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Foraging Distance of the Argentine Ant in California Vineyards

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Abstract

Argentine ants, *Linepithema humile* (Mayr) (Hymenoptera: Formicidae), form mutualisms with hemipteran pests in crop systems. In vineyards, they feed on honeydew produced by mealybugs and soft scales, which they tend and protect from natural enemies. Few options for controlling Argentine ants are available; one of the more effective approaches is to use liquid baits containing a low dose of an insecticide. Knowledge of ant foraging patterns is required to estimate how many bait stations to deploy per unit area. To measure how far ants move liquid bait in vineyards, we placed bait stations containing sugar water and a protein marker in plots for 6 d, and then collected ants along transects extending away from bait stations. The ants moved an average of 16.08 m and 12.21 m from bait stations in the first and second years of the study, respectively. Marked ants were found up to 63 m from bait stations; however, proportions of marked ants decreased exponentially as distance from the bait station increased. Results indicate that Argentine ants generally forage at distances <36 m in California vineyards, thus suggesting that insecticide bait stations must be deployed at intervals of 36 m or less to control ants. We found no effect of insecticide on distances that ants moved the liquid bait, but this may have been because bait station densities were too low to affect the high numbers of Argentine ants that were present at the study sites.

Key words: ant bait, foraging distance, grapes, invasive species, *Linepithema humile*

The Argentine ant, *Linepithema humile* (Mayr) (Hymenoptera: Formicidae), is a widespread and ecologically destructive invasive insect (Suarez et al. 2001). It has reached high numbers in urban, natural, and agricultural systems (Holway et al. 2002b) and threatens native ecosystems in North America, South Africa, Europe, and Hawaii (Suarez et al. 2001, Wetterer et al. 2009). It was first found in California in 1907 and is now widespread in disturbed low-elevation areas where soil moisture is not limiting (Suarez et al. 2001, Menke and Holway 2006, Brightwell and Silverman 2009). The Argentine ant's success and impacts are largely due to its competitive abilities. It forms highly cooperative supercolonies (Holway et al. 1998, Tsutsui et al. 2000), and it outcompetes native ants by rapidly recruiting to food sources in high numbers (Human and Gordon 1996, van Wilgenburg et al. 2010). The effects of Argentine ants can extend beyond native ant populations to other invertebrates (Human and Gordon 1997) and even to communities of vertebrates (Suarez and Case 2002) and plants (Rodriguez-Cabal et al. 2009).

In crop systems, Argentine ants contribute to pest outbreaks through their association with honeydew-producing hemipterans such as mealybugs, aphids, and scale insects. Argentine ants feed

almost exclusively on honeydew in some environments (Tillberg et al. 2007). In return, ants protect hemipteran pests from many natural enemy species (Helms 2013, Sime and Daane 2014, Calabuig et al. 2015) and may increase the abundance of several pest species in vineyards (Daane et al. 2007, Charles et al. 2010, Chong et al. 2010). In California's coastal vineyards, the Argentine ant forms mutualisms with the native grape mealybug, *Pseudococcus maritimus* (Ehrhorn) (Hemiptera: Pseudococcidae), and the invasive obscure mealybug, *Pseudococcus viburni* (Signoret) (Hemiptera: Pseudococcidae) (Daane et al. 2007). These mealybugs began reaching more damaging levels in the late 1980s, when the Argentine ant became more prevalent in California vineyards (Phillips and Sherk 1991). An additional mealybug, the invasive *Planococcus ficus* (Signoret), is also tended by the Argentine ant and has become the most damaging mealybug pest in California vineyards since its arrival in California in the early 1990s (Daane et al. 2013). In a California coastal wine-grape vineyard, mealybug numbers were up to 82 times higher on vines tended by Argentine ants than on ant-excluded vines (Daane et al. 2006), and researchers later reported that using insecticide to suppress ant numbers led to lower mealybug density and crop

damage (Daane et al. 2008). Mealybugs also transmit plant viruses (Almeida et al. 2013).

Options for controlling Argentine ants in crop systems are limited. Chemical sprays kill or repel foragers but are unlikely to affect queens or larvae in ant colonies, and foragers comprise only a small portion of the colony and will be quickly replaced (Vega and Rust 2003). Moreover, these chemicals degrade within 30 d (Rust et al. 1996) and may harm beneficial arthropods and the environment. An alternative approach is to use baits that contain a slow-acting insecticide (Hooper et al. 1998, Krushelnicky and Reimer 1998, Klotz et al. 2004). Argentine ants recruit colony members to bait stations along persistent pheromone trails (Silverman and Roulston 2003), and foragers then return to the nest with the bait and share it with nestmates through trophallaxis (Rust et al. 2004). The insecticides in baits should act slowly, thereby maximizing the number of workers, immatures, and queens that are exposed and eventually killed (Silverman and Brightwell 2008). In addition, the small amounts of insecticide that are deployed in baits are unlikely to impact the environment, and bait stations can be designed to prevent impacts to beneficial insects such as mealybug parasitoids and pollinators (Taniguchi et al. 2005, Daane et al. 2006).

