ORIGINAL RESEARCH ARTICLE

Fitness cost, cross-resistance, instability and realized heritability of deltamethrin resistance in *Tribolium castaneum* (Coleoptera: Tenebrionidae)

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Abstract

Tribolium castaneum (Herbst) is a common pest of various stored commodities, globally. It is a notorious pest in terms of developing resistance against different insecticides used for its control. In the present study, *T. castaneum* population was selected with deltamethrin to investigate aspects related to deltamethrin resistance development, such as fitness trade-off, stability, realized heritability and cross-resistance. After 12 continuous selections, deltamethrin-selected *T. castaneum* (Delta-Sel strain) developed 49.74-fold and 92.85-fold resistance as compared to field and unselected population, respectively. However, a decrease in level of deltamethrin resistance was observed when selection with deltamethrin was ceased for three generations (G_{12} to G_{15}), which suggests the unstable nature of deltamethrin resistance. The realized heritability (h^2) value for deltamethrin resistance was 0.05. The cost paid to develop resistance was observed as reduced fecundity and hatching (%), lower biotic potential, low relative growth rate, and prolonged developmental time, resulting in a decline in the growth potential of the Delta-Sel strain. No cross-resistance to imidacloprid and a very low cross-resistance to chlorpyrifos and bifenthrin was observed. Based on the results, it appears that utilizing insecticides with low or no cross-resistance by interchanging with deltamethrin can be an effective approach for managing resistance and maintaining *T. castaneum's* susceptibility to deltamethrin. These findings will be helpful for researchers to refine resistance management strategy for delaying resistance and impair survival of *T. castaneum*.

Keywords Red flour beetle · Stored product pest · Biological parameters · Risk assessment · Resistance management

Introduction

Red flour beetle, *Tribolium castaneum* (Herbst) (Coleoptera: Tenebrionidae) is a prevalent and significant pest of stored goods, known for its polyphagous feeding habits (Bakhtawar et al. 2013; Kiran et al. 2006). However, it infests various stored commodities like grains (Atta et al. 2020), flours of major staple foods especially wheat (Ajayi and Rahman 2006), stored nuts (Pires et al. 2017), dry fruits and vegetables (Sarwar

2015), and museum specimens (Abdul-Rassoul 1996), resulting in heavy economic losses every year in many developing countries (Jung et al. 2020). It degrades the quality and reduces quantity of stored foods and make these unfit for human consumption in case of heavy infestation (Nikolaou et al. 2021). *T. castaneum* also contaminates stored commodities through its feces (Krizkova-Kudlikova and Hubert 2008) and is medically important due to the production of quinones (i.e. benzoquinones) (Ladisch et al. 1967), which is carcinogenic in nature and may be dangerous and unfit for human's health (Lis et al. 2011). Both immature and adults of *T. castaneum* are the secondary pest of intact grains (Phillips and Throne 2010) but are the primary pest of processed products of grains (Astuti et al. 2020) and nuts (Pires et al. 2017). It attacks the embryo of wheat grains and affects its viability and germination rate (Lustig et al. 1977). Furthermore, *T. castaneum* is an excellent species to investigate the effectiveness of conventional and new insecticides due to its status as a widespread pest and its potential as an indicator species (Campbell et al. 2022).

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Several protectants including deltamethrin have been used to alleviate stored product pests. Among stored product pests it has also been used for the control of *T. castaneum* for many years (Munawar et al. 2020). Different formulations of deltamethrin are applied in different ways, such as directly applied singly or as a synergistic mixture on grains, treating bags used for storage, and used as dust to treat floor, cracks, and other surfaces (Quinn et al. 2018). This insecticide disturbs the normal functioning of voltage-sensitive axonal sodium-channel of the neuron by keeping the sodium channels in open state (De La Cerda et al. 2002; Ogata et al. 1988). However, the occurrence of deltamethrin resistance in *T. castaneum* presents challenges for its continuous effective use. Unfortunately, it is well-known for developing resistance to several compounds with 136 reported cases including deltamethrin (Aprd 2020). Furthermore, *T. castaneum* is among the top twenty insecticide-resistant arthropods while occupying 4th position among urban pests resistant to insecticide worldwide (Annonymous 2020; Zhu et al. 2016). Consequently, assessing the fitness costs linked with deltamethrin resistance would aid in comprehending the rate of resistance evolution and in designing an effective resistance management program.

The development of resistance to any insecticide in an insect population at the expense of its fitness or changes in biological parameters relative to its counterpart susceptible strain is termed as "Fitness cost" (Kliot and Ghanim 2012). Selection of resistance genes via insecticide use can increase (Abbas et al. 2014) or decrease fitness (Abbas et al. 2016b; Hafez and Abbas 2023; Saddiq et al. 2016a) of an insect or it may be possible that selection of resistance genes do not have any effect on the fitness component (Basit et al. 2012). If the fitness component is negatively related to resistance genes, reduction in resistance level and ultimately susceptibility of resistant individual of a population could be expected in insecticide-free environment (Banazeer et al. 2020b). Previously, though many studies illustrated the resistance of this species to deltamethrin, but fitness cost associated with deltamethrin resistance has not yet been reported in *T. castaneum*.

This study aimed to provide a foundation for the management of deltamethrin resistance by understanding the processes involved in resistance selection. Therefore, a deltamethrin-selected *T. castaneum* and a susceptible strain were used to determine the key factors involved in resistance evolution such as fitness cost, realized heritability, cross-resistance, and stability of deltamethrin resistance. The results will be helpful for researchers devising resistance management tactics to delay deltamethrin resistance and control *T. castaneum*.

