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Fitness of a Malathion-Resistant Strain of the Parasitoid *Anisopteromalus calandrae* (Hymenoptera: Pteromalidae)

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ABSTRACT Biological fitness of a malathion-resistant (R) and a malathion-susceptible (S) strain of the solitary parasitoid *Anisopteromalus calandrae* (Howard) was compared when the wasps were parasitizing immature rice weevils, *Sitophilus oryzae* (L.), in stored wheat. Despite having a >2,500-fold naturally occurring resistance, in the absence of insecticide the R strain was equal to the S strain in ability to parasitize hosts and in several developmental parameters. Development times of cohorts of male and female progeny produced over 7 d by R and S females at 25°C and 75% RH were not significantly different. There was no significant strain effect on daily fecundity. Parasitization of hosts was not significantly affected by strain–host density interactions. There was no significant effect of strain on total progeny production at different host densities, but more female progeny were produced by the susceptible strain at high host densities. Otherwise, the proportion of females among progeny of the 2 strains was not significantly different. Frequency of the R allele in Hardy–Weinberg populations, set up with an initial R allele frequency of 0.5, was lower than expected but tended to stabilize after 4 generations. Frequency of the R allele in a population started with hybrid females was not significantly different from values expected under the hypothesis of no fitness costs. Failure to detect fitness costs associated with malathion resistance in *A. calandrae* could be caused by the lack of negative pleiotropic effects associated with the R allele.

KEY WORDS *Anisopteromalus calandrae*, biological control, parasitoid, insecticide resistance, fitness, stored-products

A COMPLEX OF parasitoids and predators is associated with pest insects that infest stored grain (Brower et al. 1996). The amount of natural control that these beneficial species exert on pest insect populations is difficult to measure and likely to be variable. As a result, the best use of these beneficial species in pest management programs in the stored-grain ecosystem is through augmentative release (Brower et al. 1996). Strains of these biological control agents selected for release should be competitive with indigenous field populations of a given parasitoid or predator species, particularly if the released strain has been genetically improved or carries a desired trait such as improved searching ability or increased fecundity (Croft 1990).

Insecticide resistance is a desirable trait for parasitoids and predators used in management programs (Croft and Strickler 1983,Hoy 1985, Rosen 1985). However, insecticide resistance also may confer fitness disadvantages (Georghiou and Taylor 1977) that would reduce the stability of the trait within field populations in the absence of selection pressure. Spollen and Hoy (1992) measured relative fitness components for a genetically improved strain of *Aphytis melinus* DeBach with increased resistance to carbaryl. Except for a difference in progeny sex ratio, developmental parameters were not significantly different between the resistant and susceptible strains. Nevertheless, the laboratory-selected resistance in *A. melinus* declined slowly. In contrast to the number of beneficial species genetically improved through laboratory selection procedures (Hoy 1985, Rosenheim and Hoy 1988, Havron et al. 1991a, b), the number of parasitoid species with significant levels of naturally occurring resistance to organophosphates is quite small, and little information on relative fitness is available in these species (Croft 1990).

Malathion has been used extensively as a chemical protectant on stored cereals since the late 1950s. Because of widespread use of this phosphorodithioate insecticide, many insect pests as well as beneficial insects found in the stored-grain ecosystem have developed significant levels of resistance (Arthur 1996). The highest level of resistance in a beneficial species was found in a field strain of *Anisopteromalus calandrae* (Howard), a small pteromalid wasp that parasitizes insect larvae found within grain kernels (Baker and Weaver 1993, Baker 1995). The unique resistance in this solitary parasitoid has been stable for several years of laboratory

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rearing without any selection pressure (Baker 1995), and we have evidence that the resistance is controlled by a single, incompletely dominant gene (Baker et al. 1997).

To obtain information on the stability of the R allele when the resistant strain of *A. calandrae* is released in the field, biological components that determine fitness, such as development time, fecundity, sex ratio, and rates of parasitization, were compared in the resistant (R) and susceptible (S) strains in the absence of insecticide. In addition, changes in frequency of the R allele in Hardy–Weinberg populations were measured over 6 generations.

Materials and Methods

Insect Cultures. *Anisopteromalus calandrae* was maintained at 28°C and 60–65% RH on cultures of hard, red winter wheat infested with larvae of the rice weevil, *Sitophilus oryzae* (L.). The S strain of *A. calandrae* has been maintained in the laboratory for >20 yr. The R strain of *A. calandrae* was collected in 1992 near Bamberg, SC, and has been reared continuously in the laboratory without selection pressure. All tests with *A. calandrae* were conducted by pairing newly emerged virgin males and females of each strain. Virgin wasps were obtained by placing 3-4 infested kernels in glass tubes (13 by 100 mm) and checking daily for adult emergence.

