Sexual Differences in Insecticide Susceptibility and Synergism with Piperonyl Butoxide in the Leafminer Parasitoid *Diglyphus begini* (Hymenoptera: Eulophidae)

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ABSTRACT Susceptibility of males and females of the *Liriomyza* leafminer parasitoid *Diglyphus begini* (Ashmead) to methomyl, oxamyl, fenvalerate, and permethrin was compared with laboratory bioassays. For each insecticide and five populations tested, males were more susceptible than females. Differences in LC_{50}s between the sexes ranged from 1.3- to 15.7-fold and were greater in resistant compared with susceptible populations. Tibia length was significantly less for male than female *D. begini*. Size differences ranged from 1.1- to 1.2-fold. Piperonyl butoxide synergized oxamyl and fenvalerate in males and females, suggesting that oxidative detoxification was important in both sexes. The addition of piperonyl butoxide to oxamyl affected both sexes similarly. The synergistic effect of piperonyl butoxide with fenvalerate was significantly greater for females than males, suggesting greater oxidative detoxification of fenvalerate in females than males.

KEY WORDS Insecta, biological control, pesticide resistance, synergism

THE LEAFMINERS *Liriomyza trifolii* (Burgess) and *L. sativae* Blanchard (Diptera: Agromyzidae) are important pests of vegetable and ornamental crops throughout the world (Minkenberg & van Lenteren 1986, Parrella 1987). *Diglyphus begini* (Ashmead) (Hymenoptera: Eulophidae), an external larval parasitoid of *Liriomyza* spp., shows potential for biological control of leafminers in greenhouse and field situations (Parrella et al. 1989). In Hawaii, *D. begini* has been reared from *Liriomyza* on beans, watermelon, cucumber, tomato, chrysanthemum, and onion (Mothershead 1978, Hara 1986, Herr 1987, Johnson & Hara 1987). Some populations of *D. begini* in Hawaii have developed resistance to carbamates and pyrethroids (Mason & Johnson 1988, Rathman et al. 1990). This situation represents one of the few cases in which an insect parasitoid has evolved pesticide resistance in the field (Croft & Brown 1975, Croft & Strickler 1983, Theiling & Croft 1989, Tabashnik & Johnson 1992).

Few studies have compared susceptibility to insecticides between male and female hymenopterous parasitoids. Available data show that male hymenopterous parasitoids are usually more susceptible to insecticides than females (Pielou & Glasser 1951, Adams & Cross 1967, Lindgren et al. 1972, Abdelrahmen 1973, Schoonees & Giliomee 1982, Lasota & Kok 1986, Scott & Rutz 1988). In some cases, sexual differences in susceptibility of parasitoids were attributed to size differences (Abdelrahmen 1973, Scott & Rutz 1988). The synergist piperonyl butoxide (PB) was used to evaluate the role of oxidative metabolism in resistance (Raffa & Priester 1985, Scott 1990), but previous studies did not contrast its effects on male versus female parasitoids.

The objectives of our study were to compare male and female *D. begini* in terms of susceptibility to insecticides, size, and response to the synergist piperonyl butoxide. These data may be important in determining the resistance mechanism in *D. begini*.

Materials and Methods

Sources of Parasitoids. Leaves containing parasitized *Liriomyza sativae* and *L. trifolii* larvae were collected from five sites in Hawaii—three on the island of Oahu (PO, HO, and MO) from February to July 1989, one on the island of Hawaii (GH) from August to October 1989 and one on the island of Maui (KM) in July, 1990. Adult *D. begini* were also obtained from a California laboratory colony on five dates in June and July 1989.

PO was at the University of Hawaii Experiment Station farm at Poamoho. HO was a private commercial farm in Hawaii Kai. MO was an isolated organic garden in the Manoa Valley near the University of Hawaii. KM was a private com-

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mercial farm near Kula. GH was a heavily sprayed commercial greenhouse north of Hilo.

PO, HO, KM, and GH had received frequent pesticide applications. GH had received 34 pesticide treatments between December 1988 and May 1989, including 16 applications of fenvalerate (Asana XL 0.66 emulsifiable concentrate [EC]; E.I. Du Pont de Nemours & Company, Wilmington, Del.), 11 applications of methomyl (Lannate 1.8 EC; Du Pont), and seven applications of oxamyl (Vydate 2.0 EC; Du Pont). Application rates were 5.0–10.0 ml/liter for oxamyl and methomyl and 320–640 μl/liter for fenvalerate.