Materials and methods

Collection and culturing of *T. castaneum*

The culture of *T. castaneum* used in the experiment was collected from infested flour obtained from flour mill in District Multan (30°12′ N, 71°25′ E), Punjab, Pakistan. About 200-250 mixed sexes of *T. castaneum* adults were sieved from the infested flour and kept in a plastic jar (1000 ml capacity) to multiply and obtain homogenous culture. The population was nominated as Parental population. It was reared on a diet having 500 gm wheat flour mixed with 5% Brewer's yeast (Singh and Prakash 2015). Before utilization, the diet (wheat flour) was placed in the freezer below 0 °C for five days to sterilize it. The adults were removed from jar after 4–5 days of oviposition so that after eggs hatching, larvae completed their life cycle to produce adults. After maximum emergence, the adults were sieved out from the culture media and labelled as "Field Pop" which was further used for different experimental purposes. The culture was raised under controlled conditions of 27 ± 3 °C and $65 \pm 5\%$ relative humidity.

Insecticides

The commercial formulations of insecticides used in the experiments were Decis Super® EC containing 10% deltamethrin active ingredient (a.i.) (Bayer Crop Sciences, Pakistan), Lorsban® EC containing 40% chlorpyrifos (a.i.) (Dow Agro Sciences, Pakistan), Talstar® EC containing 10% bifenthrin (a.i.) (FMC, Pakistan) and Confidor® SL containing 20% imidacloprid (a.i.) (Bayer Crop Sciences, Pakistan).

Bioassay protocol

Toxicity bioassays were conducted by exposing *T. castaneum* adults of homogenous age (6–10 days old) on insecticide-treated filter papers (Whatman # 2). Preliminary bioassays were performed on a hit and trial basis to identify the dose causing ten to ninety percent of adults' mortality. Five different concentrations of each insecticide were prepared in acetone. The concentrations were made following the serial dilution procedure to develop a concentration–response relationship. Subsequently, filter paper of equivalent dimensions to a petri dish was treated with each concentration of insecticide and positioned within the petri dish. A total of ten adults of *T. castaneum* were introduced into each petri dish and covered with a lid to inhibit the escape attempts by adults. Each petri dish was considered as a replication and there were three replications for each insecticide concentration. Only acetone treated filter paper was used in three replications of control (Collins 1998). A total of 180 T. *castaneum* adults were tested for each bioassay. Dead adults were counted after 48 h of exposure to deltamethrin, bifenthrin, and chlorpyrifos while 72 h posttreatment of imidacloprid. Adults without any movement on touching with camel hair brush were considered as dead (Lloyd 1969).

Selection protocol for the development of deltamethrin resistance

At the start of the experiment, the parental population of *T. castaneum* was separated into two distinct groups: the first group, referred to as the "Delta-Sel" population, was exposed to deltamethrin for twelve consecutive generations, while the second group, called the "Unsel" population, was raised without any exposure to deltamethrin. To ensure enough survivors for the next generation, a suitable concentration of deltamethrin was exposed to adult beetles between 6–10 days old, with the amount increasing gradually with each passing generation. Almost 350 to 500 adults were used in each selection and the surviving adults were used to get the next progeny. The selection was done using filter paper dipped in acetone diluted insecticide solution of respective concentrations. Mortality was recorded after 48 h exposure to insecticide.

Reciprocal crosses to study fitness parameters

Two more strains were developed by crossing Delta-Sel and Unsel strains named as $Cross_1$ and $Cross_2$. To generate $Cross_1$, female adults of Delta-Sel strain were crossed with males of Unsel in a separate jar while $Cross_2$ was generated using males from Delta-Sel strain and females from Unsel. In both crosses, the male and female ratio was kept the same. Differentiation of male and female of *T. castaneum* was done at the pupal stage on the basis of the genital lobe (larger in females) with the use of a microscope (Park 1934).

Assessment of biological parameters to construct life table

To determine the impact of deltamethrin resistance on the biological parameters, newly hatched larvae were used in the experiment. A total of 150 grubs were collected from each of Unsel, $Cross_1$, $Cross_2$, and Delta-Sel strains and divided equally in three replications. Initially, weight of these neonates was recorded using a digital weighing balance (GF-300, AND) and then shifted one replication in one petri dish of 5 cm diameter. Furthermore, as the development proceeded data of various biological parameters like larval duration, pupal weight, the survival rate from 1st instar till pupation, and development time (DT) from egg to adult of both sexes were also recorded for all the strains under consideration. The newly emerged adults were coupled within three families each consisting of 5 ♀ and 5 ♂ in a petri dish and allowed to mate for oviposition. Moreover, fecundity (number of eggs laid by each female) was recorded daily till the death of females, and egg eclosion or hatching rate was calculated according to Liu and Han (2006) by formula,

$$\text{Percentage hatching} = \frac{\text{Total neonates}}{\text{Total eggs}} \times 100$$

The formula used to calculate the net reproductive or net replacement rate (R0) was as follows (Cao and Han 2006),

$$R0 = \frac{Nn+1}{Nn}$$

where (N_n) represents parental population insects and (N_{n+1}) represents offspring in the next generation.

The formula used to analyze the mean relative growth rate (MRGR) was reported by Radford (1967),

$$\text{MRGR} = \frac{[\text{WP(mg)} - \text{WL(mg)}]}{T}$$

where W_L and W_P are initial weights of larvae and pupae, respectively and T is used to indicate the duration from the first larval stage to pre-pupation.

The intrinsic rate of population growth (r_m) was determined by substituting the value R_o in the formula given by Birch (1948),

$$rm = \frac{\ln R0}{DT}$$

DT is used to express the developmental time from ova to adult eclosion.

