the effectiveness of *P. flavidulus* and *L. epona* releases in the central coast region (San Luis Obispo County) and (2) the influence of the Argentine ant, *Linepithema humile* (Mayr), on parasitoid effectiveness and distribution. At each vineyard, a 1-acre block (12 rows by 50 vines) was selected in which 30, five-vine plots were established. Treatments (ants or no ants) were assigned in a randomized block design. Ants were excluded by coating the basal 6–9 cm of the vine trunk with Tanglefoot (Tanglefoot, Grand Rapids, Michigan, U.S.A.), which was reapplied weekly. On each sample date, one vine from each five-vine plot was sampled. Samples were taken throughout the season on a biweekly or monthly schedule, depending on seasonal ant activity.

In 2001, a survey of mealybugs and parasitoid activity was made at the release sites and surrounding vineyards to determine parasitoid establishment and effectiveness.

Vine mealybug. Field studies were conducted in 2000 and 2001 in vineyards in two disparate grape growing regions: three vineyards in the Coachella Valley (Riverside County) and three vineyards in the San Joaquin Valley (Fresno County). Previous observations suggested that levels of ant tending and parasitoid activity varied greatly between these two regions. Therefore, the goal of this study was to compare vine mealybug and parasitoid population dynamics between the desert region (Coachella Valley) and the cooler San Joaquin Valley. At each location three blocks were studied to determine (1) the seasonal abundance and within-vine distribution of the vine mealybug and its parasitoids and (2) the influence of ants on parasitoid efficiency. Ants present were *Solenopsis xyloni* McCook and *Formica aerata* (Fransuor) in the San Joaquin Valley and *Formica perpilosa* Wheeler and *Solenopsis molesta* (Say) in the Coachella Valley. The six vineyards sampled represented three cultivars (Thompson Seedless, Flame Seedless, and Superior), and both drip and furrow irrigation systems; however, none of the vineyards were treated with insecticides for mealybug control and in each vineyard the sample methodology for mealybugs was similar between and within each region.

Mealybug, Parasitoid, and Ant Sampling

There are no simple and effective methods to monitor most mealybug species (but see Millar *et al.*, 2002). For both the obscure and vine mealybug studies we used a combination of timed counts and destructive sampling techniques (see Geiger and Daane, 2001). We used timed counts to estimate mealybug numbers. Each vine was divided into sections (e.g., lower trunk, cordon [the horizontal supporting arms or scaffolding of the vine], canes, leaves, grape bunches), and each section was searched for 3 or 5 minutes (sample-time varied between years and projects). The developmental stage and condition (alive or parasitized) of all mealybugs found were recorded. To complement these “timed” counts, we periodically took “destructive” samples in which all the bark, grape canes, leaves, spurs and fruit bunches on each of three vines (in each vineyard) was collected. The material was brought to the laboratory and dissected to determine the number, developmental stage and condition of the mealybugs. With the exception of crawlers, all mealybugs in samples were held for parasitoid emergence.

Information about parasitoids was collected during both the timed samples and the destructive samples. Additionally, each month we collected ca 100 mealybugs (all stages pooled, from second instars through adults), which were placed individually in gelatin capsules and held for parasitoid emergence. In the vine mealybug study, we also collected mealybugs from (1) exposed locations (e.g., leaves or grape bunches) and (2) hidden locations (e.g., deep under the bark). These mealybugs were also held in gelatin capsules for parasitoid emergence.

Ant foraging activities were estimated by a 2-minute timed count of ants moving up and down the trunk or along the cordon. The presence of foraging ants was also noted on different vine sections.

RESULTS

Obscure Mealybug

Surveys in 2001 found evidence that *P. flavidulus* had established, but *L. epona* was not recovered. Mealybug densities were high (more than 20% of grape bunches were infested) unless the vineyard block had been treated with an insecticide. *Pseudaphycus flavidulus* was found in four of six vineyard blocks surveyed, including the two release sites. Levels of parasitism were low (with less than 5% of the observed mealybugs being mummified).