Cohort Development Times. Development time of cohorts of male and female progeny produced over a 7-d oviposition period, total progeny production, progeny sex ratio, and parasitization were determined for individual parent females of each strain of *A. calandrae.* For this study, virgin females and males of each strain that had emerged within the previous 18 h were paired in glass tubes (13 by 100 mm). After 3 h, the females were placed in 16-dram plastic vials (3.2 by 8 cm) with snap-cap screen lids that contained 20 g of wheat infested with 23-d-old rice weevil larvae. Because the 20-g samples came from the same bulk sample of weevil-infested wheat, host age and density were similar for both parasitoid strains. Female wasps were removed after a 7-d oviposition period at 25°C and 75% RH. Beginning at 14 d, emerging rice weevils and male and female *A. calandrae* were counted daily until wasp emergence was complete. Controls to determine initial rice weevil host density were included. Results are based on oviposition responses of 16 S females and 15 R females.

Daily Fecundity. Daily fecundity at 25°C and 75% RH was compared in the 2 strains of *A. calandrae.* Newly emerged virgin females of both strains were mated with virgin males and transferred to plastic petri dishes (15 by 60 mm) containing 5 g of hard, red winter wheat infested with larvae of *S. oryzae* (21–24 d old. Tests with R and S females were run simultaneously with host age and host density similar for both strains. After 24 h, the females were transferred to a new petri dish containing a 5-g sample of infested wheat. In this manner, the daily fecundity of females of each strain was determined for 10 consecutive days. Male and female progeny that emerged from each batch of wheat were counted. Results are based on mean progeny production of 15 R females and 8 S females.

Host Density. The effect of host density on effectiveness of the 2 parasitoid strains was evaluated. Three host densities were prepared by allowing 50, 125, or 400 rice weevil adults (2–4 wk old) to oviposit for 4 d in 1 kg hard, red winter wheat (moisture content, 14.1%) at 28°C and 55–60% RH. The percentage of infested kernels under these conditions was 1.7 ± 0.4%, 3.9 ± 1.1%, and 9.5 ± 1.7% (mean ± SE), respectively. Samples of wheat (25 g) containing 22-d old host larvae from each density were placed in 16-dram vials. Newly emerged virgin males and females from each strain were obtained, and after pairing for 30 min, a single pair was placed in each vial. The experimental design included 10 replicates per strain per density plus 10 control replicates per density for host emergence. Number of parasitoids and hosts emerging in each vial was determined after 4 wk at 25° and 75% RH.

Allele Frequency. Changes in the frequency of the R allele in Hardy–Weinberg populations of the haplo-diploid *A. calandrae* parasitizing rice weevils at 28°C and 55–60% RH were determined in 2 experiments. Virgin males and females of the parent R and S strains, and virgin F_1 females from the RR × S hybrid cross, were collected. To obtain initial R allele frequencies of 0.5 at Hardy–Weinberg equilibrium, 25 RR females, 50 RS females, 25 SS females, 12 R males and 12 S males were combined in a 0.95-liter jar. After 3 h, the wasps were added to a 3.8-liter jar containing 1 kg of wheat infested with 22-d old host larvae. After 21 d, 100 G1 females were removed and used to begin a new generation. The remaining males and females were tested in the bioassay against a discriminating concentration (10 μg per vial) of malathion (Baker et al. 1997). This protocol was continued for 6 generations. Expected mortality with an R allele frequency of 0.5 is 25% for females and 50% for males. Percentage mortality was corrected for control mortality by the method of Abbott (1925) and compared with expected values.

In the 2nd experiment, the same number of total wasps was set up as above except the wasps were arranged into smaller groups (1 SS female, 2 RS females, 1 RR female) in glass tubes (13 by 100 mm) for mating with single S or R males. After mating overnight, all wasps were combined and placed in 1 kg of weevil-infested wheat as above. Bioassays of progeny were conducted for 5 generations.

