Development, Survivorship, and Reproduction of *Helicoverpa armigera* (Lepidoptera: Noctuidae) Under Constant and Alternating Temperatures

G. K. MIRONIDIS AND M. SAVOPOULOU-SOULTANI[1]

Aristotle University of Thessaloniki, Faculty of Agriculture, Laboratory of Applied Zoology and Parasitology, 54124 Thessaloniki, Greece

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ABSTRACT Laboratory studies were conducted to assess the effect of temperature on the survival, development, fecundity, and longevity of *Helicoverpa armigera* (Hübner) at 11 constant temperatures ranging from 12.5 to 40°C, as well as at five alternating temperature regimes (25–10, 30–15, 32.5–17.5, 35–20, and 35–27.5°C) and under a photoperiod of 16:8 (L:D) h. *H. armigera* reared at constant temperatures did not develop from egg to adult (emergence) outside the temperature range of 15–32.5°C. The alternating conditions expanded this range from 10 to 35°C. The lowest developmental thresholds of the immature stages were estimated by a linear model and ranged from 10.17 (pupal stage) to 11.95°C (egg stage) at constant temperature regimes and from 1.1 to 5.5°C, respectively at alternating temperatures. The values of developmental thresholds estimated using the nonlinear (Lactin-2) model were lower than those estimated by the linear model for constant and alternating temperature regimes except for larval and pupal stages at constant temperatures. Mean adult longevity fluctuated from 34.4 d at 15°C to 7.6 d at 35°C. Females reared under all alternating temperature regimes laid more eggs than females reared at any, except the 25°C, constant temperature treatment. The intrinsic rate of increase was highest at 27.5°C, at both the constant and the corresponding alternating temperature regimes (0.147 and 0.139, respectively). Extreme temperatures had a negative effect on life table parameters.

KEY WORDS *Helicoverpa armigera*, temperature, developmental time, survival, life table

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Helicoverpa armigera (Hübner) (Lepidoptera: Noctuidae) is a major pest of a wide range of plants, including field and horticultural crops in many parts of the world (Zalucki et al. 1986, 1994, Fitt 1989). In northern Greece, *H. armigera* completes two or three generations per year and causes annual damage, especially to cotton (EPPO/CABI 1997). In particular, during 1968 and 2003, damage to cotton crops grown in central and northern Greece was severe (Mourikis and Vasilaina-Alexopoulou 1969, EU 2005). The larvae of this bollworm also attack tomato, corn, tobacco, chick pea, pepper, okra, carnation, and gladiolus in Greece (Isaakides 1941, Pelekassis 1962).

The pest status of this species is derived, in part, from its four life history characteristics (e.g., polyphagy, high mobility, high fecundity, and a facultative diapause) that enable it to survive in unstable habitats and to adapt to seasonal changes (Fitt 1989). These characteristics may also account for the wide geographic distribution of the species within ≈45° N and 45° S latitude.

Insect development occurs within a specific temperature range. Temperature influences the rates of growth and development, the duration of life cycle, the fecundity, and the survival of insect species (Howe 1967, Andrewartha 1970). The approach most widely used to predict insect development uses a linear approximation of the developmental rate versus temperature curve. The observed relationship between insect development and temperature under controlled constant conditions tends to be nonlinear over the full range of tolerable temperature conditions to which the insect is exposed (Wagner et al. 1984, Allsopp et al. 1991). Acceleration of insect development at a low temperature and retardation at a high temperature are shown to be implicit to the assumption of the nonlinearity of development (Worner 1992). The importance of predicting the seasonal occurrence of insects has led to the formulation of many mathematical models that describe developmental rates as a function of temperature (Wagner et al. 1984). Model evaluation has been based on specific criteria: fit to data, number and biological values of the fitted coefficients, number of measurable parameters, and the accuracy in the estimation of the thresholds (Medeiros et al. 2003, 2004, Kontodimas et al. 2004, Walgama and Zalucki 2006).

[1] Corresponding author, e-mail: matilda@agro.auth.gr.

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In most natural environments, temperature usually undergoes regular diurnal variation, frequently superimposed by irregular fluctuations. Under natural conditions, insects are exposed to daily cycles of temperature (thermoperiods) whose influence on development may be different from that of exposure to constant temperatures (Beck 1983). Discrepancies are common between developmental times predicted from constant development–temperature relationships and those measured under natural fluctuating or alternating temperatures around the same mean. Ratte (1985) summarized these studies and, in a simulation experiment using a nonlinear rate–temperature relationship, showed that developmental rates under fluctuating temperatures will be slower at higher and faster at lower temperatures than at the mean constant temperature (rate summing effect). Furthermore, it is not clear how the actual and potential changes in the world's weather patterns have, or will, affect insect population dynamics and other ecological processes (Drake 2005, King 2005). Global warming may affect insect populations in different ways: by altering developmental times, equilibrium population densities, geographical distributions, and insect–plant interactions (Speight et al. 1999).

Alternating temperature regimes approach more realistically the variation existing in nature and produce higher parameter values than the optimal constant temperature (Welbers 1975, Behrens et al. 1983, Saffar et al. 1996, Vargas et al. 2000, Davis et al. 2006). However, alternating temperature produces not only specific accelerations but also retardations in the rate of development, and the intensity of this effect depends on the range of alternating temperature regimes (Eubank et al. 1973, Lamb and Gerber 1985, Petavy et al. 2001). According to Behrens et al. (1983), it is not the length of warm treatment alone, but the temperature change per se, that further intensifies the temperature-induced modifications in development. Finally, other results indicate that diurnally alternating temperatures have no effect on insect development (Hagstrum and Leach 1973, Humpesch 1982, Liu et al. 1995).

Several studies have been conducted on the effect of constant temperature on developmental time of *H. armigera* reared on host plant materials or artificial diet (Wilson et al. 1979, Qureshi et al. 1999, Jallow and Matsumura 2001, Liu et al. 2004), and Foley (1981) has studied pupal developmental rate under constant and fluctuating temperatures. However, the developmental rate for each life stage of this insect has not been studied under alternating temperature regimes, although such data are necessary to help explain population fluctuations under natural conditions.

The purpose of this study was to investigate the effects of constant and alternating temperatures on development and survival of the immature stages of *H. armigera*, as well as the effects of temperature on demographic parameters (e.g., adult survival, longevity, fecundity, and intrinsic rates of increase) in laboratory conditions. This information will lead to more appropriate phenological models for evaluation of pest management strategies and for population dynamics analysis, and it also may contribute to a better understanding of the effects of climate change on *H. armigera* phenology.

Materials and Methods

Insect Rearing. A laboratory colony of *H. armigera* was established in September 2003 from larvae collected from cotton fields in northern Greece (41° N, 023° E). The colony was reared on an artificial diet at 25°C and under a photoperiod of 16:8 (L:D) h. More than 400 larvae were used to establish the colony, and the offspring of the F_5 generation were used for the temperature experiments. The components of the diet were water (4 liters), agar (106 g), maize meal (760 g), brewer's yeast (200 g), wheat germ (184 g), ascorbic acid (28 g), benzoic acid (12 g), methyl *p*-hydroxybenzoate (9.2 g), Vanderzant's vitamin mixture for insects (0.2 g), and Wesson's salt mixture (30 g), prepared as described by Smith (1966).

