

Thermoperiodism and the Thermal Environment of the Pitcher-Plant Mosquito, *Wyeomyia smithii*

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Summary. *Wyeomyia smithii* Coq. (Diptera: Culicidae) completes its pre-adult development only within leaves of the purple pitcher-plant, *Sarracenia purpurea*. Between early June and mid-October in northern New York State, the daily temperature cycle in leaves lagged the photic cycle by 0–6 h and exhibited a mean daily amplitude of 14.5° C.

Thermoperiod acts as a potent zeitgeber. At constant temperatures, *W. smithii* respond to the shorter dark period of a symmetric skeleton photoperiod as “day”. However, a superimposed thermoperiod having the thermophase coincident with the longer dark period overrides this tendency. Thermoperiods may also perturb the photoperiodic clock but *W. smithii* compensate for the range of phase relationships between the photic and thermal cycles observed in nature.

Compared with constant temperatures, *W. smithii* develop more slowly but exhibit a 7-fold increase in fecundity when reared under fluctuating temperatures. The net result is a 50% greater capacity for increase in the latter regimen. These results suggest that maximum fitness in *W. smithii* is achieved through the action of, and not despite, thermal heterogeneity.

The length of day, or photoperiod, constitutes a highly reliable indicator of changing seasons. It is not, therefore, surprising that a great variety of insects rely upon photoperiod to cue their seasonal development (Beck, 1968; Danilevskii, 1965; Saunders, 1976). In order to capitalize on the geophysical accuracy of day length, the photoperiodic mechanism must be attuned to changes in environmental temperature. Environmental temperatures are not constant; rather, they vary both with respect to mean and amplitude within and between days. Temperature fluctuations or thermoperiods may themselves provide periodic cues which are capable of mediating dormancy in insects (Saunders, 1973; Chippendale, et al., 1976). Thus, organisms living in a photo- and thermoperiodic environment must not only compensate for variation in average temperature (temperature compensation), but also for variation in phase between light and temperature cycles (phase compensation).

The mosquito, *Wyeomyia smithii* Coq., passes its entire pre-adult life within a leaf of the purple pitcher-plant, *Sarracenia purpurea*. Photoperiod perceived by the larvae is the primary environmental cue mediating the onset, maintenance, and termination of larval diapause (Smith and Brust, 1971; Evans and Brust, 1972; Bradshaw and Lounibos, 1972, 1977). However, leaves containing *W. smithii* are exposed to great temperature extremes on the open bog mat, heating the water to as high as 42° C in north Florida (personal observations); even in Manitoba, daily temperatures in the summer vary from over 25° C to below 10° C (Evans and Brust, 1972). The present paper describes the thermal environment in leaves of *S. purpurea*, considers the interaction of thermo-

periodic and photoperiodic cues on the initiation of diapause in *W. smithii*, and measures the relative effect of constant and fluctuating temperatures on capacity for increase in this mosquito.

Materials and Methods

1. Pitcher-Plant Temperatures

Temperature recordings were made with a Tempscribe spring-wound recorder with a remote sensing bulb. The bulb was placed in a large leaf of a pitcher plant exposed to the sun on an open bog mat near Mendon, New York, approximately 42°55'N latitude, 77°30'W longitude, and 150 m altitude. Temperatures were obtained for the first week in June and continuously from the last week in June until the latter portion of October, 1971. Temperatures were read from the charts every three hours starting at midnight. They were averaged at each time of day over a seven day period to give the mean temperature at that time of day for that week.

2. Source and Maintenance of Mosquitoes

Larvae of *W. smithii* were collected from bogs near Pinckney, Livingston County, Michigan, Forge Village, Somerset County, Massachusetts, and Moore's Meadows, Burlington County, New Jersey. Laboratory populations were reared and maintained as in earlier studies (Bradshaw and Lounibos, 1972; Lounibos and Bradshaw, 1975).

3. Experimental Light and Temperature Regimes

Three types of photoperiodic regimes were used in this study: entire, symmetric, and asymmetric skeleton photoperiods. Entire or complete photoperiods consist of one light period (photophase) and one dark period (scotophase) per day; skeleton photoperiods consist of two photophases and two scotophases per day. In symmetric skeletons both photophases are of equal duration; in asymmetric skeletons, one photophase, the main photophase, is longer than the other. In both symmetric and asymmetric skeletons, the scotophases may be of varying length. The responses to symmetric skeleton photoperiods were determined in Forma model 11 incubators with programmed light control.

