

## Geography of larval dormancy in the tree-hole mosquito, *Aedes triseriatus* (Say)

CHRISTINA M. HOLZAPFEL AND WILLIAM E. BRADSHAW

Department of Biology, University of Oregon, Eugene, OR, U.S.A. 97403

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Among *Aedes triseriatus* from 30–40° N latitude, photoperiod and temperature mediate the onset and maintenance of larval diapause. Photoperiod has a significant effect not only on the initiation and maintenance of diapause but also on the rate of postdiapause development, both directly and by modifying response to temperature. The critical photoperiod for larval diapause is shorter than that for controlling rate of development. Over most of the range considered, both the critical photoperiod for the induction and maintenance of larval diapause and that for rate of development are shorter than the critical photoperiod governing embryonic diapause. Based on relative photoperiodic response and censuses of overwintering populations, we conclude that larval diapause in *A. triseriatus* is mainly a backup or fail-safe system for embryonic diapause and that the major adaptive significance of larval diapause relates to the modulation of late winter and spring development rather than to overwintering, *per se*.

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Chez *Aedes triseriatus*, à des latitudes de 30 à 40° N, la photopériode et la température sont responsables du déclenchement et du maintien de la diapause larvaire. La photopériode a une influence significative non seulement sur ces deux paramètres, mais aussi sur la vitesse de développement après la diapause, d'une part directement, et d'autre part en modifiant la réaction à la température. La photopériode critique de la diapause larvaire est plus courte que la photopériode qui détermine la vitesse du développement. Dans presque toute l'étendue de la région d'étude, la photopériode critique du déclenchement et du maintien de la diapause larvaire et la photopériode critique de la vitesse de développement sont plus courtes que la photopériode critique qui contrôle la diapause embryonnaire. D'après la réaction relative à la photopériode et le recensement des populations après l'hiver, il est permis de croire que la diapause larvaire d'*A. triseriatus* est surtout un système palliatif infaillible de la diapause embryonnaire et que son importance, du point de vue de l'adaptation, est surtout reliée au contrôle du développement à la fin de l'hiver et au printemps plutôt qu'à la survie pendant l'hiver *per se*.

[Traduit par le journal]

### Introduction

*Aedes triseriatus* is a multivoltine mosquito which is broadly distributed throughout central and eastern North America, ranging from Florida through central Texas north to Maine (Zavortink 1972). It breeds primarily in the rotholes of deciduous trees, although it may also frequent more temporary containers as well (Jenkins and Carpenter 1946; Clay and Venard 1972). *Aedes triseriatus* may overwinter either as embryos or as larvae in a photoperiodically initiated and maintained state of diapause. Embryonic dormancy may be induced among *A. triseriatus* from any latitude (Baker 1935; Kappus and Venard 1967; Clay and Venard 1972; Shroyer 1979) in temperate North America. Larval dormancy has been described as mainly occurring among southern populations (Clay and Venard 1972; Love and Whelchel 1955; Wright 1966; Wright and Venard 1971) although Clay and Venard (1972) reported that they were able to induce diapause among larvae hatched from overwintered eggs. On a geographic scale, embryonic dormancy has been most thoroughly considered by Shroyer (1979) who found that at 21°C, critical photoperiod increased by 1 h for each increase in latitude of 4.2° from Louisiana to northern Michigan. The geography of larval dormancy

has received less attention, and in the present paper, we examine photoperiodic response of larval *A. triseriatus* collected over a range of 12° latitude and 1100 m altitude.

### Materials and methods

#### Collection and rearing

To obtain large numbers of tree-hole mosquitoes, we set out 15–40 old automobile tires at nine localities in eastern North America (Fig. 1). We placed the tires at the base of trees in oak–hickory woodlots and added approximately 0.5–1.0 L of local tree-hole sediment to each tire. The basal position of our tires was intended to bias against oviposition by *Aedes hendersoni* which tend to oviposit in higher tree holes (Sinsko and Grimstad 1977; Scholl and DeFoliart 1977). Spot checks of larvae harvested from these tires revealed no *A. hendersoni*.

