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The Significance and Thermodynamics of Fluctuating Versus Static Thermal Environments on *Heliothis zea* Egg Development Rates[1]

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ABSTRACT

Egg development of *Heliothis zea* (Boddie) was studied under various static and fluctuating environmental regimes. Two computer-controlled environmental chambers were programmed to fluctuate temperatures through diurnal sinusoids of ±5°F (2.8°C) to ±20°F (11.1°C) using the same mean temperatures as regimes in statically controlled environmental chambers.

The heat-units concept of development proved not to apply to bollworm egg development. In its stead, a hypothesis is formulated based on the egg-development curve measured in static thermal conditions.

Entomological literature abounds with confusing and conflicting reports regarding the effects of fluctuating temperatures on insect development. Some indicate that fluctuating temperatures have no effect on insect development, while others report that development can be either speeded up or retarded, depending upon the insect species. For example, Hagstrum and Hagstrum (1970) reported that 26 different species displayed distinct increases in developmental rates when exposed to various fluctuating environments. On the other hand, Morris and Fulton (1970) found no evidence that fluctuating conditions within the normal temperature ranges significantly affected rate of development of *Hyphantria cunea* (Drury).

The purpose of this research was to analyze critically the developmental differences exhibited by bollworm eggs under static and fluctuating environmental regimes and to clarify the reason for insect development being advanced, retarded, or remaining unchanged when temperatures are fluctuated.

Methods and Materials

Cotton bollworm eggs were used for the environmental simulation studies. The parent colony was maintained at 77–83°F (25–28.3°C), 86–94% RH and a photoperiod of 14L (light)/10D (dark). Supplemental continuous low-intensity light (a 15-w, 2-ft long daylight fluorescent tube loosely wrapped in aluminum foil that produced less than .01 μW-cm^{-2} throughout the colony room) was used to simulate starlight. Eggs were obtained from cultures of 1000–1500 adults kept in 73.50-cm cubical aluminum cages. Three sides of each cage had removable frames covered with 0.31-cm nylon mesh, which served as egg-deposition surfaces. All eggs used were deposited during 4-h periods.

Four environmental chambers (Atmar and Ellington 1972) were used for egg incubation. Two of these were incorporated into a direct-digital chamber-control system designed around a Hewlett-Packard® 9100A digital calculator/computer and a Hewlett-Packard 9101A memory extender so that environmental subroutines could be programmed into the computer (Atmar and Ellington 1973). Records of the environment within the chambers were obtained with a Bendix-Hygrothermograph® calibrated with a Psychrometer[3] possessing a certified accuracy to meet or exceed ±0.2°F (±0.11°C) and ±1% indicated relative humidity traceable to the National Bureau of Standards.

Initial experiments involved incubating newly collected eggs in petri dishes and hand counting the young larvae hourly as they emerged. These experiments were replicated 2–5 times at each temperature.

An automatic larval collecting device was developed (Fig. 1) based on the behavorial characteristic of negative geotropism in newly emerged bollworms. Small egg pad segments were placed in 9.5×2.5-cm glass vials, covered with inverted plastic funnels. The long shank of each funnel was heated and bent

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[3] Psychrometer, Model 4A-1, Thunder Scientific Corp., Albuquerque, N. Mex.

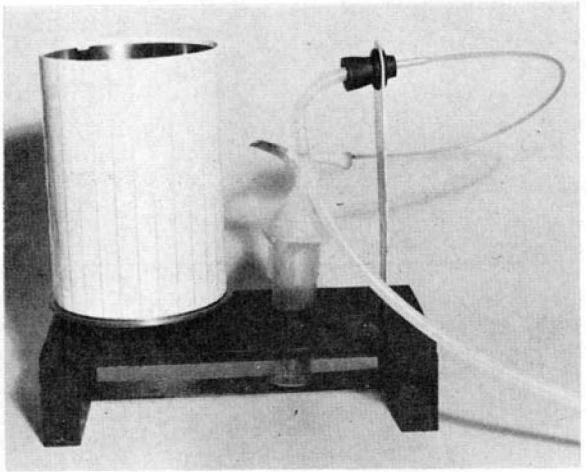

FIG. 1.—Automatic larval collector. Cotton bollworm eggs were placed in the vial. After they eclosed and migrated, the larvae were deposited on the chart of the clock mechanism by bursts of air.

