

INSECTICIDE RESISTANCE AND RESISTANCE MANAGEMENT

Resistance to Protectant Insecticides in Two Field Strains of the Stored-Product Insect Parasitoid *Bracon hebetor* (Hymenoptera: Braconidae)

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ABSTRACT Field strains of the parasitoid *Bracon (Habrobracon) hebetor* Say (Hymenoptera: Braconidae) collected in corn and peanut storage facilities in Blackville, SC, and Hawkinsville, GA, were 7.6- and 7.3-fold more resistant to malathion, respectively, than was a laboratory strain with which they were compared. We detected much higher levels of malathion resistance (>270-fold that of a susceptible strain) in a pyralid host *Plodia interpunctella* (Hübner) collected at the same facilities. Results of serial time-response bioassays with a single pesticide dose indicated that adult males of the Blackville (SCC) strain of *B. hebetor* were significantly more sensitive to malathion than were females, perhaps because of their smaller (1.3-fold) size (weight). In the timed bioassay, sensitivities of laboratory and SCC strains of the parasitoid to several common grain protectants were chlorpyrifos-methyl > pirimiphos-methyl > deltamethrin > cyfluthrin > malathion. The SCC strain of *B. hebetor* was significantly more tolerant of deltamethrin, cyfluthrin, and malathion, compared with the laboratory strain. S,S,S-tributyl phosphorothioate (DEF) synergized malathion against the SCC strain but was slightly toxic by itself. Triphenyl phosphate (TPP) substantially delayed the toxicity of malathion in the SCC strain. We discuss the relatively low level of resistance development in *B. hebetor*, compared with that of the host *P. interpunctella*, in terms of the behavioral ecology of host location by the parasitoid.

KEY WORDS *Bracon hebetor*, protectants, resistance

PESTICIDE-RESISTANT BENEFICIAL INSECTS are an important component of pest-management programs (Metcalf and Luckmann 1982). Although parasitoids are generally more sensitive to pesticides than are herbivorous insect pests (Croft 1990), strains with laboratory-selected resistance have been developed and successfully used in field trials (Hoy et al. 1990). Naturally occurring resistance to pesticides in beneficials is less well documented but has been demonstrated in several species (Schoones and Giliomee 1982, Rosenheim and Hoy 1986, Havron et al. 1991, Baker and Arbogast 1995).

In addition to the above cases of resistance, a field strain of a small pteromalid wasp, *Anisopteromalus calandrae* (Howard), collected on a farm near Bamberg, SC, was shown to be 2,800-fold

more resistant to malathion, compared with a susceptible laboratory strain, and 200-fold more tolerant of malathion than the field strain of its insect host (Baker and Weaver 1993, Baker 1995). *A. calandrae* parasitizes insects such as grain weevils whose immature stages feed internally in grain kernels. Development of the resistance in *A. calandrae* may be a result of several unique characteristics of the interaction of the insecticide, the grain (host food), and the weevil host within the stored grain ecosystem.

Among other hymenopterans that parasitize insects associated with stored products, one of the most important and effective is *Bracon (Habrobracon) hebetor* Say (Brower 1990). This braconid wasp is ectoparasitic on larvae of pyralid moths such as the Indianmeal moth, *Plodia interpunctella* (Hübner), and the almond moth, *Cadra cautella* (Walker). In the southeastern United States, these pyralids have developed significant resistance to several of the commonly used grain and peanut protectants (Zettler et al. 1973, Zettler 1982, Arthur et al. 1988). To incorporate *B. hebetor* into an integrated chemical-biological control program for these pest moth species, parasitoid strains with either laboratory-selected or naturally occurring resistance to these protectants are necessary.

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Because the presence of pesticide-resistant hosts may facilitate development of resistance in associated parasitoids (a tenant of the food limitation hypothesis [Croft and Morse 1979, Tabashnik 1986]), we examined malathion resistance in two field strains of *B. hebetor* in Georgia and South Carolina. We also determined the sensitivities of the *B. hebetor* field strains to chlorpyrifos-methyl, pirimiphos-methyl, deltamethrin, and cyfluthrin, and we evaluated resistance levels to malathion in two strains of the host *P. interpunctella* collected at the same field locations.