The responses to entire and asymmetric skeleton photoperiods were determined at constant temperatures in programmed light cabinets. Individual chambers (35 × 35 × 45 cm) were equipped with an isolated, air-cooled 4 watt cool-white fluorescent lamp at a distance of approximately 10 cm from the larvae. These cabinets were located in constant temperature rooms at 25 ± 0.5° C. Temperature in each chamber remained within 0.5° C of ambient.

Two types of chambers were used to program temperature

and light cycles. The first consisted of modified Forma model 11 refrigerated incubators. To the normal 500 ohm potentiometer which controlled the temperature, a second was added in parallel. One potentiometer was set for a low temperature, the other for a high temperature. Control of the incubator was switched from one potentiometer to the other with an Intermatic time switch. The incubator maintained temperature to within 0.5° C of the set temperature. Lighting consisted of a single 13 watt cool-white fluorescent lamp at a distance of approximately 25 cm from the larvae. The second type of chamber was constructed from a two-compartment wooden box. Each compartment (30×30×30 cm) contained a single 4 watt cool-white fluorescent lamp and a 50 watt Ohmite wire-wound resistor. The chambers were connected by ducts and a 15 ft³min⁻¹ (0.42 m³min⁻¹) blower which continuously circulated air from one chamber to the other. The lower temperature was determined by ambient temperature, the higher by setting a PSG mercury switch and relay to activate the resistor. Temperatures remained within 0.5° C of the nominal lower temperature and 1.0° C of the higher nominal temperature.

4. Life-History Parameters

To examine survivorship and fecundity of *W. smithii*, they were reared from the day of oviposition until death on long days (L:D=16:8) at constant or fluctuating temperatures. For the constant temperature, the experimental chamber consisted of a 30 gallon (113.6 liter) galvanized steel can equipped with a 4 watt cool-white fluorescent lamp. The ballast for the lamp was located outside the can and can temperatures remained within 0.5° C of ambient in a 25±0.5° C constant temperature room. For the fluctuating temperature regimen, the chambers in the wooden cabinet described above were programmed for a 31.5:18.5° C=12:12 h thermoperiod which lagged the photoperiod by 30° (2 h). To provide humidities conducive to adult survivorship, a tray of wet sand was placed in the experimental chambers for both constant and fluctuating thermal regimens.

Five batches of eggs were collected from a single large adult colony of *W. smithii* from New Jersey; 3 of them ($n=100, 108,$ and 139) were exposed to constant temperatures (25±0.5° C) and 2 batches ($n=88$ and 100) to the fluctuating temperatures (25±6.5° C). The eggs, each larval instar, and pupae were maintained in separate containers and a record kept of the number surviving each stage from egg to adult. Eggs were removed from the adult cages and counted daily. Replacement rate (R_0), mean generation time (MGT), and the capacity for increase (r_c) were calculated by the following equations:

$$R_0 = \frac{\text{total number of eggs produced by the parental generation}}{\text{number of eggs in the original sample}} = \frac{\text{number of } F_1 \text{ eggs}}{\text{number of } P_1 \text{ eggs}}$$

$$\text{MGT} = \frac{\sum t E_t}{\sum E_t}$$

$$r_c = \frac{\ln(R_0)}{\text{MGT}}$$

where E is the number of F_1 eggs oviposited on a given day and t is the age of the parental (P_1) generation in days since the latter was oviposited.

Results

1. Pitcher-Plant-Temperatures

Figure 1A shows that mean weekly temperatures ranged between 16 and 24° C from early June until early September, after which time temperatures declined. Mean weekly temperature based on readings taken at 8 times during the day were 0.2–2.0° C lower than those based on only the mean maxima and minima for the week. The amplitude of daily fluctuations in temperature averaged 14.5° C over the entire recording period and ranged from 5–26° C; mean weekly amplitudes ranged from 6–21° C (Fig. 1B). As shown by the relative temperatures at sunrise and sunset (Fig. 1C), the temperature cycle lagged the light cycle from June to mid-September; thereafter, the light and temperature cycles were approximately in phase. The weekly averaged phase angle difference between the photoperiod and the thermoperiod ranged from 0–90°.