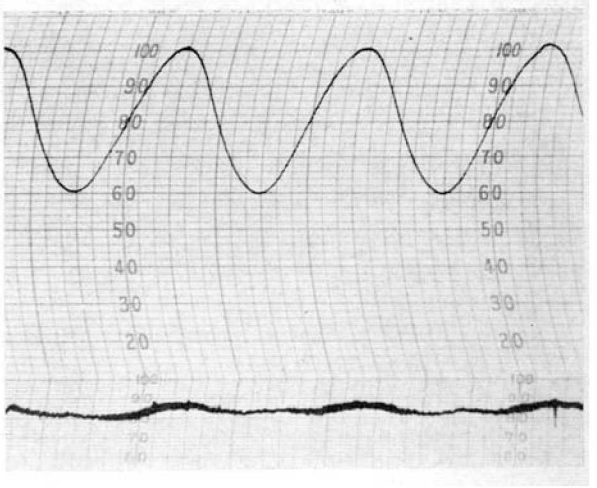

FIG. 2.—A hygrothermograph record of one of the experimental regimes demonstrating the diurnal sine wave programmed. Humidity control degrades to ± 4% RH when a 40°F (22.2°C) thermal region is transited.

to 60–70° angle. A brass tube, 0.5-mm diam, was installed at the bend point. A 1.0-cm hole—covered with a fine-mesh organdy to prevent larval escape—was cut in the funnel just above the vial and below the shank region to serve as an air-suction port. The brass tube was connected to the laboratory air supply through a timer-solenoid assembly, which allowed a 0.5-sec burst of air to rush through the assembly once every 15 sec. The resulting system created a venturi-effect that sucked the larvae through the vial-funnel arrangement and deposited them onto a sticky[4] hygrothermograph chart mounted on a Bendix-Hygrothermograph clock drum. The vial-funnel arrangement was positioned with the funnel opening about 0.5 cm. from the sticky chart. Collecting efficiency was about 95–97%. A few larvae failed to display typical negative geotropism.

To insure that the vial-funnel assembly was not moderating the hygral environment, a Brady Array® humidity sensor with a guaranteed accuracy of ±4% RH was used to measure the microenvironmental humidity. A hole was drilled into the side of a vial, the Brady Array was inserted, the hole was sealed with modeling clay, and the vial was capped with the funnel. A 78% RH was recorded without air bursts. With an air burst every 15 sec, 79–80% RH was recorded. Similarly, a hole was drilled into the lid of a glass petri dish, and humidity conditions were recorded in an identical manner. Inside the dish, the RH was 77%.

The thermal regimes used in the static environmental studies ranged from 70°F (21.1°C) to 95°F (35.0°C) in 5°F (2.8°C) increments. In comparison, the computer-controlled environmental chambers were programmed to fluctuate temperatures through a diurnal sinsoid of ±5°F (2.8°C), ±10°F (5.6°C), ±15°F (8.3°C), and ±20°F (11.1°C) with the mean temperatures the same as the static environments (Fig. 2). The sinusoidal curves were programmed for a high temperature peak at 6:00 PM and a low temperature trough at 6:00 AM. In both the static and fluctuating environments, RH was constant at 80% and the light regime was 10D/14L unless noted otherwise. Only the number of larvae that emerged, ranging from 300 to 1000 individuals/treatment (environmental regime), was recorded.

Results

Data from hand-collection experiments indicated that the speed of development of bollworms from egg deposition to larval eclosion increased by about 38%

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[5] Thunder Scientific, 604 Wyoming, Albuquerque, N. Mex.

Table 1.—Speed of development from egg deposition to larval eclosion of *H. zea* at 4 static temperatures. The data of Luckmann (1963) is included for comparison.

Environmental regime	Hand-collected results					Luckmann's results			
	Mode (hours)	Mean (hours)	Range (hours)	SD	No. indiv.	Mean (hours)	Range (hours)	SD	No. indiv.
75°F, 80% RH	86.0	85.2	14	1.98	113	86.9	17	2.1	338
80°F, 80% RH	68.4	68.9	11	1.6	450	—	—	—	—
80°F, 90% RH	68.5	69.0	11	2.1	186	—	—	—	—
85°F, 80% RH	59.3	60.3	13	1.79	667	58.7	12	2.0	233
90°F, 70% RH	53.5	52.9	16	2.0	168	51.7	16	2.4	110

between the mean static temperatures of 75°F (23.9°C) and 90°F (32.2°C). At 80°F (26.7°C) there was little difference in the speed of development between 80% and 90% RH (Table 1). These developmental rates agree closely with results of similar tests by Luckmann (1963) (Table 1).