Biotic potential (B_p) was assessed to compare the reproductive potential of Delta-Sel strain with its susceptible counterpart strain as Roush and Plapp (1982),

$$Bp = \frac{\ln \text{ fecundity}}{DTr}$$

where DT_r is the ratio of developmental time of any tested strain and Unsel strain.

Relative fitness (R_f) was calculated following Cao and Han (2006) as,

$$Rf = \frac{R0 \text{ of any tested strain}}{R0 \text{ of Unsel strain}}$$

Assessment of deltamethrin resistance stability

The change in resistance (DR) in Delta-Sel strain after three generations of rearing without exposure was assessed by computing the value of R as follows,

$$DR = \frac{[\log (LC_{50} \text{ of final bioassay}) - \log (LC_{50} \text{ of initial bioassay})]}{n}$$

where n designates the number of generations kept without insecticide stress, initial LC_{50} is when the selection was stopped and final LC_{50} is after n generation reared without exposure (Tabashnik 1994).

Cross-resistance

In order to assess potential cross-resistance of the Delta-Sel strain to three additional insecticides, bioassays were conducted using both the G_{12} Delta-Sel and the Field-Pop. Cross-resistance ratio (CRR) was calculated as:

$$CRR = \frac{LC_{50} \text{ of any insecticide tested on Delta} - \text{Sel at } G_{12}}{LC_{50} \text{ of respective insecticide tested on Field Pop at } G_1}$$

Realized heritability

The realized heritability (h^2) of deltamethrin resistance in *T. castaneum* was estimated by following the equation described by Tabashnik (1992),

$$h2 = \frac{R}{S}$$

where R represents the response to selection and S represents the difference of selection.

According to the given formula, R was calculated,

$$R = \frac{[\text{Log}\left(\text{final LC}_{50}\right) - \text{Log}\left(\text{initial LC}_{50}\right)]}{n}$$

where the final LC50 is after "n" number of selected generations and the initial LC_{50} value is at Field Pop.

Selection Differential (S) was estimated as follows,

$$S = \text{intensity of selection}(i) \times \text{phenotypic standard deviation} (\sigma p)$$

According to Falconer (1989) "*i*" was estimated using equation:

$$i = 1.583 - 0.0193336p + 0.0000428p2 + 3.65194/p$$

where *p* is the percent survivorship after selection with deltamethrin. The σp can be estimated as,

$$\sigma p = [(\text{initial slope} + \text{final slope})0.5]^{-1}$$

where initial slope is the slope obtained from probit analysis of concentration-mortality data of parental population before selection and final slope is the slope of offspring after n generations of selection with deltamethrin.

Based on the selection response of *T. castaneum* to deltamethrin in the laboratory, generations (G) were anticipated for a 10-fold rise in LC_{50} as follows,

$$G = R^{-1}$$

Statistical analysis

Toxicity data were subjected to Probit analysis (Finney 1971) to calculate median lethal concentration (LC_{50}) values with 95% Fiducial limits (FL), slope with its standard error (SE), and chi-square (χ^2) values by using POLO Plus software (Leora Software 2002). LC_{50} values were considered to be significantly different ($P < 0.01$) if their 95% FL did not overlap (Litchfield and Wilcoxon 1949). Resistance ratio (RR) was calculated by dividing LC_{50} of the Delta-Sel strain by LC_{50} of the Unsel strain. The RR and CRR values were classified based on the standard given by Torres-Vila et al. (2002). The resistance ratio values of = 1, 2 to 10, 11 to 30, 31 to 100, and > 100 indicate susceptible, tolerance to low resistance, moderate resistance, high resistance, and very high resistance, respectively.

The data on biological parameters of each of the tested population were subjected to analysis of variance (ANOVA) for comparison of means, and means of different populations were separated by test of least significant difference (at $P \leq 0.05$) employing analytical software of Statistix (version 8.1) (Annonymous 2005). Before ANOVA the biological parameters data were tested for normality with Shapiro–wilk test using Statistix (version 8.1) and no transformation was required (Annonymous 2005).

Results

Selection history for deltamethrin resistance development

Survival of red flour beetle adults exposed to different concentrations (20–1000 μg/mL) was 51.25%_42.50% for different tested generations (Fig. 1). Continuous selection of beetle with deltamethrin increased the LC_{50} value from 20.85 μg/mL at G1 to 1037.10 μg/mL at G_{12} and developed 49.74-fold resistance compared to the Field-Pop (Table 1). However, Delta-Sel strain developed 92.85-fold resistance when compared to its counterpart Unsel Pop, whereas resistance ratio of deltamethrin for Cross 1 and Cross 2 were 24.75 and 26.74-fold as compared to the Unsel (Table 2).

Stability of deltamethrin resistance in Delta-Sel strain

A decrease in LC_{50} (from 1037.10 to 595.12) was observed when the deltamethrin selection pressure was released for three generations (G_{12}-G_{15}). The rate of decline to deltamethrin resistance was -0.08. The negative value of DR indicates the unstable nature of deltamethrin resistance, but reversion of resistance would be slow (Table 1).