2. Photoperiodic Response of *W. smithii* at Constant and Fluctuating Temperatures

When reared at 25±0.5° C, long days averted and short days initiated diapause among *W. smithii* from Massachusetts, Michigan, and New Jersey (Table 1). All of the larvae exposed to 12 h of light per day remained third instars for more than 25 days (entered diapause) while all of those experiencing photophases of 15 or more h spent 5 days or less as a third instar (Mean ± 2 S.E. = 2.80 ± 0.15 days). Critical photoperiods for the initiation of diapause ranged from 13.8 to 14.6 h of light per day. When reared at 30±0.5° C and 12 h of light per day, 4–44% of the larvae did not enter diapause in the third instar but continued developing to the fourth within 2–10 days. Thus, at a constant temperature of 30° C, some individuals do not respond to the short-day photoperiod and avert diapause.

To examine the effects of temperature which fluctuate daily between 25 and 30° C, larvae from all three localities were reared in the wooden thermoperiod cabinet on a short-day regimen (L:D=12:12). Each chamber was programmed for 16 h at 30° C and 8 h at 25° C (30:25° C=16:8 h). In separate experiments, the phase of the thermoperiod was varied so that it lagged the photoperiod by 0, 90, 180, or 270°. Two-way analysis of variance (after logarithmic transformation to achieve homogeneity of variance) revealed no significant differences among localities ($F_{2,8} = 3.87$; $P > 0.05$) but indicated highly significant differences among responses to various phase angles and the constant temperature (30° C) controls ($F_{4,8} = 9.16$; $P < 0.01$). Duncan's multiple range test then indicated significant differences ($P < 0.01$) between all treatments, including response to a constant 30° C. When the mid-point of the thermophase coincided with noon or lights-off, 1–14% of the larvae developed without entering diapause (Fig. 2). By contrast, when the mid-point of the thermophase fell at midnight or lights-on, 22–72% of the larvae failed to enter diapause. These results show that the phase angle between the thermoperiod and the photoperiod may have a profound effect on the interpretation of day-length by the photoperiodic clock among *W. smithii* from widely separated populations.

3. Skeleton Photoperiods

Asymmetric Skeletons at Constant Temperature. To determine the sensitivity of the photoperiodic clock of *W. smithii* during the scotophase, larvae from New Jersey were reared at 25±0.5° C on asymmetric skeleton photoperiods. The main photophase consisted of 11 h of light and was followed by a 1 h light pulse at various times during the 13 h dark period. Twenty-five larvae

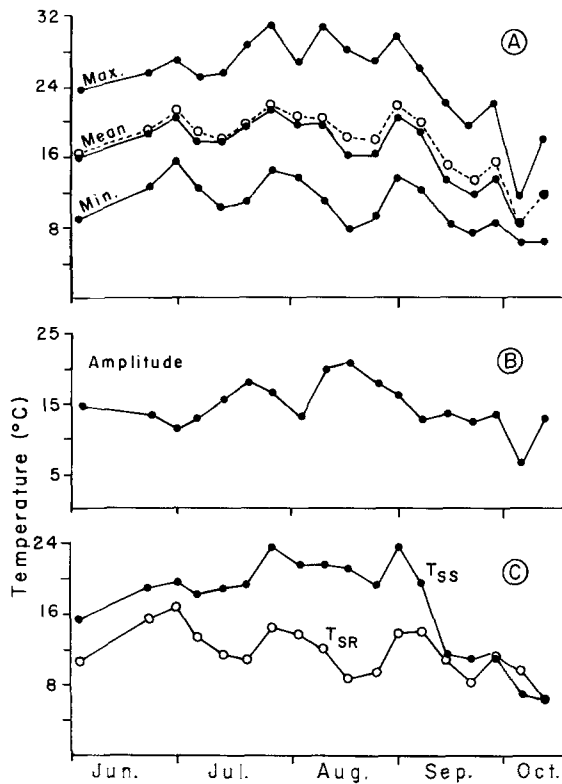


Fig. 1A-C. Temperature relationships in the leaves of *S. purpurea* exposed to the full sun in a bog near Mendon, New York. **A** Maximum (*Max.*), mean, and minimum (*Min.*) weekly mean temperatures. *Solid lines*: mean based on 8 readings per 24-h period; *broken line*: mean based on the maximum and minimum readings per 24-h period. **B** Weekly mean amplitude (daily maximum minus daily minimum). **C** Weekly mean temperature at sunrise (T_{SR}) and sunset (T_{SS})