Unless otherwise noted, we used wild-caught larvae for all of our experiments. We harvested tires during January and February. Where tires were frozen, we broke out the ice and thawed the contents in large plastic containers. We sorted mosquito larvae from the water and sediment and then, after warming for 24–48 h, pipetted out the pale first instars of *A. triseriatus* which we presumed had just hatched from overwintering eggs. We immediately refrigerated all larvae and shipped them air freight to Eugene, OR, where we maintained them at 5 ± 1°C and short-day photoperiod (8 h light (L) : 16 h

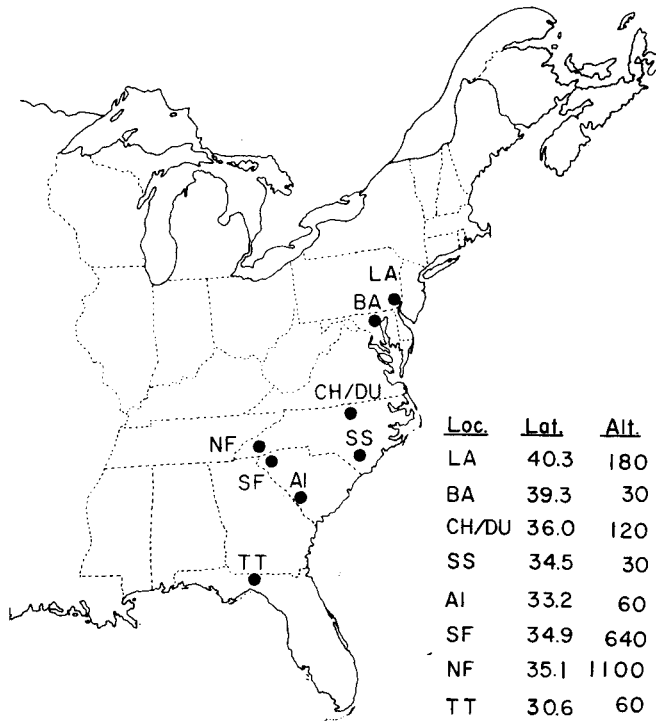


FIG. 1. Source localities of *A. triseriatus*. LA, Bucks Cty, PA; BA, Baltimore Cty, MD; CH/DU, Orange–Durham Cty, NC; SS, Bladen Cty, NC; AI, Aiken Cty, SC; SF, Oconee Cty, SC; NF, Macon Cty, NC; TT, Leon Cty, FL.

dark (D)) until the start of experiments. To induce larval diapause, we placed first instars (wild caught or laboratory reared) on short days (8 h L : 16 h D) at  $16.5 \pm 0.5^\circ\text{C}$  and fed them a mixture of ground guinea pig chow and freeze-dried brine shrimp in a ratio of 2:1, by volume.

In experiments where laboratory reared larvae were used, we collected adults of the parental generation and placed them in moist plastic cages (30 × 15 × 15 cm) at  $25 \pm 1^\circ\text{C}$  and long-day photoperiod (16 h L : 8 h D). Adult food consisted of offerings of human blood three times weekly, supplemented with molasses treated with paramethylhydroxybenzoate to inhibit mold formation. Fifty adult females were inseminated by induced mating (Holzapfel and Bradshaw 1976) and housed together in another plastic cage maintained at high humidity. Oviposition readily occurred in artificial tree holes constructed by enclosing a 50-mL paper towel lined jar within a black cardboard cylinder with a 2.5-cm hole cut in the side to allow entry. Each cylinder stood about 10 cm high and measured approximately 5 cm in diameter. F<sub>1</sub> eggs were collected by removing the paper towel lining of the jar every 2 days. Eggs were stored at  $24 \pm 1^\circ\text{C}$  under long-day conditions (16 h L : 8 h D) in high humidity chambers. Hatching was stimulated after allowing a minimum of 10 days for embryogenesis by immersing eggs in anaerobic tree-hole water treated with baker's yeast. Larvae were treated as above.