Newly hatched larvae were reared in groups of 50–100 in 200-ml plastic cups provided with small cubes of artificial diet until the third instar, after which larvae were separated into individual 9-cm-diameter petri dishes to prevent cannibalism. The larvae completed their development in the petri dishes. On emergence, 10 pairs of adults were released in an wooden frame oviposition cage (30 by 30 cm) covered with a 30-mesh saran screen on three sides and a piece of glass on the fourth that served as a sliding door. Adults were provided with 10% sucrose solution on a cotton swab. Three to four pieces of thin paper napkin were hung inside the cage as an oviposition substrate. The napkins were removed from the cage daily and replaced with fresh napkins. Napkins removed from cages were cut into smaller pieces, and pieces containing eggs were transferred into petri dishes and covered. After hatching, the larvae were transferred to cups, described above, containing artificial diet.

Survival and Development of Immature Stages. Eggs laid on the same day (<24 h old) were kept in petri dishes in controlled environment chambers (Precision Scientific, General Electric, Louisville, KY, and GRW 1000SB CMP, E. Crisagis, Athens, Greece) and exposed to 11 different constant temperatures (12.5, 15, 17.5, 20, 25, 27.5, 30, 32.5, 35, 37.5, and 40°C) and to five alternating temperatures: thermocryophase (T:C) temperatures (mean values in parentheses) 25–10 (20), 30–15 (25), 32.5–17.5 (27.5), 35–20 (30), and 35–27.5 (32.5)°C. Relative humidity was >65%, and photoperiod was held constant at 16:8 (L:D) h. The number of eggs used to start each of the temperature treatments varied from 100 to 300 for most of the temperature treatments, whereas ≈1,000 eggs were used for temperatures >35°C.

The number of eggs hatched was recorded daily, except for the eggs held at the higher temperatures, which were examined every 12 h. Larvae hatched from each temperature treatment were used for the developmental studies at the respective temperatures. Newly hatched first-instar larvae were individually

Table 1. Survivorship (percentage) of immature stages of *H. armigera* reared under constant and alternating temperatures

Temperature (°C)	*n*	Egg stage	Larval instars					Larval stage	Pupal stage	Total[a]
			First	Second	Third	Fourth	Fifth			
12.5	220	36.33	—	—	—	—	—	—	—	—
15	158	43.66	89.85	96.77	86.67	84.61	81.82	46.38	—[b]	—
17.5	153	45.06	94.20	98.46	96.87	87.10	92.59	72.46	86.00	28.10
20	135	51.66	74.29	92.31	100.00	100.00	100.00	67.14	89.36	31.11
25	108	67.66	93.15	97.05	96.97	98.44	96.83	80.82	83.05	45.37
27.5	117	63.00	97.30	100.00	100.00	100.00	100.00	95.95	92.96	56.41
30	275	32.33	92.13	97.56	100.00	97.50	85.90	65.17	77.59	16.36
32.5	257	32.66	86.90	91.78	92.54	95.16	96.61	63.10	56.60	11.67
35	277	31.00	70.93	98.36	100.00	96.67	81.03	47.67	21.95	3.96
37.5	963	8.30	82.89	80.60	85.19	93.48	83.72	26.25	14.29	0.31
40	972	—	—	—	—	—	—	—	—	—
25–10	172	44.71	97.40	96.00	100.00	100.00	100.00	92.21	87.32	36.05
30–15	100	59.00	91.53	92.59	98.00	95.92	97.87	77.96	93.47	43.00
32.5–17.5	113	69.64	92.41	90.41	100.00	96.97	100.00	81.01	96.88	55.75
35–20	205	38.50	98.73	100.00	97.44	97.37	97.30	87.34	76.81	25.85
35–27.5	154	56.55	70.11	90.16	96.36	98.11	96.15	55.17	89.58	27.92
χ^2		553.825	91.566	47.825	57.940	42.463	66.833	178.683	186.185	649.219
P		0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
df		14	13	13	13	13	13	13	12	12

n, number of eggs used to start each of the temperature treatments.
[a] Total represents survivorship of immature stages from egg to adult emergence.
[b] Pupae exposed to 15°C entered diapause.

transferred from the petri dishes to 50-ml plastic cups and were provisioned with artificial diet. After the completion of the third instar, the larvae were transferred to petri dishes. Larvae were examined daily until pupation for molting and mortality. Larval instars were determined by checking the shed head capsules. Pupal weight was recorded on day 2 after pupation. On pupation, sex was determined and recorded. The number of emerged adults was recorded daily.

Adult Longevity and Reproduction. Adults emerged from the development study were used to estimate fecundity and adult longevity for each temperature treatment. On emergence (<24 h), pairs of adults were placed individually in transparent hard plastic truncated conical cups (400 ml) covered by a transparent piece of tulle. A hole punched in the bottom of each cup was plugged with a dental wick saturated with 10% sucrose solution as a food source. Adults were transferred to new cups daily until their death, and eggs laid each day were counted under a binocular stereoscope. Preoviposition period, oviposition period, and the number of eggs laid were determined. Because of high mortality at 35°C and diapause induction at 15°C (at pupal stage), pairs of newly emerged adults derived from the laboratory colony were used for mortality and fecundity studies at 35 and 15°C, respectively.

Statistical Analysis. The effect of temperature on developmental time and reproduction was determined by analysis of variance (ANOVA). A logarithmic transformation $\log_{10}(x + 1)$ of the data were used to avoid heterogeneity of variance: untransformed means are presented in the tables. Percentages were compared using the χ^2 test (Sokal and Rohlf 1995).

The relationship between temperature (T) and mean developmental rate (r = developmental time^{-1}) of each life stage and total immature stage (egg to adult) under constant and alternating temperature regimes was determined using linear and nonlinear models.

Linear Model. The relationship between T and r was determined using linear regression where $r = a + bT$. The lower developmental threshold (T_o) and the degree-days requirements (DD) were estimated as $T_o = -a/b$ and $DD = 1/b$, where a and b were estimated by least square regression. Regressions were conducted only for those temperature ranges in which developmental rate was linear with temperature. Calculations were performed with the statistical package STATISTICA (StatSoft 2001).

Nonlinear Model. The nonlinear empirical Logan model (Logan et al. 1976) as modified by Lactin et al. (1995) was used to describe the temperature-dependent developmental thresholds under constant and alternating regimes of each life stage and total immature stage (egg-adult). The expression of the model is as follows:

$$r(T) = e^{\rho T} - e^{\rho Tmax - (Tmax - T)/\Delta} + \lambda$$

where r(T) is the mean developmental rate at temperature T (°C). Fitted parameters, ρ (rate of increase at optimal temperature), T_{max} (upper developmental threshold), Δ (difference between optimal and upper developmental threshold), and λ (which allows the curve to intercept the x-axis, allowing the estimation of a developmental threshold), were estimated using the Marquardt algorithm in SPSS 14 (SPSS 2006).