Biological parameters performance of different tested strains of *T. castaneum*

Means of biological parameters with standard errors for different strains are summarized in Table 3. Percent
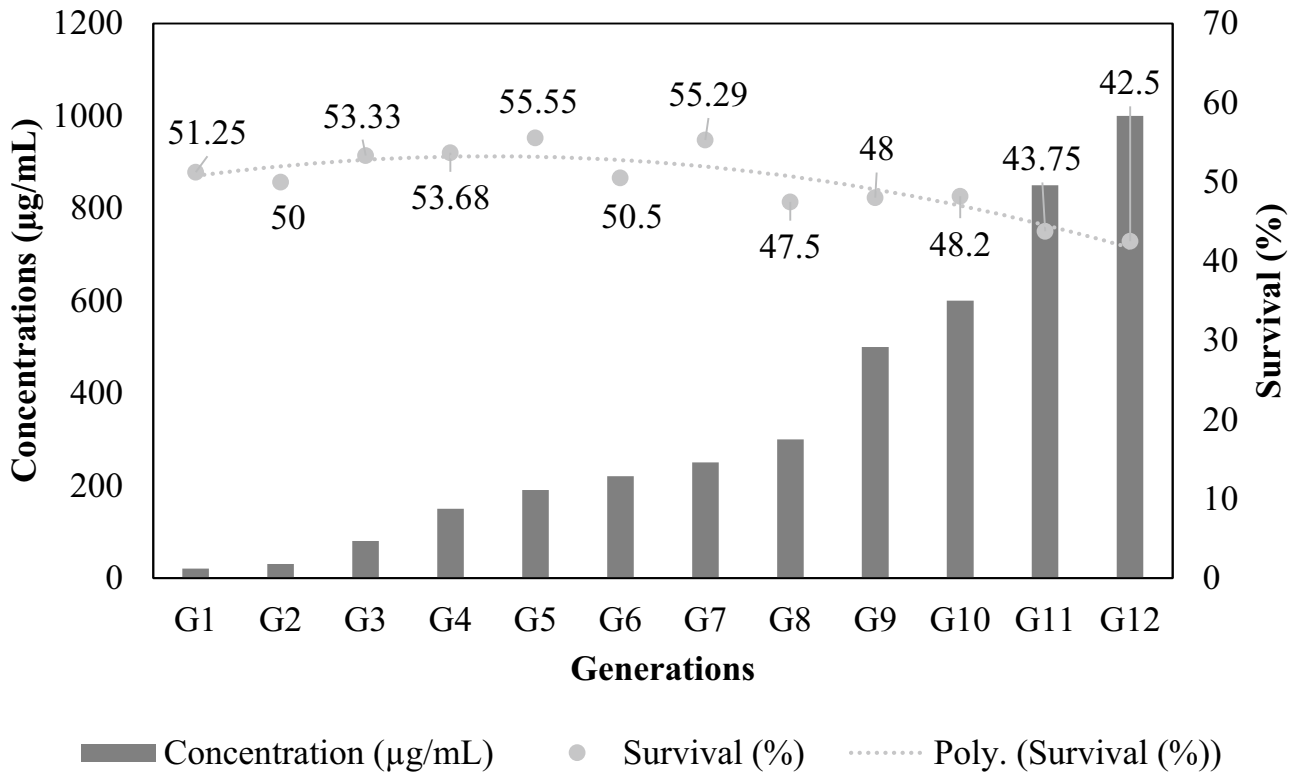
Fig. 1 Survival rate (%) of *Tribolium castaneum* selected with deltamethrin for 12 generations

survival rate from the first instar to pupae ($P = 0.65$), first instar larval weight ($P = 0.06$), and pupal weight ($P = 0.09$) did not differ significantly among all tested strains. The larval duration of both hybrid strains was significantly longer than Unsel ($P = 0.02$) but was similar to Delta-Sel. Development time of Delta-Sel from egg to adult was

Table 1 Development of deltamethrin resistance in *Tribolium castaneum*

Generation	LC$_{50}$ (95% FL[a]) (µg/mL)	Slope $\pm$ SE	N	df	X^2	P	RR[b]	RR[c]	DR[d]
Unsel (G$_{12}$)	11.17 (8.425–15.48)	1.84 ± 0.29	180	4	0.28	0.99	-	1.00	
Field Pop (G$_1$)	20.85 (14.99–33.70)	0.29 ± 1.60	180	4	0.77	0.94	1.00	1.87	
Delta-Sel (G$_2$)	24.69 (17.98–35.20)	0.27 ± 1.61	180	4	0.51	0.97	1.18	2.21	
Delta-Sel (G$_3$)	71.13 (51.57–109.85)	0.28 ± 1.59	180	4	0.35	0.98	3.41	6.37	
Delta-Sel (G$_4$)	90.26 (63.31–132.32)	0.27 ± 1.44	180	4	0.93	0.91	4.33	8.08	
Delta-Sel (G$_5$)	130.46 (94.32–183.15)	0.27 ± 1.60	180	4	1.10	0.89	6.26	11.68	
Delta-Sel (G$_6$)	159.22 (108.42–289.55)	0.27 ± 1.31	180	4	0.15	0.99	7.64	14.25	
Delta-Sel (G$_7$)	236.74 (175.29–319.17)	0.28 ± 1.79	180	4	1.06	0.89	11.35	21.19	
Delta-Sel (G$_8$)	330.99 (229.45–550.17)	0.27 ± 1.35	180	4	0.05	0.99	15.87	29.63	
Delta-Sel (G$_9$)	583.33 (416.34–888.94)	0.27 ± 1.48	180	4	0.09	0.99	27.98	52.22	
Delta-Sel (G$_{10}$)	735.69 (521.95–1157.68)	0.27 ± 1.45	180	4	0.12	0.99	35.28	65.86	
Delta-Sel (G$_{11}$)	866.86 (598.76–1423.53)	0.26 ± 1.33	180	4	0.36	0.98	41.58	77.61	
Delta-Sel (G$_{12}$)	1037.10 (731.23–1657.80)	0.27 ± 1.42	180	4	0.16	0.99	49.74	92.85	
Delta-Sel (G$_{15}$) *	595.12 (472.29–818.41)	1.70 ± 0.23	180	4	0.61	0.96	28.54	53.28	-0.08