Materials and Methods

Insect Strains. The laboratory (Savannah) strain of *B. hebetor* has been maintained at the USDA laboratory in Savannah, GA, for >20 yr. Two field strains of *B. hebetor* were collected. The first strain was obtained by combining two collections of *B. hebetor* aspirated from corn bins on farms located near Bamberg and Blackville, SC, in March 1993. This combined strain was named the SCC strain. A strain of *P. interpunctella* was also collected from the farm at Blackville. The second *B. hebetor* strain was collected in April 1993 from peanuts infested with *P. interpunctella* at the Central Georgia Cooperative in Hawkinsville, GA. Both *B. hebetor* strains were reared at 25°C and 50–60% RH on larvae of the laboratory strain of *P. interpunctella*. *P. interpunctella* was reared on the diet of Silhacek and Miller (1972).

Dose-Response Bioassay. Laboratory bioassays were done in 20 ml glass vials (28 by 60 mm) with the procedure of Baker and Weaver (1993). Dose-response bioassays were used to compare the response of adults of the three *B. hebetor* strains to technical malathion (95% [AI], American Cyanamid, Princeton, NJ). Preliminary tests were used to obtain the approximate LD₅₀ for each strain. From these data, a logarithmic series of doses was selected to give two doses below the LD₅₀, two doses above the LD₅₀, and one dose at the approximate LD₅₀. Doses tested ranged from 0.1 to 0.63 µg per vial for the Savannah strain and from 0.63 to 4.0 µg per vial for the SCC strain (F₅ adult progeny) and Hawkinsville strain (F₃ adult progeny). Adults tested were generally between 2 and 5 d old and had access to a line of honey when they emerged in each culture jar. Mortality was assessed after a 24-h contact period, followed by an additional 24-h period at 25°C and 75% RH. For each dose, including hexane-treated control vials, we used five replicates with 10 adults per replicate. Two to four tests were done on different dates, and mortality data were pooled across dates.

Resistance ratios of F₂ progeny of Blackville and Hawkinsville strains of *P. interpunctella* were determined by topical application of 1 µl of technical malathion (950 µg [AI]/µl) to the thoracic dorsum of wandering fifth instars (Arthur et al. 1988). Dilutions of the technical material were not toxic. At

least 85 larvae of each strain were tested. Treated insects were placed in petri dishes lined with filter paper and held at 27°C and 60% RH. Mortality rates were calculated when adult emergence had ceased. Resistance ratios were determined by dividing the dose for the field strains by the dose required to produce the equivalent percentage mortality in the laboratory (susceptible) strain (LD₅₀ and LD₉₅, 0.315 and 0.709 mg/g, respectively) assayed by Zettler (1982).

Adult Weights. Adult weights of 2- to 3-d-old *B. hebetor* reared on *P. interpunctella* were obtained by weighing 20 individual males and 20 individual females from each of three separate cultures of the Savannah and SCC F₅ strains on a Mettler UMT2 microbalance. Adults had access to a line of honey in the culture jars from emergence until they were removed and weighed.

Time-Response Bioassays. Serial time-dose-response bioassays were used to compare responses of male and female *B. hebetor* from the Savannah and SCC strains to different doses of malathion in the glass vials. Serial time-response bioassays were used to compare responses of Savannah and SCC strains to a single dose of chlorpyrifos-methyl (Dow, Midland, MI), pirimiphos-methyl (Zeneca, Wilmington, DE), deltamethrin (Roussel UCLAF, Paris, France), cyfluthrin (Miles, Kansas City, MO), and malathion. This latter bioassay was also used to determine the effect of the carboxylesterase inhibitors triphenyl phosphate (TPP, Aldrich, Milwaukee, WI) and S,S,S-tributyl phosphorotrithioate (DEF, Miles) on sensitivity to malathion in the Savannah and SCC strains. In each bioassay, the *B. hebetor* were briefly anesthetized with CO₂ and placed in vials. Knockdown was determined at 5-, 10-, 15-, or 30-min intervals at 22°C, depending on the strain-pesticide-dose interaction.