Life Table Parameter Analysis. Life table studies were conducted for each temperature regimes as described by Carey (1993). Immature-stage survival data were obtained from the experiment described above. A sex ratio of 1:1 females/males (Reed 1965) was used for the development of the life table parameters. The following parameters were calculated: $R_o = \Sigma Lx_i mx_i$

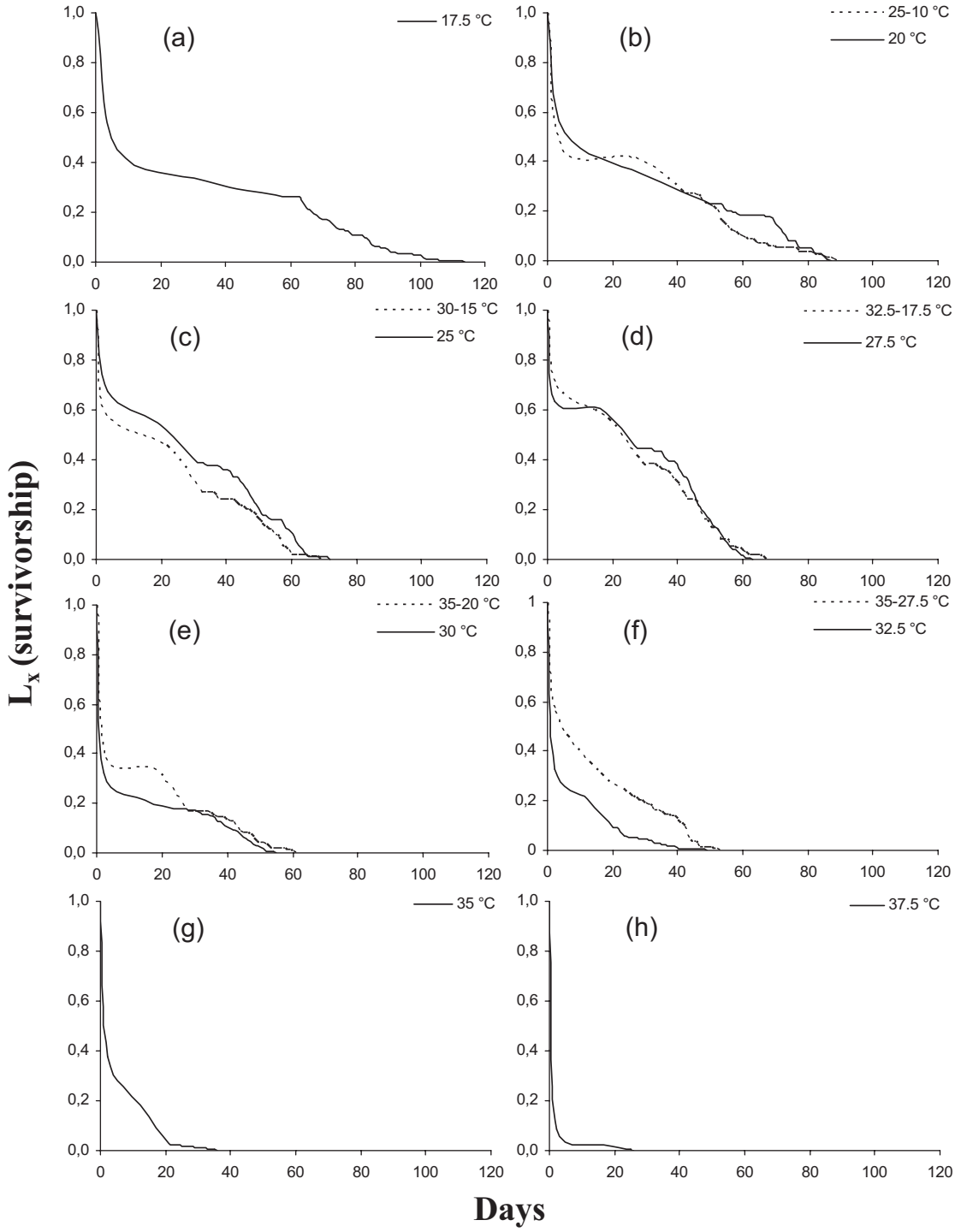

Fig. 1. Total survivorship (L_x) at constant (___) and corresponding alternating (- - - - - -) temperature regimes. The 12.5, 15, and 40°C are not represented because of the low number of values.

(net reproductive rate), $T = \Sigma x_i l x_i m x_i$ (mean generation time), $r = \ln R_o / T$ (intrinsic rate of increase), $\lambda =$ anti-lnr (finite rate of increase), $DT = \ln 2 / r$ (doubling time), where lx_i is the number of surviving insects at the beginning of age class x_i, Lx_i is the survivorship of age class x_i, and mx_i is the number of female offspring produced per female in each age class x_i. The average number of the offspring produced by each female in

Table 2. Mean developmental time (days ± SE) of immature stages and pupal weight (mg ± SE) of *H. armigera* reared under constant and alternating temperatures

