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Temperature, deltamethrin-resistance status and performance measures of *Plutella xylostella*: complex responses of insects to environmental variables

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Abstract. 1. Worldwide, the excessive use of insecticides has resulted in field-evolved insecticide-resistant populations of diamondback moth (DBM), *Plutella xylostella*. A deltamethrin-resistant DBM population from the field was divided into two subpopulations in the laboratory. One population (S-strain) was maintained with no further exposure to insecticides, whereas the other population (R-strain) was maintained under a regime of intermittent selection with deltamethrin.

2. Individuals from both strains were reared at constant temperatures in the range 10–35 °C in the absence of deltamethrin, and the effects of rearing temperature on various traits were investigated. At the time of experimentation, the R-strain was 20-fold more resistant to deltamethrin than the S-strain.

3. Temperature differentially affected developmental time, adult life span, pupal weight, and fecundity of both strains. Although both strains laid eggs after being reared at 10 °C, few of these eggs were fertile. The R-strain developed significantly faster than the S-strain. The integrated performance of the S-strain and R-strain was greatest at 25 and 15 °C, respectively.

4. The present study provides important information on the complexities of the outcomes of the interactions between ectotherms and temperature. Specifically, temperature-trait relationships may not be unimodal, and ectotherm genotypes (in this case insecticide-resistance status) and abiotic stresses can interact with unpredictable outcomes.

5. Current models predicting DBM population dynamics and relative abundance in different locations do not consider different thermal biologies of different genotypes. The present study shows the dramatic effects of environment on many parameters used in these models and will help to enhance their accuracy, and thus their utility.

Key words. Deltamethrin, performance, *Plutella xylostella*, pyrethroids, resistance, temperature.

Introduction

The diamondback moth (DBM) *Plutella xylostella* L. (Lepidoptera: Plutellidae) is a highly migratory and destructive specialist herbivore of *Brassica* plants. DBM is one of the most widespread insects, and it can colonise both tropical and temperate regions around the world (Lim, 1986; Talekar & Shelton, 1993).

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The life span and reproduction rates of DBM are highly variable depending on the specific plant host upon which it develops and the local environmental conditions. In particular, the number of generations that DBM can complete each year is determined by local temperatures. DBM can be highly migratory, and adults are able to fly thousands of kilometres over consecutive days (Talekar & Shelton, 1993). In the last 80 years, many laboratory studies have been published on the development of DBM at different constant temperatures. The critical lower and upper temperature thresholds for development have been estimated to be 7.4 and 38.0 °C, respectively (Liu *et al.*, 2002; Furlong & Zalucki, 2017), although they are able

to complete development at alternating temperatures in the range 4–38 °C (Liu *et al.*, 2002). The development rate of DBM is highest at constant 30 °C (Li *et al.*, 2016), fecundity is maximised at 15 °C and the highest growth rate (mass per day) is at 20 °C (tested at 5 °C intervals from 10 to 30 °C) (Garrad *et al.*, 2016).

Intensive use of insecticides, together with the rapid development and high reproduction rates of DBM, facilitates the selection of insecticide resistance. The pest has developed resistance to every class of insecticides (both synthetic insecticides and toxins derived from the soil bacterium *Bacillus thuringiensis*) used against it in the field (Furlong *et al.*, 2013). For example, DBM was the first agricultural pest to develop resistance to DDT in 1953 (Ankersmit, 1953) and the first insect to evolve resistance to *B. thuringiensis* (Tabashnik *et al.*, 1992).

The increased frequency of the alleles that confer resistance in DBM may have impacts on associated fitness traits in the absence of the insecticide (Crow, 1957). In most cases, a fitness cost will reduce the level of resistance in a population when the selection pressure of the insecticide is removed because the negative effects of pleiotropy are more strongly expressed. For example, a field-evolved chlorantraniliprole-resistant DBM population exhibited significantly longer larval and pupal durations and male life span, higher hatching rates, and lower larval weight and fecundity in the absence of chlorantraniliprole (Ribeiro *et al.*, 2014). Similarly, the survival, hatching rates, and fecundity of a DBM strain resistant to *B. thuringiensis* decreased significantly in the absence of *B. thuringiensis* (Groeters *et al.*, 1994). A spinosad-resistant strain of DBM had longer developmental time, lower pupal weight and decreased fecundity compared with the susceptible field population (Sayyed *et al.*, 2008). Lower reproduction rates were also found in tebufenozide-resistant DBM (Cao & Han, 2006). Temperature extremes could interact with such effects of resistance and even exacerbate the fitness costs, as demonstrated in spinosad-resistant DBM (Li *et al.*, 2007). However, resistance in insects may not always incur a fitness cost. For example, there were no significant differences in developmental time, mortality, or fecundity across a fenvalerate-resistant DBM strain collected in Thailand and its revertant in the laboratory (Motoyama *et al.*, 1992).

Pyrethroid insecticides are broad-spectrum synthetic pyrethrins that paralyse and kill insects by targeting the α subunit of their voltage-gated sodium channels (Soderlund & Bloomquist, 1989). Resistance to pyrethroids can be conferred by non-metabolic and metabolic mechanisms in DBM, as detected in many field populations around the world (Furlong *et al.*, 2013). Point mutations in the *para* gene, which encodes the voltage-gated sodium channel and results in insensitivity to pyrethroid, represent a non-metabolic mechanism found in pyrethroid-resistant DBM. This mechanism is known as 'knockdown' resistance, and it was discovered in other pyrethroid-resistant insects (including house flies and cockroaches) before the decreased sensitivity of the nervous system to pyrethroids was detected electrophysiologically in pyrethroid-resistant DBM (Hama *et al.*, 1987; Schuler *et al.*, 1998). Field-evolved pyrethroid-resistance in DBM collected from 16 field sites in southern Australia was related to at least three different mutations (L1014F, T929I and F1020S) in the *para* sodium channel gene (Endersby *et al.*, 2011). Metabolic mechanisms of pyrethroid resistance, which may involve detoxification by the microsomal P450-dependent monooxygenase system, esterases or glutathione S-transferases, have also been reported in DBM (Sun *et al.*, 1992; Eziah *et al.*, 2009). It is possible that the resistance in any one individual comprises more than one mechanism (Schuler *et al.*, 1998; Lambkin & Furlong, 2011).

Deltamethrin is a pyrethroid that is widely used against agricultural and urban pests. We used a field-evolved deltamethrin-resistant strain in the present study. The population was divided in two, and the two subpopulations were maintained separately: one was maintained without exposure to insecticides so that insecticide-resistance attenuated, whereas the other was intermittently selected with deltamethrin to maintain expression of deltamethrin-resistance. Because the two experimental populations had the same genetic background, comparisons of fitness traits across them at different temperatures could be expected to reveal any costs of deltamethrin-resistance under different thermal conditions. Furthermore, the present study has the same emphasis on understanding the complexities of how insects respond to different temperatures. Various life traits and intergenerational effects were investigated and compared. These results have considerable significance for understanding the individual performance, population dynamics and geographical limits of these highly migratory ectotherms.

