

Geographic Variation in the Photoperiodic Response of the Western Tree-Hole Mosquito, *Aedes sierrensis*¹

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Aedes sierrensis (Ludlow) (Diptera: Culicidae) relies upon photoperiod to initiate a 4th instar diapause at 16.5°C. Short days elicited 100% diapause among larvae from central Oregon and northern California, but thereafter the incidence of diapause declines with

latitude so that in southern California only 35% of the sample populations entered diapause. Among that portion of the population capable of responding to day length, the critical photoperiod increased by one h for each 4.8° increase in latitude of origin.

Many insects depend upon the length of day (photoperiod) to cue their seasonal development (Danilevskii 1965, Beck 1968, Lees 1955, Danilevskii et al. 1970, Tauber and Tauber 1976). Among these species are several mosquitoes whose larvae overwinter in a photoperiodically mediated state of dormancy or diapause. Typically, these mosquitoes breed in containers, such as *Wyeomyia smithii* in the pitcher plant, *Sarracenia purpurea* (Smith and Brust 1971, Evans and Brust 1972, Bradshaw and Lounibos 1972, Lounibos and Bradshaw 1975), or several species in the rot-holes of deciduous trees: *Anopheles barberi* (Baker 1935), *Orthopodomyia signifera* (Baker 1935, Bradshaw 1973), *Toxorhynchites rutilus* (McCrary 1965)³ (Jenner and McCrary 1964, Bradshaw and Holzapfel 1975, Holzapfel and Bradshaw 1976), *Aedes triseriatus* (Wright 1966)⁴ (Love and Whelchel 1955, Wright and Venard 1971, Clay and Venard 1972) and *Aedes sierrensis* (Garcia and Ponting 1972). All the above mosquitoes but *A. sierrensis* occur primarily in eastern North America. *A. sierrensis*, a widespread species on the Pacific slope, ranges from British Columbia, Idaho, and Montana in the north to southern California (Peyton 1956, Neilsen et al. 1967, 1968). One would expect considerable variation in the photoperiodic response of this species to enable it to develop in synchrony with the changing seasons throughout this wide area. Here we consider such variation among 5 populations of *A. sierrensis* from a range of over 10° latitude.

MATERIALS AND METHODS

We collected overwintering larvae of *A. sierrensis* from tree-holes at 4 sites in California (Mt. Palomar, San Diego Co., 33°18' N; Lockwood, Monterey Co., 36°04' N; Auburn, Placer Co., 39°00' N; Yreka, Siskiyou Co., 41°52' N) and one site in Oregon (Halsey, Linn Co., 44°21' N). We packed the larvae on ice, transported them to Eugene, Ore., and reared

them to adulthood at 21±0.5°C and 16 h of daily illumination. Larval food consisted of ground rat chow and freeze-dried brine shrimp in a ratio of 2:1 by volume; adult food consisted of molasses with a few drops of para methyl hydroxy benzoate added to inhibit mold. We maintained the adults at 24±1°C and 16 h of daily illumination in plastic cages (28×15×15 cm) and provided them with a mock tree-hole for oviposition. We constructed the latter by covering a 50-ml paper-towel-lined jar of water with a closed, black cardboard cylinder (ca. 10 cm high and 5 cm diam). A 2.5-cm hole bored into the side of this cylinder provided access to the oviposition site. The mosquitoes mated readily without recourse to induced mating and were offered human or mouse blood 2–3 times/wk. The F₁ eggs from these field-caught populations provided the larvae for the experiments below.

After allowing 10 days for embryogenesis at 24±1°C and 16 h of daily illumination, we immersed the eggs in stagnant water at the same temperature to stimulate hatching. We then exposed samples of 20 freshly hatched 1st instars each to a variety of photoperiods at 16.5±0.5°C. We checked the larvae daily and placed any freshly molted animals into a new dish. We determined the percentage of each sample which had pupated within 50 days of hatching, eliminating from consideration any which had died before that time. We analyzed the data according to methods found in Snedecor (1956).

RESULTS AND DISCUSSION

As shown in Fig. 1, long days promoted development among larvae from all latitudes. Short days were completely effective in halting development among larvae from the 2 northernmost localities, but with decreasing latitude of origin, short days were progressively less effective in preventing development. All the larvae which had not developed by the end of 50 days were 4th instars. Short days may therefore elicit a 4th instar diapause among all the populations we considered, but their efficacy in inducing diapause is reduced in the more southerly populations.

We do not yet know whether *A. sierrensis* is capable of entering diapause at another stage of its life cycle, as does the eastern tree-hole mosquito, *Aedes*

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³ McCrary, A. B. 1965. The effect of photoperiod, temperature, and food on diapausing and developing larvae of *Toxorhynchites rutilus* (Coq.). M. S. Thesis. University of North Carolina, Chapel Hill, N. C. 49 pp.