Temperature (°C)	Egg stage	Larval instars					Larval stage	Pupal stage	Total[a]	Pupal weight
		First	Second	Third	Fourth	Fifth				
12.5	19.11 ± 0.20a	—	—	—	—	—	—	—	—	—
15	13.57 ± 0.09b	9.31 ± 0.29a	7.87 ± 0.12a	8.22 ± 0.19a	10.41 ± 0.72a	19.81 ± 1.67a	68.00 ± 2.04a	—	—	273.9 ± 11.9abc
17.5	6.60 ± 0.04c	4.30 ± 0.09b	3.14 ± 0.07b	3.84 ± 0.18b	5.14 ± 0.24b	10.74 ± 0.27b	27.30 ± 0.38b	23.81 ± 0.27a	57.18 ± 0.33a	245.6 ± 4.1cd
20	5.12 ± 0.02d	4.17 ± 0.06b	3.06 ± 0.06b	2.98 ± 0.06c	4.06 ± 0.10b	8.60 ± 0.32b	23.87 ± 0.47c	20.80 ± 0.25b	49.56 ± 0.52b	242.3 ± 4.6cd
25	3.31 ± 0.02f	3.27 ± 0.11c	1.91 ± 0.09de	2.03 ± 0.06def	2.31 ± 0.16de	5.18 ± 0.21c	15.52 ± 0.26e	12.35 ± 0.17d	30.77 ± 0.30de	310.5 ± 5.6a
27.5	2.40 ± 0.02i	2,56 ± 0.10d	1.91 ± 0.05d	2.03 ± 0.07def	3.53 ± 0.31c	5.06 ± 0.09c	13.78 ± 0.20fg	11.29 ± 0.10de	27.41 ± 0.23f	279.1 ± 4.4abc
30	2.10 ± 0.01j	2.22 ± 0.07de	1.60 ± 0.07ef	1.69 ± 0.10fg	3.03 ± 0.26cde	4.00 ± 0.23cd	12.58 ± 0.25g	9.07 ± 0.12f	23.41 ± 0.31g	276.1 ± 5.7abc
32.5	2.01 ± 0.01k	2.04 ± 0.04e	1.21 ± 0.06g	1.57 ± 0.07g	2.55 ± 0.20cde	3.37 ± 0.13d	10.24 ± 0.21i	8.63 ± 0.14f	20.91 ± 0.34h	288.3 ± 7.8ab
35	2.04 ± 0.02jk	2.00 ± 0.00e	1.02 ± 0.02g	1.12 ± 0.10h	2.49 ± 0.29e	4.51 ± 0.15cd	10.36 ± 0.14i	8.56 ± 0.29f	21.11 ± 0.33h	288.7 ± 5.8ab
37.5	2.11 ± 0.03j	2.01 ± 0.07e	1.19 ± 0.09g	1.76 ± 0.15efg	3.05 ± 0.54cde	3.75 ± 0.49d	14.52 ± 0.76ef	8.33 ± 0.67f	22.44 ± 0.88gh	188.4 ± 19.5e
40	—	—	—	—	—	—	—	—	—	—
25–10	4.19 ± 0.02e	3.16 ± 0.05c	3.16 ± 0.10b	3.33 ± 0.09bc	3.03 ± 0.10cd	5.03 ± 0.37cd	22.70 ± 0.28c	15.64 ± 0.15c	42.43 ± 0.34c	308.8 ± 3.6a
30–15	2.74 ± 0.02g	3.05 ± 0.04c	2.17 ± 0.08cd	2.21 ± 0.06d	2.27 ± 0.07cde	4.31 ± 0.30cd	18.74 ± 0.48d	10.85 ± 0.22e	32.37 ± 0.72d	291.2 ± 8.3ab
32.5–17.5	2.55 ± 0.01h	3.30 ± 0.10c	1.98 ± 0.06d	2.09 ± 0.08de	2.33 ± 0.07cde	3.72 ± 0.22d	15.98 ± 0.28e	11.00 ± 0.11e	29.45 ± 0.31e	281.1 ± 4.3abc
35–20	2.57 ± 0.01h	2.15 ± 0.06e	2.48 ± 0.09c	2.34 ± 0.13d	2.78 ± 0.19cde	4.41 ± 0.19cd	14.91 ± 0.27ef	10.51 ± 0.13e	27.76 ± 0.33f	273.2 ± 4.4abc
35–27.5	2.08 ± 0.01jk	2.13 ± 0.08e	1.53 ± 0.07f	2.19 ± 0.18def	3.30 ± 0.32cde	4.64 ± 0.27cd	13.53 ± 0.36fg	8.79 ± 0.13f	24.43 ± 0.41g	259.6 ± 6.9bcd
F	12684.953	250.475	176.542	109.567	40.051	58.831	624.792	592.718	620.402	17.555
df	14, 1186	13, 724	13, 724	13, 724	13, 724	13, 646	13, 726	12, 522	12, 522	13, 549
P	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

Means within a column followed by the same letter are not significantly different ($P < 0.05$, Tukey HSD test).
[a] Total represents mean developmental time of immature stages from egg to adult emergence.

Table 3. Linear regression model parameters and R^2 values for temperature-dependent developmental rates of *H. armigera* immature stages

Stage	Temperature	Parameter estimates				
		b ± SE	a ± SE	T_o	DD	R^2
Egg	Constant	0.0252 ± 0.0013	−0.3013 ± 0.0341	11.95	39.68	0.985
	Alternating	0.0174 ± 0.0029	−0.0963 ± 0.0808	5.53	57.47	0.920
Larva	Constant	0.0042 ± 0.0010	−0.0442 ± 0.0067	10.52	238.09	0.980
	Alternating	0.0024 ± 0.0001	−0.0052 ± 0.0040	2.17	416.16	0.988
Pupa	Constant	0.0052 ± 0.0003	−0.0529 ± 0.0086	10.17	192.30	0.984
	Alternating	0.0035 ± 0.0006	−0.0037 ± 0.0186	1.06	285.71	0.898
Total[a]	Constant	0.0021 ± 0.0001	−0.0201 ± 0.0019	9.57	476.19	0.995
	Alternating	0.0013 ± 0.0001	−0.0029 ± 0.0025	2.23	769.23	0.985

a, intercept; b, slope; T_o, lower developmental threshold in °C; DD, cumulative degree-days required for stage development.
[a] Total represents the development of immature stages from egg to adult emergence.

the interval x to x + 1 (gross fecundity rate, M_x), was recorded until death.

Results

Survival and Development of Immature Stages. *Helicoverpa armigera* achieved complete development from egg to adult emergence between 17.5 and 37.5°C constant temperatures and at all alternating temperature regimes examined (Table 1). At a constant temperature of 37.5°C, only 3 of 21 pupae emerged to adults. At 12.5°C, 36% of eggs hatched successfully but all newly hatched larvae died; at 40°C, no eggs hatched. At 15°C, the insects entered diapause at the pupal stage. Lower constant temperatures (17.5, 20°C) caused less mortality than higher constant temperatures (35, 37.5°C).

The survival rates of the total immature stage (egg to adult emergence) differed slightly between constant and corresponding alternating temperature regimes at the low and moderate temperatures (20–27.5°C). However, at higher mean temperatures (30 and 32.5°C), alternating conditions were more favorable than constant ones for survival (Table 1). Survival of the immature stages was significantly different among the temperature regimes (Table 1).

Alternating temperatures enhanced age-specific survivorship at the lowest and highest temperature regimes (Fig. 1, b, e, and f). Mortality rates remained approximately constant with age (type II curve) for constant and alternating temperature regimes within a range of 17.5–27.5°C (Fig. 1, a–d). Under constant and corresponding alternating temperature regimes, survivorship increased to a maximum at 27.5°C and decreased as temperature increased (Fig. 1d). At higher temperature regimes, the shape of the age-specific survivorship curve changes progressively to type III. This indicates that, above 30°C, the death rate for *H. armigera* increased with most of the mortality occurring in early stages.

At constant temperature regimes, the developmental times of *H. armigera* decreased as temperature increased up to 32.5°C in the egg and larval stage, whereas in the pupal stage, the developmental rate became proportional to temperature (Table 2). For all alternating temperature regimes, the developmental stage duration varied inversely with temperature. The total developmental time of immature stages was significantly longer at constant 20°C and significantly shorter at constant 27.5, 30, and 32.5°C temperatures than at alternating temperatures with similar means (Table 2). At 25°C, developmental times were not significantly different between constant and corresponding alternating temperature regimes. Pupae exposed to 15°C entered diapause and were therefore not included in the analyses. Pupal stage duration was longer at constant 20 and 25°C than at alternating 25–10 and 30–15°C, respectively, whereas the opposite was observed at mean of 30°C. The highest mean pupal weight was observed at 25 and 25–10°C (≈300 mg), whereas at 37.5°C, the pupal weight was just over one half this value (≈180 mg). Except for insects reared at a mean of 20°C, there were no significant differences in pupal weight of insects reared at constant and the corresponding alternating temperature regimes (Table 2).