*Deltamethrin resistance stability was evaluated by uplifting the deltamethrin selection pressure for three generations (G$_{12}$-G$_{15}$)

[a]Fiducial limits

[b]Resistance ratio = LC$_{50}$ of Delta-Sel/LC$_{50}$ of Field-Pop

[c]Resistance ratio = LC$_{50}$ of Delta-Sel/LC$_{50}$ of Unsel

[d]Decrease rate of deltamethrin resistance

Table 2 Toxicity of deltamethrin to selected (Delta-Sel), unselected (Unsel), Cross$_1$ (Delta-Sel♀ + Unsel♂) and Cross$_2$ (Delta-Sel♂ + Unsel♀) of *Tribolium castaneum*

Population	LC$_{50}$ (95% FL) (µg/mL)	Slope ± S.E	N	df	X^2	P	RR[a]
Unsel (G$_{12}$)	11.17 (8.43–15.48)	1.84 ± 0.29	180	4	0.28	0.99	
Delta-Sel (G$_{12}$)	1037.10 (731.23–1657.80)	0.27 ± 1.42	180	4	0.16	1.00	92.85
Cross$_1$	276.47 (193.45–429.39)	1.39 ± 0.27	180	4	0.30	0.98	24.75
Cross$_2$	298.65 (214.98–451.04)	1.53 ± 0.28	180	4	0.35	0.98	26.74

[a]Resistance ratio = LC$_{50}$ of Delta-Sel, Cross$_1$ and Cross$_2$/LC$_{50}$ of Unsel

longer as compared to Unsel, but it was similar for both hybrid strains ($P = 0.0005$). The parameters like fecundity (eggs/female) ($P = 0.01$), percent hatchability ($P = 0.02$), and the number of next generation larvae ($P = 0.004$) in Delta-Sel, Cross$_1$, and Cross$_2$ were significantly different from Unsel. Mean relative growth rate (MRGR) of the Delta-Sel was similar to Cross$_2$ but significantly lower than that of the Unsel ($P < 0.05$). Moreover, MRGR of both crosses was also significantly different from Unsel. The net reproductive rate of Unsel was significantly higher than that of other tested strains ($P = 0.003$). Cross$_1$, Cross$_2$ and Delta-Sel strains had a significantly lower intrinsic rate of natural increase ($P = 0.002$) and biotic potential ($P < 0.05$) as compared to Unsel. The calculated values of relative fitness for Unsel, Delta-Sel, Cross$_1$, and Crosss$_2$ were 1.00, 0.54, 0.62, and 0.66, respectively.

Cross-resistance of deltamethrin to other insecticides

Cross-resistance results indicated very low cross-resistance to bifenthrin (2.53- fold) and chlorpyrifos (5.43). No cross-resistance was observed to imidacloprid (1.76-fold) in the Delta-Sel strain (Table 4).

Realized heritability and resistance risk assessment

The value of h^2 was 0.05 for deltamethrin resistance after twelve generations of selection (Table 5). The generations anticipated for a 10-fold increase in deltamethrin resistance varies inversely with h^2 and mortality. Therefore, it was assumed that $\sigma p = 0.52$, $h^2 = 0.05$ as well as the mortality after deltamethrin selection are around 50%, 60%,

Table 3 Means (± SE) of various biological parameters of different tested strains of *Tribolium castaneum*

Analyzed parameters	Mean (± SE)				ANOVA parameters (df = 3,8)
	Unsel	Delta-Sel	Cross$_1$	Cross$_2$	
Neonates	150	150	150	150	
Survival rate from 1st instar to pupae (%) *	77.55 ± 5.93	72.67 ± 2.73	79.66 ± 2.02	74.33 ± 4.70	F = 0.56; P = 0.65
1st instar larval weight (mg) *	0.37 ± 0.05	0.24 ± 0.03	0.25 ± 0.02	0.28 ± 0.02	F = 3.71; P = 0.06
Larval duration (days)	13.53 ± 0.29 b	16.37 ± 1.40 ab	17.17 ± 1.10 a	18.5 ± 0.29 a	F = 5.29; P = 0.02
Pupal weight (mg) *	1.89 ± 0.02	1.64 ± 0.10	1.67 ± 0.06	1.67 ± 0.06	F = 2.98; P = 0.09
Pupal duration	8.67 ± 033 c	14.97 ± 0.32 a	12.16 ± 0.17 b	12.63 ± 0.63 b	F = 42.2; P = 0.00
Development time from egg to adult (days)	31.2 ± 0.72 b	42.33 ± 2.19 a	41.87 ± 0.71 a	40.33 ± 0.33 a	F = 19.7; P = 0.0005
Fecundity (eggs/female)	76.67 ± 8.35 a	48.67 ± 1.45 b	52.67 ± 2.85 b	55.33 ± 2.40 b	F = 7.32; P = 0.01
Hatchability (%)	85.06 ± 2.76 a	69.72 ± 1.80 b	73.91 ± 2.35 b	76.44 ± .08 b	F = 6.49; P = 0.02
Number of next generation larvae	326.67 ± 39.30 a	169.67 ± 9.02 b	195.33 ± 15.53 b	210.67 ± 3.00 b	F = 10.3; P = 0.004
Net reproductive rate (Ro)	2.18 ± 0.26 a	1.13 ± 0.06 b	1.3 ± 0.10 b	1.4 ± 0.02 b	F = 10.4; P = 0.003
Mean relative growth rate (MRGR)	0.17 ± 0.00 a	0.09 ± 0.01 c	0.12 ± 0.01 b	0.11 ± 0.00 bc	F = 39.6; P = 0.00
Intrinsic rate of natural increase (rm)	0.020 ± 0.00 a	0.003 ± 0.00 b	0.006 ± 0.00 b	0.010 ± 0.00 b	F = 12.9; P = 0.002
Biotic Potential (BP)	4.33 ± 0.12 a	2.88 ± 0.17 b	2.95 ± 0.03 b	3.10 ± 0.06 b	F = 41.1; P = 0.00
Relative fitness [a]	1.00	0.54	0.62	0.66	