Response of male and female *B. hebetor* of the Savannah and SCC (F₅-F₆) strains was determined at dose levels of malathion equivalent to 1, 2, 5, and 10 times the LD₉₉ (6.1 µg per vial) of the SCC strain obtained from the dose-response bioassays. The 2-, 5-, and 10-fold dose bioassays were run simultaneously whereas the 1-fold dose bioassay was run ≈6 wk later. Results are based on two or three tests at 22°C on different days, with each test having three replicate vials (10 adults per vial) per sex per strain per dose. Control vials of solvent only were included for both sexes.

Comparative responses of mixed sexes of Savannah and SCC (F₆-F₇) strains of *B. hebetor* to technical chlorpyrifos-methyl (95% [AI]), pirimiphos-methyl (90.8% [AI]), malathion, deltamethrin (98% [AI]), and cyfluthrin (93.4% [AI]) were determined at the LD₉₉ of the SCC strain for malathion (6.1 µg [AI] per vial). Results are based on three tests run at 22°C on different days, each with three replicate vials (10 adults per vial) per strain per pesticide. Control vials were included.

Table 1. Responses of the Savannah (susceptible) strain and two field strains of *B. hebetor* exposed to malathion at 25°C and 75% RH in the glass vial bioassay

Probit parameter ^a	<i>B. hebetor</i> strain		
	Savannah	SCC ^b	Hawkinsville ^c
<i>n</i>	374	477	461
χ^2	3.05	3.15	10.27
Slope	4.8 ± 0.7	3.9 ± 0.4	5.8 ± 0.8
LD ₅₀	0.21 (0.17–0.23)	1.59 (1.44–1.72)	1.51 (1.30–1.72)
LDR at LD ₅₀	—	7.6 (6.4–9.1)	7.3 (6.2–8.7)
LD ₉₉	0.63 (0.51–0.87)	6.10 (4.93–8.29)	3.82 (2.94–6.63)
LDR at LD ₉₉	—	9.7 (6.9–13.7)	6.1 (4.2–8.8)

^a Parameters: *n*, number of adults assayed; χ^2 , calculated value of chi-square; slope ± SEM; LD₅₀ and LD₉₉ (μg per vial) with (95% FL); LDR, lethal dose ratios relative to the Savannah strain.

^b F₅ progeny.

^c F₃ progeny.

The synergists DEF and TPP were combined with malathion at a weight ratio of 5:1 and response to the mixture was determined for *B. hebetor* from the Savannah and SCC (F₇) strains. In these timed assays, a malathion dose of 2-fold the LD₉₉ for the SCC strain (12.2 μg per vial) was used. Results are based on three tests on separate dates with three replicate vials (10 adults per vial) for each synergist–strain combination in each test. Control vials for effects of TPP, DEF, as well as solvent were included.

Data Analysis. Dose–mortality data were analyzed by probit regression (SAS Institute 1988). Lethal dose ratios with 95% CL were obtained from the probit parameters by the method of Robertson and Preisler (1992).

Strain and culture differences between weights of male and female *B. hebetor* were analyzed with analysis of variance (SAS Institute 1987). The classification variables were strain, culture (nested within strain), sex, sex by strain, and sex by culture (nested within strain).

Mortality data from serial time–dose–response assays were analyzed as the percentage of killed insects per number of live insects at the beginning of each time interval (Robertson and Preisler 1992). Effects of count times are treated as categorical variables that are added to the effect of dose and analyzed by using a complementary log–log (CLL or Gompertz) model with a binomial error distribution (Preisler and Robertson 1989). This analysis was done with GLIM (Payne 1987); details of programming are given by Robertson

Table 2. Percentage of mortality of F₂ progeny of field strains of larvae of the Indianmeal moth, *Plodia interpunctella*, topically treated with 1 μl of technical malathion

Strain	<i>n</i>	Dose (mg/g)	% mortality	R
Hawkinsville, GA	85	63.6	26	273
Blackville, SC	95	82.6	32	324

Resistance ratios estimated from the LD₂₆ and the LD₃₂ (0.233 and 0.255 mg/g, respectively) of a malathion-susceptible strain (Zettler 1982).