To collect parasitoids from all Hawaii field sites except MO, leaves from field-grown long bean (PO and HO) and tomato (PO, KM, and GH) were sampled, brought into the laboratory, dried at 24°C for 2–3 d, and placed in emergence cages. Male and female adult parasitoids were aspirated daily from the cages into glass vials and kept at 24°C with honey for 1–4 d before the bioassays were done.

To obtain parasitoids from MO, bean plants ('Henderson Bush,' Burpee Seed, Warminster, Pa.) were grown in a greenhouse in vermiculite and exposed to adult *L. trifolii* in the laboratory. When the plants were 12 d old and infested with second- and third-instar *L. trifolii*, they were placed at the MO site for 24–48 h. After they were removed from the field, plants were kept in a holding cage in the laboratory for 7–10 d. Leaves were cut off the plants, dried, and placed in emergence cartons (Johnson et al. 1980). Adult parasitoids from MO were aspirated and handled in the same manner as parasitoids from the PO, HO, KM, and GH sites.

The California *D. begini* colony was established in April 1989 from 569 males and 362 females that emerged from weeds surrounding an artichoke field in Salinas, Calif. This population was reared in the laboratory at the University of California, Davis for several generations on *L. trifolii* on chrysanthemum before adults were sent to Hawaii (K. M. Heinz, personal communication).

Insecticides. Four formulated insecticides were used: methomyl (Lannate 1.8 EC; Du Pont), oxamyl (Vydate 2.0 EC; Du Pont), permethrin (Ambush 2.0 water soluble liquid [L]; ICI Americas, Wilmington, Del.), and fenvalerate (Pydrin 2.4 L; Shell, Houston, Tex.).

Field rates for methomyl and oxamyl were calculated as 1,080 and 1,200 mg (AI) per liter, respectively, based upon recommended label rates of 216 (methomyl) and 240 (oxamyl) g (AI)/liter or 1.0 and 1.1 kg formulated material/ha, respectively. Field rates for permethrin and fenvalerate were calculated as 240 mg (AI)/liter, based upon recommended label rates of 240 g (AI)/liter (permethrin) and 288 g (AI)/liter (fenvalerate) or 0.24 kg formulated material per ha.

Bioassays. Our bioassay procedure was similar to a technique described by Rathman et al. (1990). Adult parasitoids (2 to 4 d old) were anesthetized with CO_2 for 30 s and sorted by sex ≈24 h before exposure to pesticide residue. ***Diglyphus begini*** males and females were placed in separate 36-ml clear plastic cups (Anchor Hocking, Minneapolis, Minn.) with a fine camel's-hair brush. The cups were covered with an organdy square and capped with a plastic lid, the center portion removed. All insects were kept at 24°C and provided with undiluted honey before they were tested.

Serial dilutions of formulated insecticide were prepared in 50 ml of distilled water plus 1 ml of 10% Triton Ag-98 (Rohm & Haas Company, Newark, N.J.). Control treatments contained 50 ml of distilled water plus 1 ml of 10% Triton Ag-98. Dilutions were poured into 36-ml clear plastic cups and poured back into the original beaker after 10 s. After 2 h drying time, unanesthetized insects were gently tapped into treated cups, which were then covered with an untreated square of organdy and capped with the rim of a plastic snap-top lid. Males and females were placed in separate cups. A single drop of undiluted honey was placed in the center of the organdy, and the cup was inverted on a wire screen.

All tests were conducted at 24°C in constant light. Mortality was recorded after 24 h. Parasitoids that were completely immobilized were scored as dead. For each date, a series of five or six concentrations plus an untreated control were run for each sex. Each concentration was replicated four times, with a total of five individuals per replicate. Approximately 120 males and 120 females were tested on each date from the same dilution series. Tests were repeated on at least two different dates (except HO when tested against permethrin). Because differences between dates were not significant, the data were pooled across dates for analysis. The MO population was not tested with permethrin.

Size Measurements. Hind tibia length (an index of parasitoid size) was measured to the nearest 0.01 mm at 20× magnification with an ocular micrometer. Legs were removed from 20 male and 20 female *D. begini* randomly selected from CA, GH, and PO and mounted in Hoyer's solution before measurements were made.