Means with different letters in a row are significantly different at $P < 0.05$

Delta-Sel, deltamethrin-resistant strain; Unsel, unselected strain; Cross 1, Delta-Sel ♀ × Unsel ♂; and Cross 2, Unsel ♀ × Delta-Sel ♂

*Parameters with no significant difference among tested mean

[a]Rf = Ro of any tested strain/Ro of Unsel

Table 4 Cross-resistance of Delta-Sel to three other insecticides

Insecticide	Generation	LC$_{50}$ (95% FL) (µg/mL)	Slope $\pm$ SE	N[a]	df[b]	X^{2c}	P[d]	CRR[e]
Chlorpyrifos	Field Pop (G$_1$)	1.36 (0.954–2.13)	1.37 $\pm$ 0.21	180	4	0.29	0.99	1.00
	Delta-Sel (G$_{12}$)	7.39 (5.25–9.66)	1.24 $\pm$ 0.21	180	4	0.18	1.00	5.43
Bifenthrin	Field Pop (G$_1$)	7.03 (5.45–11.56)	1.55 $\pm$ 0.19	180	4	1.13	0.89	1.00
	Delta-Sel (G$_{12}$)	17.84 (8.36–25.53)	1.73 $\pm$ 0.28	180	4	1.81	0.77	2.53
Imidacloprid	Field Pop (G$_1$)	12.71 (10.07–17.58)	1.72 $\pm$ 0.20	180	4	0.87	0.93	1.00
	Delta-Sel (G$_{12}$)	22.42 (16.72–26.49)	0.72 $\pm$ 0.19	180	4	1.08	0.90	1.76

[a]Total number of adults exposed in each bioassay

[b]Degree of freedom

[c]Chi-squared, goodness of fit

[d]Probability

[e]Cross resistance ratio = LC$_{50}$ of deltamethrin resistant (Delta-Sel) strain/LC$_{50}$ of field population (Field Pop)

70%, 80%, 90% in each generation, then the LC$_{50}$ values could increase 10-fold in 7.08, 5.81, 4.85, 4.04 and 3.20 generations respectively (Fig. 2). Similarly, the LC$_{50}$ values could increase 100-fold in 14.16, 11.63, 9.69, 8.08 and 6.41 generations, respectively (Fig. 2).

Discussion

Deltamethrin resistance in *T. castaneum* may has serious consequences for the grain industry as it was supposed to be a good alternative to organophosphate protectants. However, in this study, Delta-Sel showed high level of resistance to deltamethrin as compared to its counterpart Unsel. The results demonstrated that this pest had the potential for the development of resistance to deltamethrin. In previous studies, after selection with deltamethrin, 370.5-fold (Singh and Prakash 2013) and 78.6-fold resistance in *T. castaneum* (Padhee et al. 2002), 100-folds in *Phenacoccus solenopsis* Tinsley (Saddiq et al. 2016a), and 63-folds in *Spodoptera litura* (Fabricius) (Ahmad et al. 2007) was observed. The possible reason for resistance development in this stored grain pest may be the detoxification mediated by overexpression of P450 gene (regulated by cap 'n' collar C (CncC) and muscle aponeurosis fibromatosis (Maf)

transcription factors) as reported in *T. castaneum* (Kalsi and Palli 2015; Zhu et al. 2010). It may also be due to the continuous exposure of the laboratory population to greater selection pressure than insecticide dosages applied in the field or storage (Fu et al. 2018).

The examination of the fitness cost of a resistant population under laboratory conditions is important for devising a resistance management strategy to prevent the spread of resistance. Therefore, we explored this aspect to fill the knowledge gap, based on the fitness cost of deltamethrin resistance. Insecticides have potential to alter the biological parameters of the individuals that are exposed continuously (Alam et al. 2020). Often, the development of resistant strain resulted in fitness investment due to changes in biological characteristics which prevent the expansion of resistant genes in insects (Zhang et al. 2018). The current study's outcomes indicated that Delta-Sel experienced fitness drawbacks, as evidenced by reduced fecundity, hatchability (%), and a decreased number of larvae in the following generation. In addition, the Delta-Sel strain had a significantly longer development time from egg to adult than that of Unsel. These deleterious effects on biological parameters may be due to the diversion and allocation of a large portion of energy from basic physiological processes, to compensate the fitness cost associated with deltamethrin