Change in R allele frequency when the population was initiated with hybrid (SR) females also was determined. For this study, virgin SS females were mated with virgin R males. One hundred female progeny (SR genotype) that emerged from this cross (and that would have mated with S males in the culture jar) were used to initiate the population. Results of bioassays of the parents used to start this population were as expected. Mortality was 0 of 62

Table 1. Mean ± SE cohort development time, total progeny production during a 7-d oviposition period, progeny sex ratio, and percentage of parasitization of hosts by single parent females from malathion-susceptible (S) and malathion-resistant (R) strains of *A. calandrae* parasitizing rice weevil larvae in stored wheat at 25°C and 75% RH

Strain	*n*	Cohort development time, d[a]		Total progeny per ♀[b]		Proportion ♀[c]	% Parasitization[d]
		♂♂	♀♀	♂♂	♀♀		
S	16	17.8 ± 0.15b	18.9 ± 0.11a	14.4 ± 0.8b	47.1 ± 2.4a	0.77 ± 0.01a	67.8 ± 2.7a
R	14	17.5 ± 0.14b	19.0 ± 0.16a	16.5 ± 1.9b	40.6 ± 2.9a	0.71 ± 0.03a	66.2 ± 2.9a

Means in a column (or group) followed by the same letter are not significantly different at 0.05.

[a] GLM (data were weighted by number of progeny produced): strain, $F = 0.56$; df = 1, 57; $P = 0.46$; sex, $F = 68.9$; df = 1, 57; $P < 0.01$; strain × sex interaction, $F = 0.93$; df = 1, 57; $P = 0.34$. Means are based on mean development times of progeny produced by individual females weighted by the number of progeny produced per female, and are based on progeny from 16 S females and 15 R females (1 R female produced only male progeny).

[b] GLM (Box-Cox transformed data): strain, $F = 0.41$; df = 1, 56; $P = 0.53$; sex, $F = 204.4$; df = 1, 56; $P < 0.01$; strain × sex interaction, $F = 3.26$; df = 1, 56; $P = 0.08$. Untransformed means based on progeny from 16 S females and 14 R females are reported in table.

[c] GLM (arcsine-transformed proportions were weighted by number of progeny produced): $F = 4.03$; df = 1, 27; $P = 0.055$. Weighted untransformed means are reported and are based on progeny from 16 S and 13 R females.

[d] GLM (arcsine-transformed data): $F = 0.14$; df = 1, 28; $P = 0.71$. Untransformed means are reported.

for females and 42 of 42 for males. Bioassays of progeny from 2 subsequent generations were conducted as described above.

Analyses. General linear models analysis (SAS Institute 1987) was used to test for differences between strains and sexes. Box-Cox transformation was used when variances were nonhomogeneous (Box and Cox 1964). The arcsine transformation was used for proportions and percentages; however, untransformed data are presented in tables and figures. Chi-square was used to estimate significance of changes in allele frequency (Snedecor and Cochran 1967).

Results

Cohort Development Times. Male progeny from both strains of *A. calandrae* had a significantly shorter development time (≈1 day) compared with female progeny (Table 1), but there was no significant difference in mean development time at 25°C and 75% RH between the 2 strains for cohorts of either sex. In this experiment, there were also no significant differences in total numbers of female or male progeny, proportion female progeny, or percentage parasitization of host larvae between the 2 parasitoid strains.

Daily Fecundity. Females from both strains of *A. calandrae* produced the most progeny when they were 4–5 d old (Fig. 1). Maximum daily numbers of female progeny produced per female were 10.6 ± 2.2 at day 4 and 8.1 ± 3.7 at day 5 in the S and R strains, respectively. Although females of the S strain tended to produce more progeny, the difference between strains was not significant. There was a significant effect of parent female age on numbers of progeny produced. However, there was no significant strain × parent female age interaction (GLM: strains, $F = 2.03$; df = 1, 210; $P = 0.16$; parent female age, $F = 8.54$; df = 9, 210; $P < 0.01$; and strain × parent female age interaction, $F = 1.01$; df = 9, 210; $P = 0.43$). Sex ratio of progeny did not change as a function of parent female age or strain (GLM [arcsine-transformed proportion females weighted by number of progeny produced]: strain, $F = 3.82$; df = 1, 21; $P = 0.06$; parent female age, $F = 0.48$; df = 9, 164; $P = 0.89$; strain × parent female age interaction, $F = 0.45$; df = 9, 164; $P = 0.91$).