Two main types of ant baits are available: dry granular baits and liquid sucrose-based baits. Liquid-sucrose baits are more attractive to Argentine ants than granular baits (Klotz et al. 2002) because they more closely mimic hemipteran honeydew, which is typically the main food source of Argentine ants (Silverman and Brightwell 2008). Small amounts of several insecticides (e.g., boric acid, thiamethoxam, imidacloprid, spinosad) can suppress Argentine ants when added to liquid-sucrose baits (Klotz et al. 2004, Cooper et al. 2008, Brightwell et al. 2010). For economic and logistical reasons, growers will be more likely to use baits if they can be deployed at relatively low densities. A thorough knowledge of ant-foraging patterns is necessary to determine how many bait stations to deploy per unit area (Daane et al. 2008). In this study, we used immunological markers (Hagler and Jackson 2001) to measure whether the presence of insecticide-treated bait reduces ant movement; how far ant bait is moved by foraging Argentine ants in vineyards; and whether bait movement is greater along vine rows than across rows. Vineyard rows provide continuous grape vine habitat, connected by wire trellising; therefore, we expected that ants would move further along than across rows.

Materials and Methods

Experimental Sites

The study was conducted in two commercial vineyards in 2004, using seven different vineyard blocks with high Argentine ant population densities (five blocks were in 'vineyard one' and two blocks in 'vineyard two'), and in 2005, a subset of three of these blocks was studied. The vine blocks were Pinot Noir cv., Pinot Meunier cv., and Chardonnay cv., managed for premium wine grapes. No insecticides were applied at these sites during the study, although sulfur was used to control powdery mildew. Each block was split into two adjacent plots of approximately 100 × 100 m in area (30–40 vineyard rows), and each plot was centered on a single grape vine, where a bait station was placed. Bait stations in adjacent plots were at least 80 m apart (range 81–172 m). Bait stations were based on Reiersen et al. (1998) ant monitoring tubes and consisted of 50-ml plastic Falcon centrifuge tubes filled with 45 ml of 25% sugar water. Holes were drilled into the tubes' screw-on caps, which were fitted over squares of permeable Weed Block mesh (Easy Gardener Inc., Waco, TX) that allowed ants to extract sugar water but prevented leakage when the

tubes were inverted. Window screen was glued onto the top of the cap, to prevent bees from accessing the sugar water while allowing free movement of Argentine ants. The tubes were tied upside down on grape vine trunks ~0.6 m from the ground using plastic flagging tape.

In 2004, the two plots within each of the seven blocks were randomly assigned to one of two treatments, to receive either nontoxic or toxic bait. In 2005, only nontoxic baits were used in the three tested blocks. In nontoxic plots, the central bait station contained a solution of 25% sucrose (table sugar, by weight) and 0.2% citric acid (Sigma Chemical, St. Louis, MO) as a preservative in distilled water. In toxic plots, dispensers contained a solution of 25% sucrose, 0.2% citric acid, and 0.5% boric acid (Sigma Chemical). To train ants to the locations of the bait stations and increase the consumption of the protein-labeled bait by ants, a 250-ml centrifuge tube containing unlabeled bait was placed on the central vine of each plot 5–9 d before being replaced with protein-labeled bait containing the same ingredients plus 0.5 mg/ml of rabbit IgG protein (Sigma Chemical Co., product number I8140). Preliminary data indicated that IgG was detectable at concentrations above 0.125 mg/ml in ants fed sugar water but was not consistently detectable below this threshold, and that increases in detectability were negligible after 0.5 mg/ml. In 2004, the protein-labeled baits were deployed from 29 June to 3 July (both plots within each block received baits on the same day), and in 2005, all plots received protein-labeled baits on 12 July. Immediately before the protein-labeled bait was deployed, eight ants were collected from four vines immediately surrounding the bait station in each plot, to serve as negative controls for the protein marker. The protein-labeled bait stations remained in the field for 6 d and were replaced every 2 d.