Materials and methods

Insects and plants

Common cabbage plants (*Brassica oleracea L. capitata* cv. sugarloaf) were grown in individual pots (diameter 15 cm) with organic potting medium and an organic fertiliser (Osmocote, N : P : K = 16 : 35 : 10; Scotts Australia, Baulkham Hills, NSW, Australia) in a glasshouse at the University of Queensland (St Lucia, QLD, Australia). Good quality young leaves from 4–5-week-old plants, which are good hosts for DBM (Badenes-Perez *et al.*, 2004), were used for the culture and experiments. The DBM were collected from commercial cabbage crops in Gatton (27°33′S, 152°18′E), south-east Queensland in 2014. One generation after collection from the field this DBM population showed increased susceptibility to deltamethrin compared with the standard susceptible Waite population in laboratory bioassays (Etebari *et al.*, 2015). The population was divided in two and both cultures were maintained on fresh cabbage leaf material under a LD 16 : 8 h light/dark photocycle at 23 ± 1 °C. The deltamethrin resistant strain of DBM (R-strain) was selected with deltamethrin (Suncis, Santa Clarita, CA, U.S.A.; 25 g AI kg^{-1}) intermittently. Early third-instar larvae of the R-strain were selected with deltamethrin by exposing them to leaves treated with an approximate LC_{50} (i.e. the lethal concentration expected to cause 50% mortality of the population) of deltamethrin using the leaf-dip method. Larvae were exposed to treated leaves for 48 h at 23 ± 1 °C, and survivors were used to continue the R-strain. Insects were exposed to selection intermittently

every few generations for more than 2 years. The susceptible line (S-strain) was not exposed to any insecticide. At the time of experimentation, the R-strain was 20-fold more resistant to deltamethrin than the S-strain [R-strain: LC_{50} (95% confidence interval) = 123 (87–174) p.p.m., slope = 1.31 ± 0.14; S-strain: LC_{50} (95% confidence interval) = 6 (4–8) p.p.m., slope = 2.34 ± 0.25; reported in part by Barbosa, 2019].

Performance at different rearing temperatures

The survival and developmental time of each stage, pupal weight, adult life span, and fecundity of the S-strain and R-strain, when provided with fresh common cabbages as a larval food source, were measured at constant rearing temperatures of 10, 15, 20, 25, 30, and 35 °C. The experiment began by placing one 4–5-week-old potted common cabbage plant in an oviposition cage containing either > 80 R-strain or > 80 S-strain adult DBM. The plant was left in the cage for 3 h (light; 23 ± 1 °C) to accumulate eggs. The egg collection was repeated four to eight times with intact plants for each treatment. Portions of cabbage leaf containing eggs were then removed from plants and placed into Petri dishes (diameter 9 cm) containing a moistened filter paper. The dishes were then immediately placed into incubators at 10, 15, 20, 25, 30, and 35 °C (temperature ±1 °C; LD 12:12 h; 50–70% RH). Depending on previously reported survival at different temperatures, 26–159 eggs of each strain were placed to obtain sufficient surviving moths at each rearing temperature (Liu *et al.*, 2002). The eggs were checked three times per day at 08.00, 14.00, and 20.00 hours and, as soon as a larva hatched, it was transferred to a portion of fresh leaf in a Petri dish (diameter 6 cm). Individual larvae were reared separately in this way and fresh leaves were supplied to each one daily and the filter paper underneath was moistened frequently. Each larva was observed twice per day at 08.00 and 20.00 hours to record the time of death, each stage of development through to pupation, and adult emergence. Each pupa was weighed on a microbalance (XS3DU; Mettler-Toledo, Greifensee, Switzerland; $d = 1$ μg/10 μg) within 24 h of developing. Once an adult emerged, its sex was determined, and a cotton roll soaked with water was put into the Petri dish to keep the moth from dehydration. Water was supplied daily until the adult died, and adult life span was recorded.

The other group of each DBM strain was reared through to adulthood at each constant temperature as described previously and newly emerged adults were used to investigate the effect of rearing temperature on fecundity in both strains at 25 ± 1 °C (LD 12 : 12 h; 50–70% RH). Soon after emergence, adult female moths were paired with an individual male from the same treatment and held in a Petri dish (diameter 6 cm) to allow mating. A piece of common cabbage leaf was placed in each dish to stimulate oviposition and to act as an oviposition substrate, and a cotton roll soaked with water was put into the Petri dish to keep the moth from dehydration. The pieces of leaf were replaced daily, and the number of eggs laid on each was recorded until the female died. The leaf portion was then placed into a clean Petri dish (diameter 6 cm) that was sealed with Parafilm (Bemis Company, Inc., Neenah, WI, U.S.A.) and incubated (25 ± 1 °C; LD 12 : 12 h). The number of eggs that hatched on each leaf was recorded after 5 days (sufficient time for them to hatch at this temperature) (Liu *et al.*, 2002), allowing fertility rates to be measured for each strain at each temperature.

Integrated performance

Whole-organism performance or fitness is an estimate of net population growth (Angilletta, 2009). Integrated performance (R) is defined as the reproductive rate of a female over one generation and is a measure of the efficiency of reproduction. It was calculated as:

$$R = \frac{F}{DL} \quad (1)$$

where F is the mean fecundity of female DBM and DL is the mean duration of a life cycle of individuals at a given constant temperature.

Statistical analysis

Statistical analysis was conducted in R (R Core Team, 2019). Before conducting an analysis of variance (ANOVA), the homogeneity of variances was examined by Bartlett's tests. Normality of distribution of dependent variables was also examined. The effects of temperature and strain (which indicates deltamethrin-resistance status) on duration of a life cycle and adult life span were tested with two-way ANOVA with White-corrected covariance matrices applied; *post hoc* analyses were conducted with Games–Howell tests. The effects of strain at each temperature on duration of a life cycle were compared with one-way ANOVA. The impacts of temperature and strain on pupal weight and fecundity were tested with two-way ANOVA; *post hoc* analyses were conducted with Tukey's honestly significant difference tests.

Results

DBM from the S-strain and the R-strain could complete their life cycles at all constant temperatures tested in the range 10–30 °C. First-instar larvae of both strains died soon after hatching at 35 °C (Table 1). Both temperature ($F_{4,384} = 13026.26$, $P < 0.001$) and strain ($F_{1,384} = 31.72$, $P < 0.001$) significantly affected the time to complete the life cycle and there was a significant interaction between these main effects ($F_{4,384} = 6.17$, $P < 0.001$) (Table 2). As expected, the duration of the life cycle decreased with increasing temperature from 10 to 30 °C. At 10 °C, it took 88.7 ± 0.51 days ($n = 81$) for the S-strain and 85.8 ± 0.51 days ($n = 74$) for the R-strain to complete their life cycles but, at 30 °C, it took only 11.1 ± 0.10 days ($n = 34$) and 10.6 ± 0.07 days ($n = 52$) for the S-strain and R-strain, respectively (Fig. 1a). However, at 35 °C, the time it took for eggs to hatch was shorter than at 25 °C but longer than at 30 °C (Table 1). Generally, the time it took to complete each developmental stage declined with increasing temperature for both strains (Table 1). Neonates took longer to complete development to the next instar than any other larval stage, and the

Table 1. Developmental time [mean ± SE (number of individuals that completed the stage)] of each stage, in days, of the susceptible field strain (S-strain) and deltamethrin-resistant strain (R-strain) of *Plutella xylostella* when reared at constant temperatures.

