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Fitness Consequences of Malathion-Specific Resistance in Red Flour Beetle (Coleoptera: Tenebrionidae) and Selection for Resistance in the Absence of Malathion

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ABSTRACT

Malathion resistance in the red flour beetle, *Tribolium castaneum* (Herbst), is a worldwide problem and is very stable once it becomes widespread in natural populations. In the absence of insecticide the proportion of resistant phenotypes may rapidly decline but the development of resistance does not always involve reduced fitness. Malathion-specific resistance in T. *castaneum* seems not to involve any loss of fitness in laboratory or field conditions. Susceptible beetles were in competition with resistant beetles at different initial frequencies and modifications of susceptible gene frequency were estimated in these laboratory populations over 10 generations. A significant decrease in susceptible gene frequency was observed in *Tribolium* populations over time. The selection coefficient of the susceptible allele was estimated and the fitness of susceptible alleles in all tests was observed to range from 0.89 to 0.93 compared with the fitness of resistant genotypes, which was assumed to be 1. Data provided evidence that the resistant strains exhibited fitness advantages in the absence of malathion. We also compared the biotic potential (fecundity and developmental time) of the susceptible strain, the homozygous malathion-specific resistant strain, and their hybrids. Malathion-specific resistant strains showed an 8-23% increase in biotic potential relative to the susceptible strain. These findings are consistent with those of malathion-specific resistance in T. *castaneum;* the fitness of the insects seems independent of the genetic background and the fitness of the resistant insects is not affected by this resistance mechanism.

KEYWORDS : *Tribolium castaneum,* Coleoptera, insecticide, malathion resistance, fitness, selection

Because of the intensive use of malathion in grain storage and on stored grain since the late 1950s, mal-athion-resistance in red flour beetle, *Tribolium castaneum* (Herbst), is widespread. The first case of resistance was reported in 1961 (Parkin et al. 1962), and by 1974 this phenomenon was regarded as a common attribute of this species (Champ and Dyte 1976). Although malathion use has declined or even been abandoned in some countries from the early 1970s because of the widespread occurrence of malathion resistance in red flour beetle populations (Champ 1984), malathion-specific resistance is very stable in *T. castaneum* wild populations. Moreover, the malathion-specific resistant phenotype in *T. castaneum* populations has almost completely replaced the susceptible one throughout most of the world (Beeman and Nanis 1986). To explain this stability, it was assumed that there were no pleiotropic effects of the mutation and no or few reproductive disadvantages between malathion-specific resistant and susceptible strains.

Because resistant insects were not present at high frequency before the use of insecticides, it is not surprising that resistant and susceptible strains should differ in properties other than their adaptation to insecticides, such as developmental time, fecundity, and fertility. Differences in the biological parameters affecting the net reproductive rate and the innate capacity of insect populations to increase are of particular interest to insecticide resistance management. Although the majority of fitness studies has shown that there are fitness costs associated with insecticide resistance (Ferrari and Georghiou 1981, Argentine et al. 1989, Parello and Trumble 1989, White and Bell 1990, Cochran 1993, McKenzie 1994), in some cases, in the absence of treatment, there is no fitness difference between resistant and susceptible strains or the resistant strain has a fitness advantage (Roush and Hoy 1981, Beeman and Nanis 1986, McKenzie 1993, Spollen et al. 1995, White and Bell 1995).

In this study, we evaluated fitness consequences of malathion resistance in *T. castaneum* to understand why persistence of this resistance mechanism occurs in wild populations. We compared the biotic potential (B_P) of susceptible and malathion-specific resistant strains of *T. castaneum.* With this information, we can better assess the likelihood of insecticide resistance increasing to cause widespread control failures against stored-product pests.

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Materials and Methods

Strains. Two red flour beetle strains were used in this study. A strain specifically resistant to malathion, called PRm, was originally collected from a grain store in the Philippines in 1976. The other strain, Asm, is susceptible to malathion and originated from storage facilities at Abidjan, Ivory Coast, in 1984. The beetles were reared on whole wheat flour enriched with brewer's yeast (10:1 wt:wt) and kept in the dark at 30 ± 3°C and 65 ± 5% RH. The PRm strain was exposed to a continuous dose of malathion (148 µg/cm^2 on filter paper) for 37 generations and was selected for homozygous malathion resistance by exposure malathion (14.8 µg/cm^2 on filter paper) for a discriminating time of 3 h. The homozygous susceptible Asm strain was maintained without pesticide exposure for 8 yr. Separate cultures were started with homozygous resistant PRm eggs and homozygous susceptible Asm eggs and heterozygous eggs laid by the susceptible female parents (PRm male x Asm female) or by the resistant female parents (Asm male x PRm female).