and Preisler (1992). Probability of death values were obtained from the GLIM output. The second procedure was a probit analysis developed for correlated data (Throne et al. 1995). This matrix-based procedure, which provides confidence limits on slope, intercept, and estimated LT (lethal time), was used to analyze serial time–response assays when only one dose of each pesticide was tested. Mortality data (proportion killed) were transformed into probit, logit, and Gompertz units. In addition, time (x-axis) was (1) untransformed or (2) transformed to logarithm units. Thus, the data were fit to six models. Probability of dying was obtained from back transformations of the transformation giving the best fit to the data as determined by a chi-square goodness-of-fit test. When interactions were compared (e.g., strain–pesticide interactions), the model giving the best overall fit for the two strains was used even though a different model may have been a better fit for one of the strains. Programs for these analyses were written and run in Mathematica (Throne et al. 1995). Where appropriate, slopes and intercepts from the output were also compared with a *z* test (Snedecor and Cochran 1967).

Results

Dose–Response Bioassays. Probit regression parameters for the response of Savannah, SCC, and Hawkinsville strains of *B. hebetor* to malathion (Table 1) indicated that the probit model fit the data reasonably well. LD₅₀ values for the three strains were 0.21, 1.59, and 1.51 μg per vial, respectively. Lethal-dose ratios indicated that the SCC and Hawkinsville strains were 7- to 9-fold less sensitive to malathion, respectively, than the Savannah (laboratory) strain at the LD₅₀ and LD₉₉.

Resistance in *P. interpunctella* Host Larvae. Larvae of *P. interpunctella* from Hawkinsville, GA, and Blackville, SC, collected at the same sites as the *B. hebetor* were >270-fold more resistant to malathion compared with the Savannah laboratory (susceptible) strain of *P. interpunctella* (Table 2).

Response of Male and Female *B. hebetor* to Malathion. We detected a clear trend for male *B.*

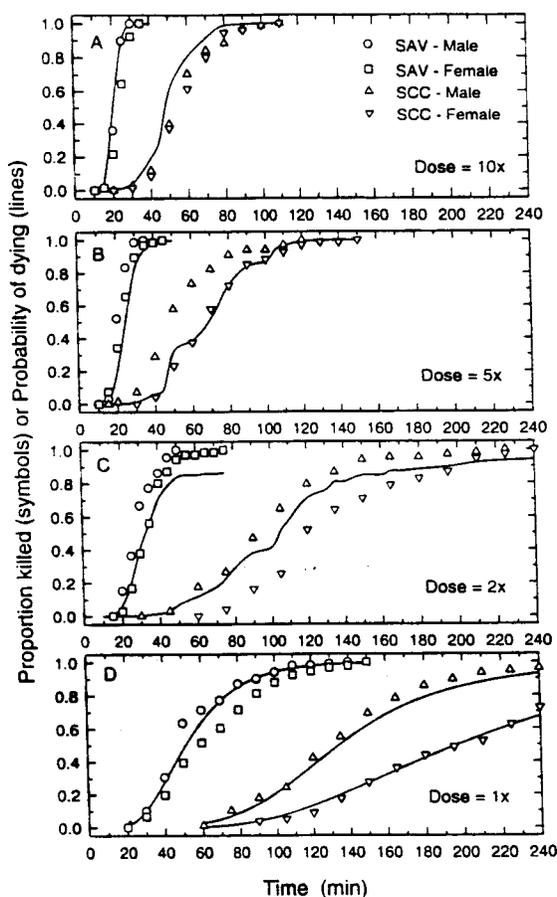


Fig. 1. Serial time response of males and females from the Savannah and SCC strains of *B. hebetor* to dose multiples of the LD_{99} for malathion of the SCC strain ($6.1 \mu\text{g}$ per vial) bioassayed in glass vials at 22°C . A-10-fold dose = $61 \mu\text{g}$ per vial; B-5-fold dose = $30.5 \mu\text{g}$ per vial; C-2-fold dose = $12.2 \mu\text{g}$ per vial; and D-1-fold dose = $6.1 \mu\text{g}$ per vial. Data in Fig. 1 A-C were analyzed with the CLL model by using GLIM. CLL lines were not significantly different so combined data for both sexes were used to prepare probability of dying curves for each strain-dose combination. Data in D were analyzed with the matrix-based procedure because this test was conducted separately. Back transforms giving probability of dying were obtained from combined sex data of the Savannah strain because sex differences were not significant. Sex differences in LT_{50} s at the 1-fold dose were significant ($P < 0.05$) in the SCC strain and back transforms (log-logit) were obtained for each sex.