Ants were sampled on the day that the protein-labeled bait stations were removed, 6 d after they were deployed. We chose this time interval because a preliminary laboratory study using whole ant colonies showed that IgG was detectable up to 7 d after ants were fed labeled sugar water but was only marginally detectable after 10 d. Ants were collected using an aspirator and were placed individually into 1.5-ml microcentrifuge tubes before placing them in a cooler. Ants were collected from the vine and from the ground immediately surrounding the vine at each sample location. Searching continued until 16 ants were collected or until 8 min had elapsed; if fewer than 16 ants were collected from the sample vine, additional ants were collected from the two adjacent vines within the same row.

In 2004, ants were sampled along two perpendicular transects running away from the bait station, one running along vineyard rows and the other running across vineyard rows (Fig. 1). Ants were collected from the vine with the bait station and then within the bait station rows at 5, 10, 15, 20, 25, 30, 35, and 40 vines from the bait station (9, 18, 27, 36, 45, 54, 63, and 72 m at vineyard one, and 7.5, 15, 22.5, 30, 37.5, 45, 52.5, and 60 m at vineyard two). The difference in sample distances between the vineyards was because of different vine spacing. Ants were also collected 1, 2, 3, 4, 6, 8, 10, 14, and 18 rows from the bait station (2.5, 5, 7.5, 10, 15, 20, 27, 34, and 44 m) at each vineyard, although row 18 was not sampled in the two blocks at the second vineyard, where blocks were smaller and plots were only 16 rows wide. In 2005, ants were collected along four transects extending away from the bait station along and across rows in all four cardinal directions (Fig. 1); the same transect distances were sampled as in 2004, except that ants were not collected along rows at vine 40 and across rows at row 18, and rows 8 and 11 were sampled (20.0 and 27.0 m from the bait station) in place of vine 10 across rows. Based on results from 2004, we decided that monitoring ants at shorter distances would be more informative

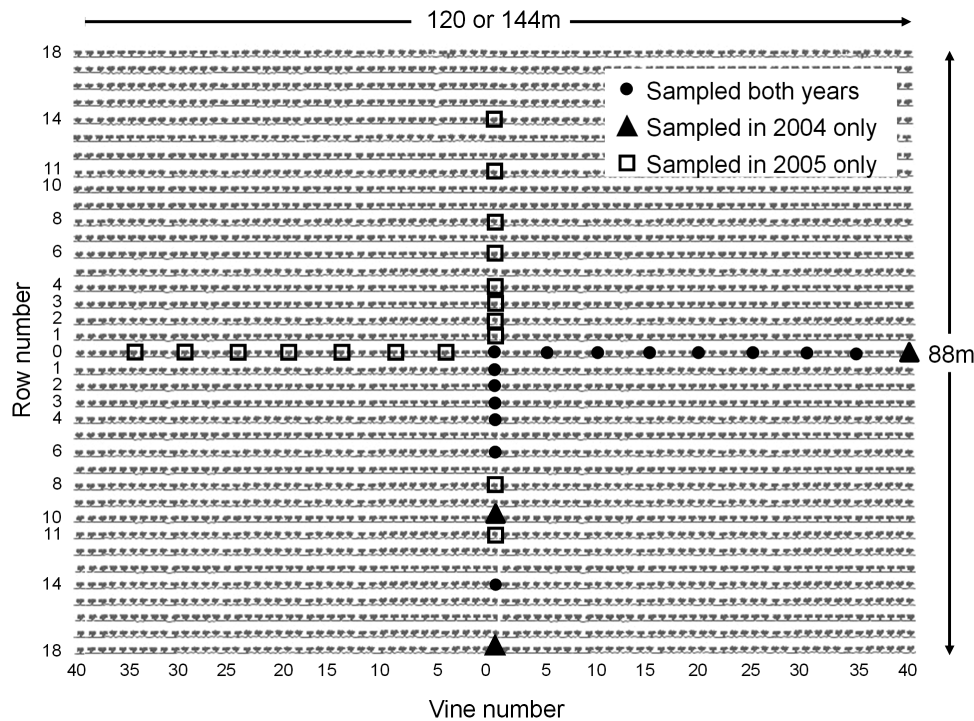


Fig. 1. Locations sampled along transects in both years (closed circles), in 2004 only (closed triangles), or in 2005 only (open squares). In 2004, ants were sampled along two perpendicular transects in each plot extending from the bait station, running either along or across vineyard rows. In 2005, ants were collected along four transects extending along and across rows in all four cardinal directions. In 2004, ants were collected from the vine with the bait station and then along rows at 5, 10, 15, 20, 25, 30, 35, and 40 vines from the bait station and across rows at 1, 2, 3, 4, 6, 8, 10, 14, and 18 rows from the bait station. The same distances were sampled in 2005, except that vine 40 along rows and vine 18 across rows were not sampled, and vines 8 and 11 were sampled rather than vine 10.

than sampling at the furthest distances from bait stations, where marked ants often were not found.