Modeling Developmental Rates. Based on these results, the lowest threshold and degree-day requirement for the development of each immature life stage of *H. armigera* were estimated by the linear model (Table 3). The ranges of constant temperatures used in the regression analysis were 12.5–30, 15–32.5, and 17.5–32.5°C for egg, larval, and pupal stages, respectively. All alternating temperature regimes were used in the estimations. Higher coefficients of determination (R^2) were obtained for each immature stage and for the total immature stage (egg to adult emergence) at constant than at alternating temperature regimes except for the larval stage (Table 3). The lowest developmental thresholds (T_o) of the various stages ranged from 10.17 to 11.95°C at constant temperature regimes and from 1.1 to 5.5°C at alternating ones. The T_o for development from egg to adult at constant and alternating temperature regimes was 9.6 and 2.2°C, respectively. Lower developmental thresholds were observed when the insects were exposed to alternating compared with constant temperatures, whereas the opposite was observed for the degree-days for each life stage and for development from egg to adult (Table 3).

The nonlinear Lactin-2 model, when fitted to developmental rate values, gave a good fit to the data sets

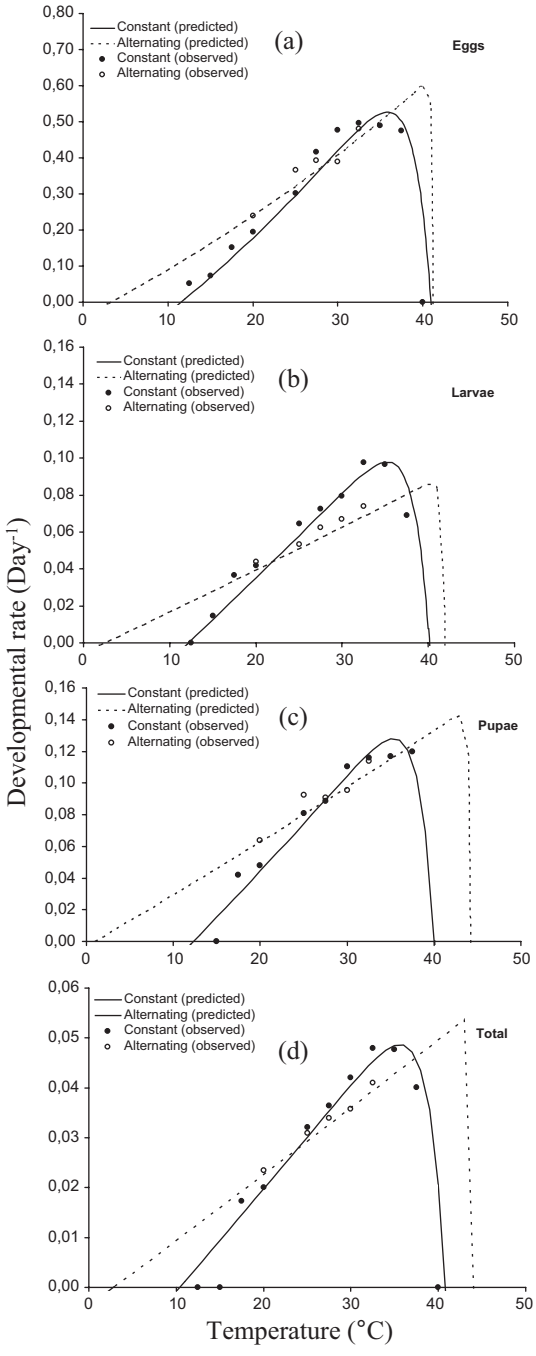

Fig. 2. Developmental rate (day^{-1}) of (a) egg stage, (b) larval stage, (c) pupal stage, and (d) total immature stage (egg stage up to adult) of *H. armigera* as a function of constant (●) and alternating (○) temperature (°C). Fitted curves according to Lactin et al. (1995).

over the range of temperature used (Fig. 2; Table 4). Observed developmental rate values for constant and alternating temperature regimes were compared with predicted values from the Lactin-2 model for egg, larval, pupal, and total immature (egg to adult) stages (Fig. 2). In the range of 20–32.5°C, the responses obtained were approximately linear for all developmental stages. The resulting coefficients of determination ranged between 0.90 and 0.99 and were higher at constant than at alternating temperatures except for the larval stage (Table 4). Lower values of developmental thresholds were estimated by the Lactin-2 model than by the linear model for constant and alternating temperature regimes, except for the larval and pupal stages at constant temperatures (Tables 3 and 4). The optimal developmental temperatures estimated for egg, larval, pupal, and total immature (egg to adult) stages were 34.84, 34.22, 35.37, and 34.61 under constant and 39.26, 39.35, 41.92, and 42.35°C under alternating temperature regimes (Table 4). Above the optimal temperature, developmental rate decreased. The upper developmental thresholds (t_{max}) for each immature stage and for the total immature (egg to adult) stage were estimated between 39.11 and 43.54°C, with higher values at alternating than at constant temperature regimes (Fig. 2; Table 4). However, the range from the optimal temperature to the upper developmental threshold was greater at constant (≈5°C) than at alternating temperature (≈1°C; Table 4).

Adult Longevity and Reproduction. The average life span of adult *H. armigera* at constant and alternating temperature regimes fluctuated from 7.65 to 34.40 d at the highest and lowest temperature, respectively (Table 5). Adult longevity of both sexes did not differ significantly between constant and alternating temperatures with similar means, except for 35–27.5°C, where the mean female adult life span was significantly shorter than that at a constant 32.5°C (Table 6). However, constant and alternating temperatures produced different average adult life spans; male life spans are longer at constant, but shorter at alternating, temperature regimes than females.

Fecundity varied significantly with temperature at constant but not at alternating temperature regimes, except for 35–27.5°C (Table 5). However, it should be noted that fecundity at alternating temperature regimes was, in most cases, higher than that at the corresponding constant temperature regime, although the differences were not significant (Table 5). The duration of the preoviposition period of *H. armigera* was also affected by temperature. It was the highest at 15°C and lowest at 35–20°C. The number of eggs laid per female per day (M_x) was approximately similar at 25 and 27.5°C, at both constant and alternating temperature regimes (Fig. 3, d and e). However, at means of 20, 30, and 32.5°C, females laid more eggs at alternating than at constant temperature regimes. The M_x decreased at low and high constant temperatures (Fig. 3).