Malathion Susceptibility and Dominance of Resistance. Adult beetles (2-4 wk old) were tested for malathion resistance with an insecticide contact bio-assay. For each concentration tested, 100 adults were exposed for 24 h to a filter paper impregnated with an acetonic solution of malathion (943 µl*)* at concentrations ranging from 0 to 30% (wt:vol) at 25°C. Controls were exposed to acetone-impregnated papers. Afterward, the number of dead adults was observed. We considered adults to be dead when the beetles were motionless or exhibited completely uncoordinated movements. Mortality was determined 24 h later and compared with controls that were treated with malathion only. Data were pooled, and LC_{50}, LC_{90}, and their corresponding resistance factors were determined by Logit-Probit regression analysis (Raymond 1993). Dominance levels were measured as $D = (R_{F1} - 1)/(R_R - 1)$, where R_R and R_{F1} are the resistance factors at LC_{50}; and R_R and R_{F1} are defined by LC_R/ LC_S and LC_{F1}/LC_S, respectively, where LC_R, LC_S, and LC_{F1} are the insecticide concentrations (in percent) needed to obtain 50% mortality for homozygous resistant, homozygous susceptible, and heterozygous individuals (Bourguet et al. 1997).

Selection for Malathion-Specific Resistance in Absence of Insecticide. To assess the relative fitness of resistance allele(s) in absence of selective pressure, resistant phenotypes were placed in competition with susceptible insects without insecticide. The frequencies of the resistant and susceptible phenotypes were monitored for 10 consecutive, nonoverlapping generations. Population cages were made of 900-ml glass jars containing whole wheat flour enriched with brewer's yeast (10:1 wt:wt). The initial frequency of resistant allele was set at 0.05, 0.10, 0.20, or 0.30 at a Hardy-Weinberg equilibrium by adding R^{mal}/R^{mal}, R^{mal}/S^+, or S^+/S^+ beetles in the proper ratios, where R^{mal} represents the allele of malathion-specific resistance and S^+ of insecticide susceptibility. Six independent lines were monitored for each initial R^{mal} frequencies. To ensure nonoverlapping generations, parent beetles were discarded after 3 wk, which is less than the immature developmental period. After 8 wk, the progeny were collected from every jar. One hundred adults were randomly selected and used to initiate the next generation. In addition, F_1 adult progeny of each population were tested for malathion susceptibility as describe by Haubruge et al. (1997). Three replicates of 200 insects were confined on a filter paper impregnated with a 1% malathion concentration (14.8 µg/ cm^2) for 3 h at 25°C This discriminating dose was 10 times the LC_{99} of the susceptible strain Asm, but did not kill any of the resistant heterozygotes and homo zygotes.

Table 1. Expected frequencies of the different genotypes of susceptible homozygous, resistant homozygous or heterozygous and their fitness

Genotype	R^{mal}/R^{mal}	R^{mal}/S^+	S^+/S^+
Frequency	p^2	2pq	q^2
Fitness *(w)*	$W_{RR} = 1$	$W_{RS} = 1$	$w_{ss} = 1 - C_s$

C_s, p, and q are the selection coefficient, the frequency of resistant, and the frequency of susceptible alleles, respectively.

Estimates of Selection Coefficients and Relative Fitness. The frequencies of the different genotypes and their fitness can be summarized at Table 1. If the malathion-specific resistance is inherited as a single dominant or codominant gene (see *Results)* and the frequency of susceptible genotype *(S^+/S^+)* decreased in *Tribolium* populations, the fitness of the resistant homozygous *(w_{RR})* and heterozygous *(w_{RS})* were assumed to be 1.0. The fitness of susceptible homozygous *(w_{ss})* was assumed to be 1 — C_s.