hebetor in both Savannah and SCC strains to be more sensitive than females to malathion in the serial time-dose-response assays (Fig. 1 A-C). This trend was more apparent at lower doses. Nevertheless, analysis of response data for 2-, 5-, and 10-fold doses indicated no important difference in the CLL lines between the sexes of a given strain, although there was a significant difference ($P < 0.05$) between strains. From results of the GLIM

output, we did the bioassay with the LD_{99} for the SCC strain and analyzed these data with the matrix-based method for correlated data. Results of these analyses are presented in Fig. 1D and Table 3. Based on failure of 95% CL to overlap, we concluded that LT_{50} s for males and females of the SCC strain differed significantly, but males and females of the Savannah strain did not differ significantly at this dose. For the SCC strain, LT_{50} s were 134.3 min for males, compared with 196.8 min for females.

Adult Weights of *B. hebetor* Strains. Analysis of variance of adult weights of males and females of the Savannah and SCC strains is given in Table 4. Males from both strains weighed substantially less than females, and adults of the SCC strain weighed significantly less than those from the Savannah strain. Within a given culture, there are always some very small adults and this is indicated by the wide range of weights obtained within a given sex for each strain.

Sensitivity of *B. hebetor* Strains to Protectants. The order of sensitivity of the Savannah and SCC strains of *B. hebetor* to the tested pesticides was identical; specifically, chlorpyrifos-methyl > pirimiphos-methyl > deltamethrin > cyfluthrin > malathion (Fig. 2). Probit parameters of these data are presented in Table 5.

Based on the criterion of failure of 95% CL of LT_{50} s to overlap, both strains were significantly ($P < 0.05$) more sensitive to chlorpyrifos-methyl than to the other pesticides. In this bioassay, the Savannah strain responded similarly to pirimiphos-methyl and deltamethrin and was less sensitive to cyfluthrin and malathion. LT_{50} s for the Savannah strain ranged from 11.6 min for chlorpyrifos-methyl to 38.3 min for malathion.

We detected significant ($P < 0.05$) differences in the timed response to the pesticides in the SCC strain. LT_{50} s ranged from 11.0 min for chlorpyrifos-methyl to 120.8 min for malathion. We also identified significant differences between LT_{50} s of the Savannah and SCC strains for deltamethrin, cyfluthrin, and malathion. In every case, slopes of the response of the Savannah and SCC strains to a given pesticide were significantly different by the χ^2 test.

Effect of Synergists on Response of *B. hebetor* to Malathion. Adults of both Savannah and SCC strains had lower LT_{50} s for malathion + DEF compared with malathion alone, although these differences were only important for the SCC strain (based on nonoverlap of confidence intervals) (Table 6). Nevertheless, occasional mortality occurred in control vials treated with DEF. In several cases, significant mortality ($\approx 75\%$) occurred when adults in control vials treated with DEF were left overnight whereas no mortality occurred in vials treated with solvent.

LT_{50} s of adults of both Savannah and SCC strains that were exposed to malathion + TPP were significantly longer (based on failure of 95%

Table 3. Response of males and females from Savannah and SCC strains of *B. hebetor* to the LD₉₉ for malathion of the Savannah strain (6.1 µg per vial) in a serial-time laboratory bioassay in glass vials at 22°C

Strain	Sex	Transform	Parameters ^a				
			LT ₅₀ (min)	95% CL	Slope ± SEM	χ ²	df, P
Savannah	Male	Log-probit	49.7	46.3–53.2	5.8 ± 0.4	10.94	9, 0.138
Savannah	Female	Log-probit	51.4	47.8–55.3	5.4 ± 0.3	18.02	11, 0.046
SCC	Male	Log-logit	134.3	125.2–143.9	10.3 ± 0.8	5.93	9, 0.199
SCC	Female	Log-logit	196.8	172.8–224.1	8.6 ± 0.8	18.57	9, 0.019

^a Parameters from the matrix-based procedure for correlated data of Throne et al. (1995). χ², calculated value of chi-square; df, degrees of freedom for chi-square; P, probability of a greater chi-square.