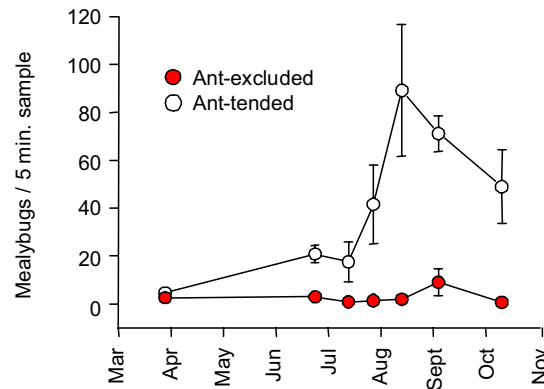


Figure 1. Ant exclusion trial in a central coast vineyard showed significantly more mealybugs on ant-tended vines. Edna Valley Vineyards, San Luis Obispo, California, 1999.

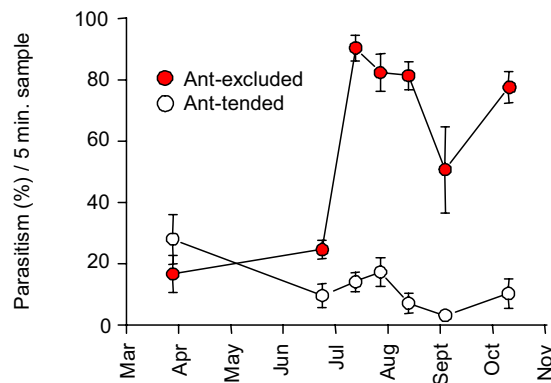


Figure 2. Ant exclusion trial in a central coast vineyard showed significantly less parasitoid activity on ant-tended vines. Edna Valley Vineyards, San Luis Obispo, California, 1999.

In all vineyard blocks that were infested with mealybugs, there were also large populations of the Argentine ant. In one of the ant exclusion trials (Edna Valley Vineyards), the Tanglefoot barrier effectively prevented ants from foraging on treated vines. Mealybug densities were significantly reduced (Fig. 1) and parasitism levels increased (Fig. 2) when ants were completely excluded. At the site of this trial, 72% of all parasitoids recovered were *P. flavidulus* and 18% were *L. epona*. In the second vineyard block with an ant exclusion trial (McGregor Vineyard), the Argentine ant population was much larger and ants occasionally broke through the sticky barriers by walking over a bridge of dead ants, even though the Tanglefoot was reapplied weekly. At that site, the between-treatment differences in mealybug density and percentage parasitism were not nearly as great (data not shown). When ant exclusion was only partial, only *P. flavidulus* was recovered. In laboratory experiments, *P. flavidulus* was more efficient at foraging for mealybugs in the presence of the Argentine ant, as compared with *L. epona* (data not provided).

Vine Mealybug

Seasonal abundance and distribution. In the Coachella Valley, vine mealybug density increased rapidly to an early peak in April, followed by a rapid decline after harvest (from late April through June in the Coachella Valley) and then a relatively low, but steady density for the remainder of the season (Fig. 3). For the three vineyards monitored, peaks in crawler density suggest the occurrence of four generations (data not provided).

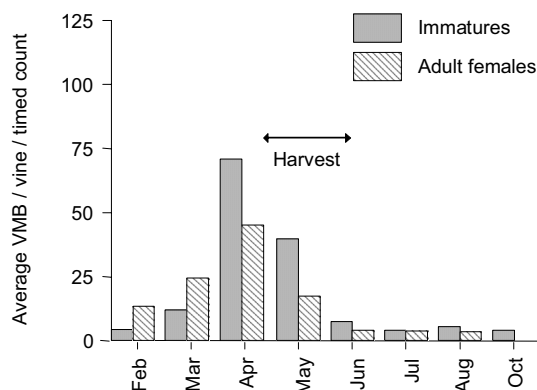


Figure 3. Seasonal abundance of immature (crawlers excluded) and adult vine mealybug in the Coachella Valley. Data combined from three vineyard blocks sampled in Coachella and Thermal, California, 2001.

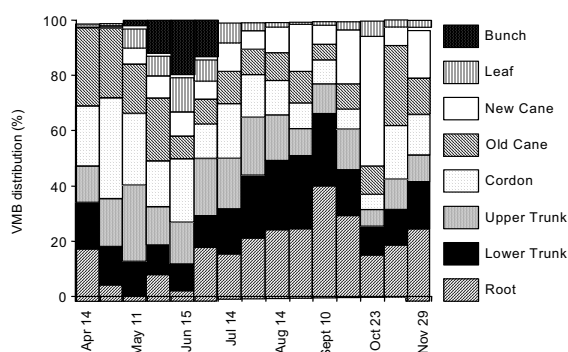


Figure 4. Vine mealybug population distribution (%) on the vine in the Coachella Valley. Note a continual presence of mealybugs on the roots. Data combined from three vineyard blocks sampled in Coachella and Thermal, California, 2001.