#### Statistical treatment of data

Regressions or correlations requiring fits to sigmoid curves were carried out similarly to those of Jordan and Bradshaw (1978). We first transformed the sigmoidally distributed independent variable to a linear distribution by

$$[1] Y_{tr} = \ln [(MAX - Y_i)/(Y_i - MIN)]$$

where  $Y_i$  is the individual observation, MAX is the largest value of  $Y_i$ , and MIN is the smallest value of  $Y_i$ . To avoid either a zero denominator or numerator in equation 1, we added 0.1% or 0.01 to the maximum value and subtracted 0.1% or 0.01 from the minimum value of percentage or rate data, respectively. In dealing with real data, there may be repeated asymptotic values (e.g., zeros at the leading and 100's at the trailing end of sigmoid percentage distributions); these values will flatten out regression lines. Where inflection points of the curve are important, we delete from a given distribution all but one of the upper and one of the lower asymptotic values, retaining those closest to the mode. Regression of  $Y_{tr}$  on a set of independent variables yields the regression equation

$$[2] \hat{Y}_{tr} = a + bX_1 + cX_2 + \dots nX_m$$

where  $a, b, c, \dots n$  are constants determined by regression. Backtransformation to the original coordinate system is given by

$$[3] Y = \frac{MAX + MIN e^{\hat{Y}_{tr}}}{1 + e^{\hat{Y}_{tr}}}$$

When dealing with percentage data, the asymptotes may be set *a priori* (but see Jordan and Bradshaw 1978 for an exception); when dealing with other data, the asymptotes are not necessarily so apparent. Furthermore, under a given experimental condition expected to yield a maximum or minimum response, there will be a scatter of points. The asymptote in this case is best represented by the mean rather than extreme value of the scatter of points. Thus, for nonpercentage data such as rates, we ran the initial regression on mean values but tested for goodness of fit by correlating all of the original, individual observations with those predicted from regression.

Critical photoperiod is normally defined (Lees 1955; Beck 1968; Danilevskii et al. 1970) as the number of hours of light per day which induces 50% of an insect population to enter or maintain diapause. If one is dealing with sigmoidally distributed data, the critical photoperiod may be taken as the inflection point on the sigmoidal curve (Jordan and Bradshaw 1978). From equation 1, it can be seen that this inflection point, being half way between the asymptotes, would have an expected value of zero. Hence, the inflection point may be found by solving equation 2 for photoperiod with  $\hat{Y}_{tr}$  set equal to zero.

#### Sex ratio

We estimated the sex ratio of overwintering populations from the frequency of adult males and females emerging from our photoperiod experiments. To avoid complications due to differences in response to temperature and photoperiod between males and females, we tallied the numbers of each sex only from temperature–photoperiod combinations which evoked 100% development during the course of the experiment.

## Results

### Age distribution and sex ratio in winter collections

In January 1975, during a warmer than normal winter

TABLE 1. Departure of winter temperatures (mean monthly temperature for December, January, and February) from normal ( $^{\circ}\text{C}$ ) for climatic divisions surrounding or near collection sites of *Aedes triseriatus* during 1975 and 1977

Collection site	Climatic division	December 1974	January 1975	February 1975	December 1976	January 1977	February 1977
TT	Florida, northwest	0.0	+1.6	+2.2	-2.6	-5.8	-2.9
AI	South Carolina, central	+0.7	+2.6	+2.1	-1.3	-6.1	-1.3
SS	North Carolina, southern coastal	+0.7	+2.1	+2.2	-1.6	-6.4	-1.7
CH/DU	North Carolina, central Piedmont	+0.1	+1.6	+1.4	-1.8	-6.6	-1.2
NF,SF	North Carolina, southern mountains	+0.3	+2.2	+2.1	-1.4	-6.9	-1.4
LA/BA	New Jersey, southern	+2.3	+2.8	+1.3	-2.4	-5.8	+0.3
Mean	Eastern North America, 30-40° N	+0.7	+2.2	+1.9	-1.8	-6.3	-1.4

(Table 1), we found larvae of *A. triseriatus* as far north as Pennsylvania (LA); tanned first and second instars were abundant farther south in North Carolina (CH/DU, SS). Larvae in all instars were abundant in north Florida (TT) (Fig. 2).