Synergist Studies. We first tested piperonyl butoxide (Incite 8.0 [L]; Loveland Industries, Greeley, Colo.) alone at concentrations of 0.959–9,590 mg (AI) per liter to determine its toxicity to *D. begini*. To maximize the potential for synergism (Scott 1990), we selected the highest concentration of piperonyl butoxide (9,590 mg [AI]/liter) that caused no mortality to either males or females from either KM or HO (total, $n = 80$).

To test for synergism, we compared responses to 110 mg (AI) per liter of oxamyl and 580 mg (AI) per liter of fenvalerate with and without piperonyl butoxide (9,590 mg [AI]/liter). The insecti-

Table 1. Toxicity of oxamyl and methomyl to male and female *D. begini*

Population[a]	n	Sex[b]	Slope ± SE	LC_{50} (95% CL)[c]	F:M[d]	Resistance ratios[e]
			Oxamyl			
PO	210	F	2.3 ± 0.3	280 (210–400)	3.1	10.0
	484	M	3.4 ± 0.3	91 (77–110)		6.1
HO	240	F	2.0 ± 0.3	570 (430–830)	5.2	20.3
	240	M	2.6 ± 0.3	110 (82–150)		7.3
GH	229	F	2.6 ± 0.3	420 (350–510)	4.2	15.0
	241	M	2.5 ± 0.3	100 (80–130)		6.7
MO	214	F	1.8 ± 0.3	68 (46– 96)	3.4	2.4
	213	M	2.4 ± 0.4	20 (14– 25)		1.3
CA	332	F	3.1 ± 0.4	28 (22– 34)	1.9	1.0
	240	M	2.7 ± 0.4	15 (12– 19)		1.0
			Methomyl			
PO	259	F	2.6 ± 0.4	130 (110–170)	3.2	16.2
	401	M	2.1 ± 0.3	40 (33– 54)		6.7
HO	239	F	3.2 ± 0.4	120 (95–150)	4.0	15.0
	240	M	3.4 ± 0.4	30 (25– 37)		5.0
GH	240	F	3.0 ± 0.4	180 (130–260)	3.3	10.0
	239	M	2.7 ± 0.4	55 (39– 83)		9.2
MO	217	F	2.8 ± 0.4	15 (11– 20)	1.9	1.9
	477	M	1.8 ± 0.2	8 (7– 10)		1.3
CA	246	F	2.3 ± 0.3	8 (6– 12)	1.3	1.0
	246	M	2.9 ± 0.4	6 (5– 8)		1.0

[a] PO, Poamoho, Oahu; HO, Hawaii Kai, Oahu; GH, Glenwood, Hawaii; MO, Manoa, Oahu; CA, California.
[b] Data for female *D. begini* from Rathman et al. (1990).
[c] Milligrams (AI) per liter.
[d] F:M is the LC_{50} of females for a given population divided by LC_{50} of males for a given population.
[e] LC_{50} of a population for a given pesticide divided by LC_{50} of most susceptible population (CA).

cide concentrations were the LC_{50}s estimated for HO males.

Analysis. Mortality data were analyzed with the probit option of POLO-PC (LeOra Software 1987). Control mortality was <5% for males and <3% for females. LC_{50} values were compared between sexes for five populations and four insecticides. A difference between two LC_{50} values was considered significant if the 95% confidence limits did not overlap. Resistance ratios were calculated separately for each sex by dividing the LC_{50} for a given population by the LC_{50} of the most susceptible population. Regression analysis (Statview 512, Abacus Concepts, Berkeley, Calif.) was used to examine toxicity differences between the sexes in populations tested with methomyl, oxamyl, permethrin, and fenvalerate. Female-to-male ratios (LC_{50} of females divided by LC_{50} of males) were plotted versus log LC_{50} for males and females from each of five populations (PO, HO, MO, GH, and CA). Previously reported data for female *D. begini* (Rathman et al. 1990) are used for comparison with males. Statistical analysis of size differences between the sexes was by Student's t test. In the synergist studies, percentages were transformed by arcsine to normalize variances before analysis. For each insecticide (fenvalerate and oxamyl) a separate three-way analysis of variance was used to test for main effects of sex, treatment (piperonyl butoxide), population (KM versus HO), and interactions. We evaluated the sex × treatment interaction to determine if the extent of synergism differed between males and females.