Life Table Parameters. The estimated life table parameters for *H. armigera* for the constant and alternating temperature regimes are presented in Table 6. The intrinsic (r) and finite (λ) rates of increase were highest for both constant and alternating temperature regimes at 27.5°C. The highest net reproductive rate was at 25 and at 32.5–17.5°C. Increasing temperature

Table 4. Nonlinear (Lactin et al. 1995) model parameters ± SE and R^2 values for temperature-dependent developmental rates of *H. armigera* immature stages

Stage	Temperature	Parameter estimates							
		ρ	T_{max}	Δ	λ	R^2	t_{min}	t_{opt}	t_{max}
Egg	Constant	0.0165 ± 0.0007	42.024 ± 0.2909	2.0503 ± 0.0271	−1.1906 ± 0.0271	0.987	10.58	34.84	39.99
	Alternating	0.0125 ± 0.0028	40.8390 ± 0.0000	0.2781 ± 0.0000	−1.0295 ± 0.1108	0.916	2.33	39.26	40.56
Larva	Constant	0.0042 ± 0.0003	43.1521 ± 2.1172	1.8197 ± 0.7098	−1.048 ± 0.0068	0.983	11.17	34.22	39.11
	Alternating	0.0022 ± 0.0003	41.8090 ± 0.0065	0.3410 ± 0.0000	−1.0034 ± 0.0002	0.989	1.55	39.35	40.95
Pupa	Constant	0.0053 ± 0.0004	43.3886 ± 0.7293	1.6854 ± 0.3733	−1.0674 ± 0.0107	0.974	12.31	35.37	40.00
	Alternating	0.0032 ± 0.0010	44.2448 ± 0.0000	0.3409 ± 0.0000	−1.0000 ± 0.0301	0.897	1.01	[illegible]	43.54
Total[a]	Constant	0.0020 ± 0.0001	45.1604 ± 2.0243	1.8842 ± 0.5243	−1.0197 ± 0.0028	0.994	9.42	[illegible]	39.81
	Alternating	0.0012 ± 0.0000	43.2127 ± 0.0043	0.0957 ± 0.0000	−1.0023 ± 0.0001	0.985	1.85	42.35	42.92

ρ, rate of increase to optimum temperature; T_{max}, lethal temperature; Δ, difference between the lethal temperature and the optimum temperature of development; λ, parameter that makes the curve intersept the x-axis; t_{min}, t_{opt}, and t_{max}, lower, optimum, and maximum developmental threshold in degrees Celsius.

[a] Total represents the development of immature stages from egg to adult emergence.

resulted in shorter mean generation times for both constant and alternating temperature regimes. The longest population doubling time occurred at alternating 25–10°C and at constant 17.5°C. Life table parameters of *H. armigera* were more favorable for alternating temperatures than for corresponding constant ones in the upper and lower temperature boundaries.

Discussion

A comparative analysis of survival and development rates at all life history stages of *H. armigera* reared under constant and corresponding alternating temperatures regimes is presented in this study.

High alternating temperature regimes increased total survival rate in relation to mean constant high temperature of 30 and 32.5°C. Over a wide constant thermal range, 15–27.5°C, total survival is stable and apparently not affected by temperature. Below 15°C, survival decreased rapidly, reaching zero at 12.5°C. At warmer temperatures, survival also decreased very quickly above 28°C and fell to zero at 40°C. Dhileepan et al. (2005) found that the survival rate of *Aconophora compressa* (Walker) at alternating temperatures was higher than that at constant temperatures, but the general trend of lower survival at higher temperatures was similar to that found in our study. Our results show that *H. armigera*, when reared at constant temperatures, could not develop from egg to adult emergence (capable of egg production) out of the temperature range of 17.5–32.5°C. Nevertheless, alternating temperatures allowed *H. armigera* to complete its life cycle over a much wider range, 10–35°C, than did constant temperatures. Calculations by Richards and Suanraksa (1962) showed that the energy expenditure for embryonic development at alternating temperature regimes was less than that needed at corresponding constant temperatures. They also showed that the energy reserves were sufficient for considerable periods below the constant temperature threshold, provided that enough time was spent at much higher temperatures. Howe (1967) noted that outside the survival range, the effects of temperature on survival

Table 5. Reproductive parameters and longevity expectation of *H. armigera* at constant and alternating temperatures and results of ANOVA

Temperature (°C)	Longevity (d)		Fecundity (eggs/♀)	Averague eggs/d	Preoviposition period (d)	Oviposition period (d)
	♂♂	♀♀				
15[a]	34.40 ± 7.28dA	25.20 ± 3.26dA	101.90 ± 36.76bc	4.04 ± 0.41e	9.60 ± 1.61a	13.50 ± 2.27abc
17.5	26.00 ± 3.42cdA	16.55 ± 1.91cdB	309.15 ± 60.95bc	18.40 ± 1.70cde	4.74 ± 0.34b	12.11 ± 1.78abc
20	23.68 ± 2.05cdA	20.47 ± 2.88cdA	433.93 ± 127.37abc	21.20 ± 2.31cde	3.00 ± 0.34bc	12.85 ± 2.20abc
25	23.11 ± 2.07bcdA	20.44 ± 2.17cdA	1007.69 ± 250.73a	49.31 ± 4.62a	1.57 ± 0.17cd	14.50 ± 2.10ab
27.5	21.06 ± 1.29bcdA	17.53 ± 1.46cdA	794.79 ± 103.24ab	43.52 ± 3.14ab	1.95 ± 0.19cd	13.16 ± 1.25abc
30	19.52 ± 1.30bcdA	16.75 ± 1.25cdA	695.80 ± 125.47abc	41.29 ± 3.43ab	1.22 ± 0.21cd	11.33 ± 1.19abc
32.5	13.54 ± 2.21abA	6.91 ± 1.98aB	140.09 ± 47.54bc	20.01 ± 3.43cde	1.71 ± 0.94cd	6.86 ± 2.10bc
35[a]	9.75 ± 1.24aA	7.65 ± 0.78abA	92.15 ± 28.21c	12.25 ± 1.98de	2.00 ± 0.37cd	4.71 ± 0.70c
25–10	15.95 ± 2.13abcA	19.76 ± 2.83cdA	659.44 ± 165.69abc	33.51 ± 3.51abc	2.21 ± 0.19cd	15.83 ± 2.65ab
30–15	17.54 ± 1.86abcdA	22.21 ± 2.43cdA	930.50 ± 175.20a	42.02 ± 3.64ab	1.36 ± 0.13cd	17.86 ± 2.06a
32.5–17.5	16.58 ± 2.02abcA	19.29 ± 1.59cdA	915.48 ± 147.33a	47.85 ± 4.35a	0.80 ± 0.12d	13.75 ± 1.10abc
35–20	17.69 ± 2.09bcdA	18.76 ± 1.39cdA	968.90 ± 178.90a	51.64 ± 4.51a	0.61 ± 0.14d	14.06 ± 1.35ab
35–27.5	14.12 ± 1.70abcA	14.11 ± 1.73bcA	369.44 ± 102.02bc	26.18 ± 2.15bcd	0.91 ± 0.25d	15.00 ± 1.68ab
F	5.765	7.709	5.336	2.763	29.505	3.274
df	12, 239	12, 220	12, 220	12, 220	12, 220	12, 220
P	0.000	0.000	0.000	0.000	0.000	0.000

Means within a column followed by the same letter (lowercase) are not significantly different ($P < 0.05$, Tukey HSD test).
Means between sexes in a particular temperature followed by the same letter (uppercase) are not significantly different ($P < 0.05$, *t*-test).
[a] Adults were reared at 25°C.