Temperature (°C)	Strain	*n*	Egg	First instar	Second instar	Third instar	Fourth instar	Prepupa	Pupa (female)	Pupa (male)	Pupa (total)
10	S-strain	159	18.2 ± 0.11 (159)	14.4 ± 0.21 (135)	8.6 ± 0.13 (129)	9.2 ± 0.15 (125)	11.3 ± 0.19 (120)	3.8 ± 0.11(118)	23.0 ± 0.31 (35)	24.9 ± 0.32 (46)	24.1 ± 0.24 (81)
10	R-strain	150	17.4 ± 0.09 (148)	12.9 ± 0.26 (105)	9.0 ± 0.18 (103)	9.7 ± 0.22 (99)	10.8 ± 0.16 (94)	3.7 ± 0.07 (92)	22.4 ± 0.43 (36)	23.8 ± 0.41 (38)	23.1 ± 0.30 (74)
15	S-strain	51	6.7 ± 0.05 (44)	5.1 ± 0.25 (32)	2.4 ± 0.09 (31)	3.3 ± 0.07 (31)	3.5 ± 0.09 (31)	1.2 ± 0.05 (31)	10.2 ± 0.14 (17)	11.4 ± 0.15 (13)	10.7 ± 0.15 (30)
15	R-strain	26	6.1 ± 0.05 (26)	4.1 ± 0.16 (24)	2.8 ± 0.13 (23)	3.2 ± 0.11 (23)	3.5 ± 0.11 (22)	1.3 ± 0.07 (22)	9.8 ± 0.22 (12)	11.1 ± 0.20 (9)	10.3 ± 0.21 (21)
20	S-strain	39	4.5 ± 0.00 (39)	3.1 ± 0.08 (32)	2.3 ± 0.08 (31)	2.7 ± 0.22 (31)	3.3 ± 0.16 (31)	1.3 ± 0.23 (28)	5.6 ± 0.11 (9)	6.2 ± 0.20 (16)	6.0 ± 0.14 (25)
20	R-strain	49	4.6 ± 0.03 (33)	2.6 ± 0.10 (33)	1.9 ± 0.04 (32)	2.2 ± 0.11 (31)	3.6 ± 0.22 (28)	1.0 ± 0.05 (25)	5.5 ± 0.10 (13)	6.0 ± 0.18 (11)	5.7 ± 0.11(24)
25	S-strain	46	2.7 ± 0.06 (41)	2.2 ± 0.07 (36)	1.1 ± 0.05 (36)	1.3 ± 0.07 (36)	1.8 ± 0.06 (36)	0.7 ± 0.04 (36)	3.5 ± 0.08 (21)	4.0 ± 0.06 (14)	3.7 ± 0.07 (35)
25	R-strain	39	3.0 ± 0.06 (32)	2.2 ± 0.08 (20)	1.1 ± 0.06 (18)	1.4 ± 0.08 (18)	1.6 ± 0.06 (18)	0.8 ± 0.09 (18)	3.1 ± 0.10 (12)	3.3 ± 0.11 (6)	3.2 ± 0.08 (18)
30	S-strain	84	2.5 ± 0.00 (53)	1.6 ± 0.07 (47)	1.1 ± 0.05 (39)	0.9 ± 0.04 (39)	1.4 ± 0.05 (39)	0.5 ± 0.01 (39)	3.0 ± 0.05 (23)	3.4 ± 0.06 (11)	3.1 ± 0.05 (34)
30	R-strain	81	2.4 ± 0.02 (77)	1.7 ± 0.03 (74)	0.8 ± 0.05 (67)	1.3 ± 0.06 (60)	1.2 ± 0.07 (55)	0.6 ± 0.03 (55)	2.8 ± 0.06 (29)	3.0 ± 0.05 (21)	2.9 ± 0.04 (52)
35	S-strain	144	2.8 ± 0.04 (34)	–	–	–	–	–	–	–	–
35	R-strain	131	2.8 ± 0.07 (14)	–	–	–	–	–	–	–	–

–, no individuals survived to that stage.

Table 2. Summary of the analysis of variance statistics for the effects of temperature and strain (which indicates deltamethrin-resistance status) on the duration of a life cycle, adult life span, pupal weight, and fecundity of *Plutella xylostella*.

Source	d.f.	*F*	*P*
Duration of a life cycle			
Temperature	4	13026.26	< 0.001
Strain	1	31.72	< 0.001
Temperature × Strain	4	6.17	< 0.001
Residuals	384		
Adult life span			
Temperature	4	230.12	< 0.001
Strain	1	0.10	0.753
Temperature × Strain	4	2.50	< 0.05
Residuals	353		
Pupal weight (females)			
Temperature	4	155.36	< 0.001
Strain	1	4.32	< 0.05
Temperature × Strain	4	5.75	< 0.001
Residuals	191		
Pupal weight (males)			
Temperature	4	120.25	< 0.001
Strain	1	0.04	0.837
Temperature × Strain	4	0.07	0.990
Residuals	176		
Fecundity			
Temperature	4	40.67	< 0.001
Strain	1	0.18	0.674
Temperature × Strain	4	2.04	0.094
Residuals	114		

pupal stage took the longest of all immature stages to complete (Table 1). The duration of a life cycle of S-strain insects was significantly longer than those of the R-strain at 10 ($F_{1,153} = 15.34$, $P < 0.001$), 15 ($F_{1,49} = 14.12$, $P < 0.001$), 20 ($F_{1,47} = 12.56$, $P < 0.001$), and 30 °C ($F_{1,84} = 16.58$, $P < 0.001$), although there was no significant difference at 25 °C ($F_{1,51} = 0.11$, $P = 0.744$) (Fig. 1a).

Adult life span also declined significantly with increasing temperature ($F_{4,353} = 230.12$, $P < 0.001$), although strain ($F_{1,353} = 0.10$, $P = 0.753$) had no effect on adult life span (Fig. 1b and Table 2). The maximum adult life span of an individual of the S-strain was 20.5 ± 1.31 days ($n = 71$) and, for the R-strain, it was 19.5 ± 1.21 days ($n = 55$) and, in both cases, insects were reared at 10 °C. By contrast, the S-strain and R-strain adults died in only 3.7 ± 0.08 days ($n = 34$) and 3.8 ± 0.16 days ($n = 51$) after eclosion, respectively, when reared at 30 °C (Fig. 1b).