CL to overlap) than those for adults in vials treated with malathion. The delay was especially apparent in the SCC strain. Slopes of log-logit transformed data comparing malathion and the malathion + TPP treatment in the SCC strain were significantly different ($P < 0.05$) by the z test. We observed no mortality in control vials treated with TPP with either strain.

Discussion

Because peanut and grain storage facilities in the southeastern United States have historically been treated with malathion on a seasonal basis, lepidopterous pests (e.g., *C. cautella*, and *P. interpunctella*) associated with these commodities have developed significant malathion resistance (Zettler et al. 1973, Zettler 1982). Populations of *B. hebetor* that parasitize larvae of these pyralid moths occur naturally in these facilities (Keever et al. 1985). Although resistance to organophosphorous insecticides is not that well documented among hymenopterous parasitoids (Croft 1990), the malathion resistance that we found in the two field strains of *B. hebetor* is not surprising considering their probable exposure to residual pesticide treatments.

Sex Differences. The serial time-response bioassays with residual malathion were particularly effective in demonstrating increased sensitivity of males to malathion in the Savannah and SCC strains of *B. hebetor*. These differences would have been much more difficult to document with typical dose-response bioassays. Another advantage of the serial time-response bioassay is that fewer test in-

sects are needed. This can be important when testing field strains where few individuals may be available.

Sex differences in sensitivity of parasitoids to pesticides have been noted in other studies. For example, male *Bracon mellitor* Say were more sensitive than were females to a number of pesticides (Adams and Cross 1967, O'Brien et al. 1985). Adult males of the pteromalid *Urolepis rufipes* (Ashmead) were 1.3- to 2.8-fold more sensitive than females to seven pesticides (Scott and Rutz 1988). In these cases, the differences in sensitivity were thought to be related to the smaller size of the males. Males of the parasitoid *Diglyphus begini* (Ashmead) were more sensitive than were females to methomyl, oxamyl, fenvalerate, and permethrin (Rathman et al. 1992). These differences

Table 4. Adult weights of males and females from two strains of the parasitoid *B. hebetor* reared on *P. interpunctella* larvae at 27°C and 50–60% RH

Strain	n	Adult wt (mg)	
		Males	Females
Savannah	60	0.770 ± 0.29a (0.254–1.239)	0.956 ± 0.039b (0.349–1.447)
SCC	60	0.664 ± 0.023b (0.338–1.020)	0.859 ± 0.029c (0.425–1.340)

Means ± SEM with (range). Obtained by weighing 20 ♂ and 20 ♀ 2- to 3-d-old adults from each of three separate cultures for each strain. Means in a row or column followed by the same letter are not significantly different at $P = 0.05$ (ANOVA).

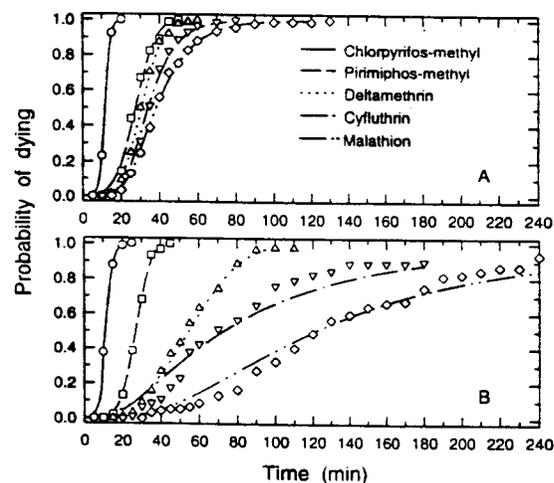


Fig. 2. Probability of dying curves (lines) obtained from back transformation of serial time-response data (symbols) of *B. hebetor* from Savannah (A) and SCC (B) strains to pesticides used as protectants bioassayed in glass vials at 22°C. Pesticides were compared at the LD₉₉ for malathion of the SCC strain (6.1 µg per vial) and analyzed with the matrix-based procedure of Throne et al. (1995). Transformations used for comparing strains against a given pesticide are given in Table 5. Chlorpyrifos-methyl (circles), pirimiphos-methyl (squares), deltamethrin (triangles), cyfluthrin (upside-down triangles), and malathion (diamonds).