Table 6. Summary of life table parameters of *H. armigera* at constant and alternating temperatures

Parameter	Temperature (°C)											
	Constant							Alternating				
	17.5	20	25	27.5	30	32.5	35	25–10	30–15	32.5–17.5	35–20	35–27.5
Net reproductive rate (R_o)	48.58	56.02	203.14	185.93	63.13	10.54	9.37	91.40	122.78	170.70	80.09	44.17
Mean generation time (T)	64.06	60.11	40.56	35.31	32.17	32.28	27.53	53.01	41.04	36.96	37.17	32.99
Intrinsic rate of increase (r)	0.06	0.07	0.13	0.15	0.13	0.07	0.08	0.09	0.12	0.14	0.12	0.12
Finite rate of increase (λ)	1.06	1.07	1.14	1.16	1.14	1.08	1.08	1.09	1.12	1.15	1.13	1.12
Doubling time (DT)	11.44	10.36	5.29	4.69	5.38	9.51	8.53	8.15	5.91	4.99	5.88	6.04

and development were confounded with time of exposure. Bursell (1964) claims that a process of physiological acclimation may take place when the insects are exposed to sublethal temperatures before they are exposed to critical ones. This process enables the insects to survive at critical temperatures. The cumulative effects of these processes, especially in temperate regions like Greece, may well raise the mortality thresholds by a degree or more, which must be taken into account when applying laboratory data to field conditions.

Insects have frequently been shown to develop more rapidly at fluctuating than at constant temperatures when the maximum and minimum of the fluctuating temperature are within the optimal range of development for the organism (Hagstrum and Hagstrum 1970). Foley (1981) found faster development of *H. armigera* pupae at fluctuating temperatures with a mean of 24°C than at the corresponding constant temperature. Our data showed that the developmental times of the entire immature stage of *H. armigera* at constant temperatures tended to be shorter above 25°C and longer below this temperature than at alternating temperature regimes with the same means. In the same way, other authors (Behrens et al. 1983, Lamb and Gerber 1985, Roltsch et al. 1990, Hagstrum and Milliken 1991, Petavy et al. 2001, Fantinou et al. 2003) have confirmed this acceleration in developmental time at low to moderate fluctuating temperature regimes relative to corresponding constant temperature. These differences in developmental time also tended to increase with the amplitude of fluctuating temperature. The acceleration of development at fluctuating temperature below developmental threshold is most likely because different components (e.g., enzymes) of the development sequence have different temperature coefficients (Rock 1985). A thermoperiodic regime might satisfy all of the rate limiting conditions, whereas a relatively low constant temperature would not (Sharpe and DeMichele 1977, Beck 1983b). Another aspect for consideration regarding the acceleration of development is the thermal units accumulated when the cryophase of the thermoperiod is below developmental threshold compared with the thermal units accumulated at constant low temperature (Yeargan 1980).

Results obtained from constant temperature experiments are often not applicable directly to the field (Lamb 1961), where animals are subjected to diurnal variation in temperature. Fluctuating temperatures are normal for many species: they show differing abilities to withstand constant temperature because the thermal optimum in fluctuating temperature may differ from the constant temperature optimum (Cloudsley-Thompson 1953). Moreover, constant temperature studies underestimated thresholds, whereas fluctuating temperatures widened threshold limits (Messenger 1964).

When temperature goes beyond the optimal, degree-day models cannot be applied, and are, in fact, unsuitable for predicting insect development (Davis et al. 2006). Similarly, our results from the constant temperature developmental model failed to predict development under alternating temperature regimes. Lower developmental thresholds were estimated, for both linear and Lactin-2 models, when the insects were exposed to alternating compared with constant temperatures (Tables 4 and 5). Insect response to variable temperatures, whether linear or nonlinear, can explain the shift in thresholds often observed for insect development. For example, Behrens et al. (1983) found that alternating temperatures with an amplitude of 12°C reduced the temperature threshold for embryonic development of the cricket, *Gryllus bimaculatus* (De Geer), from 16.6°C at constant temperatures to 11.8°C. Similarly, Fantinou et al. (2003) estimated lower developmental thresholds of the various stages of the corn borer, *Sesamia nonagrioides* (Lefebvre), when the insects were exposed to alternating temperature (threshold range: 6.2–7.2°C) than when they were exposed to constant temperature (threshold range: 8.9–10.8°C). Worner (1992) suggested that disparate results between observed development and those predicted by the model could be the results of an inadequate model, an unknown physiological mechanism, or both.

The data from our study fit the linear and Lactin-2 models very well as indicated by the high R^2 values, both at constant and alternating temperatures. The estimate of the λ value for all cases was <0, indicating that a developmental threshold can be estimated by the Lactin-2 model (Lactin et al. 1995). The Lactin-2 model estimated lower developmental threshold values for the egg, larval, and total immature stages very similar to those estimated by the linear model. Estimates of the lower developmental threshold for the pupal stage, however, differed between the two models. Roltsch et al. (1990) claimed that the error involved in nonlinear, temperature-dependent developmental models may relate to the critical assumption