Temperature ($F_{4,367} = 274.82$, $P < 0.001$) and sex ($F_{1,367} = 118.62$, $P < 0.001$) had significant impacts on the pupal weight of both strains. When looking at the two sexes separately, strain ($F_{1,191} = 4.32$, $P < 0.05$) and its interaction with temperature ($F_{4,191} = 5.75$, $P < 0.001$) (Table 2) significantly affected the pupal weight of females, although neither had an effect on male pupal weight (Table 2). The pupal weight of females and males generally decreased with increasing temperature (Fig. 1c,d). In addition, the pupal weight of R-strain females was significantly higher than that of S-strain

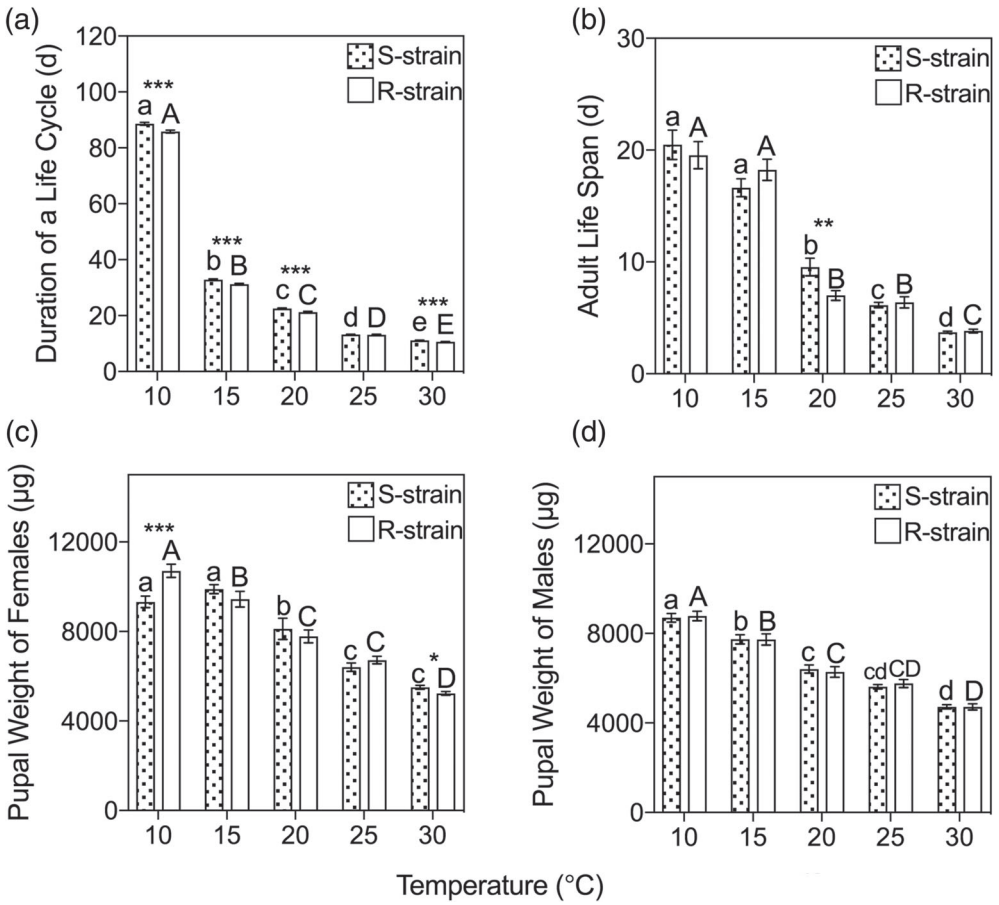

Fig. 1. Mean ± SE duration of a life cycle (a), adult life span (b), female pupal weight (c), and male pupal weight (d) of the susceptible field strain (S-strain; dotted columns) and the deltamethrin-resistant strain (R-strain; empty columns) of *Plutella xylostella* at constant temperatures. Characters above columns show the results of *post hoc* analyses. Lowercase letters represent comparisons within the S-strain, and uppercase letters represent comparisons within the R-strain among different temperatures (95% confidence interval). Stars above characters indicate the *P* value (no stars: $P > 0.05$; *$0.05 > P > 0.01$; **$0.01 > P > 0.001$; ***$P < 0.001$) of one-way analysis of variance comparing the parameter across these two strains at a given temperature.

females at 10 °C ($F_{1,63} = 12.25$, $P < 0.001$) and lower at 30 °C ($F_{1,50} = 5.24$, $P < 0.05$) (Fig. 1c), and the pupal weight of each sex did not differ significantly across strains at any temperature (Fig. 1c,d).

Temperature significantly affected fecundity ($F_{4,114} = 40.67$, $P < 0.001$) and fecundity was not affected by strain ($F_{1,114} = 0.18$, $P = 0.674$), and there was no interaction between strain and temperature ($F_{4,114} = 2.04$, $P = 0.094$) (Table 2). Females of both strains produced most eggs at 15 °C and the least at 30 °C (Table 3). At 10 °C, female moths could produce eggs, but only a small number, in each case produced by a single female of each strain (S-strain, $n = 19$; R-strain, $n = 10$), hatched (Table 3).

For both strains, the changes of adult life span, pupal weight of females, fecundity, and development rates in response to different temperatures differed markedly (Fig. 2). The optimal temperatures for integrated performance of the S-strain and the R-strain were 25 and 15 °C, respectively. The minimum integrated performance was for those insects exposed constantly to 10 °C. The integrated performance of the S-strain was lower at 20 °C than at 15 or 25 °C. The integrated performance of the R-strain at 20 °C was between 15 and 25 °C (Fig. 3).

Discussion

Effects of temperature

Temperature profoundly affects developmental and reproductive variables of DBM in different ways. In natural environments, the population dynamics and migratory behaviour of DBM are affected by local conditions. In cool regions, such as the South Island of New Zealand, there are approximately six generations each year (Muggeridge, 1930). In the southern subtropical provinces in China, DBM can complete 20 generations each year with continuous populations of overlapping generations. In temperate regions in northern China, DBM does not occur all year round, although it is able to complete two to three generations after migrating from the south during the spring

Table 3. Numbers of eggs (mean ± SE) laid by females of the susceptible field strain (S-strain) and the deltamethrin-resistant strain (R-strain) of *Plutella xylostella* at constant temperatures, and the proportion of those that were viable.

Temperature (°C)	Strain	N*	n†	Nf‡	No. Eggs	Group§	Number of viable eggs	Proportion
10	S	25	19	1	79.9 ± 8.6	ab	0.2 ± 0.2	0.2%
10	R	25	10	1	59.8 ± 12.5	A	0.6 ± 0.6	1.0%
15	S	13	13	9	200.9 ± 19.8	c	136.1 ± 31.1	67.7%
15	R	15	12	12	226.0 ± 18.5	B	212.5 ± 19.2	94.0%
20	S	13	12	10	73.8 ± 12.2	ab	70.2 ± 13.5	95.0%
20	R	15	13	13	89.2 ± 15.6	A	86.9 ± 15.0	97.50%
25	S	15	11	11	109.5 ± 14.9	b	102.5 ± 13.2	93.7%
25	R	22	17	15	65.4 ± 14.3	A	59.6 ± 14.4	91.3%
30	S	10	8	4	29.8 ± 7.5	a	19.9 ± 8.7	66.8%
30	R	12	9	7	43.0 ± 12.3	A	40.0 ± 12.4	93.0%

∗Numbers of females that were tested for fecundity.
†Numbers of females that eventually laid eggs.
‡Numbers of females that laid viable eggs.
§The results of *post hoc* analyses. Lowercase letters represent comparisons within the S-strain, and uppercase letters represent comparisons within the R-strain among different temperatures (95% confidence interval).