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The fitness of the susceptible genotype compared with the resistant genotype over 10 generations may be estimated from the change in frequency of that genotype during this time. The method of Clarke and Murray (1962) is appropriate when the gene frequency change is low as it is here (Muggleton 1986). Assuming the existence of a Hardy-Weinberg equilibrium among the tested *Tribolium* populations, estimates of gene frequencies q_0 and q_n at the beginning and after each generation (n) were obtained. A simple expression is available for the change in q as a result of one generation of selection: $[\Delta q = C_s \cdot q^2(1 - q)/1 - C_s(1 - q^2)]$ (Falconer 1960). By integrating this over 10 generations an estimate of selection coefficient (C_s) and his variance [$V_{(Cs)}$] could be calculated as (Clarke and Murray 1962):

$$C_s = \frac{\ln\left[\frac{q_0(I - q_{10})}{q_{10}(I - q_0)}\right] + \frac{I}{q_{10}} - \frac{I}{q_0}}{t + \ln\frac{(I - q_{10})}{(I - q_0)}}$$

$$V_{(Cs)} = \left(\frac{I}{q_{10}} + \frac{I}{I - q_{10}} + \frac{I}{q_{10}^2}\right)^2 \frac{q_{10}(1 - q_{10})}{2N_n} + \left(\frac{I}{q_0} + \frac{I}{I - q_0} + \frac{I}{q_0^2}\right)^2 \frac{q_0(I - q_0)}{2N_0} \Bigg/ \left[t + \ln\left(\frac{I - q_{10}}{I - q_0}\right)\right]$$

Egg Fertility and Biotic Potential (B_P). The fertility of the eggs laid by homozygous and heterozygous females was estimated for the four strains. One hundred adults were placed in 90-mm petri dish with 20 g of the rearing medium. Every 4 d, the eggs laid during a 24-d period were removed. One hundred eggs were randomly selected and placed in a 55-mm petri dish with 5 g of the rearing medium. After 6 d, the number of hatched larvae was counted.

Both fecundity (F) and developmental time (DT) affect the reproductive potential of the insects. It is therefore interesting to pool these two parameters to compare the fitness of resistant homozygous and heterozygous strains to that of the susceptible strain. We used the biotic potential (B_P) adapted from Roush and Plapp (1982) as follows:

$$B_P = ln\ F/DT_r$$

where F is the fecundity (mean number of larvae/ female), and DT_r is the ratio between the mean developmental time of the considered strain and that of the susceptible strain.

The fecundity and the ratio between the mean developmental time of the two homozygous strains (Asm and PRm) and those of their two reciprocal hybrids (PRm male x Asm female and Asm male x PRm female) were estimated and pooled to calculate the B_P of the resistant insects.

To compare fecundity, pupae of every T. *castaneum* strain were sexed and maintained individually in a vial with the rearing medium to ensure the beetle virginity. Adult pairs consisting of a male marked with a black pencil and a female were placed at 30 ± 3°C and 60 ± 5% RH in a 90-mm petri dish with 20 g of the rearing medium. After 4 d, the males were discarded and the females placed individually in a 55-mm petri dish with 5 g of the rearing medium. The females were allowed to lay eggs for 4 d and were discarded afterward. After 2 wk (a period long enough to allow all larvae to hatch under the rearing conditions), the number of larvae was counted in each dish. Fecundity studies were replicated 34 times for each strain. For developmental time estimates, 100 eggs laid during a 24-h period were placed at 30 ± 3°C and 60 ± 5% RH in a 55-mm petri dish with 20 g of the rearing medium. Three weeks later, emerging adults were counted at least once every day and developmental time means calculated. The experiments were replicated three times for each strain. The ratio between the mean developmental time of homozygous and heterozygous resistant strains were scaled against one of the susceptible strain Asm. B_p was calculated on these scaled values, which we referred to as relative developmental time **(DT_r).**

Statistical Analysis. The statistical analysis software Minitab version 12.2 for Windows (Minitab 1998) was used to analyze the results. One-way analysis of vari-anc (ANOVA) and Tukey's multiple comparison test were performed to compare the four strains (significant differences were considered when P values were <0.05).