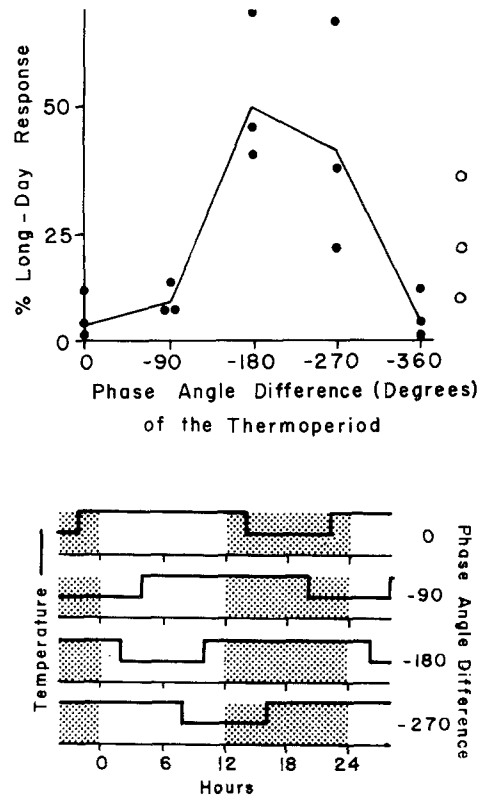


Fig. 2. Effect of phase angle difference between the thermal and photic cycles on development. The lower figure shows the phase relationships between the 16:8=30°:25° C thermoperiod and the 12:12=L:D photoperiod. The upper figure plots long day response (% development) to this normally short-day photoperiod as a function of phase angle difference

Table 1. Effect of photoperiod on the initiation and maintenance of diapause and on the duration of the third instar at constant temperatures

Popula- tion	Critical photo- period at 25° C	Percentage of diapause at			Duration of the third instar at 25° C and L:D =16:8
		25° C		30° C	
		L:D =16:8	L:D =12:12	L:D =12:12	
Mich.	14.5 h	0	100	22 ± 6 (2) ^a	2.5 ± 0.7 (22) ^a
Mass.	14.6 h	0	100	10 ± 11 (4)	2.8 ± 0.8 (35)
N.J.	13.8 h	0	100	39 ± 7 (2)	2.0 ± 0.2 (23)

^a Mean ± 2 SE (sample size)

were exposed to each regimen in each of 1-3 replicates. *W. smithii* exhibited two periods of sensitivity, one in the early and the other in the late subjective night (Fig. 3). The former appeared broadly distributed, the latter as a sharp peak. The most effective pulse in the early subjective night ended 15 h after lights-on of the main photophase; the most effective pulse in the late subjective night began 15 h before lights-off of the main photophase. The maximum long-day response is thus obtained by asymmetric skeletons mimicking and entire photoperiod of L:D=15:9.

Symmetric Skeletons at Constant and Fluctuating Temperatures. When provided with symmetric skeleton photoperiods whose scotophases are of unequal length, insects generally respond to the shorter dark period as "day" and consequently exhibit a short-day response (Saunders, 1976, pp. 129-132). When *W. smithii* are reared at 25 ± 0.5° C on a L:D:L:D=1:13:11:9 skeleton to approximate an entire L:D=15:9 or 9:15 photoperiod, 4-20% of the larvae did not enter diapause. When reared on the same skeleton but provided with a 29:18° C=15:9 h thermoperiod whose thermophase coincided with the longer dark period, 85-88% of the larvae developed to the fourth instar within 10 days of becoming a third (Fig. 3). Thus, thermoperiodic cues provide sufficient stimulus to overcome the natural tendency of *W. smithii*'s photoperiodic clock to interpret the shorter dark period as "day".