Results

Susceptibility Differences Between the Sexes. Male *D. begini* were more susceptible than females to all four insecticides tested (Tables 1 and 2). In 18 of 19 pairwise comparisons between the sexes for each population and each insecticide, LC_{50}s for males were significantly lower than LC_{50}s for females. In the exceptional case, the California population tested with methomyl, the male LC_{50} was less than the female LC_{50}, but the difference was not significant (Table 1). In the pairwise comparisons, differences between the sexes ranged from 1.3- to 15.7-fold (mean, 5.7 ± 0.93 [$\bar{x}$ ± SEM]).

Sexual differences in LC_{50}s were generally greater for resistant (PO, HO, and GH) (mean, 6.4 ± 1.2) than susceptible (CA, MO) (4.4 ± 1.4) populations. Regression analysis indicated a significant relationship between female-to-male ratios and female LC_{50}s (r^2 = 0.33; df = 18; P = 0.01) (Fig. 1) but not male LC_{50}s (r^2 = 0.09; df = 18; P = 0.21). Resistance ratios for females were approximately double the resistance ratios for males for oxamyl, methomyl, and fenvalerate, but not for permethrin. In the exceptional cases, GH and HO males had higher resistance ratios

Table 2. Toxicity of fenvalerate and permethrin to adult male and female *D. begini*

Population[a]	n	Sex[b]	Slope ± SE	LC_{50} (95% CL)[c]	F:M[d]	Resistance ratios[e]
			Fenvalerate			
PO	193	F	1.9 ± 0.5	5,700 (4,000–16,000)	12.9	14.2
	598	M	1.1 ± 0.1	440 (310– 640)		3.7
HO	340	F	2.9 ± 0.4	3,100 (2,700– 3,700)	5.3	7.7
	240	M	2.9 ± 0.4	590 (450– 760)		4.9
GH	240	F	1.8 ± 0.3	6,900 (5,000–11,000)	6.3	17.2
	241	M	1.6 ± 0.2	1,100 (780– 1,600)		9.2
MO	298	F	1.7 ± 0.2	1,400 (1,000– 1,900)	8.8	3.5
	256	M	1.5 ± 0.2	160 (100– 220)		1.3
CA	227	F	2.7 ± 0.5	400 (240– 580)	3.3	1.0
	241	M	1.1 ± 0.2	120 (31– 210)		1.0
			Permethrin			
PO	239	F	2.9 ± 0.4	1,100 (850– 1,300)	15.7	5.8
	330	M	1.4 ± 0.1	70 (50– 100)		3.9
HO	120	F	2.5 ± 0.4	620 (200– 2,300)	10.5	3.3
	120	M	1.3 ± 0.2	60 (30– 140)		7.5
GH	388	F	3.2 ± 0.4	2,400 (2,000– 2,900)	3.4	12.6
	240	M	2.1 ± 0.3	700 (550– 930)		38.9
CA	290	F	1.6 ± 0.2	190 (130– 310)	10.5	1.0
	370	M	1.1 ± 0.2	18 (8– 28)		1.0

[a] PO, Paomoho, Oahu; HO, Hawaii Kai, Oahu; GH, Glenwood, Hawaii; MO, Manoa, Oahu; CA, California.
[b] Data for female *D. begini* from Rathman et al. (1990).
[c] Milligrams (AI) per liter.
[d] F:M is the LC_{50} of females for a given population divided by LC_{50} of males for a given population.
[e] LC_{50} of a population for a given pesticide divided by LC_{50} of most susceptible population (CA).

(38.9 and 7.5) than GH females (12.6 and 3.3) for permethrin (Tables 1 and 2).

Size Differences Between the Sexes. Within each of three populations examined (PO, GH, and CA), tibia length was significantly less for males than females. The ratio of female to male hind tibia length ranged from 1.1 to 1.2 (Table 3).