Changes in the vine mealybug within-vine distribution showed greater seasonal variation than did mealybug density. The most notable aspect of the within-vine distribution is that some vine mealybugs were found on the roots on all sample dates (Fig. 4). The proportion of the mealybug population on the roots was smallest during the late April through June period, when grape bunches are maturing and when the mealybug density was peaking. As the vine mealybug population entered the warmest summer months the proportion of the population found underground and on the lower portion of the vine trunk increased. These data suggest that the vine mealybug was seeking protection (probably from heat) underground.

There was also a clear association with ants, and we believe the underground habitat would not be nearly as suitable if not for ants (mostly *F. perpilosa*) tending the mealybugs and improving the underground habitat by moving soil away from the root sections and creating small caverns for mealybugs along the ant trails. The ants also removed honeydew, which kept the underground refuge habitable. Above ground, most of the vine mealybug feeding, even on the new canes, was under a thin bark layer. In fact, very few of the mealybugs were ever truly in exposed locations (leaves and fruit) for long periods. The greatest period of exposure was from May to June, when the mealybugs began feeding on leaves and grape bunches. Ants did not tend these sections as consistently or aggressively as those they did the roots and trunk sections.

In the San Joaquin Valley, the vine mealybug seasonal abundance pattern showed an initial increase about one month later than in the Coachella Valley (compare Figs. 3 and 5). Unlike in the Coachella Valley, mealybug abundance continued to increase until July and August, followed by a reduction in August and September (Fig. 5). The late-season reduction was not accompanied by an increase in summer temperatures but was associated with increased parasitism levels. All stages were found throughout the summer feeding on leaves and canes in exposed locations, suggesting that San Joaquin Valley temperatures had little effect on vine mealybug densities. For example, there appears to be five to six generations per year in the San Joaquin Valley, which is one or two more than in the Coachella Valley. These results suggest that vine mealybug may have upper temperature thresholds that either slow development or increase mortality (masking the increase in density of each new generation) of the vine mealybug populations in the Coachella Valley.

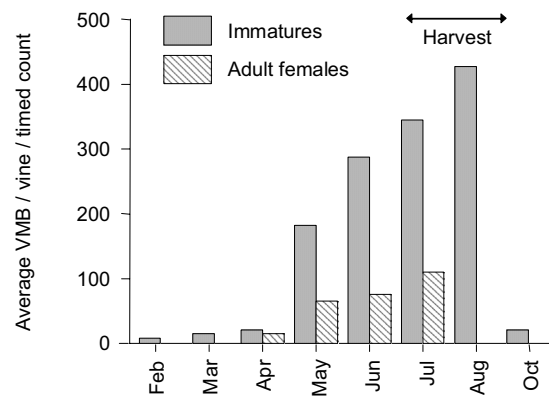


Figure 5. Seasonal abundance of immature (crawlers excluded) and adult vine mealybug in the San Joaquin Valley. Data are from a raisin vineyard near Del Rey, California, 2001.

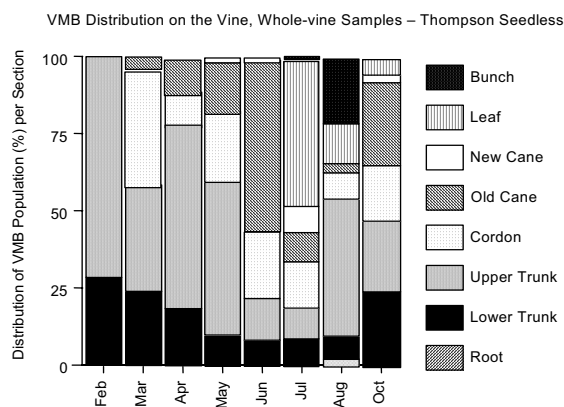


Figure 6. Vine mealybug population distribution (%) on the vine in the San Joaquin Valley. Data are from a raisin vineyard near Del Rey, California, 2001.

In both the Coachella and San Joaquin valleys, there was a seasonal movement of mealybugs vertically up the vines that corresponded with warmer spring temperatures and the maturation of the grape crop. However, in contrast with the Coachella Valley, few mealybugs overwintered on the roots in the San Joaquin Valley. In fact, the greatest proportion of the vine mealybug population was

found on the upper trunk, cordon, or canes (Fig. 6). Perhaps more surprising, there was no summer migration down to cooler areas underneath the soil during the months of July and August, as was found in the Coachella Valley vineyards. Throughout the growing season, a significant proportion of vine mealybugs remained on the canes and the leaves in exposed positions.