Samples taken in January 1977; during a colder than normal winter (Table 1), showed dramatic changes in the distribution of instars as well as numbers of individuals when compared with 1975 (Fig. 2). In the winter of 1977, we found no larvae north of southern North Carolina (SS); even at this latitude and southwards, we encountered an order of magnitude fewer larvae than we had observed in the winter of 1975. At all locations warming of the tire contents produced prolific hatching of first instars within 24-48 h.

In 1975, the frequency of males from north Florida (TT) was highest among larvae collected as overwintering fourth instars and lowest among those caught as second instars (Table 2). Although 95% confidence limits indicated no significant difference in the percentage of males among third and fourth instars, both these instars had a significantly higher proportion of males than would be expected from an equal distribution of the two sexes. Among the  $F_1$  progeny of the larvae collected in 1975, there was an equal frequency of males and females, indicating a primary sex ratio of 1:1 in this population.

In 1977 (Table 2), males predominated among overwintering fourth instars and females among first instars which hatched upon warming of the tire contents. However, only among the fourth instars was the sex ratio significantly distorted from an equal distribution.

#### Temperature and photoperiod effects on larval diapause and development

To assess the state of dormancy among overwintering larvae, we exposed wild-caught, fourth instars from North Carolina (collected 2 February 1974, at SS) to a variety of photoperiods at 25, 21, and 16.5 $^{\circ}\text{C}$ . Ten larvae were exposed to each treatment; they were fed

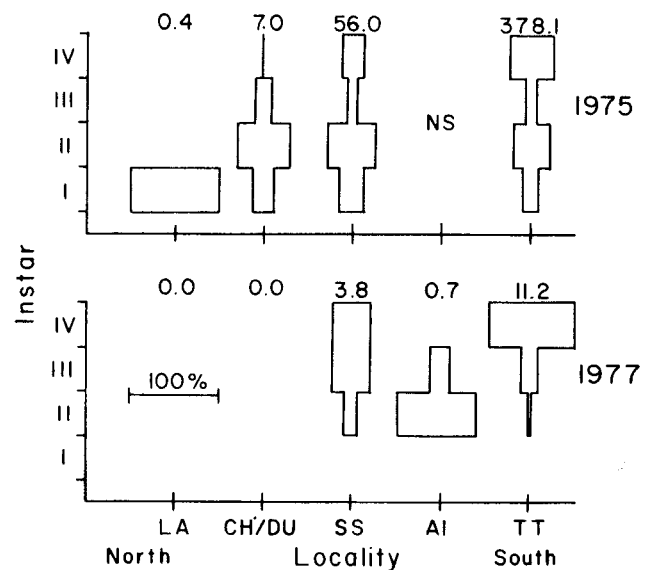


FIG. 2. Age distribution of *A. triseriatus* overwintering in tires during 1975 and 1977. The percentage of the population in a given instar is shown by the width of the bar. Average population size per tire is shown at the top of each age distribution. NS, not sampled.

and checked daily for 80 days, at the end of which time the experiment was terminated and development scored. Those remaining as fourth instars were presumed to be in diapause. Figure 3A shows that the duration of the fourth instar was less than 80 days at all temperatures and photoperiods; at each temperature, however, photoperiod had a significant effect on the duration of the fourth instar. This effect of photoperiod became progressively more pronounced as temperature declined. Thus, while photoperiod did not maintain dormancy among wild-caught, overwintering fourth instars, it had a substantial effect on the rate of development.