Enzyme-Linked Immunosorbent Assay and Analysis

Ants were stored at -4°C until they could be analyzed for protein presence using the anti-rabbit IgG sandwich enzyme-linked immunosorbent assay (ELISA) described by Hagler et al. (1992). The collected ants were scored positive for the presence of the protein mark if the ELISA optical density value was three standard deviations above the mean for the negative controls (i.e., the ants collected in the immediate vicinity of bait stations before the protein-labeled bait stations were deployed), after Hagler (1997).

The proportion of marked ants were calculated for each transect distance in each plot, and the average and maximum distances that marked ants moved from bait stations were calculated for each direction (along/across rows) in each plot; effects on these parameters were then assessed using mixed-model analysis of variance and the lmer function in R version 3.2.2 (R Development-Core-Team 2015). Transect direction (along/across rows) was included as a fixed factor and block as a random factor in all models; treatment (nontoxic/toxic bait) was included as an additional fixed factor in analyses of 2004 data, and transect distance was included as a fixed factor for analyses of proportions of marked ants. Proportions of marked ants were logit transformed before analysis. Only transect distances that were shared (i.e., roughly equivalent) between the two directions were included in these analyses: for 2004, along rows from vines 5–25 (9–45 m) from the bait station at vineyard one, and along rows from vines 5, 10, 15, 25 and 30 (7.5, 15, 22.5, 37.5 and 45 m) from the bait station at vineyard two, and across rows from vines 4–18 (9.8–44.1 m) from the bait station; for 2005, along rows from vines 5–20 (9–36 m) from the bait station and across rows

from vines 4–14 (9.8–34.3 m) from the bait station. Relationships between proportions of marked ants and transect distance were linear when only these distances were included in analyses, making linear models appropriate. Data from central vines with bait stations were excluded from these analyses because they provided no information about movement of ants.

To examine the possible effects of the insecticide treatment on Argentine ants across the entire data set, proportions of marked ants from plots with nontoxic and toxic baits were fitted to separate negative exponential models that included data from all transect distances (see the following section) because the relationship between proportions of marked ants and transect distance was nonlinear across all transect distances. Parameter estimates did not differ between these curves, indicating that they were similar, and these data are not shown here.

To describe the foraging range of ants, proportions of marked ants out of total ants collected were fitted with a three-parameter negative exponential equation (with a lower limit) using the drm function in R: $f(x) = c + (d - c) \times \exp(-x/e)$, where c is the lower limit, d is the upper limit (intercept), and e indicates decay rate. The upper limit parameter (c) was dropped when not significantly different from 0. Separate models were fitted for each direction (along/across rows), and analyses were run with and without data from central vines with bait stations, to ensure that the high proportions of marked ants recorded at this distance did not inordinately affect the results.

Results

Argentine ants were the only ant species observed at the feeding stations and sample locations. A total of 3,411 and 2,829 ants were

collected and 15.9 and 11.8% scored positive for the protein marker in 2004 and 2005, respectively. On average, marked ants that moved away from bait stations (i.e., excluding ants collected from vines with bait stations) were collected 16.08 m from a bait station in 2004 and 12.21 m from a bait station in 2005. In 2004, no marked ants were collected at the maximum sampled distance across vineyard rows (34 or 44 m) in 7 out of 14 plots; no marked ants were collected in any plots at the maximum sampled distance along vineyard rows (60 or 72 m). In 2005, no marked ants were collected in 4 out of 6 plots at the maximum sampled distance across vineyard rows (34 m) and in 4 out of 6 plots at the maximum sampled distance along vineyard rows (63 m).

In 2004, proportions of marked ants and average and maximum distances that marked ants moved per plot were not affected by insecticide treatment or direction (Table 1). In 2005, proportions of marked ants were significantly higher along than across rows, although the average distance that ants moved did not differ between directions, and maximum distance was affected only marginally (Table 1). In both years, proportions of marked ants declined with distance from bait stations across the subset of transect distances that were included in these analyses (2004: $F_{1,118} = 8.35$, $P = 0.005$; 2005: $F_{1,45} = 11.38$, $P = 0.002$).