(Li *et al.*, 2016). Migration could explain the seasonal distribution of DBM populations in areas with unfavourable thermal conditions during cold seasons. Direct observations (French & White, 1960; Shaw & Hurst, 1969), light and pheromone trap studies, and radar monitoring (Chapman *et al.*, 2002) all indicate that the annual influxes of DBM into the U.K., which can cause outbreaks in some years, originate from areas bordering the Baltic Sea and continental Europe, rather than from endemic populations (Talekar & Shelton, 1993). In North America, populations in the southern states could be the origin of DBM populations in northern parts of the U.S.A. and Canada, where DBM cannot survive the harsh winter (Dosdall *et al.*, 2004). Studies in China provide genetic and field evidence for mass migration of DBM towards the north in spring (Wei *et al.*, 2013).

Previous laboratory studies have shown that DBM, similar to many other ectotherms, has a sensitive response to temperature. Development rate is the trait most frequently used to define the performance of insects in response to temperature in many studies, and it is even used as a surrogate for fitness (Angilletta, 2009; Sinclair *et al.*, 2016). Other traits are, however, also used in thermal studies of insect performance, such as rates of increase in mass, metabolic rates, and fecundity. The results reported in the present study demonstrate that using a single trait to define the performance of an insect in response to temperature is of limited value.

In response to a given temperature, a trait might manifest differently across distinct strains of the same species, and there can be a lack of consistency in responses across different traits. For example, in the present study, both strains of DBM laid the most eggs at 15 °C, and the least at 30 °C. By contrast, they took approximately 1 month to complete one life cycle at 15 °C but only one-third of that time at 30 °C (Fig. 2). In such cases, concluding that either 15 or 30 °C is the optimal temperature for DBM would not be convincing.

The development rates increased with rising temperatures from 10 to 30 °C for both strains, although adult life span decreased at higher temperatures. The responses of pupal weight of females and fecundity to different temperatures also varied and showed that heavier females do not necessarily produce more eggs (Fig. 2). The different responses to temperature in the traits investigated demonstrate that no single trait adequately reflected how DBM performs under given thermal conditions. The responses of the multiple traits measured in this study provide more comprehensive information on the effects of temperature on the insect.

Decreasing temperature significantly prolonged the duration of the life cycle of both strains. Accordingly, the time required to complete each developmental stage was also reduced at higher temperatures. However, there are limits to this generalisation because the duration of the egg stage at 35 °C was longer than at 30 °C (Table 2), demonstrating that higher temperature does not always result in shorter developmental time, especially under extreme conditions. By comparison, the life cycle was completed fastest at 30 °C. On its own, this measurement might suggest that 30 °C is more favourable for development than lower temperatures. The time to complete a life cycle increased by only 2–3 days from 30 to 25 °C. This may be a result of these temperatures being close to the optimal for thermal performance, whereas a slight increase in temperature beyond 30 °C decreases development rates more markedly. With each 5 °C change from 25 to 15 °C, the duration of the life cycle decreased by approximately 10 days. The most drastic change occurred between 10 and 15 °C, resulting in an increase of 30 days for the time to complete the life cycle at the lower temperature (Fig. 1a). The time to complete development was extremely long for both strains at 10 °C (Fig. 1a,b). Although this harsh temperature slowed development significantly, it did not appear to impact any given development stage more than any other (Table 1).

Adult life span was also shortened significantly by increasing temperature. Longer adult life, in moths reared at lower temperatures, might be a result of their relatively larger body sizes resulted from lower rearing temperatures (Fig. 1c,d) and lower metabolic rates (Gillooly *et al.*, 2001). Pupal weights of both female and male DBM were lower at higher temperatures (Fig. 1c,d), and this resulted in smaller adults. DBM does not

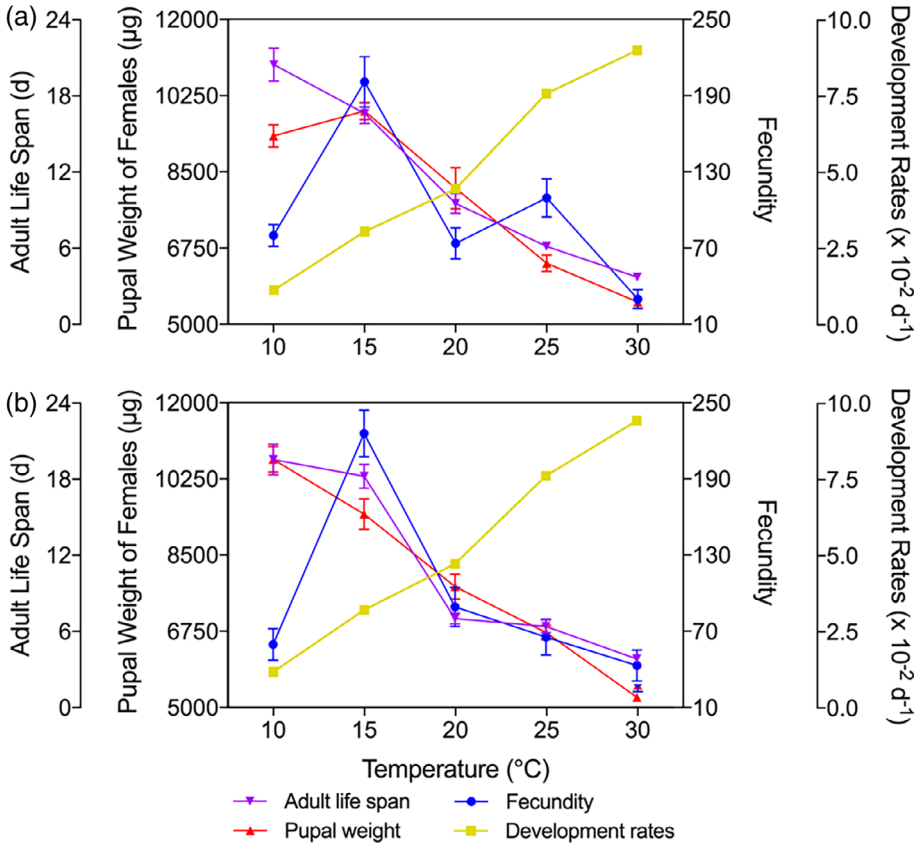

Fig. 2. Comparisons among the changes of mean ± SE adult life span, female pupal weight, fecundity, and development rates of the susceptible field strain (S-strain) (a) and the deltamethrin-resistant strain (R-strain) (b) of *Plutella xylostella* in response to different constant temperatures. [Colour figure can be viewed at wileyonlinelibrary.com].

need to feed as an adult (Talekar & Shelton, 1993), and so the resources used for metabolism and activities at the adult stage rely heavily on resources accumulated during the larval stage. We tested adult life span at the original rearing temperatures, such that adult metabolism could be affected by both ambient temperature and the long-term effects of temperature during their immature stages. The heavier pupae that developed at lower temperatures in this study support the temperature-size rule for ectotherms, which contends that, at lower ambient temperatures, the growth rate of ectotherms is relatively faster than their development rates, resulting in a larger body size upon maturity (Stevenson, 1985).