To examine the combined effects of temperature and photoperiod on the initiation and maintenance of dormancy, we reared the  $F_1$  progeny of the above larvae from the day of hatch under the same conditions described above until they had pupated or had spent 80 days as fourth instars. As shown in Fig. 3B, only larvae

TABLE 2. Sex ratio of overwintering and laboratory reared *Aedes triseriatus* from north Florida (TT)

Conditions of collection	Number of adults examined	% males among resulting adults	$\chi^2$
Collected as overwintering fourth instars, January 1975	127	72±8*	25.6†
Collected as overwintering third instars, January 1975	91	69±10	13.5†
Collected as overwintering second instars, January 1975	66	56±12	1.0‡
F <sub>1</sub> progeny of 1975 collections, reared in the laboratory	219	50±7	0.1‡
Collected as overwintering fourth instars, January 1977	52	83±10	22.2†
Collected as freshly hatched first instars, January 1977	60	43±13	1.1‡

\*± 95% confidence limits.

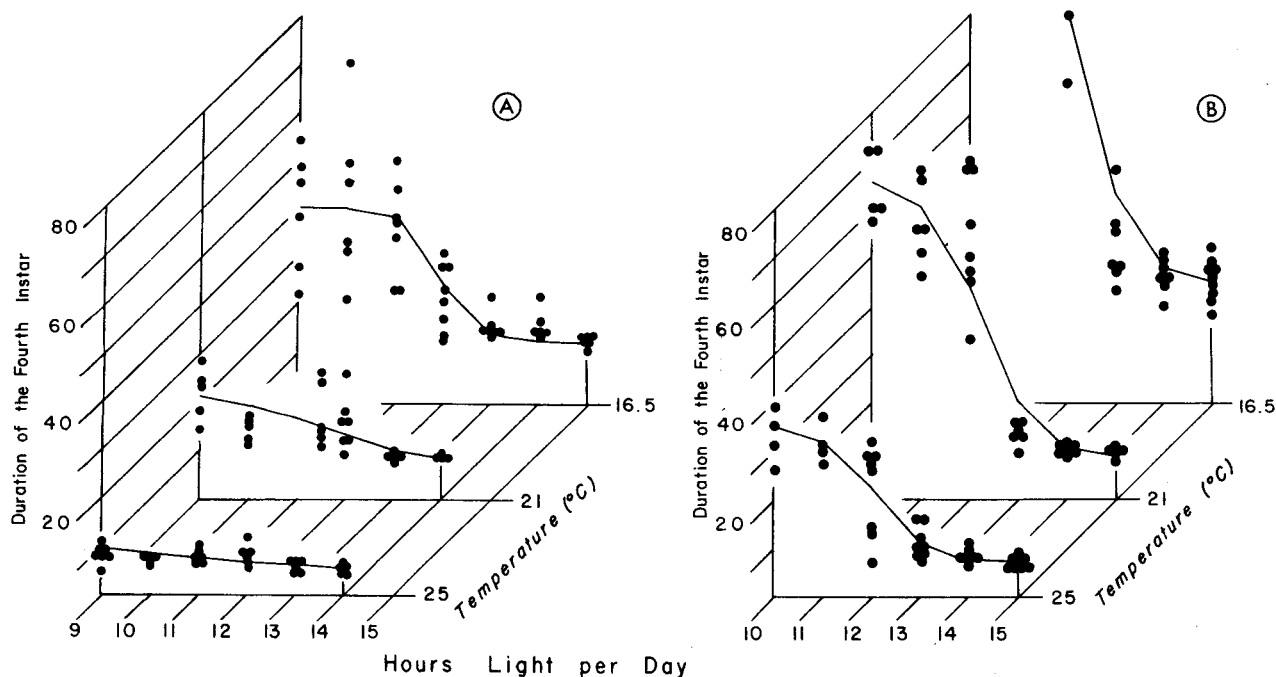
† $P < 0.01$  that frequency of males is 50%‡ $P > 0.05$  that frequency of males is 50%.