The dispersal distances of marked ants across all transect distances were well described by negative exponential decay models in both years (Figs. 2 and 3). The upper limit (d) and decay rate (e) parameters were significant in both directions in both years, whether distance 0 was included in analyses or not, whereas the lower limit (c) was significantly different from 0 only for data collected across rows in 2004 (Table 2). The proportions of marked ants decreased exponentially as distance from the bait station increased, and similar foraging distributions were observed in samples collected along and across vineyard rows. In both years, the proportion of marked ants declined by about 50% between the bait station and the first sample location (2.5 m and 9 m away from bait stations across and along

rows, respectively). The proportion of marked ants across rows was predicted to approach its lower limit at 15 m; for 2004, predicted values never decreased below a lower limit of 0.08 (Fig. 2), but for 2005, they approached 0 at 15 m (Fig. 3). Along rows, the proportion of marked ants was predicted to approach 0 at 36 m in both years (Figs. 2 and 3).

Discussion

In the first year of the study, we uncovered no effect of the insecticide on proportions of marked ants or on distances that ants moved the protein marker from bait stations. These results differ from Ripa et al. (1999), who found that liquid baits treated with fipronil lowered percentages of marked Argentine ants and reduced the foraging distance of ants by one-half to two-thirds. One possible explanation for this discrepancy is that the insecticide used in the current study (boric acid) may be slower acting than fipronil. Ripa et al. (1999) observed an effect of fipronil very quickly, in only 24 h. Although boric acid has been effective in suppressing numbers of Argentine ants in past studies (e.g., Rust et al. 2004, Nelson and Daane 2007, Cooper et al. 2008, Daane et al. 2008, Brightwell and Silverman 2009), it may not affect ant foraging distance if it acts too slowly.

Still, this does not explain why proportions of marked ants remained unchanged in the presence of insecticide in the current study, even after 11–16 d of exposure. We suspect that the effects of the insecticide were limited by the low bait-station densities that we deployed, only about one bait station per ha, far lower than in past studies reporting strong effects of boric acid on Argentine ants (Cooper et al. 2008). Fewer ants and mealybugs and less grape damage were observed when boric acid was deployed in bait stations at maximum densities of 223 per ha (Daane et al. 2008) or 620 per ha (Daane et al. 2006). Using boric acid as an insecticide, Nelson and Daane (2007) tested a range of bait-station densities in vineyards and found that the lowest tested density of 54 per ha had a

Table 1. Proportions of marked ants per transect distance and average and maximum distances per plot (in meters) that marked ants moved from bait stations (means \pm SE), and results of ANOVAs testing the effects of direction (along vs. across vineyard rows) and treatment (nontoxic vs. toxic baits) on these variables

Response variable	Direction/treatment	Mean \pm SE	ANOVA results ^a		
			Direction	Treatment	Block
a) 2004					
Proportion ants marked	Along	0.12 \pm 0.03	$F_{1,118} = 0.02$, $P = 0.89$	$F_{1,12} = 0.01$, $P = 0.94$	$\chi^2 = 11.44$, $P = 0.003$
	Across	0.10 \pm 0.02			
	Nontoxic	0.11 \pm 0.02			
	Toxic	0.12 \pm 0.03			
Average distance	Along	17.10 \pm 1.59	$F_{1,17} = 0.05$, $P = 0.83$	$F_{1,14} = 0.71$, $P = 0.41$	$\chi^2 = 0.10$, $P = 0.75$
	Across	16.55 \pm 1.87			
	Nontoxic	16.55 \pm 1.87			
	Toxic	18.73 \pm 1.96			
Maximum distance	Along	27.14 \pm 3.78	$F_{1,19} = 0.48$, $P = 0.50$	$F_{1,19} = 0.01$, $P = 0.92$	$\chi^2 < 0.01$, $P = 0.99$
	Across	28.99 \pm 5.20			
	Nontoxic	26.44 \pm 5.19			
	Toxic	29.92 \pm 3.73			
b) 2005					
Proportion ants marked	Along	0.07 \pm 0.02	$F_{1,45} = 11.08$, $P = 0.002$		$\chi^2 < 0.01$, $P = 0.99$
	Across	0.02 \pm 0.01			
Average distance	Along	17.32 \pm 2.08	$F_{1,7} = 0.25$, $P = 0.63$		$\chi^2 = 2.08$, $P = 0.15$
	Across	15.47 \pm 2.38			
Maximum distance	Along	31.50 \pm 3.07	$F_{1,7} = 4.31$, $P = 0.08$		$\chi^2 = 2.99$, $P = 0.08$
	Across	22.54 \pm 4.80			

^aThe decimal values given by Satterthwaite's approximation for degrees of freedom were rounded to the nearest whole number.