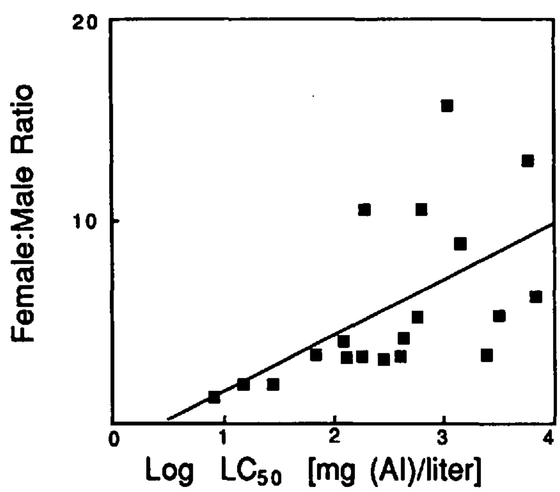

Fig. 1. Female:male ratios (LC_{50} of females divided by LC_{50} of males) versus log LC_{50} for females from a given population. Females were exposed to methomyl (Lannate), oxamyl (Vydate), fenvalerate (Pydrin), and permethrin (Ambush) for 24 h and mortality recorded. The five populations tested were: PO, Poamoho, Oahu; HO, Hawaii Kai, Oahu; MO, Manoa, Oahu; GH, Glenwood, Hawaii; and CA, California.

Synergist Studies. Addition of piperonyl butoxide to either fenvalerate or oxamyl increased mortality in males and females from both populations tested (Table 4). The effect of piperonyl butoxide (treatment effect) was highly significant with both insecticides ($P < 0.0001$ in each case) (Table 5). Significant effects of sex (Table 5) confirmed earlier results showing that females were less susceptible than males (Tables 1 and 2).

The interaction between sex and treatment was significant for fenvalerate, but not oxamyl (Table 5). Synergism by piperonyl butoxide with fenvalerate was greater for females than males. The effect of piperonyl butoxide with oxamyl was similar for both sexes.

Population differences between HO and KM were suggestive but not significant (Table 5).

Table 3. Comparison of hind tibia length for male and female *D. begini* (two-tailed t test)

Population[a]	n	Sex	Tibia length (μm), $\bar{x}$ ± SEM	t	P	F:M[b]
PO	20	F	41.1 ± 0.7			
	20	M	38.3 ± 0.6	3.14	0.005	1.1
GH	20	F	40.6 ± 0.9			
	20	M	34.7 ± 0.5	5.01	0.0002	1.2
CA	20	F	42.0 ± 0.9			
	20	M	37.3 ± 0.9	4.75	0.003	1.1

[a] PO, Poamoho, Oahu; GH, Glenwood, Hawaii; CA, California.
[b] F:M is the ratio of mean female hind tibia length to mean male hind tibia length.

Table 4. Toxicity of fenvalerate and oxamyl with and without piperonyl butoxide (PB) to *D. begini* males and females

Population[a]	Treatment[b]	% Mortality, $\bar{x} \pm$ SEM[c] Males	Females
KM	Fenvalerate	46.7 ± 6.7[d]	11.9 ± 5.0
	Fenvalerate + PB	65.3 ± 6.8	52.7 ± 7.0
HO	Fenvalerate	59.2 ± 5.4	24.2 ± 4.1
	Fenvalerate + PB	68.0 ± 2.2	58.4 ± 3.6
KM	Oxamyl	51.9 ± 5.8	5.3 ± 3.5
	Oxamyl + PB	70.4 ± 5.8	31.9 ± 7.2
HO	Oxamyl	28.7 ± 8.2	7.4 ± 4.5
	Oxamyl + PB	90.0 ± 0.0	61.2 ± 3.5

[a] HO, Hawaii Kai, Oahu; Kula, Maui.
[b] Fenvalerate (580 mg [AI]/liter); oxamyl (110 mg [AI]/liter) with and without piperonyl butoxide (PB) (9,590 mg [AI]/liter). Mortality with 9,590 mg (AI)/liter of PB (no insecticides) was 0.0% for both males (n = 20) and females (n = 20).
[c] Arcsine transformation of percent mortality.
[d] KM: $\bar{x} \pm$ SEM of 10 replications of five parasitoids; HO: $\bar{x} \pm$ SEM of five replications of 10 parasitoids.

The significant population × treatment interaction (Table 5) with oxamyl reflects a greater effect of piperonyl butoxide on HO than KM (Table 4). Other interactions with population were not significant (Table 5).