4. Effect of Constant and Fluctuating Temperatures on Life-History Parameters

W. smithii developed faster in response to a constant temperature of 25° C than to a 31.5:18.5° C thermoperiod with a mean daily temperature of 25° C (Fig. 4). This faster development at constant 25° C resulted both in younger age at first reproduction and younger age at peak reproduction. Consequently, *W. smithii* at constant temperatures had a shorter mean generation time than

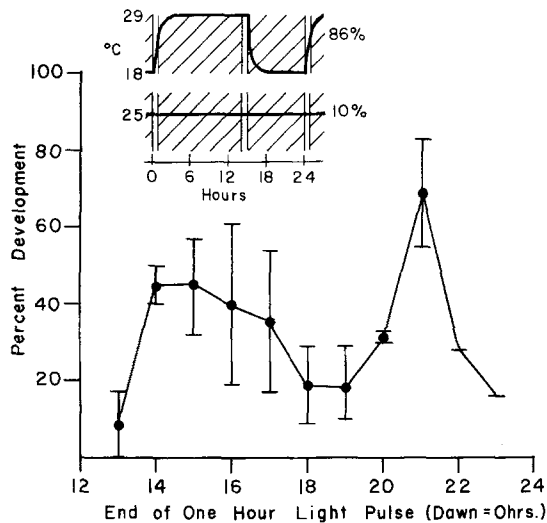


Fig. 3. Developmental response to a short-day photoperiod with a one hour light pulse added at various times during the scotophase. Main photophase=0–11 h. Inset: mean developmental response of mosquitoes reared on symmetric skeletons mimicing a 15:9 or 9:15=L:D cycle. Top: with a 29:18°C=15:9 h thermoperiod with the thermophase superimposed over the longer dark period; bottom: at a constant 25°C

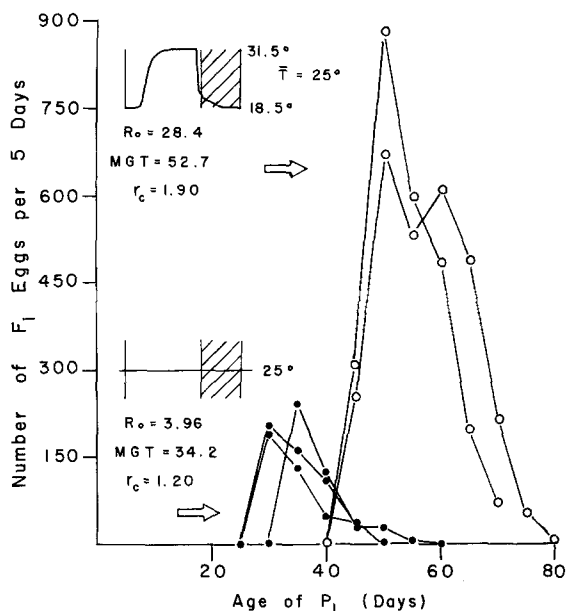


Fig. 4. Effect of constant and fluctuating temperatures on the capacity for increase among *W. smithii* from New Jersey. R_0 , replacement rate; MGT , mean generation time; r_c , capacity for increase. The insets show the relationship between the 16:8=L:D photoperiod and the constant (25°C) or fluctuating (31.5:18.5°C=12:12 h) temperature

those experiencing the thermoperiod. However, fecundity was far greater under the latter conditions and replacement rate was enhanced more than seven-fold. The greater replacement rate more than compensated for the longer generation time so that *W. smithii* exposed to fluctuating daily temperatures exhibited 58% greater capacity for increase than those exposed to the constant temperature.

Discussion

1. The Thermal Environment and Phase Compensation

In the leaves of *S. purpurea*, a strong thermoperiod prevails (Fig. 1). During the summer, thermoperiods lag photoperiods, resulting in cool dawns and warm dusks; later, during the fall, the photic and thermal days are more in phase. While thermoperiod can act as an effective zeitgeber in *W. smithii* (Fig. 3), the degree to which the mosquito's photoperiodic clock may be perturbed by thermoperiod depends upon the phase relationship of the two cycles (Fig. 2). Thermoperiods which lag the photoperiod by 180 or 270° promote development on an otherwise short-day regimen. While these responses cannot immediately be used to speculate on the underlying mechanism of day-length measurement, they do show that the photoperiodic clock of *W. smithii* is phase-compensated for the range of phase relationships between the photo- and thermoperiods normally encountered in its natural habitat.