Host Density. Host densities established in these studies were 29 ± 5.7, 45 ± 8.8, and 94 ± 14.5 weevils per 25 g wheat. The mean number of progeny produced by individual parent females from both strains of *A. calandrae* was a function of host density ($F = 87.0$; df = 2, 53; $P < 0.01$) (Fig. 2). However, there was no significant difference between progeny production of the S and R strains ($F = 1.45$; df = 1, 53; $P = 0.23$; host density × strain interaction: $F = 0.82$; df = 2, 53; $P = 0.45$). Percentage parasitization ranged from 64.4 to 72.3% but did not vary with either host density or strain (GLM [arcsine-transformed percentage parasitization weighted by number of weevils + number of parasitoids emerged]: host density, $F = 0.10$; df = 2, 53; $P = 0.90$; strain, $F = 0.99$; df = 1, 53; $P = 0.33$; host density-strain interaction, $F = 0.40$; df = 2, 53; $P = 0.67$). Proportion females did vary with host density and there was a significant strain × host density inter-

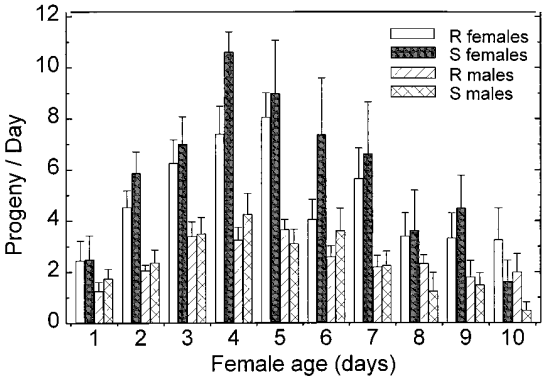

Fig. 1. Daily fecundity of parent females of S and R strains of *A. calandrae* parasitizing rice weevil larvae in wheat for 10 d at 25°C and 75% RH. Mean ≈ SE number of male and female progeny emerging per day was used as a measure of fecundity.

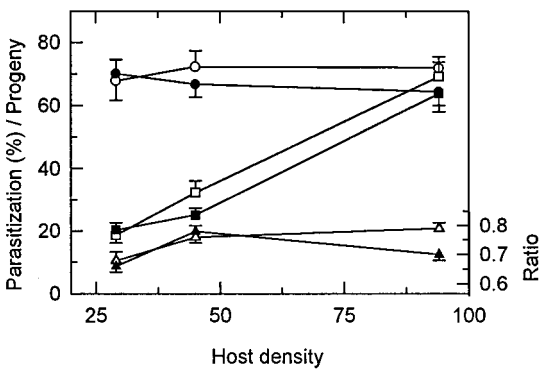

Fig. 2. ○, effect of host density on mean ± SE percentage of parasitization of hosts; □, total progeny produced per parent female; and △, progeny sex ratio (proportion female progeny) by S (hollow) and R (solid) strains of *A. calandrae* parasitizing rice weevil larvae in hard, red winter wheat at 25°C and 75% RH.

action (GLM [arcsine-transformed proportion females weighted by number of progeny produced]: host density, $F = 9.9$; df = 2, 53; $P < 0.01$; strain, $F = 1.20$; df = 1, 53; $P = 0.28$; host density × strain interaction, $F = 5.15$; df = 2, 53; $P < 0.01$). The S strain produced a higher proportion of female progeny at the highest density.

Allele Frequency. Based on the ratio of female and male genotypes used to initiate the experiments, and assuming random mating between male wasps and all female genotypes as well as a stable gene frequency, 75% of female progeny should have the RR or RS genotype and be phenotypically resistant when exposed to our discriminating concentration of malathion. Exposure to malathion should kill 25% of female progeny (i.e., those with SS genotype). Similarly, 50% of male progeny should be R and 50% should be S and die in the bioassay. In experiment 1, the initial mortality for both female and male progeny significantly exceeded these values (i.e., there were fewer individuals with the R allele than expected). Mortality tended to stabilize after 4 generations (Table 2). In this experiment, mortality of female progeny increased from ≈50 to 65% and remained stable at ≈65%. Mortality of male progeny was ≈75 to 85% during the entire study.

In experiment 2, mortality of G1 female progeny (28.7%) was not significantly different from expected. However, mortality of female progeny increased to ≈50% in the G2, then remained relatively stable for the duration of the study. Mortality of male progeny fluctuated throughout the study but generally was similar to that of male progeny in the 1st experiment.

When hybrid SR females mated to S males were used to initiate the parasitoid population, mortality of female and male progeny was not significantly different from expected during the 2-generation study (Table 2). Expected mortality of G1 progeny was 50% for both females and males. Expected mortality of G2 progeny was 37.5% for females and 75% for males.