Table 2. Toxicity of malathion to strains of T. castaneum: Asm (susceptible), PRm (malathion-specific resistant), H_1 (Asm male x PRm female), and H_2 (PRm male x Asm female)

Strain	*n*	Slope ± SE	LC_{50}	95% CL	χ^2	df	RF_{50}
Asm	100	14.35 ± 1.08	0.04	0.01-0.10	6.79	5	1
PRm	100	5.20 ± 0.30	8.61	7.54-12.41	4.17	8	211.85
H_1	100	3.28 ± 0.29	7.96	6.43-14.45	3.49	3	174.78
H_2	100	3.12 ± 0.32	9.12	6.78-13.89	3.55	2	224.58

n, Sample size per dose. RF50, resistance factor 50.

Results

Malathion Susceptibility of Strains and Dominance of Resistance. The malathion-specific resistant strain PRm was 212-fold resistant to malathion compared with the susceptible Asm strain at the LC_{50} (Table 2). The degree of dominance (Bourguet et al. 1997) was 0.9 and 1.0 for the heterozygous (PRm male x Asm female) strain and the heterozygous (Asm male x PRm female) strain, respectively. The reciprocal crosses gave almost identical results, confirming an autosomal mode of inheritance. Repeated backcross-ing of resistant hybrids to the Asm susceptible strain consistently yielded two offspring classes (resistant and susceptible) (data not shown). There was no segregation of the resistant class into partially resistant subclasses even after four consecutive generations of backcrossing. These observations provide evidence that resistance is primarily controlled by a single, dominant allele or closely linked alleles as previously reported (Beeman 1983, White and Bell 1988).

Selection for Malathion-Specific Resistance in the Absence of Insecticide: Selection Coefficients and Relative Fitness. Our results show that when resistant phenotypes are in competition with the susceptible T. *castaneum* phenotype, their frequency within populations increases slightly. After 10 generations, there is evidence of directed selection of the resistant allele because the mean frequency of the S^+ allele decreases under its original value in all initial frequencies tested (Fig. 1; Table 3). The selective advantage of R^{mal} allele implied by the decline of the susceptible phenotype in the populations can be quantified by estimating the selection coefficient (C_s) and the fitness *(w)* of the different genotypes (Table 2). Although the fitnesses *(w_{RR}* and *w_{RS}) are* assumed to be 1.0, the fitness of susceptible homozygous *(w_{ss})* ranged from 0.891 to 0.930 after 10 generations for the different initial R^{mal} frequencies. These data suggest that even in the absence of malathion, the malathion-specific resistant phenotypes of T. *castaneum* have a selective advantage compared with the susceptible phenotype.

Table 3. Selection coefficients and fitness of malathion susceptible genotype ($S+/S^+$)ofT. castaneum in relation with the hiitial frequency of resistant allele (R^{mal}) over 10 consecutive nonover-lapping generations

Initial R^{mal} Frequency	Initial S^+ Frequency	Final S^+ Frequency	Selection Coefficient	$V_{(Cs)}$[a]	s^+/s^+ fitness
(p_0)	**(q_0)**	(q_{10})	(C_S)		***(w_{ss})***[b]
0.05	0.95	0.83	0.109	0.00068	0.891
0.10	0.90	0.78	0.081	0.00051	0.919
0.20	0.80	0.63	0.091	0.00045	0.909
0.30	0.70	0.57	0.070	0.00055	0.930

[a] $V_{(Cs)}$, variance of selection coefficient.

[b] $w_{ss} = 1 - C_s$.

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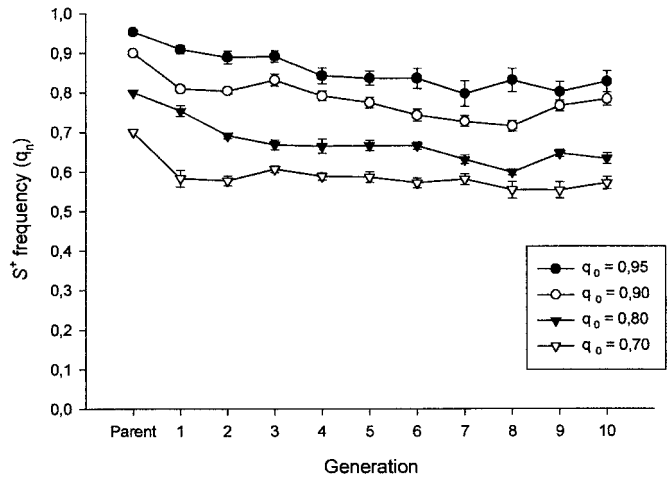

Fig. 1. Evolution of the frequency of malathion susceptible allele (S^+) in T. castaneum populations during 10 consecutive and nonoverlapping generations. Six independent lines were monitored for each of four initial R^{mal} frequencies. Each symbol (mean ± SE) shows the frequency of S^+ allele in the population.