Both strains showed greatest fecundity at 15 °C (Table 3) and, at this temperature, fecundity was more than twice that at the other temperatures. Typically, it is assumed that larger females will produce more eggs than smaller individuals (Leather, 1988; Honěk, 1993). In the present study, the large females of each strain, which were produced at 10 °C, laid only a limited number of eggs and almost none of these hatched (Table 3). The cause might be incomplete development of the reproductive system of DBM when reared at 10 °C, which requires further experimentation. Most male DBM that were reared at 10 °C might fail to copulate successfully, and it was possible that those that did so failed to produce viable sperm. By contrast, a larger proportion of female DBM reared at this temperature could develop viable eggs if mated with healthy males reared at 25 °C (L. Wang *et al.*, unpublished data). This suggests their tolerance to cold conditions differs across the sexes (e.g. Gilad & Scharf, 2019), and it raises several ecologically and physiologically significant questions. In particular, the viability or fertility of eggs is rarely tested in studies investigating the effects of different thermal conditions on the fecundity of insects. The minimum temperature threshold for DBM development from egg to adult and from second instar larva to adult has been estimated to be between 4 and 8 °C, respectively (Liu *et al.*, 2002; Bahar *et al.*, 2014). However, neither study investigated the effects of low rearing temperature on the eggs produced by these insects. As such, these studies likely underestimate the intergenerational effects of harsh conditions, and therefore estimates of the potential net growth of those populations are likely to be inaccurate.

The fecundity of both strains was similar at 20 °C to that at 25 °C (Table 3), although the pupal weights of insects reared at 20 °C were significantly higher than those reared at 25 °C (Fig. 1a). This suggests that the extra body mass gained from slower development may not necessarily be fully invested in increasing reproduction. Female moths of both strains that were reared at 30 °C laid the fewest eggs (Table 3). Their smaller

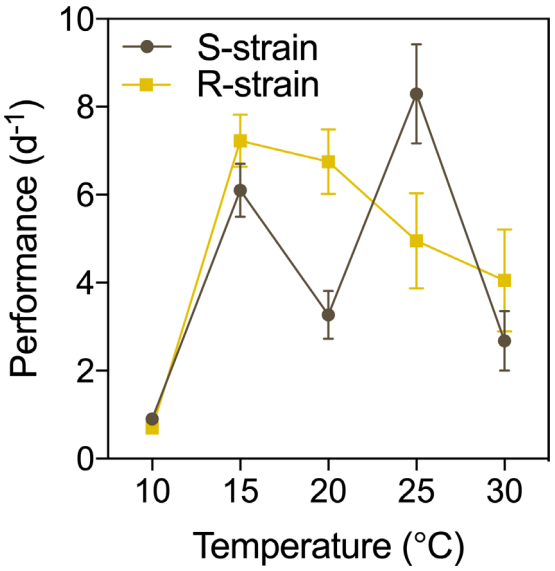

Fig. 3. Mean ± SE integrated performance (individuals/*d*, the reproductive rate of a female over one generation) of the susceptible field strain (S-strain) and the deltamethrin-resistant strain (R-strain) of *Plutella xylostella* at different constant temperatures. [Colour figure can be viewed at wileyonlinelibrary.com].

bodies might indicate they had been provisioned with fewer resources, or they may somehow have been physically damaged by the relatively harsh thermal conditions.

The integrated performance, which represents the reproductive rate of a female DBM over one generation, is a measure of the effectiveness of female DBM to contribute to future population growth. A temperature of 20 °C is suitable for *Brassica* growth and colonisation by DBM, and so it was not expected that the integrated performance would be lower at 20 °C than at 15 and 25 °C for the S-strain or similar to that at 15 and 25 °C for the R-strain. This may be the result of an integrated effect resulting from different sensitivity and thermal optima of different metabolic processes, which may or may not be related to insecticide-resistance in DBM, or it may be the result of better plant defences against herbivory at 20 °C. Whether similar patterns are evident in other insects is worthy of further investigation. In both strains, integrated performance was minimal at 10 °C (Fig. 3), suggesting an extremely low potential for population growth at relatively low temperatures. Furthermore, the low viability of eggs produced by moths reared at 10 °C could exacerbate this situation.

In summary, exposure of DBM to different temperatures clearly affects their developmental and reproductive outputs differentially, and these differentials will, in return, result in a range of impacts on the population dynamics and population genetics of these organisms. Higher development rates could result in faster generation times and potentially faster development of resistance to xenobiotics, whereas longer adult life spans may suggest more time to achieve reproductive success, search for hosts, and migrate. For example, an adult with a longer life span as a result of developing in a cooler season may have more time to move to a warmer location.

Effects of resistance

Insecticide resistance usually results in increased 'fitness costs' in resistant insects as a result of the higher energetic costs associated with metabolic mechanisms of resistance and/or changes to the frequency of alleles conferring resistance that may also affect fitness (Crow, 1957). In such cases, in the absence of selection pressure, susceptibility to insecticides is likely to increase over time (Muggleton, 1983). If insecticide resistance does not carry a fitness cost, then the insecticide-resistant phenotype may be maintained without a selection pressure (ffrench-Constant & Bass, 2017). The present study aimed to identify the difference in the developmental time, adult life span, pupal weight, and fecundity across the deltamethrin-resistant DBM strain and its homogenous susceptible field strain at different temperatures. The time required to complete a life cycle differed significantly across the R-strain and S-train, and this main effect had a significant interaction with temperature (Table 2). The R-strain completed its life cycle in a significantly shorter time than the S-strain at 10, 15, 20, and 30 °C, although the time to complete a life cycle did not differ between the strains at 25 °C. However, resistant strains taking longer to develop is the more common outcome of such interactions (Sayyed *et al.*, 2008; Ribeiro *et al.*, 2014) and such studies are cited as evidence for that the investment required for the expression of resistance results in slower development. In the present study, resistance to deltamethrin did not impede development, rather, it accelerated it. Changes in the frequency of associated alleles or the involvement of the metabolic enzymes in increased metabolism, if metabolic resistance is involved, in the deltamethrin-resistant DBM may play a role in this phenomenon. In several studies (Sayyed *et al.*, 2008; Ribeiro *et al.*, 2014), fitness costs are compared across strains that may be inherently different genetically, irrespective of their different exposure and responses to insecticide; for example, when a trait of an insecticide-resistant field population is compared with that trait in an unrelated laboratory insecticide-susceptible strain. The conclusions from such studies should be treated with caution.

The pupal weight of female DBM was significantly impacted by strain and its interaction with temperature, whereas strain did not affect the pupal weights of male DBM (Table 2). The only significant differences found across the strains at different temperatures were higher pupal weights of R-strain females at 10 °C and S-train females at 30 °C (Fig. 1c). This might suggest that R-strain females can cope better with cold conditions and that S-strain females can cope better with higher temperature extremes in terms of gaining biomass. Strain did not affect the fecundity at either of these temperatures, again suggesting that larger females do not necessarily produce more eggs.

The integrated performances of the S-strain and the R-strain were maximised at 25 and 15 °C respectively, indicating that the difference in their deltamethrin-resistance status resulted in changes in their optimal temperatures for population growth. Besides this, no detrimental fitness costs as a result of deltamethrin-resistance were detected in any of the traits measured. Indeed, deltamethrin-resistance might even result in faster development and subsequently higher rates of net growth

of populations. Furthermore, if there are no significant costs of expressing resistance, susceptibility may be difficult to recover even when exposure to deltamethrin is stopped for multiple generations. Thus, there could be other negative or even other positive effects of carrying resistance to deltamethrin to explore.