Discussion

The R strain of *A. calandrae*, collected on a farm storage near Bamberg, SC, has been reared in the laboratory since 1992 without any malathion-induced selection pressure. The >2,500-fold malathion resistance in this parasitoid has remained essentially constant (Baker 1995). The stability of the

Table 2. Change in frequency of R allele in populations of *A. calandrae* reared for multiple generations at 28°C and 60% RH on hard red winter wheat infested with rice weevil larvae

Generation	♀ progeny		♂ progeny	
	r/*n*	% Mortality	*r*/*n*	% Mortality
		Hardy–Weinberg experiment 1		
G1	207/421	49.2	59/76	77.6
G2	29/58	50.0	43/54	79.6
G3	202/335	60.3	145/178	79.5
G4	323/483	65.5	129/167	75.0
G5	308/478	64.4	177/278	77.6
G6	300/321	66.7	300/341	83.8
		Hardy–Weinberg experiment 2		
G1	70/234	28.7*	146/231	59.9
G2	339/728	46.6	174/237	73.4
G3	83/139	51.7	30/49	56.7
G4	206/484	42.6	145/193	71.8
G5	293/464	57.5	167/192	83.0
		Hybrids		
G1	477/898	53.1*	108/190	56.8*
G2	71/167	42.5*	61/80	76.3*

Hardy–Weinberg populations were initiated with an R allele frequency of 0.5 based on Hardy–Weinberg equlibrium. For a stable R allele frequency of 0.5, expected mortality during discriminating dose tests with malathion in the Hardy–Weinberg populations is 25% for females and 50% for males. For hybrids, expected mortality is 50% for females and males in G1 and 37.5% and 75% for females and males, respectively, in G2. Mortality was assessed after a 24-h contact period in a glass vial bioassay with a malathion concentration of 10 μg per vial at 25°C and 75% RH; *r*, number dead; *n*, number tested; percentage mortality, corrected for control mortality; *, not significantly different from expected ratio by chi-square.

resistance during this extended laboratory rearing may in part be caused by the coevolution of fitness modifiers during the prolonged exposure of this strain to malathion as well as to the dominance of the R allele (Baker et al. 1997).

When we measured several individual fitness components in the S and R strains of *A. calandrae* in the absence of insecticide, the only difference we found was a tendency for S females to produce more female progeny than the R females. We did not find any significant differences between strains in cohort development times for either sex, progeny sex ratio (except in the density study), or parasitization effectiveness. Thus, even though the genetic background of the field and laboratory strains was probably different, their measured biological parameters were nearly identical. Failure to find fitness costs in the resistant strain may be caused by the lack of negative pleiotropic effects associated with the R allele.

Malathion-resistant strains of stored-product insects often show reduced intrinsic population growth rates compared with susceptible laboratory strains. A malathion-resistant strain of *Cryptolestes ferrugineus* (Stephens) produced ≈50% fewer eggs and had a longer larval development time compared with a susceptible strain (White and Bell 1990), and both fertility and fecundity of a malathion-resistant strain of *Plodia interpunctella* (Hübner) were reduced (Halliday 1990). However, the reduction in fitness is not necessarily associated with the genes responsible for the resistance. When alleles conferring malathion resistance from 2 stored-product beetles were backcrossed into susceptible genomes, no negative effect on overall fitness resulting from the R allele could be demonstrated in *Tribolium castaneum* (Herbst) (Beeman and Nanis 1986) or *C. ferrugineus* (White and Bell 1990).

In the current study, the frequency of the R allele in Hardy–Weinberg populations of *A. calandrae* containing all possible genotypes was significantly lower than expected in the G1 generation. Reasons for this are not understood. Nevertheless, the frequency of the R allele tended to stabilize after 4 generations, indicating that it was fully competitive with the S allele. Additional evidence for stability of the R allele was obtained when the *A. calandrae* population was initiated with hybrids. Frequency of the R allele was as expected during the 2-generation study.

Probably the most important fitness character of beneficial insects carrying a desirable trait and used in augmentative release programs is maintenance of the ability to locate and parasitize the target pest insect successfully. Based on evidence from our laboratory studies, the strain of *A. calandrae* carrying the malathion resistance gene searches as effectively as the susceptible strain even in the absence of insecticide. However, in stark contrast to the S strain, this naturally occurring R strain also retains its effectiveness in the presence of commercial application levels of malathion on wheat (Baker and Throne 1995).

It is apparent that the R strain of *A. calandrae* can compete successfully in the stored-grain ecosystem with parasitoids lacking the R allele. Even if this is not the case for other strains or parasitoid species carrying a desirable trait, multiple releases of parasitoids throughout the storage period may be able to overcome any fitness disadvantages the released parasitoid might have relative to the resident population.

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