Table 5. Survey of responses of Savannah and SCC strains of *B. hebetor* to insecticide protectants in a glass vial laboratory bioassay at 22°C. Pesticides compared at the LD₉₉ of the SCC strain for malathion (6.1 µg per vial)

Pesticide	Strain	Transform	Parameters				
			LT ₅₀ (min)	95% CL	Slope ± SEM	χ ²	df, P
Chlorpyrifos	Sav	Logit	11.6	10.9–12.2	0.72 ± 0.08	0.61	1, 0.754
Chlorpyrifos	SCC	Logit	11.0	10.2–11.8	0.5 ± 0.06	0	1, 55.53
Pirimiphos-methyl	Sav	Probit	27.4	23.8–31.0	0.12 ± 0.01	16.5	6, 0.009
Pirimiphos-methyl	SCC	Probit	26.7	25.4–28.1	0.16 ± 0.01	3.89	5, 0.292
Deltamethrin	Sav	Probit	30.6	28.7–32.5	0.11 ± 0.01	5.12	8, 0.216
Deltamethrin	SCC	Probit	54.7	50.1–59.3	0.05 ± 0.0	10.8	11, 0.169
Cyfluthrin	Sav	Log	34.1	30.2–38.4	6.8 ± 0.5	23.1	10, 0.007
Cyfluthrin	SCC	Log	72.7	53.9–98.8	2.9 ± 0.3	46.4	16, 0.000
Malathion	Sav	Log	38.3	36.2–40.4	5.9 ± 0.4	5.69	14, 0.043
Malathion	SCC	Log	120.0	99.1–148.4	3.5 ± 0.3	38.9	21, 0.006

Parameters obtained from the procedure of Throne et al. (1995) for correlated data. χ², calculated chi-square goodness-of-fit statistic; df, degrees of freedom for chi-square; P, probability of a greater chi-square.

in sensitivity were thought to be partly related to size. However, there was also evidence for differences in metabolism of fenvalerate among males and females, as well as behavioral differences between males and females in the bioassay itself, that might account for the increased sensitivity of males.

In our studies, adult females of *B. hebetor* were 1.2-fold heavier than males in the Savannah strain and 1.3-fold heavier than males in the SCC strain. In lieu of any evidence for metabolic differences between sexes, as well as no apparent behavioral differences observed between males and females in the vial bioassay, we assume the increased sensitivity of males is primarily the result of their smaller size.

Survey of Pesticide Selectivity. Both the Savannah and SCC strains of *B. hebetor* showed selectivity to the five pesticides tested in the serial time-response bioassays. The SCC strain was significantly more tolerant of deltamethrin and cyfluthrin than was the Savannah (laboratory) strain. A similar increased tolerance for pyrethroids relative to chlorpyrifos-methyl and pirimiphos-methyl was noted in a field strain of *A. calandrar* (Baker 1994).

Pyrethroids are generally less toxic than organophosphorous insecticides to adult parasitoids

(Wilkinson et al. 1979, Elzen et al. 1987, Mason and Johnson 1988). Reasons for these differences in sensitivity remain to be determined. Bull et al. (1987) postulated that the increased tolerance of *Microplitis croceipes* (Cresson), a braconid parasitoid of *Heliothis* spp., for pyrethroids and DDT could have been caused by (1) years of heavy use of DDT for control of *Heliothis* spp. in cotton and other crops, (2) selection for DDT resistance or tolerance in *M. croceipes* during this time period, and (3) the similarity in modes of action of DDT and pyrethroids. Interestingly, DDT was used extensively as a warehouse treatment in the past. As a result, if *B. hebetor* has been predisposed to chlorinated hydrocarbon pesticide residues, the increased tolerance of the SCC strain for pyrethroids may be explained by a similar hypothesis.