As in the Coachella Valley, in the San Joaquin Valley the ants (*F. aerata* and *S. xyloni*) tended mealybugs more extensively near the ground level. While ants were observed on the trunk, leaves, and canes, the mealybugs in those locations were left unattended for longer periods. Unlike in the Coachella Valley, in the San Joaquin Valley we did not observe a close association between ants (*F. aerata* and *S. xyloni*) and mealybugs at the base of the vine's trunk.

Resident parasitoid effectiveness. In the Coachella Valley, mummies or parasitoids were recovered from March through September. Two encyrtid primary parasitoids were recovered—*A. pseudococci* (75% of all recovered parasitoids) and *L. abnormis* (13%)—as well as a signiphorid hyperparasitoid, *Chartocerus* sp. (12%). Levels of parasitism were low, never exceeding 12% of the collected mealybugs on any sample date. *Anagyrus pseudococci* and *L. abnormis* were recovered at the end of March and then sporadically until the beginning of October. No parasitism was observed from mid-October until March in the following season.

While the largest numbers of mealybugs were on the roots and lower trunk during most of the season, no parasitoids were recovered from the root zone, and very few were recovered from the lower trunk (Fig. 7). However, other researchers have found mummified mealybugs in the root zone (K. Godfrey, California Department of Food and Agricultural, pers. comm.); although the mealybugs may have been parasitized above ground and then later moved or were carried by ants underground.

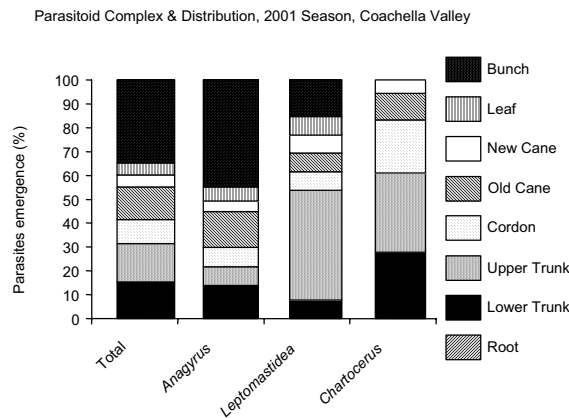


Figure 7. Data combined from all sample methodologies and all vineyards sampled show no parasitoids were recovered from the root sections. Coachella and Thermal, California. 2001 season.

Parasitism levels were much greater in the San Joaquin Valley (Fig. 8) than in the Coachella Valley, with *A. pseudococci* being the dominant parasitoid. From biweekly collections of live mealybugs, the first parasitoids were reared from February collections; however, the percentage parasitism remained low (less than 2%) until June. As the mealybugs moved to the leaves in July, there was a dramatic increase in parasitism to 70–80% of exposed vine mealybugs. By late October, the only live mealybugs were those in hidden locations, deep under the bark and inside the feeding holes of wood boring larvae. Of these mealybugs in hidden locations, less than 2% were parasitized (data combined from all three vineyards sampled). Corresponding to the seasonal period of increased parasitism, we found the greatest proportion of vine mealybug population had moved to feeding locations on the

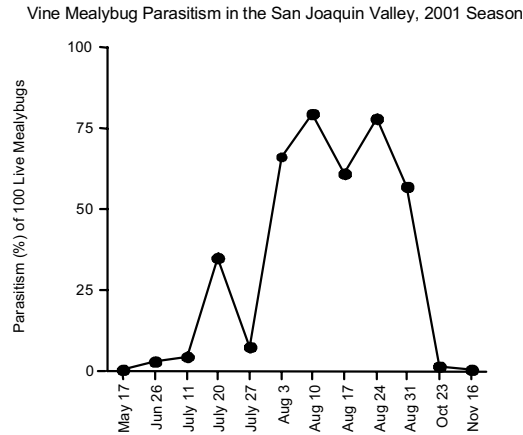


Figure 8. In the San Joaquin Valley, there was high parasitoid activity after August. Most (greater than 90%) parasitoids recovered were *Anagyrus pseudococci*. Sanger, California. 2001 season.

canes and leaves, which often placed them in exposed locations. While foraging *F. aerata* were present on almost every vine, the ants only occasionally tended mealybugs in the upper vine sections. In terms of available refuge, these mealybugs were leaving vine sections where either the vine structure or the foraging ants provided relatively good protection from parasitoids and moving to sections that were more exposed to parasitoids, perhaps for a better food source.