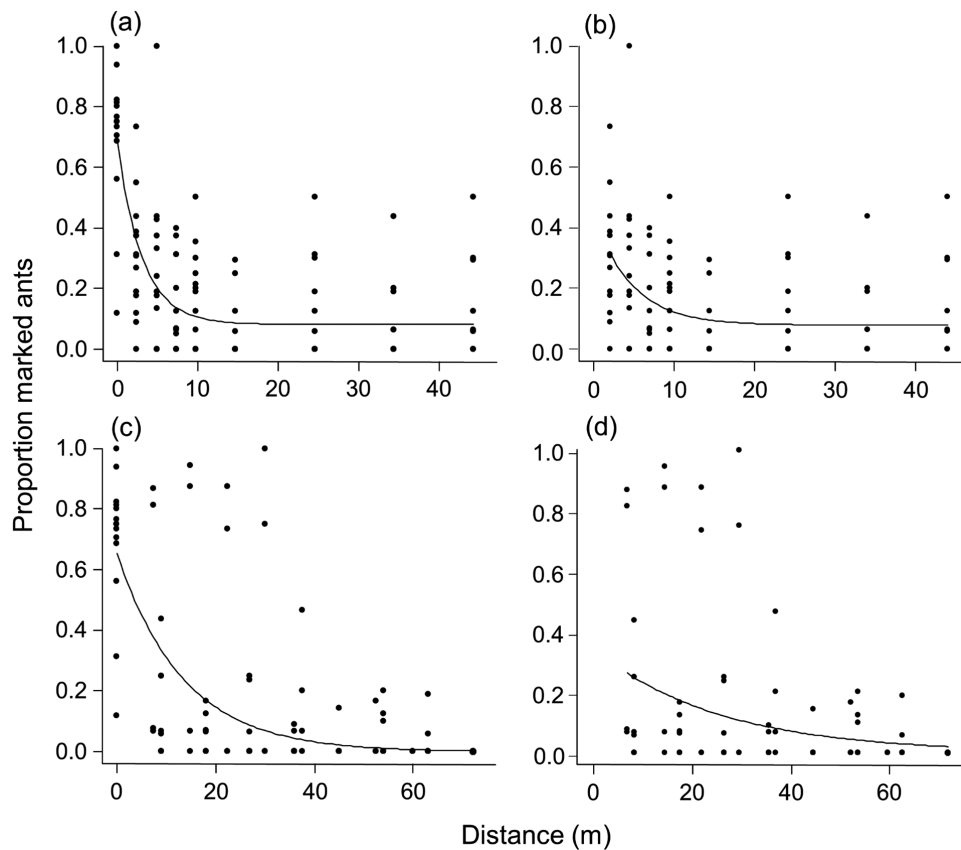


Fig. 2. Relationship between proportions of marked ants and distance from bait stations in 2004, across (a, b) or along (c, d) vineyard rows, and either including all transect distances (a, c) or excluding vines with bait stations (b, d).

suppressive effect on Argentine ant numbers; therefore, bait-station density may need to exceed a threshold somewhere between 1 and 54 bait stations per ha for a detectable effect on Argentine ants to emerge, as discussed further in the following section.

High ant densities at our sites may have weakened any effects of the insecticide. We measured ant activity in our study plots in June 2004 using bait stations containing sugar water, and after accounting for evaporation, ants removed an average of 26.9 g of sugar water from each tube per day (data not shown). An Argentine ant worker is capable of ingesting approximately 0.3 mg of sucrose solution (Reierson et al. 1998) and a loss of 26.9 g represents approximately 90,000 ant visits per tube per day. Vega and Rust (2003) and Nelson and Daane (2007) baited areas with similarly high Argentine ant densities, and speculated that ants repopulated treated plots from untreated areas. Any ants that were killed by the insecticide in the current study may simply have been replaced; we are unable to assess this possibility because we sampled only live ants. Extensive ant movement between plots seems unlikely in the current study, however.

Indeed, ant movement appeared to be largely confined to research plots. No marked ants were recovered at the maximum sampled distance in 2004 (72 m along vineyard rows) or in 4 out of 6 plots at the maximum sampled distance in 2005 (63 m along vineyard rows). Furthermore, predicted percentages of marked ants in exponential decay models reached their lower limit along rows at 36 m and across rows at 15 m. Ants may move further but only over periods longer than 6 d. These results are broadly in line with Heller et al. (2008), who found that marked ants did not move more than 50 m over a 2 wk sample period, and with Ingram and Gordon

(2003), who used genetic analysis to determine that local dispersal of ants occurred over distances of <100 m. Our estimate is slightly larger than Song et al. (2015), who reported that Argentine ants foraged at distances of 20 m or less; their study took place in a natural area, where vegetation may have been denser and more heterogeneous than in vineyards. The foraging ranges of ants can contract in denser vegetation (Usnick 2000).