Egg Fertility and B_p. Egg fertility did not differ among the four strains (Table 4; one-way ANOVA, $F = 0.03$; df = 3, 20; P = 0.994). There was a significant difference in fecundity of the females of the four strains (one-way ANOVA, $F = 48.07$; df = 3, 132; P < 0.0001). The fecundity of the susceptible females was significantly lower than that of the females of the three resistant strains (Tukey's test, P < 0.05). Measurements of developmental time showed that DT of heterozygous resistant and susceptible strains was generally shorter than the DT of homozygous resistant strain. However, there is a significant difference between the DT of the four strains (one-way ANOVA, F = 208.81; df = 3, 893; P < 0.0001) and the DT of the susceptible strain is the shortest (Tukey's test, P < 0.05). For malathion resistance and fecundity, the (PRm male x Asm female) heterozygous strain had a greater fitness advantage than the homozygous resistant strain with regard to DT, probably due to the heterosis effect (Table 4).

The B_P of every strain is reported in Table 4. Mal-athion-specific resistance in T. *castaneum* does not involve any reduction of B_P. Moreover, the biotic potential of the resistant phenotypes is slightly higher than that of the susceptible strain.

Although we observed that heterozygous resistant insects were more fit than homozygous resistant, the ratio of their $B_p = B_pPRm/ (\{B_pHl + B_pH2\}/2)$ was 1.11, this is not really in contradiction with the assumption made in the model to estimate the coefficient of selection (C_s) of the R^{mal} gene, where the fitness of the two heterozygous and the homozygous resistant insects was assumed to be equal.

Discussion

Malathion-Specific Resistance was Assessed Genetically in *T. castaneum* by Conventional Experiments.

Although Beeman (1983) determined that this resistance mechanism was inherited as a semidominant trait, we suggest that it is inherited as a monogenic autosomal dominant Mendelian trait. However, Wool et al. (1982) determined that it was inherited as a dominant or overdominant character. McKenzie and Whitten (1982) reported that pesticide resistance evolving in an agricultural environment is usually controlled by one or a few genes. Moreover, pleiotropic effects of insecticide resistance gene(s) on fitness traits are among the factors that could affect the persistence of resistance in a population of mixed genotypes (Georghiou 1983). It has been assumed that resistance gene(s) have fitness costs resulting in low frequency of resistant phenotypes before the population is in contact with the insecticide. Moreover, fitness values varying from 0.5 to 0.8 for resistant insects compared with susceptible insects have been observed in populations of mosquitoes (Ferrari and Georghiou 1981), blowflies (McKenzie and O'Farrell 1993), and beetles (Muggleton 1983) in the absence of insecticide.

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Table 4. Fertility, fecundity, developmental time, and biotic potential of T. castaneum strains: Asm (susceptible), PRm (malathion-specific resistant), H_1 (Asm male x PRm female), and H_2 (PRm male x Asm female)

Strain	*n*	Fertility (%)	*n*	F	ln F	*n*	DT	DT_r	B_P	C_{BP}
Asm	600	72.2 ± 2.1	34	33.9 ± 3.3a	3.52	206	29.8 ± 0.1a	1.00	3.52	1
PRm	600	73.0 ± 7.4	34	71.8 ± 2.6bc	4.27	227	34.1 ± 0.2d	1.13	3.79	1.08
H_1	600	72.1 ± 5.4	34	65.5 ± 2.4b	4.18	243	31.0 ± 0.1c	1.03	4.08	1.16
H_2	600	74.0 ± 4.1	34	75.9 ± 2.7c	4.33	219	30.4 ± 0.1b	1.00	4.32	1.23

Within the same column, there is a significant difference ($P < 0.05$, Tukey's test) between values followed by a different letter. Mean ± SE. F, fecundity (number of larvae emerged from the eggs laid during the egg laying period); DT, development time (in days); B_P, biotic potential; DT_r, ratio between the development time of the considered strain by the one of the susceptible strain; C_{BP}, ratio of the biotic potential between the considered strain and the susceptible strain.