Table 5 Realized heritability (h^2) of deltamethrin resistance in *T. castaneum*

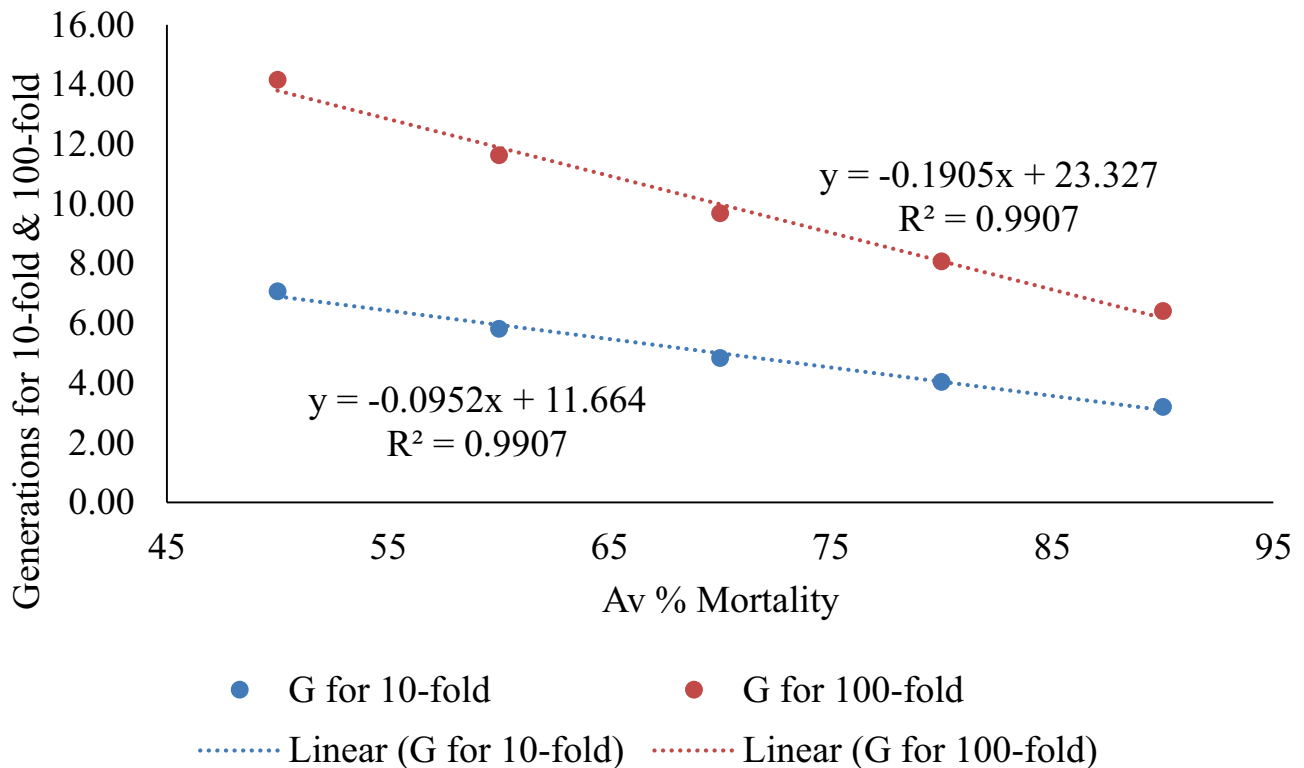| Generations	Insecticide	Initial[a] LC$_{50}$ log	Final[b] LC$_{50}$ log	R[c]	p[d]	i[e]	Initial slope	Final slope	σp	S[f]	h^2 = R/S
G$_1$-G$_{12}$	Deltamethrin	1.32	3.02	0.141	50	0.8	0.29	0.27	3.57	2.84	0.05

[a]LC$_{50}$ at Field Pop

[b]LC$_{50}$ at Delte-Sel

[c]Selection response

[d]Average survival (%), ΣP_n (n = 1, 2, 3…)/n, where n designates total number of generations under selection

[e]Selection intensity

[f]Selection differential

Fig. 2 The number of generations of *Tribolium castaneum* required for a 10-fold and 100-fold increase in LC_{50} of deltamethrin (slope = 0.28, $h^2 = 0.05$) at different mortalities

resistance (Sousa et al. 2009). Moreover, a noteworthy reduction was detected in Delta-Sel's net reproductive rate, mean relative growth rate, intrinsic rate of natural increase, and biotic potential relative to Unsel. The decline in Delta-Sel's growth potential seemed primarily attributable to the decrease in fecundity and percentage hatching. (Abbas et al. 2016a). These results suggest that resistant strain would not increase as rapidly as Unsel in the absence of selection pressure (Kliot and Ghanim 2012). Finally, the Delta-Sel strain showed reduction in relative fitness (0.66) with respect to Unsel. A similar relative fitness (0.86) was reported for spinosad resistance in *T. castaneum* (Khalid et al. 2023). Our data confirm the findings by Pimentel et al. (2007) who reported reduced fecundity, prolonged developmental time and reduction in growth rate in phosphine resistant *T. castaneum*. Bajracharya et al. (2016) demonstrated a fitness expense related to phosphine resistance in *Rhyzopertha dominica* (F.). Furthermore, decreased relative fitness associated with deltamethrin resistance has also been reported in different insects pests such as *Anophlese labranchiae* (Tabbabi and Daaboub 2018), *P. solenopsis* (Saddiq et al. 2016a), *T. infestans* (Germano and Ines Picollo 2015), and *Heliothus virescens* (Sayyed et al. 2008). Thus, our findings are in agreement with the general statement that insecticide-resistant strains

exhibit a disadvantage in fitness as compared to susceptible ones in the absence of insecticide pressure (Denholm and Rowland 1992).