It should be noted that we did not measure ant foraging distance per se, but rather movement of the protein marker, which could have been exchanged between ants via trophallaxis. The actual foraging distance of ants in the current study may have been smaller than the total distance that the marker traveled if trophallaxis occurred. Each worker likely feeds 4–12 other workers (Markin 1970), who then pass the food along to other workers, so that up to 156 workers are fed by the initial ant within 48 h (Rust et al. 2004). Although we did not measure the transfer rate of the marker between ants, it almost certainly occurred and may have led to an overestimate of foraging distance.

Argentine ants in the current study may have been confined to a relatively limited foraging range by various factors that are known to influence the location of their nests. Argentine ants prefer moist habitats (Walters and Mackay 2003), and dry soil conditions can halt their spread (Holway et al. 2002a). Although irrigation provides regular water subsidies in vineyards, localized differences in terrain and soil composition can affect the spatial distribution of soil moisture within vineyard plots (Ramos and Martinez-Casasnovas 2006), and may have influenced the location of ant nests and, thus, the foraging range of ants, in our plots. The location of food sources can also determine the location of Argentine

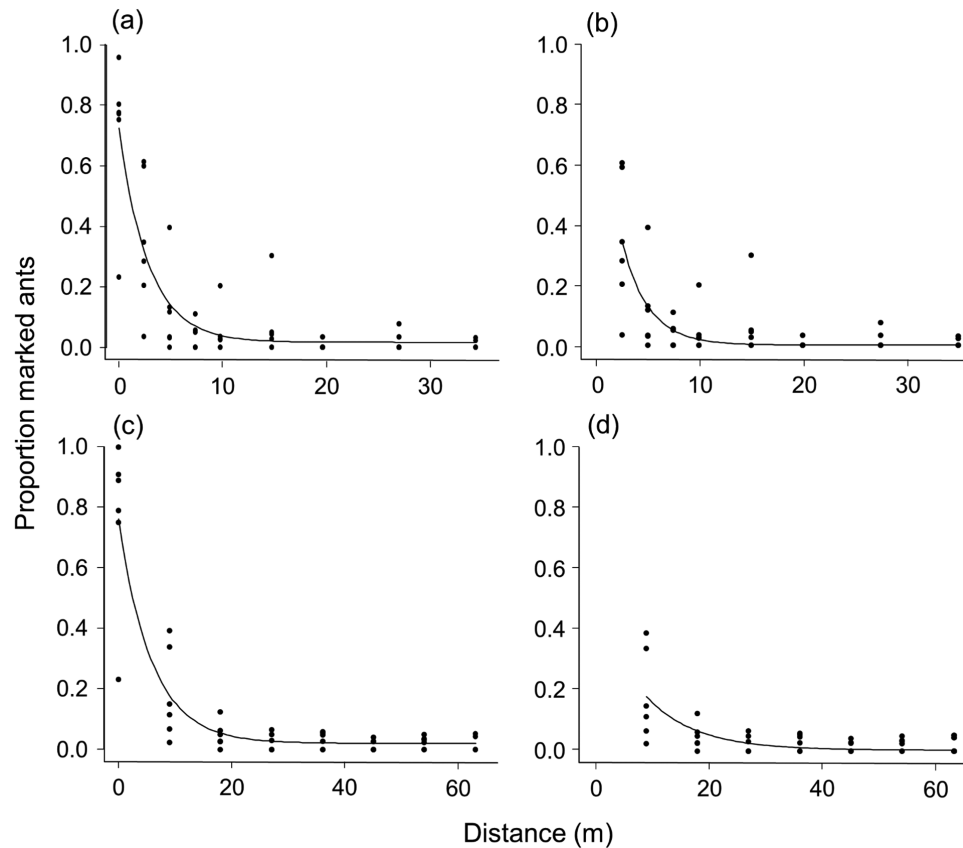


Fig. 3. Relationship between proportions of marked ants and distance from bait stations in 2005, across (a, b) or along (c, d) vineyard rows, and either including all transect distances (a, c) or excluding vines with bait stations (b, d).