The developmental mode rather than the mean was used to analyze bollworm development. The typical emergence pattern is slightly skewed to the left (Fig. 3). Individual emergence tapers off slowly when the mode of the distribution is reached, resulting in a distorted distribution mean.

The speed of development was not affected by continuous light when compared with a more normal photoperiod (10D/14L) in an otherwise similar environmental regime (Fig. 3). Emergence data using the auto-collector were taken from 4 static environmental regimes (the data collected at 70°F (21.1°C) and at 95°F (35.0°C) were collected by hand). These data are presented in Table 2 and are represented graphically in Fig. 4. The modal emergence time was plotted with the range of emergence (from emergence onset to termination) for each static regime. Since the auto-collector was allowed to run approximately 12–24 h after the onset of emergence, the range and standard deviation of bollworm emergence times were both increased (when compared with hand-collected data), because a few of the very slowly developing individuals were not excluded from the data set. Auto-collected modal-emergence data were pooled, since treatment replication within each regime produced nearly identical results. The

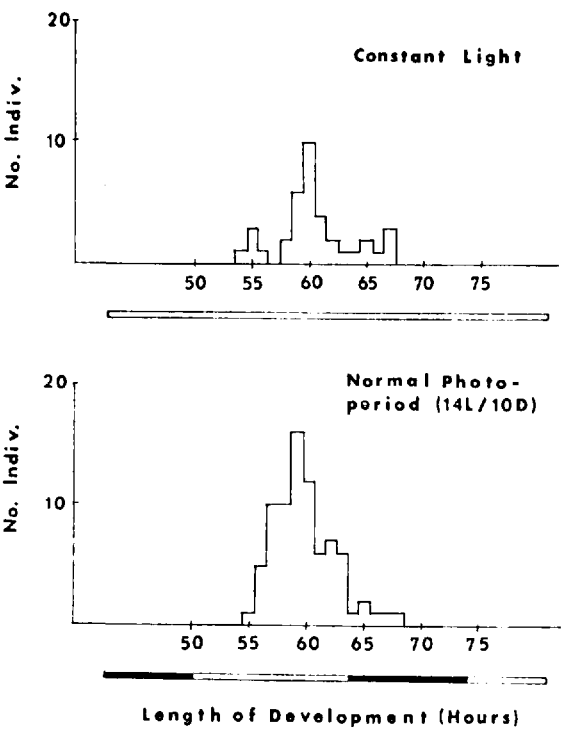

FIG. 3.—Auto-collected data from eggs reared under constant light vs. a normal photoperiod in an environmental regime of 85°F (29.4°C) and 90% RH.

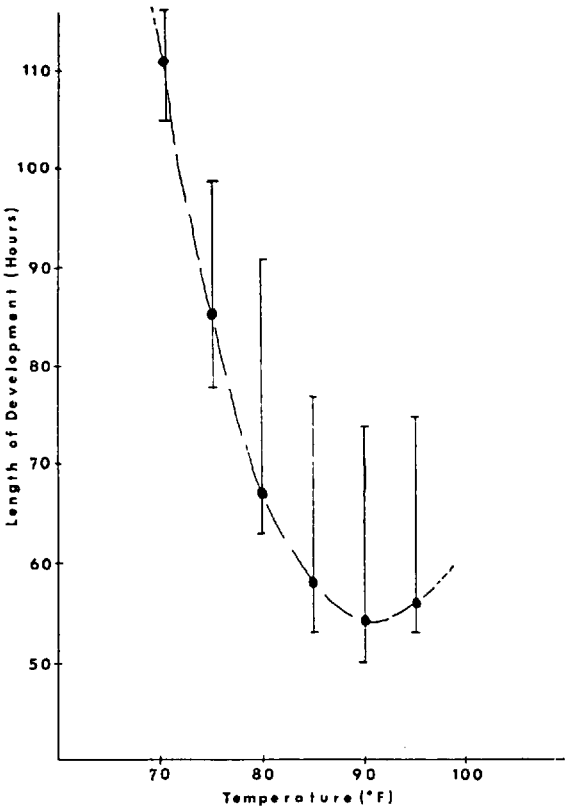

FIG. 4.—The parabolalike larval emergence curve for *H. zea* at static temperatures and constant 80% RH. The black dots represent the modal emergence time at the indicated temperature. The range of emergence is represented by a solid line at each temperature.