Our results confirm those of Beeman and Nanis (1986) who showed a stability of R^{mal} allele in *Tribo-lium* laboratory populations over six generations in the absence of malathion. However, these studies did not report estimates of fitness and selection coefficient values. Our fitness estimates show that the proportion of malathion-specific resistant individuals increases slightly in populations of T. *castaneum* during 10 generations in the absence of insecticide. The homozygous and heterozygous resistant strains of T. *castaneum* have a higher fitness than the homozygous susceptible strain. As reported for other species and other resistance mechanisms (Roush and McKenzie 1987, McKenzie 1996 and references therein), in T. *castaneum,* malathion-specific resistance is not associated with reduced fitness. In T. *castaneum,* our B_P study shows that developmental stages of the susceptible homozygous strain develop at a slightly faster rate than those of the resistant heterozygous and homozygous strains. However, lower fecundity of susceptible insects is likely to lead to overall lower population growth rates than in the resistant strains. As suggested by Dyte (1990), malathion-specific resistance in T. *castaneum* does not involve any loss of fitness under laboratory or field conditions.

Dieldrin, diazinon, and malathion-resistant strains of the sheep blowfly *Lucilia cuprina* showed reduced fitness compared with susceptible strains when resistance has first evolved. However, due to the continued use of diazinon, besides the development of resistance, a fitness modifier was selected. Modified dia-zinon-resistant phenotypes show similar developmental stability and relative fitness compared with susceptible insects (McKenzie 1993). In T. *castaneum,* the malathion-specific resistance gene(s) has no pleiotropic fitness costs. Because fitness costs have never been noted in malathion-specific resistant T. *castaneum* populations, it seems that there has been no coadaptation with a fitness gene modifier or that the fitness modifier is closely linked to the malathion-specific resistance gene (s). In T. *castaneum,* resistance allele fitness studies have shown that the resistant allele had no major fitness costs (Beeman and Nanis 1986). Our results combined with those of Beeman and Nanis (1986) suggest that *in T. castaneum* the fitness of malathion-resistant insects is not dependent on their genetic background. A similar independence of fitness and genetic background also was observed in *L. cuprina* and dieldrin resistance (McKenzie 1996) and *Musca domestica* and diazinon resistance (Whitehead et al. 1985).

When a single gene is involved in insecticide resistance, the fitness of the heterozygous relative to the susceptible homozygous is critical because the resistance gene is carried primarily as the heterozygous when the gene is at low frequency during the early stages of resistance (Roush and Plapp 1982). We observed that the two heterozygous malathion-specific resistant strains had a heterosis advantage that confers on them the best fitness. Resistant heterozygous insects therefore have a double selective advantage. In addition to a better fitness than homozygous susceptible insects, they also can tolerate high malathion concentrations.

Because selection will not reduce the frequency of resistant genes by acting against resistant phenotypes when the corresponding insecticide is not being used, chemical control strategies based on the relative fitness disadvantage of insecticide-resistant insects will not succeed for malathion-specific resistance in T. *castaneum.* However, White and Bell (1988), regarding the vulnerability of the heterozygous first instars, postulated that resistance could be reversed by introducing susceptible insects within the population. Nevertheless, this method seems to be more effective with nonspecific malathion resistant strains (Wool and Manheim 1980) than with malathion-specific resistant *T. castaneum* strains (White and Bell 1988).

Because world trade in cereals implies the circulation of freight from one storage place to another, it allows the dispersal of pests from different geographic areas and therefore of different genetic backgrounds and selective life histories. This will sometimes result in the introduction of resistant phenotypes in silos already contaminated with susceptible insects. Because genetic background does not influence fitness in the case of malathion-specific resistance and that no fitness disadvantage accompanies resistance genotypes in insects, the dispersal of resistant individuals will result in the development of malathion-specific resistance in the untreated populations. This may finally result in the failure of control of these populations with malathion.

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