Synergists. Plapp et al. (1963) found that S,S-tributyl phosphorotrithioate (DEF) was an effective synergist for malathion-resistant houseflies, *Musca domestica* L. However, DEF was also one of the few synergists that showed toxicity to the houseflies in a glass jar bioassay as well as to larvae of *Culex tarsalis* (Coquillett) that were bioassayed in distilled water. Because DEF caused mortality in *B. hebetor* in our glass vial bioassays, even though there was only slight mortality within the actual bioassay time interval, it is difficult to inter-

Table 6. Effect of synergists DEF and TPP on sensitivity of Savannah and SCC strains of *B. hebetor* to malathion in a glass vial laboratory bioassay at 22°C

Strain	Synergist	Parameters				
		LT ₅₀ (min)	95% CL	Slope ± SEM	χ ²	df, P
Savannah	—	28.9	26.5–31.5	9.9 ± 0.9	3.82	3, 0.231
Savannah	DEF	25.9	23.9–27.9	12.2 ± 1.3	1.51	1, 0.306
Savannah	TPP	45.4	42.2–48.8	10.9 ± 0.9	6.54	4, 0.124
SCC	—	77.4	69.5–86.2	7.4 ± 0.6	6.54	10, 0.181
SCC	DEF	62.5	56.3–69.2	7.7 ± 0.7	6.06	8, 0.224
SCC	TPP	169.5	129–222	4.8 ± 0.4	29.34	13, 0.004

Parameters obtained from the procedure of Throne et al. (1995) for correlated data. All data were transformed by the log-logit transformation before analysis. χ², goodness-of-fit chi-square; df, degrees of freedom for chi-square; P, probability of a greater chi-square. Malathion used at a dose equivalent to two times the LD₉₉ of the SCC strain (12.2 µg per vial). Synergists tested at 5:1 weight ratio.

pret the synergistic effect of the DEF + malathion mixture regarding possible resistance mechanisms.

Triphenyl phosphate (TPP) is a potent synergist for malathion (Plapp et al. 1963). TPP has been used to characterize malathion resistance as being due to a specific carboxylesterase in a number of stored-product insects (Dyte and Rowlands 1968, Haliscak and Beeman 1983, Navarro et al. 1986, Zettler and Cuperus 1990). Malathion resistance in the stored-product insect predator, *Xylocoris flavipes* (Reuter) (Heteroptera: Anthocoridae) was completely abolished with TPP (Baker and Arbogast 1995). However, in our serial time-response bioassays with *B. hebetor* in the glass vials, TPP significantly reduced the effectiveness of malathion against the SCC strain. This antagonistic effect of TPP has been noted before by Dyte et al. (1966). Also, Plapp et al. (1963) found that TPP decreased the toxicity of parathion to *M. domestica* in glass jar bioassays; they postulated that TPP interfered with the uptake of parathion from the vial surface. TPP may also interfere with uptake of malathion by *B. hebetor* in our vial assay. However, additional studies are needed to determine the mechanism of the TPP antagonism and to characterize the malathion resistance in this parasitoid more fully.

Resistance Development in *B. hebetor*. Compared with the resistance ratios of pyralid larvae that infest stored peanuts and grain in the Southeast, the malathion resistance of *B. hebetor* was low in the field strains that we tested. Several factors may be responsible. First, *B. hebetor* is a generalist and attacks a variety of lepidopterous hosts in ecosystems that are not necessarily treated with pesticide. *B. hebetor* foraging in these alternate ecosystems would not be under exposure to the selecting agent and could, through immigration, continually dilute parasitoid populations that would otherwise develop resistance. Second, pyralid larvae are generally found on or near the surface of stored peanuts or grain that they infest. *B. hebetor* can paralyze and oviposit on or near these larvae without actively foraging throughout the grain mass. As a result, successful host finding may occur without the parasitoid coming into extensive direct contact with protectants. Although pesticides applied directly to host larvae can be toxic to *B. hebetor* (Press et al. 1981), it is not known if toxic effects of pesticides or their metabolites can be passed directly from pyralid larvae to adult parasitoids. In addition to reduced exposure of adult parasitoids to protectants, larval parasitoids feeding on paralyzed pyralid larvae would receive little direct exposure to previously applied pesticides. In conclusion, ecological and behavioral factors among foraging adults and feeding larvae of *B. hebetor* may result in reduced selection pressure even in storage facilities extensively treated with pesticides.

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