Table 2. – Response of *H. zea* larval eclosion from eggs held under various static and fluctuating temperatures and a constant RH of 80%.

Environmental regime		Mode (hours)	Mean (hours)	Range (hours)	SD	No. individuals
70°F	Static	111	111.3	10	2.36	269
	±10°	103	103.08	10	1.6	381
	±20°	99.5	99.2	18	2.7	288
75°F	Static	85.5	87.67	31	4.7	545
	±10°	85	85.96	23	2.5	454
	±20°	84	83.9	9	1.15	318
	±25°	85	84.8	9	1.51	164
80°F	Static	67.75	75.65	24	3.06	410
	± 5°	70.8	71.6	24	3.19	603
	±10°	73	74.5	16	3.78	289
	±20°	76	75.3	9	1.7	224
85°F	Static	57.6	58.1	24	2.28	677
	± 5°	58	59.8	24	3.5	215
	±10°	63.5	66.4	18	4.36	271
90°F	Static	54.4	56.5	24	3.6	806
	± 5°	54.5	55.6	19	3.0	557
	±10°	59.2	60.7	24	1.67	290
95°F	Static	56	57.5	22	3.8	215
	± 5°	57	60.3	23	4.2	194
	±10°	62	64.9	23	5.9	236

parabolic shape of the development curve (Fig. 4) agrees well with the typical development curve described by Clarke (1967). The critical upper thermal limit for bollworm eggs is between 95° and 100°F (35–37.8°C). At 90°F (32.2°C) the mortality rate was 40–50%, which was normal for most experiments conducted in moderate-temperature regimes. The mortality rate increased to 60–70% at 95°F (35°C) and became 100% at 100°F (37.8°C).

Table 2 presents results from the fluctuating regimes and compares them with those from the static environmental regimes. These data, as with the data from the static regimes, were pooled within each regime to increase population numbers. The larval emergence times of the fluctuating regimes are advanced, retarded, or essentially remain unchanged from the same static temperature. This, too, is in agreement with the results published throughout the literature concerning insect reactions to fluctuating environments. A series of experiments was conducted to test the validity of the heat units concept in fluctuating environments. Because the static-regime data obtained here agreed so closely with Luckman's (1963) data, the developmental threshold of 54°F (12.2°C) determined by Luckmann was used. In one experiment, the results of which are depicted in Fig. 5, the heat units required for complete development at a static 80°F (26.7°C) was 1768 degree (°F)-hr. Actual modal egg eclosion took place 7 h later at 1976 degree (°F)-h. Satisfactory agreement could be obtained only when the phase of the diurnal sine wave was adjusted so as to give agreement.

Discussion

The concept of heat units (day-degrees) is held by many entomologists to be significant in determining the developmental rates for insects (Luckmann 1963, Morris and Bennett 1967, Bakersville and Ewin 1969, Morris and Fulton 1970). Implicit in the concept is the assumption that the insect developmental velocity (defined as the percent development per unit time) is strictly proportional to the heat quantity input above some threshold value. This assumption is a result of the statistical method of fitting a linear regression line to observed data, and it tends to obscure the well-known observation that metabolic reactions tend to accelerate exponentially with increasing temperature until a critical limit is reached where some mechanism such as protein denaturization begins to occur. At this critical limit, the reaction rate begins to slacken and mortality increases. This phenomenon was described in insects by Clarke (1967) and has also been noted in plants by Lowry (1969).

For many long-term developmental processes which experience randomized, small-amplitude fluctuations, the heat-units concept provides a satisfactory first-order approximation. This concept is not true in a large-amplitude, periodically fluctuating thermal environment such as might be experienced by insect eggs deposited on the upper leaves of a host plant.