Table 2. Results of negative exponential models showing effects of transect distance on proportions of marked ants along and across vineyard rows

Direction	Parameter ^a	Estimate ± SE	<i>t</i>	<i>P</i>
a) 2004				
Along	<i>d</i>	0.66 ± 0.06	10.97	<0.0001
	<i>e</i>	13.29 ± 2.68	4.96	<0.0001
Across	<i>c</i>	0.08 ± 0.03	3.30	0.001
	<i>d</i>	0.68 ± 0.05	14.15	<0.0001
	<i>e</i>	3.08 ± 0.68	4.53	<0.0001
b) 2004, no distance 0				
along	<i>d</i>	0.35 ± 0.10	3.71	<0.001
	<i>e</i>	25.28 ± 8.13	3.11	0.002
Across	<i>c</i>	0.08 ± 0.03	2.94	0.004
	<i>d</i>	0.48 ± 0.13	3.56	<0.001
	<i>e</i>	4.67 ± 2.04	2.29	0.02
c) 2005				
Along	<i>d</i>	0.76 ± 0.04	17.41	<0.0001
	<i>e</i>	6.43 ± 1.00	6.41	<0.0001
Across	<i>d</i>	0.72 ± 0.05	14.28	<0.0001
	<i>e</i>	3.04 ± 0.44	6.96	<0.0001
b) 2005, no distance 0				
Along	<i>d</i>	0.50 ± 0.24	2.09	0.04
	<i>e</i>	8.78 ± 3.44	2.55	0.01
Across	<i>d</i>	0.91 ± 0.34	2.67	0.01
	<i>e</i>	2.51 ± 0.78	3.20	0.003

^aIn the negative exponential equation, $f(x) = c + (d - c) \times \exp(-x/e)$, where *c* is the lower limit, *d* is the upper limit (intercept), and *e* indicates decay rate. The lower limit (*c*) was dropped when not significantly different from 0.

ant nests (Holway and Case 2000). Patchy and relatively stable food sources such as populations of honeydew-producing hemipterans can be more efficiently exploited by minimizing travel distances (Hölldobler and Lumsden 1980). Thus, Argentine ants may forage within defined areas where food is available.

Surprisingly, ants did not appear to consistently move further along than across rows; proportions of marked ants were higher along rows in 2005 but not in 2004 when more plots were sampled. In contrast, Ripa et al. (1999) reported that marked ants dispersed about twice as far along than across rows of trees in a citrus orchard (72 h after the bait was deployed, ants had moved 54 m along rows and 24 m across rows in plots that did not receive insecticide), and that fewer ant trails were observed extending across rows. They speculated that more continuous shade and the closer proximity of trees caused ants to move further along rows. Buczkowski et al. (2014) similarly reported that pipes and shade between trees allowed Argentine ants to move more extensively along than across rows in orchards. Perhaps, the distance between vines is not sufficiently different along versus across rows (1.5 or 1.8 vs 2.4 m at our sites) to influence the direction that ants travel. Although we have observed ants traveling along rows on trellis wires, far larger proportions of ants may travel along the ground.

The development of a control program for the Argentine ant requires that the optimal number of bait stations per ha be determined. The greater the distance that ants transport the toxin, the smaller the number of bait stations required for ant control. Our results indicate that Argentine ants generally will forage within a relatively small range in vineyards (<36 m along rows, and possibly as low as 15 m across rows, although our analyses did not uncover

a consistent effect of direction on ant foraging distance) and may partly explain why Argentine ant suppression steadily increased with incremental increases in bait-station density in a past study (Nelson and Daane 2007) and why ant control occurred only within relatively narrow areas in past studies (e.g., Vega and Rust 2003, Krushelnycky et al. 2004). If Argentine ants forage at distances of <36 m in vineyards, it would follow that bait stations may need to be deployed at intervals of 36 m or less, or at densities of at least 8–9 per ha (1 bait station per 36 × 36 m area), to affect ant levels across a given area of vineyard. However, more bait stations may be required to significantly suppress ant populations; the lower limit reached by our negative exponential models likely represents the outer edge of the ants' foraging and most ants likely foraged over shorter distances than 36 m. Furthermore, the effectiveness of liquid bait stations will also depend on ant densities, and more bait stations may be required as ant densities increase (Daane et al. 2006). Baits may be especially effective in spring, when overall ant numbers are low and colonies are growing (Nelson and Daane 2007). It is likely that widespread commercial adoption of liquid baits will not reach its full potential until better delivery systems are developed, such as the use of gel formulation delivery systems (Buczowski et al. 2014, Tay et al. 2017).

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