Does resistance always carry a fitness cost (ffrench-Constant & Bass, 2017)? There were no significant differences in the fitness (duration of stages, rates of pupation, adult emergence, and fecundity) across fenvalerate-resistant DBM collected in Thailand and its revertant at 15, 20, 25, 30, and 35 °C (Motoyama *et al.*, 1992). The intrinsic rates of population increase of highly and moderately *B. thuringiensis*-resistant subpopulations of DBM were similar to one another (Sayyed & Wright, 2001). When considering other parameters, a DBM line resistant to fenvalerate had significantly smaller eggs and a lower survival rate than the susceptible line (Chen *et al.*, 2006a). The fenvalerate-resistant and susceptible lines were exposed to unfavourable dry and hot environments without selection pressure of fenvalerate in their subsequent study, and the resistant line showed higher mortality and its susceptibility to fenvalerate returned within 10 generations (Chen *et al.*, 2006b). Similar to the present study, it also reveals that abiotic stressors could strongly direct the evolution of insecticide-resistant populations of insects. Furthermore, the strength of fitness costs can be affected by host plant suitability. The survival of homozygous *B. thuringiensis*-resistant DBM, homozygous *B. thuringiensis*-susceptible DBM, and their F1 hybrids was reduced in both the presence and absence of *B. thuringiensis* on well defended (=less suitable) host plants. However, on better quality host plants, the overall fitness costs to homozygous-resistant and homozygous-susceptible insects were greater than those to heterozygous (revertant) insects (Raymond *et al.*, 2011).

Summary and future studies

In summary, previous adaptation of DBM lines to stress could result in different responses to thermal conditions, including in life-history traits, reproduction, and thermal tolerance (e.g. present study; Zhang *et al.*, 2017). It would be worth investigating the physiological mechanisms of DBM in dealing with different thermal conditions. Furthermore, temperature not only impacts individual fitness and population dynamics of DBM, but also drives their migration. The temperature threshold for DBM to start migration should be studied, and it may also indicate what temperature DBM inherently prefers in the natural environment, as well as how their seasonal and geographical distribution may shift with a changing climate. Studies on patterns of the evolution and distribution of resistant populations in the field under different environmental conditions, including fluctuating temperature regimes, could have great significance for integrated pest management programmes especially under global changes.

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References

Angilletta, M.J. (2009) *Thermal Adaptation: A Theoretical and Empirical Synthesis*. Oxford University Press, Oxford, U.K.

Ankersmit, G. (1953) DDT-resistance in *Plutella maculipennis* (Curt.) (Lep.) in Java. *Bulletin of Entomological Research*, **44**, 421–425.

Badenes-Perez, F.R., Shelton, A.M. & Nault, B.A. (2004) Evaluating trap crops for diamondback moth, *Plutella xylostella* (Lepidoptera: Plutellidae). *Journal of Economic Entomology*, **97**, 1365–1372.

Bahar, M., Soroka, J., Grenkow, L. & Dosdall, L. (2014) New threshold temperatures for the development of a North American diamondback moth (Lepidoptera: Plutellidae) population and its larval parasitoid, *Diadegma insulare* (Hymenoptera: Ichneumonidae). *Environmental Entomology*, **43**, 1443–1452.

Barbosa, M.G. (2019) *Strategies in the resistance management of Plutella xylostella (Lepidoptera: Plutellidae) and Spodoptera frugiperda (Lepidoptera: Noctuidae): rotation of insecticides and biological control with parasitoid*. PhD thesis, Federal University of Ceara, Fortaleza, Brazil.

Cao, G.C. & Han, Z.J. (2006) Tebufenozide resistance selected in *Plutella xylostella* and its cross-resistance and fitness cost. *Pest Management Science*, **62**, 746–751.

Chapman, J.W., Reynolds, D.R., Smith, A.D., Riley, J.R., Pedgley, D.E. & Woiwod, I.P. (2002) High-altitude migration of the diamondback moth *Plutella xylostella* to the UK: a study using radar, aerial netting, and ground trapping. *Ecological Entomology*, **27**, 641–650.

Chen, X.D., Sanada-Morimura, S., Yanagi, S. & Nakasuji, F. (2006a) Genetic relationships between development of insecticide resistance and reduction of egg size as a negative effect on the fitness of the diamondback moth *Plutella xylostella* (Lepidoptera: Yponomeutidae). *Applied Entomology and Zoology*, **41**, 479–486.

Chen, X.D., Sanada-Morimura, S., Yanagi, S. & Nakasuji, F. (2006b) Rapid recovery of susceptibility under harsh environmental conditions in fenvalerate-resistant strains of the diamondback moth, *Plutella xylostella* (Lepidoptera: Yponomeutidae). *Applied Entomology and Zoology*, **41**, 641–650.

Crow, J.F. (1957) Genetics of insect resistance to chemicals. *Annual Review of Entomology*, **2**, 227–246.

Dosdall, L.M., Mason, P.G., Olfert, O., Kaminski, L. & Keddie, B.A. (2004) The origins of infestations of diamondback moth, *Plutella xylostella* (L.). in canola in western Canada. *Proceedings of the Fourth International Workshop on the Management of Diamondback Moth and Other Crucifer Pests, Melbourne, 15–26 November 2001*, pp. 95–100. Melbourne, Australia.

Endersby, N., Viduka, K., Baxter, S., Saw, J., Heckel, D.G. & McKechnie, S. (2011) Widespread pyrethroid resistance in Australian diamondback moth, *Plutella xylostella* (L.), is related to multiple mutations in the *para* sodium channel gene. *Bulletin of Entomological Research*, **101**, 393–405.

Etebari, K., Furlong, M.J. & Asgari, S. (2015) Genome wide discovery of long intergenic non-coding RNAs in diamondback moth (*Plutella xylostella*) and their expression in insecticide resistant strains. *Scientific Reports*, **5**, 14642.

Eziah, V.Y., Rose, H.A., Wilkes, M. & Clift, A.D. (2009) Biochemical mechanisms of insecticide resistance in the diamondback moth (DBM), *Plutella Xylostella* l. (Lepidopterata: Yponomeutidae), in

the Sydney region, Australia. *Australian Journal of Entomology*, **48**, 321–327.

ffrench-Constant, R.H. & Bass, C. (2017) Does resistance really carry a fitness cost? *Current Opinion in Insect Science*, **21**, 39–46.

French, R. & White, J. (1960) The diamond-back moth outbreak of 1958. *Plant Pathology*, **9**, 77–84.

Furlong, M.J. & Zalucki, M.P. (2017) Climate change and biological control: the consequences of increasing temperatures on host-parasitoid interactions. *Current Opinion in Insect Science*, **20**, 39–44.

Furlong, M.J., Wright, D.J. & Dosdall, L.M. (2013) Diamondback moth ecology and management: problems, progress, and prospects. *Annual Review of Entomology*, **58**, 517–541.