In contrast to the heat-units concept, we chose to assume that the developmental rate was principally a function of temperature and that equal heat units do not necessarily produce identical results.

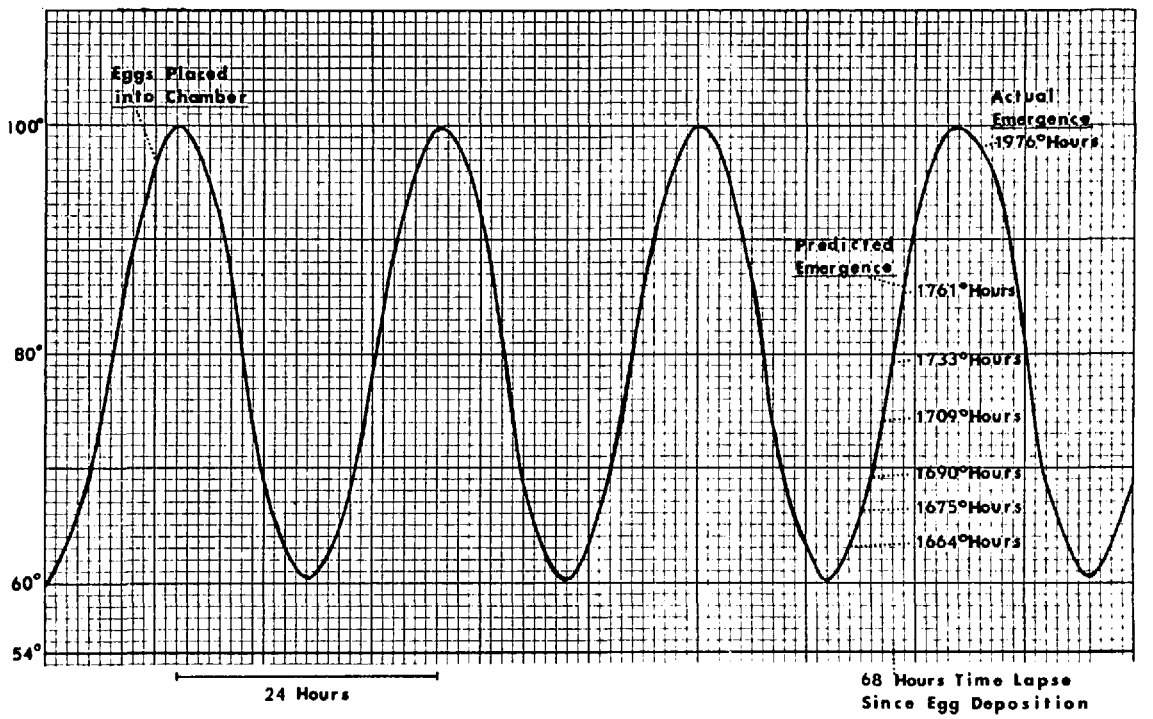

FIG. 5.—An illustration of the heat-units concept using a temperature fluctuation of 80° ± 20°F. The eggs were placed in the chamber at 4:00 PM. The predicted emergence was at 1:00 PM 3 days (69 h) later, but emergence actually occurred at 8:00 PM or 7 h later than predicted.

The developmental "trajectory" taken by a developing egg is indeterminate as it is difficult to measure anything other than ovipositional and eclosion times. However, 2 models can be proposed:

(1) a linear trajectory: % Dev = a t

and

(2) an exponential trajectory: $\%\,\mathrm{Dev} = e^{a\,t}$

where a is the developmental velocity coefficient and % Dev is the percent development to time t. As it happens, the trajectory is inconsequential for a monotonically increasing model, and the choice only modifies the magnitude of the developmental velocity coefficient. In case (1),

$$a = \frac{100}{t_E} \tag{1}$$

and in case (2),

$$a = \frac{\ln(100)}{t_E} \tag{2}$$

where t_E is the modal eclosion time $\%\,\mathrm{Dev} = 100$. For simplicity, the 1st model was chosen.

The generalized parabola, $(Y-y) = K\,(X-x)^2$, fits the measured modal eclosion curve very well. Hence, the time to modal eclosion, as a function of temperature, t_E, can be closely approximated by

$$t_E(T) = \frac{(T-91)^2}{8.0} + 54 \tag{3}$$

where $K = 1/8$, $x = 91°F$, and $y = 54$ h.