⁴ Wright, J. E. 1966. Diapause induction, maintenance, and termination studies on larvae of *Aedes triseriatus* (Say) (Diptera: Culicidae). Ph.D. Thesis, The Ohio State University, Columbus, Ohio.

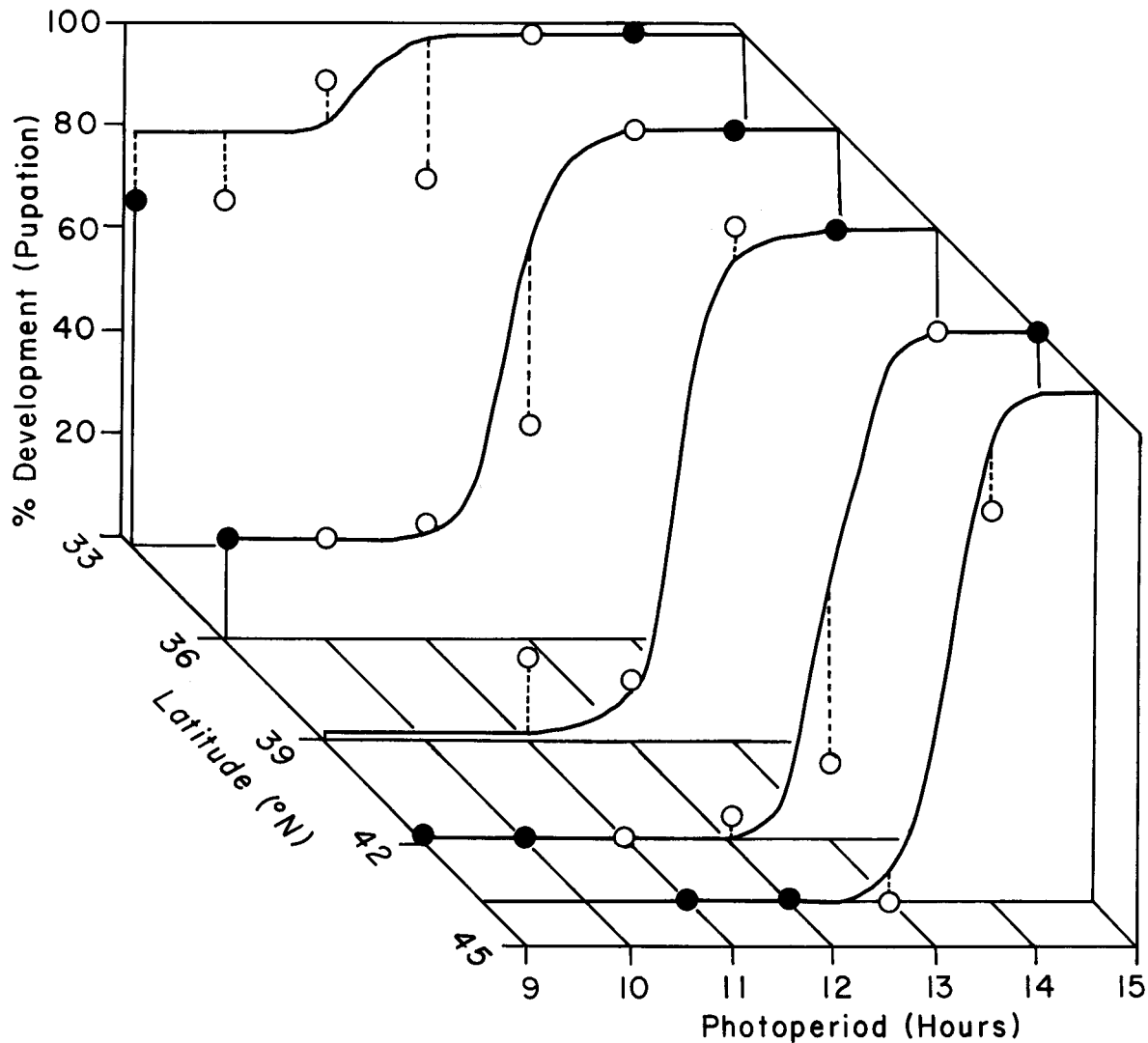


FIG. 1.—Photoperiodic response of *Aedes sierrensis* from different latitudes. Open circles were entered into the regression resulting in Eq. (2); solid circles were not entered into this regression but were used to test goodness of fit for Eq. (6). The lines were drawn from Eq. (6).

triseriatus, which may diapause as either an embryo or 4th instar (Wright 1966)* (Kappus and Venard 1967, Clay and Venard 1972, Love and Whelchel 1955, Wright and Venard 1971). The larvae of *A. sierrensis* used in our experiments are the F_1 generation of mosquitoes caught as overwintering larvae in Jan., suggesting either that many of the larvae caught in southern California were not in diapause or that heritability for the expression of fourth instar diapause is very low. California summers are especially dry (Visher 1954), and may constitute a harsher environmental stress than the relatively mild and moist winters. Further north, winters are more severe, and the data in Fig. 1 suggest that at higher latitudes the entire larval population of *A. sierrensis* should enter an hibernal diapause.