DISCUSSION

For both the obscure mealybug on the central coast of California and the vine mealybug in the Coachella Valley, parasitism levels were low. Data collected on percentage parasitism in ant exclusion studies and from observations made on ant foraging suggest that ants reduced parasitoid effectiveness. As noted previously, ants have long been associated with the interference of biological control. However, comparing the ant tending in the three mealybug studies (central coast, Coachella Valley and San Joaquin Valley), we found very different types of ant-mealybug-parasitoid interactions. In the central coast, the Argentine ant populations were extremely dense throughout the vine, providing an almost continual tending of all mealybugs present anywhere on the vine. In the Coachella Valley, the dominant ant (*F. perpilosa*) was very active near the vine trunk and provided a better underground habitat (on the vine roots) for the mealybugs by creating free space in their network of tunnels and removing honeydew in this enemy-free space. This close association between ant and mealybug became crucial during seasonal periods when most vine mealybugs were underground or near the soil surface. In the Central Valley, the primary ants (*F. aerata* and *S. xyloni*) did not appear to have as close an association with the vine mealybug as ant species in the other regions studied. *Formica aerata*, in particular, provided neither improved shelter nor constant tending and honeydew removal. In this region, as the vine mealybugs moved up the vine and onto the leaves, they were more exposed to parasitism. Still, high rates of parasitism late in the season were not enough to provide economic control (Malakar-Kuennen and Daane, unpub.).

We think that a better understanding of the effects of foraging ants can be had by describing the area of refuge that they provide to mealybugs. In refuge theory (enemy-free space), the proportion of the host (here, mealybug) population in a refuge is immune to attack from natural enemies (Hawkins *et al.*, 1993); therefore, a large refuge allows a greater proportion of the host population to escape natural enemies. We found that mealybug-tending ants in the three systems studied created different sized refuges from parasitoids. In the central coast vineyards studied, the obscure mealybug was in exposed locations on leaves or canes during a good portion of the season. However the aggres-

sive tending by Argentine ants created a large biological refuge that covered almost the entire vine. In the Coachella Valley, the vine mealybug was not in exposed locations for much of the season, with a large proportion of the population residing underground on the roots throughout the year. This underground habitat was created or improved by mealybug tending ants, especially *F. perpilosa*, which clearly enlarged the root habitat available for vine mealybug and moved mealybugs throughout the protective refuge. In the San Joaquin Valley, the two ant species found associated with the vine mealybug (*F. aerata* and *S. xyloni*) were neither in larger numbers, like the Argentine ant in the central coast vineyards, or in close association with the mealybugs, like *F. perpilosa* in the Coachella Valley. As a larger proportion of the San Joaquin Valley vine mealybug population moved onto exposed locations during the summer months, there was no corresponding movement of *F. aerata* with the mealybugs, which were left exposed and available to *A. pseudococci* attack.

In this study, we investigated three different mealybug systems in California vineyards, all three with important ant-mealybug interactions. In each case there was a different relationship between ants, mealybugs, and their parasitoids. These results would not have been predicted from a literature review or observations in other regions. For one of our studied insects, the vine mealybug, parasitoids are reported to play an important role in pest suppression (Berlinger, 1977; Duso, 1989). However, the prolonged periods of underground habitation, with ant tending, are not reported for vineyards in other regions. Similarly, while a certain level of parasitoid mortality from foraging ants might be predicted to occur anywhere, the size and aggressiveness of California populations of the invasive Argentine ant, while tending the obscure mealybug, are not duplicated in the ant's South American home range, making field comparisons of impact on parasitoids difficult. We have often observed Argentine ants to catch and kill adults of *P. flavidulus* and *L. epona* immediately after their release. Other researchers have also observed homopteran-tending ants disturbing or killing adult parasitoids (Hübner and Völkl, 1996; Heimpel *et al.*, 1997; Völkl and Kroupa, 1997; Barzman and Daane, 2001), but placing this interference in the context of a biological increase in the pest refuge has not been commonly discussed. These data illustrate that it is difficult to predict natural enemy effectiveness before field release from observations of natural enemy effectiveness in the country of origin or in the laboratory.

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