Thus the bollworm-specific developmental rate coefficient becomes

$$a\,(T) = \frac{100}{t_E(T)} = \frac{800}{(T-91)^2 + 432} \tag{4}$$

by substitution. This resulting equation is plotted against the measured developmental rate coefficients in Fig. 6.

Under fluctuating environmental conditions, the developmental-rate coefficient also becomes a function of time. In the idealized conditions programmed into the environmental chambers, the time-dependent temperature equation is

$$T\,(t) = T\mu + A \sin\,(\omega t + \phi) \tag{5}$$

where $T\mu$ is the mean temperature, A is amplitude of the fluctuations, ω is the angular frequency, and ϕ is the phase shift.

Combining Eq. (4) and Eq. (5) and integrating, % development to time t is equal to:

$$\%\,\mathrm{Dev} = \int_0^t \frac{800\,d\tau}{[T\mu + A \sin\,(\omega\tau + \phi) - 91]^2 + 432} \tag{6}$$

for bollworm eggs. Modal eclosion occurs when the intergral is integrated from $t = 0$ to $t = t_E$. To determine t_E for differing environmental conditions, a FORTRAN computer program was written to integrate Eq. (6) by iterative approximation until 100% development was reached. Table 3 presents these results. The agreement is generally quite good.

The significant results from this analysis are:

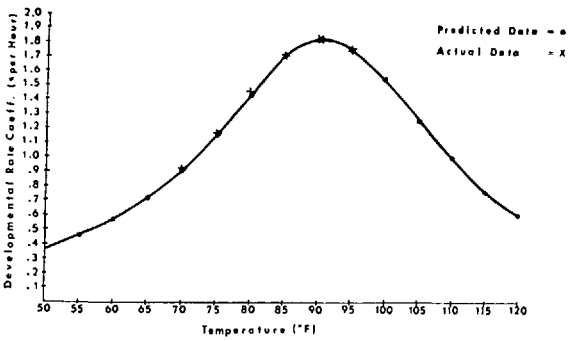

FIG. 6.—The bollworm egg developmental rate coefficient, a(T), plotted as a function of temperature. The measured developmental rates also are plotted.

(1) There is probably no true developmental threshold associated with cotton bollworm eggs. Especially at the colder temperatures, below 54°F (12.2°C), Eq. (6) predicts a finite, much shorter developmental time than does the heat-units concept. Other mortality factors such as egg desiccation and disease may eventually preclude mass eclosion, but it is not excluded by definition.

(2) Moderate thermal fluctuations around the optimal temperature (as defined by the apex of the parabolalike larval emergence curve) produce relatively little change in developmental times. Larger fluctuations can produce only retardations. Moderate thermal fluctuations (less than the difference between the mean temperature and the apical temperature) around a mean temperature on the "wings" of the parabola (either a higher or lower temperature) will produce only advances in developmental times which may be a significant percentage of the total time. Only when the fluctuating temperature traverses the apical region of the emergence curve does a retardation of the minimal development time for some mean temperature occur.

Table 3. – Comparison of predicted (Eq. 6) vs. actual modal bollworm egg development times. Relative humidity held constant at 80%.

Mean temperature		Temperature fluctuation				
		Static (hours)	±5 (hours)	±10 (hours)	±20 (hours)	±25 (hours)
95°F	Actual	56	57	62	—	—
	Predicted	56.5	58.2	62.2	77.0	85.7
90°F	Actual	54.4	54.5	59.2	—	—
	Predicted	54.5	56.0	60.0	75.0	84.0
85°F	Actual	57.6	58	63.5	—	—
	Predicted	58.7	59	62	75.2	82.7
80°F	Actual	67.75	70.8	73	76	—
	Predicted	69.5	69.7	71.0	77.2	82.5
75°F	Actual	85.5	—	85	84	85
	Predicted	86.5	84.2	81.2	80.7	86.0
70°F	Actual	111.0	—	103	99.5	—
	Predicted	109.5	106.2	101.7	96.2	96.2

(3) The observed advances and retardations in the developmental times of various insect species when exposed to fluctuating or static thermal conditions appear to be a consistent result and not so anomalous as often reported, implying that this manner of analysis should be used when investigating insect developmental behavior under fluctuating thermal conditions.

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