Previous workers have shown in a variety of insects the relative importance of warm or cool photo- and scotophases. Warm photophases and cool scotophases tend to enhance the short-day effects of a given photoperiod; cool photophases and warm scotophases promote long-day effects (Danilevskii, 1965, pp. 116–119; Beck, 1968, pp. 146–149; Chippendale et al., 1976; Ratte, 1979). Apart from Ratte (1979), these studies have considered only two phase relationships, namely, synchronous photo- and thermoperiods and regimens where the photo- and thermoperiods are 180° out of phase. In nature, thermo- and photoperiods are rarely in phase; rather, the former tends to lag the latter but by considerably less than 180° (Geiger, 1965). The present study illustrates the importance of considering the intermediate phase relationships (Fig. 2). A thermoperiod lagging the photoperiod by 90° elicits a short-day response; the same thermoperiod, when experienced 90° in advance of the photophase elicits a substantial long-day response. Phase compensation therefore involves not only the absolute phase angle difference between the light and temperature cycles but its direction as well. Furthermore, that *W. smithii* compensates for a delayed (natural) but not advanced (unnatural) thermoperiod underscores the adaptive nature of such compensation.

2. Fitness in Constant and Fluctuating Environments

Just as photoperiodic responses have most frequently been determined at constant temperatures, so too have the majority of other characteristics of fitness such as developmental rate, oxygen consumption, fecundity, and upper and lower lethal limits (Wigglesworth, 1965; Clements, 1963). Much of this work has been carried out under the assumption, tacit or overt, that there exists an optimal temperature for a given phenomenon. Fluctuating temperatures are rarely considered, perhaps because the theory of optimization would hold that variable temperatures must necessarily include those which deviate from the optimum.

Fluctuating thermal environments may be more beneficial than is generally realized. Corixid bugs, fruit flies, and alfalfa aphids are able to survive and develop at extreme temperatures of a thermoperiod which would be lethal or halt development if experienced as a constant temperature (Sweeney and Schnack, 1977; Messenger, 1964; Messenger and Flitters, 1959). Thermoperiods greatly enhance fecundity by 80–300% over constant temperature without dramatically altering developmental rate in crickets (Hoffman, 1975) or pink bollworms (Welbers, 1975). Pea aphids exhibit 1–16% greater capacity for increase when reared in fluctuating rather than constant temperatures (Siddiqui and Barlow, 1973).

The cabbage aphid realizes a 27% increase in fitness when reared out of doors on broccoly with an average daily temperature amplitude of 29° C than it does indoors on the same plant and the same mean temperature with a daily amplitude of 2° C (Root and Olson, 1969). None of these insects, however, shows the dramatic 50% rise in fitness shown by *W. smithii* (Fig. 4). *W. smithii* pass their pre-adult development in 0–100 ml of water which can warm rapidly in the sun during the day and give off heat equally rapidly to the surrounding bog at night. Their small habitat thus leaves them little opportunity for horizontal and vertical behavioral thermoregulation which is available both the aphids and corixids above and to many other mosquito larvae (Haufe and Burgess, 1956).

Organisms which have evolved in fluctuating thermal environments with a high autocorrelation or high correlation with some other cue are generally capable of greater phenotypic response than organisms having evolved in more uniform environments. Inland plantains from a more thermally variable location exhibit a higher level of homeostatic ability in thermally fluctuating regimens than do plants of the same species from a maritime environment (Teeri, 1978). The range of thermal tolerance in both Puerto Rican *Drosophila* (Levins, 1969) and North American toads (Snyder and Weathers, 1975) correlates with the range of temperatures they are likely to encounter in nature. Finally, several intertidal invertebrates show greater thermal accommodation than permanently submerged ones (Newell, 1969; Newell and Northcroft, 1967). Evolution in these environments may, however, involve more than the ability to simply cope with thermal fluctuations. The very predictability of these fluctuations may result in reliance upon its regularity as illustrated by phase-compensation in *W. smithii*. Furthermore, as shown by capacity for increase in *W. smithii*, organisms may actually require thermal-temporal compartmentalization to maximize overall fitness.

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