Table 5. Analysis of variance table for arcsine-transformed percent mortality to fenvalerate and oxamyl alone and after adding piperonyl butoxide (PB) for *D. begini* males and females from two populations

Source of variation	df	F	P
Fenvalerate			
Main effects[a]			
Treatment[b]	1	28.28	0.0001
Sex	1	22.85	0.0001
Population[c]	1	2.97	0.091
Interactions			
Sex × treatment	1	6.09	0.017
Sex × population	1	0.02	0.884
Treatment × population	1	0.72	0.401
Sex × treatment × population	1	0.03	0.873
Error	52		
Oxamyl			
Main effects[a]			
Treatment[d]	1	76.84	0.0001
Sex	1	54.83	0.0001
Population[c]	1	2.32	0.134
Interactions			
Sex × treatment	1	0.002	0.9686
Sex × population	1	3.65	0.0616
Treatment × population	1	14.70	0.0003
Sex × treatment × population	1	0.73	0.398
Error	52		

[a] Arcsine transformation of percent mortality.
[b] Fenvalerate [580 mg (AI)/liter] with and without piperonyl butoxide (PB) [9,590 mg (AI)/liter]. Mortality with 9,590 mg (AI)/liter of PB (no insecticides) was 0.0% for both males (n = 20) and females (n = 20).
[c] Hawaii Kai, Oahu (HO) and Kula, Maui (KM).
[d] Oxamyl [110 mg (AI)/liter] with and without piperonyl butoxide (PB) [9,590 mg (AI)/liter]. Mortality with 9,590 mg (AI)/liter of PB (no insecticides) was 0.0% for both males (n = 20) and females (n = 20).

Discussion

Male *D. begini* were more susceptible than females to methomyl, oxamyl, fenvalerate, and permethrin. These results are consistent with several other studies that have documented the differential response of male and female hymenopterous parasitoids to insecticides. Factors that might account for sexual differences in susceptibility include differences in size, metabolism, and behavior.

Abdelrahmen (1973) examined the relationship between weight, sex, and toxicity in the citrus red scale parasitoid *Aphytis melinus* DeBach (Aphelinidae). Weight differences in adult *A. melinus* accounted for much of the variation in dose–response curves for malathion. Males were smaller than females and had lower LC_{50} values. Males of the pteromalid *Urolepis rufipes* (Ashmead) were 1.3- to 2.8-fold more susceptible than females to seven insecticides, and the difference was attributed to the smaller size of males (1.7-fold) (Scott & Rutz 1988).

We found that for *D. begini*, tibia length was 1.1- to 1.2-fold greater for females than males (Table 3). However, differences in susceptibility ranged from 1.3- to 15.7-fold (Tables 1 and 2). Although the slight size difference might account for some of the difference in susceptibility, it probably cannot explain the entire difference. If size difference were the sole or primary cause of the difference in susceptibility, then greater size differences in populations should be observed, along with greater susceptibility differences between the sexes.

The sexual difference in size was virtually identical for two resistant populations (PO and GH) and a susceptible population (California) (Table 3). In contrast, the sexual difference in susceptibility was generally much greater for resistant populations compared with susceptible populations (Tables 1 & 2; Fig. 1).

Piperonyl butoxide synergized both oxamyl and fenvalerate in male and female *D. begini* from two populations, suggesting that monooxygenases are important in detoxification in this species (Raffa & Priester 1985). Female *D. begini* may be more metabolically active than males; however, the data from studies with fenvalerate and oxamyl were not in agreement. There was a significant interaction between sex and treatment for fenvalerate, but not for oxamyl (insecticide with and without piperonyl butoxide).

Bioassay data indicating significant differences in susceptibility between male and female parasitoids should be interpreted carefully. In laboratory bioassays, female *D. begini* may be less active than males and rest on the untreated organdy covering the bioassay cups. This behavior could account for the susceptibility differences observed. In the field, however, female *D. begini* searching for hosts may spend more time on treated leaf surfaces, than males, thereby receiving greater exposure to pesticide residue. Evidence for this has been documented in other species. For example, mortality for adult *Aphidius smithi* Sharma & Subba Rao (Aphidiidae) after an 8-h exposure to carbaryl [Sevin 50 WP at 1.25 g (AI)/liter] was higher for females than males and was influenced by their behavior (McGregor & Mackauer 1989). Female *A. smithi* searched on foliage; males were observed resting on plants or on the sides of cages.

The mechanism(s) for conferring resistance in *D. begini* remain undetermined and require more detailed study with different synergists and with both susceptible and resistant populations. Further studies are also needed to determine whether male and female *D. begini* pick up the same amount of toxicant from treated surfaces.

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