Garrad, R., Booth, D. & Furlong, M. (2016) The effect of rearing temperature on development, body size, energetics and fecundity of the diamondback moth. *Bulletin of Entomological Research*, **106**, 175–181.

Gilad, T. & Scharf, I. (2019) Separation between maternal and paternal effects on offspring following exposure of adult red flour beetles to two stressors. *Ecological Entomology*, **44**, 494–501.

Gillooly, J.F., Brown, J.H., West, G.B., Savage, V.M. & Charnov, E.L. (2001) Effects of size and temperature on metabolic rate. *Science*, **293**, 2248–2251.

Groeters, F.R., Tabashnik, B.E., Finson, N. & Johnson, M.W. (1994) Fitness costs of resistance to *Bacillus thuringiensis* in the diamondback moth (*Plutella xylostella*). *Evolution*, **48**, 197–201.

Hama, H., Kono, Y. & Sato, Y. (1987) Decreased sensitivity of central nerve to fenvalerate in the pyrethoroid-resistant diamondback moth, *Plutella xylostella* Linne (Lepidoptera: Yponomeutidae). *Applied Entomology and Zoology*, **22**, 176–180.

Honěk, A. (1993) Intraspecific variation in body size and fecundity in insects: a general relationship. *Oikos*, **66**, 483–492.

Lambkin, T.A. & Furlong, M.J. (2011) Metabolic mechanisms only partially explain resistance to pyrethroids in Australian broiler house populations of lesser mealworm (Coleoptera: Tenebrionidae). *Journal of Economic Entomology*, **104**, 629–635.

Leather, S.R. (1988) Size, reproductive potential and fecundity in insects: things aren't as simple as they seem. *Oikos*, **51**, 386–389.

Li, Z.M., Liu, S.S., Liu, Y.Q. & Ye, G.Y. (2007) Temperature-related fitness costs of resistance to spinosad in the diamondback moth, *Plutella xylostella* (Lepidoptera : Plutelidae). *Bulletin of Entomological Research*, **97**, 627–635.

Li, Z.Y., Feng, X., Liu, S.S., You, M.S. & Furlong, M.J. (2016) Biology, ecology, and management of the diamondback moth in China. *Annual Review of Entomology*, **61**, 277–296.

Lim, G.S. (1986) Biological control of diamondback moth. *Proceedings of the First International Workshop on Diamondback Moth Management, 11–15 March 1985*, *Tainan, Taiwan*, pp. 159–171. Tainan, Taiwan.

Liu, S.S., Chen, F.Z. & Zalucki, M.P. (2002) Development and survival of the diamondback moth (Lepidoptera : Plutellidae) at constant and alternating temperatures. *Environmental Entomology*, **31**, 221–231.

Motoyama, N., Suganuma, T. & Maekoshi, Y. (1992) Biochemical and physiological characteristics of insecticide resistance in diamondback moth. *Proceedings of the Second International Workshop on Diamondback Moth and Other Crucifer Pests,10-14 December 1990*, *Tainan, Taiwan*, pp. 411-418. Tainan, Taiwan.

Muggeridge, J. (1930) The diamond-back moth. Its occurrence and control in New Zealand. *New Zealand journal of agriculture*, **41**, 253–264.

Muggleton, J. (1983) Relative fitness of malathion-resistant phenotypes of *Oryzaephilus surinamensis* L. (Coleoptera: Silvanidae). *Journal of Applied Ecology*, **20**, 245–254.

R Core Team. (2019) *R: A Language and Environment for Statistical Computing*. Version 3.5.0. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Raymond, B., Wright, D.J. & Bonsall, M.B. (2011) Effects of host plant and genetic background on the fitness costs of resistance to *Bacillus thuringiensis*. *Heredity*, **106**, 281–288.

Ribeiro, L.M., Wanderley-Teixeira, V., Ferreira, H.N., Teixeira, A.A. & Siqueira, H.A. (2014) Fitness costs associated with field-evolved resistance to chlorantraniliprole in *Plutella xylostella* (Lepidoptera: Plutellidae). *Bulletin of Entomological Research*, **104**, 88–96.

Sayyed, A.H. & Wright, D.J. (2001) Fitness costs and stability of resistance to *Bacillus thuringiensis* in a field population of the diamondback moth *Plutella xylostella* L. *Ecological Entomology*, **26**, 502–508.

Sayyed, A.H., Saeed, S., Noor-Ul-Ane, M. & Crickmore, N. (2008) Genetic, biochemical, and physiological characterization of spinosad resistance in *Plutella xylostella* (Lepidoptera: Plutellidae). *Journal of Economic Entomology*, **101**, 1658–1666.

Schuler, T.H., Martinez-Torres, D., Thompson, A.J., Denholm, I., Devonshire, A.L., Duce, I.R. *et al.* (1998) Toxicological, electrophysiological, and molecular characterisation of knockdown resistance to pyrethroid insecticides in the diamondback moth, *Plutella xylostella* (L.). *Pesticide Biochemistry and Physiology*, **59**, 169–182.

Shaw, M. & Hurst, G. (1969) A minor immigration of the diamond-back moth *Plutella xylostella* (L.) (Maculipennis Curtis). *Agricultural Meteorology*, **6**, 125–132.

Sinclair, B.J., Marshall, K.E., Sewell, M.A., Levesque, D.L., Willett, C.S., Slotsbo, S. *et al.* (2016) Can we predict ectotherm responses to climate change using thermal performance curves and body temperatures? *Ecology Letters*, **19**, 1372–1385.

Soderlund, D.M. & Bloomquist, J.R. (1989) Neurotoxic actions of pyrethroid insecticides. *Annual Review of Entomology*, **34**, 77–96.

Stevenson, R. (1985) Body size and limits to the daily range of body temperature in terrestrial ectotherms. *The American Naturalist*, **125**, 102–117.

Sun, C.N., Tsai, Y.C. & Chiang, F.M. (1992) Molecular mechanisms of insecticide resistance. *Resistance in the Diamondback Moth to Pyrethroids and Benzoylphenylureas*, Vol. **505**, pp. 149–167. American Chemical Society, Washington, D.C.

Tabashnik, B.E., Schwartz, J.M., Finson, N. & Johnson, M.W. (1992) Inheritance of resistance to *Bacillus thuringiensis* in diamondback moth (Lepidoptera: Plutellidae). *Journal of Economic Entomology*, **85**, 1046–1055.

Talekar, N.S. & Shelton, A.M. (1993) Biology, ecology, and management of the diamondback moth. *Annual Review of Entomology*, **38**, 275–301.

Wei, S.J., Shi, B.C., Gong, Y.J., Jin, G.H., Chen, X.X. & Meng, X.F. (2013) Genetic structure and demographic history reveal migration of the diamondback moth *Plutella xylostella* (Lepidoptera: Plutellidae) from the southern to northern regions of China. *PLoS ONE*, **8**, e59654.

Zhang, L., Chen, J., Yang, B., Kong, X., Bourguet, D. & Wu, G. (2017) Thermotolerance, oxidative stress, apoptosis, heat-shock proteins and damages to reproductive cells of insecticide-susceptible and-resistant strains of the diamondback moth *Plutella xylostella*. *Bulletin of Entomological Research*, **107**, 513–526.

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