Ordinarily, one determines the critical photoperiod by finding the 50% intercept on a plot of percent development as a function of photoperiod. Determining the critical photoperiod for *A. sierrensis* is more elusive, since a certain portion of the population may not be photoperiodic. This portion of the population should not enter into the calculation of the critical photoperiod. We therefore define the critical photoperiod among that portion of the population which is potentially photoperiodic by the inflection points of the curves in Fig. 1. We provide below a method for fitting a continuous function to the individual points in Fig. 1 and, at the same time, calculating the critical photoperiods.

Each of the 5 series of points in Fig. 1 approximately describes a sigmoid curve. To fit all these

points to one continuous function, we first transformed percentage of pupation for the i^{th} locality and j^{th} photoperiod, $\%P_{ij}$ by:

$$\text{Tr}\%P_{ij} = \ln((100 - \%P_{ij})/(\%P_{ij} - \text{MIN}\%_i)) \quad (1)$$

where $\text{MIN}\%_i$ is the minimum percentage of pupation observed among samples from the i^{th} locality. When $\%P_{ij}$ equaled 100% or $\text{MIN}\%_i$, we subtracted 0.01% from or added 0.01% to $\%P_{ij}$, respectively. We then entered into regression only the $\text{MIN}\%$ and 100% values which resulted from daylengths closest to the inferred inflection points, shown by open circles on Fig. 1, and regressed $\text{Tr}\%P_{ij}$ on experimental photoperiod and latitude, longitude, and altitude of origin. We found significant correlations between $\text{Tr}\%P_{ij}$ and only latitude and photoperiod ($R = 0.83$, $P < 0.001$; $t(\text{photoperiod}) = 5.51$, $P < 0.001$; $t(\text{latitude}) = 3.53$, $P < 0.005$):

$$\text{Tr}\%P = 23.0 - 5.14 (\text{Photoperiod}) + 1.05 (\text{Latitude}) \quad (2).$$

Since we had used actual minimum percentage of development in Eq. (1), we next fit the actual minimum percentages of development to a sigmoid curve with upper and lower asymptotes of 100% and 0%, respectively, by transforming the minimum percentages, $\text{Tr}\text{MIN}\%_i$:

$$\text{Tr}\text{MIN}\%_i = \ln((100 - \text{MIN}\%_i)/\text{MIN}\%_i) \quad (3)$$

and regressing $\text{Tr}\text{MIN}\%_i$ on latitude ($r = 0.94$, $t = 4.77$, $P < 0.025$) whence:

$$\text{Tr}\text{MIN}\% = 0.9937 (\text{Latitude}) - 34.455. \quad (4).$$

Backtransformation then yields the minimum percentage of development calculated from regression, $\text{MIN}\%$:

$$\text{MIN}\% = 100/(1 + e^{\text{Tr}\text{MIN}\%}). \quad (5).$$

Finally, we combined Eq. (5) into the backtransformation of Eq. (1) to produce the actual percentage of pupation calculated from regression, $\%P$:

$$\%P = (100 + (e^{\text{Tr}\%P} (\text{MIN}\%)))/(1 + e^{\text{Tr}\%P}) \quad (6)$$

where $\text{MIN}\%$ is calculated from Eq. (5) and $\text{Tr}\%P$ from Eq. (2). To test for goodness of fit, we regressed $\%P$ calculated from Eq. (6) on all the actual percentages of pupation shown in Fig. 1. We found the fit to be close ($r^2 = 0.947$) and used Eq. (6) to draw the curves in Fig. 1.

By setting $\%P$ equal to 50% and calculating $\text{MIN}\%$ using Eq. (5), we solved Eq. (6) for photoperiod by successive approximation. The critical photoperiods, to the nearest 0.05 h, for Mt. Palomar,

Lockwood, Auburn, Yreka, and Halsey were 11.25, 11.85, 12.45, 13.05, and 13.55 h, respectively, indicating that the critical photoperiod of *A. sierrensis* increases one hour for every 4.8° in latitude. This value compares favorably with Beck's (1968) generalization of one h/5° latitude, but is somewhat higher than the one h/5.4° latitude calculated for another mosquito, *Wyeomyia smithii* (Bradshaw 1976, Bradshaw and Lounibos 1977).

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