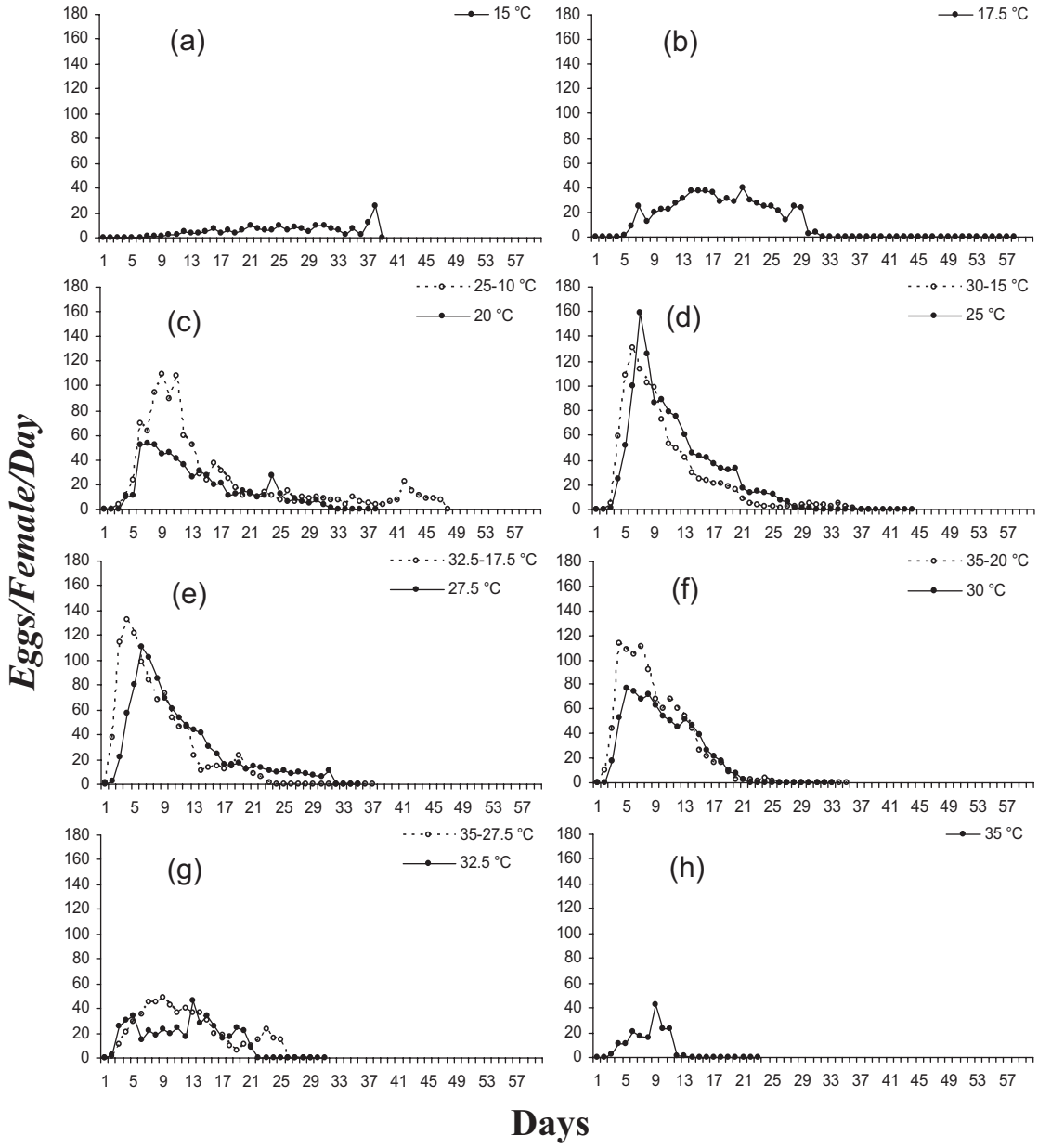

Fig. 3. Number of eggs per female per day (M_X) under constant (_●_) and corresponding alternating (···○···) temperatures regimes. Values at 15 and 35°C are from adults derived from a laboratory colony reared at 25°C. See text for details.

that enzyme systems respond almost instantaneously to temperature changes. The estimated lethal thresholds seemed to be close to the high temperatures tested, at which high mortality rates were observed.

The developmental threshold for total larval development estimated by the linear model (≈11°C) was similar to those reported by many authors (Twine 1978, Qureshi et al. 1999, Jallow and Matsumura 2001, Bartekova and Praslicka 2006) for laboratory insect strains reared on artificial diet or plant material. Kay (1981), incubated eggs of *H. armigera* under constant temperatures (range, 8.0–39.4°C) and found a developmental threshold of 11.7°C, which is similar to the egg developmental threshold (11.9°C) found in our study. However, Bartekova and Praslicka (2006) in Slovakia determined a higher egg developmental threshold of 14.8°C. In another study of constant temperatures on the development of *H. armigera* in Australia, Foley (1981) reported higher developmental thresholds (14.8°C) for nondiapausing pupae and a thermal constant of 160 DD, which is considerably less than the 200 and 211 DD determined by Wilson et al. (1979) and Twine (1978), respectively, and the 192 DD from our study. Furthermore, higher devel-

opmental thresholds for pupal stage were reported for the Chinese and Australian populations (≈14°C) (Qureshi et al. 1999, Jallow and Matsumura 2001) than for the Greek (10.17°C) and Slovakian (8.2°C) populations (Bartekova and Praslicka 2006). Differences between the results obtained in this study and those of other studies could be attributed to the different origin of *H. armigera*, i.e., strain, host and geographical region, as well as to the different experimental conditions, i.e., rearing techniques. Populations from different geographical regions may differ in various reproductive and life history aspects (Vargas and Carey 1989, Papadopoulos et al. 2002).

Fecundity and adult longevity in *Heliothis* species are influenced by temperature, humidity, and larval and adult nutrition (Liu at al. 2004, Adjei-Maafo and Wilson 1983, Nadgauda and Pitre 1983). Also, Zhou et al. (2000) found that the temperature and photoperiod conditions during larval and pupal development significantly affect adult reproductive physiology of *H. armigera.* The capacity of *H. armigera* to produce eggs, as measured by mean total fecundity of adults, reflects a response pattern similar to that of other studies with *Heliothis* spp. at constant temperature in that prolonged exposure of immature stages to temperature >35°C reduces adult survival, fecundity, and egg hatchability (Twine 1978, Henneberry and Butler 1986). In our results, females laid more eggs when entire immature stages were exposed to alternating temperature regimes with means between 20 and 32.5°C than when entire immature stages were subjected to even the most favorable constant temperature conditions, with the exception of 25°C. The optimum temperature, on the basis of fecundity, was apparently 25°C. However, preoviposition period and reproductive values at these alternating temperature regimes were more favorable than those at constant temperatures (Table 5). In the same way, Davis et al. (2006) found that the green peach aphid developed faster and had greater fecundity under fluctuating conditions. Fluctuation between high and low temperatures may provide recovery time or permit adaptations that result in higher survival and fecundity at extreme warm or cold constant temperature conditions (Vargas et al. 2000, Fantinou et al. 2003, Davis et al. 2006). In our study, as temperature increases, the duration of adult life span gradually decreases, reaching the minimum at the highest constant temperature examined; yet, the life span of adults tended to be independent of the pattern of alternating temperature changes to which immature stages were exposed in our experiments (Table 5).

The intrinsic rate of population increase, computed from life table data, is a good bioclimatic index, in that it reflects the joint influence of temperature on development, reproduction, and survival characteristics of a population (Messenger 1964). Alternating temperatures result in higher r values than do constant temperatures, because of shorter mean generation time and higher oviposition and reproduction (Kieckhefer and Elliott 1989). In our results, this index is positive at both constant (0.15) and corresponding alternating (0.14) temperature regimes, meaning that *H. armigera* could be expected to persist or increase in number between 17.5 and 35°C, with a maximum value at 27.5°C (Table 6). This high r value at this alternating temperature regime could be attributed to the considerably higher net reproductive rate per female (R_o = 170.70). Moreover, Kersting et al. (1999) established that the population of cotton aphid, *Aphis gossypii* Glover, which was kept at constant 30°C, had the highest r value among all temperatures tested but did not differ significantly from that at 25–30°C. In contrast, Vargas et al. (2000) found higher intrinsic rates of population increase at 29–18°C alternating temperature regimes than at a constant 24°C for three Hawaiian fruit fly species (Diptera: Tephritidae).

This study suggests that demographic parameters for climatic simulations differ when measured at constant or alternating temperatures. In addition, such alternating temperature conditions allow *H. armigera* to complete its life cycle over a much wider range of temperature levels than do constant conditions. Such general findings are quite important when attempts are made to evaluate geographic distribution or development, reproduction, and longevity in the field. Nevertheless, results, when based on constant or alternating simulations, need to be validated under field conditions.

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Development, survivorship and reproduction of Helicoverpa armigera (Lepidoptera: Noctuidae) under fluctuating temperatures

Mironidis, George K.

01 P Huxley Page 1

26/5/2021 9:44

02 P Huxley Page 6

26/5/2021 9:47

03 P Huxley Page 8

26/5/2021 9:53