The study of the energetic cost of insecticide resistance in $Cross_1$ (Delta-Sel ♀ + Unsel ♂) and $Cross_2$ (Unsel ♀ + Delta-Sel ♂) is also crucial for creating an ideal resistance management strategy. Hybrid progenies are more prone to carry resistant genes as compared to resistant strain in the initial stage of resistance development (Jia et al. 2009). Therefore, we also determined the fitness parameters of $Cross_1$ and $Cross_2$. Our results showed relative fitness of 0.62 and 0.66, associated with deltamethrin resistance, in $Cross_1$ and $Cross_2$, respectively. These results suggest that fitness traits in both crosses, comparative to Unsel, recover slowly. The reduced relative fitness of both crosses may be due to allelic drift in hybrids (heterozygotes) or due to the detrimental effect of recessive genes as a result of inbreeding depression resulting in the slow recovery of beneficial characters (Shah et al. 2015). However, results suggest that mixing of the selected and unselected population may also play a role in promoting the susceptibility of pests by diluting resistant genes (Hufbauer and Roderick 2005).

Resistance stability of an insecticide is considered as an important barrier in the effectiveness of insecticides (Ninsin and Tanaka 2005). Resistance to insecticides is considered

harmful for the pests if it is stable in a spray-free environment. In our findings, unstable resistance (DR = -0.08) was observed against deltamethrin, when the Delta-Sel strain was left unexposed to deltamethrin for a few generations. The deltamethrin resistance declined from 49.74-fold to 28.54-fold (about a 43% decrease) after three non-selected generations (G_{12}-G_{15}). The unstable resistance could be associated with high fitness costs of Delta-Sel allocated towards detoxification or to regain fitness (Gassmann et al. 2009). Previously unstable resistance to deltamethrin has been reported in *P. solenopsis* (Saddiq et al. 2016b) and *Earias vittella* Fabricius (Jan et al. 2015). The present results suggest that deltamethrin insecticide could become ineffective to control *T. castaneum* until it is suspended temporally or rotated with a chemical having different mode of action to re-establish the deltamethrin susceptibility (Sayyed et al. 2005).

The selection of resistance resulting from the exposure of populations with an insecticide may reduce the susceptibility of that population to other insecticides because of cross-resistance. It can occur among the same or different chemical groups. In our study, the Delta-Sel strain exhibited no cross-resistance to imidacloprid (1.76) and a very low cross-resistance to chlorpyrifos (5.43-fold) and bifenthrin (2.53-fold). Previously, alternate to our results high level of cross-resistance to pyrethroids and a moderate level of cross-resistance to chlorpyrifos has been reported in deltamethrin resistant *T. castaneum* (Padhee et al. 2003). Similar to our results very low cross-resistance to profenofos and low cross-resistance to lambda-cyhalothrin and acetamiprid was observed in deltamethrin selected population of *P. selenosis* (Afzal et al. 2018). Moreover, deltamethrin selected populations of *R. dominica* and *P. solenopsis* showed negligible cross-resistance to organophosphate (Lorini and Galley 2001; Saddiq et al. 2016a). No cross-resistance between deltamethrin and imidacloprid and very low cross-resistance with chlorpyrifos in the Delta-Sel strain was expected because of differences in chemical groups and modes of action of these insecticides. However, very low cross-resistance between deltamethrin and bifenthrin (both pyrethroids) suggests that multiple mechanisms might be involved. These results indicate that all these insecticides with no and/or very low cross-resistance can be used in alternation with deltamethrin for effective management of resistance and to retain susceptibility of deltamethrin against *T. castaneum*.

Realized heritability (h^2) is a useful parameter that is utilized to evaluate genetic variability and the potential for an insect pest to develop resistance to a specific insecticide. It refers to the proportion of phenotypic variation that results from additive genetic variation (Falconer 1989). In the present study, after 12 rounds of selection, the estimated h^2 value for the deltamethrin resistance was only 0.05. The lower h^2 value suggested that there were fewer heritable characters of deltamethrin resistance which transferred to next generations at 12 rounds of selections (Mansoor and Shad 2020). Lower realized heritability reflects lower genetic variations and higher phenotypic variations for deltamethrin resistance (Falconer and Mackay 1996). Furthermore, resistance risk assessment in pests based on estimated value of h^2 plays a vital role in the effectiveness and rational use of an insecticide in the field. In this study, we estimated that the generations needed for the 10-fold resistance of *T. castaneum* to deltamethrin were 7.08–3.20 at 50–90% selection intensity, respectively. Similarly, other scientists have documented that generations required for a 10-fold increase in resistance may change by varying the selection intensity. For example, Afzal et al. (2018) reported that a 10-fold increase in deltamethrin resistance in *P. solenopsis* would require 29 and 3 generations at 10% and 90% selection intensity, respectively. In another study, Abbas and Shad (2015) reported that a 10-fold increase in lambda-cyhalothrin resistance in *M. domestica* would occur in 32 generations at 30% and 9 generations at 90% selection intensity, respectively. Moreover, lower h^2 for pyrethroid resistance has been reported in *M. domestica* (Khan 2019b) and BR4 strain of *R. dominica* to deltamethrin (Lorini and Galley 2000) and in *O. hyalinipennis* to bifenthrin ($h^2 = 0.09$) (Banazeer et al. 2020a) and permethrin (Khan 2019a).

Conclusion

In summary, deltamethrin resistance confers fitness disadvantage in *T. castaneum* resistant strain. No cross-resistance to imidacloprid and very low level of cross-resistance to chlorpyrifos and bifenthrin was observed in the Delta-Sel strain. Additionally, the decline in resistance at a slow rate suggests that further consistent use of this chemical should be avoided as it could improve the fitness of *T. castaneum*. Therefore, the rotational use of deltamethrin with other insecticides (have no or minimal cross-resistance) and a resistance monitoring strategy should be taken to prolong the effectiveness of deltamethrin for controlling *T. castaneum*.

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Data availability The data supporting the findings of this study are available within the article.

Declarations

Conflict of interests The authors have no relevant financial or non-financial interest to disclose.

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