FIG. 3. Duration of the fourth instar of *A. triseriatus* at 16.5°C among (A) larvae caught as fourth instars in nature and (B) their F<sub>1</sub> progeny reared in the laboratory. Lines were fit by regression (equation 1) of transformed mean duration on photoperiod at each temperature and connect points predicted (equation 3) from that regression.

experiencing temperatures of 16.5°C spent 80 days or more as fourth instars, i.e., entered diapause. At 21 and 25°C, all larvae pupated after spending less than 80 days in the fourth instar but the duration of the fourth instar was strongly affected by photoperiod at both temperatures.

The data presented in Fig. 3 show that larval diapause is induced and maintained only by short days at low

temperatures. To further investigate the temperature-photoperiod interaction, we collected and reared larvae from South Carolina (AI) and Florida (TT) on short days (8 h L : 16 h D) at 16.5°C and then exposed the resulting diapausing fourth instars to eight photoperiods at 16.5 and 12°C. Fourth instars were fed and checked daily for 100 days after which time the experiment was terminated and development scored.

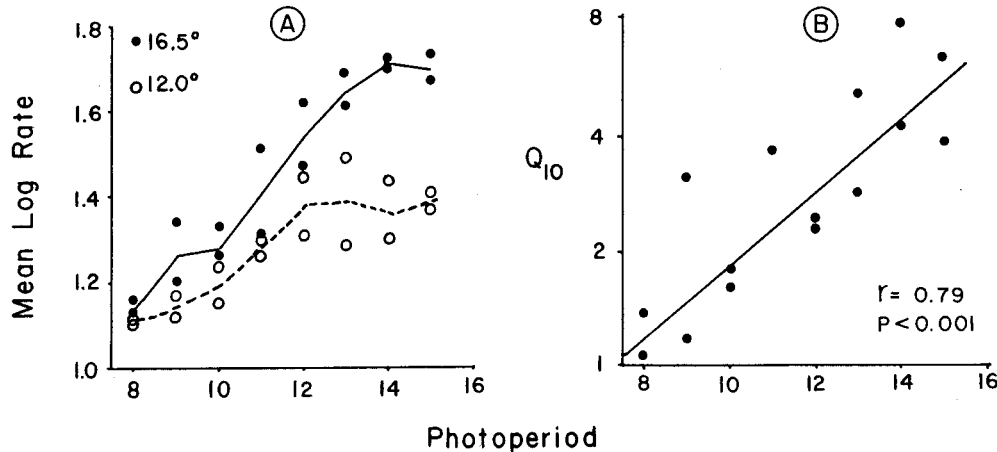


FIG. 4. Interaction of photoperiod and temperature at lower temperatures. (A) Effect of photoperiod on the rate (log (1000/days)) of completion of the fourth instar at 12 and 16.5°C; (B) effect of photoperiod on  $Q_{10}$  at these lower temperatures.

As expected from the above results, rate of development was depressed at the lower as compared with the higher temperature (Fig. 4A). Three-way analysis of variance indicated significant effects of locality ( $F_{1,31} = 10.48$ ;  $P < 0.01$ ), photoperiod ( $F_{7,31} = 29.30$ ;  $P < 0.01$ ), and temperature ( $F_{1,31} = 69.04$ ;  $P < 0.01$ ). However, photoperiod accounted for 63% of the variance in mean log rate of development and temperature for an additional 21%, but locality for only 3%. Among the first-order interactions, only that between temperature and photoperiod was significant ( $F_{7,31} = 3.48$ ;  $P < 0.01$ ). Thus, response to temperature was mainly a function of photoperiod, and the  $Q_{10}$  for rate of completion of the fourth instar was proportional to photoperiod (Fig. 4B).

#### Geography of diapause maintenance

To determine the effects of photoperiod on the maintenance and termination of larval diapause in the laboratory, we could not rely upon wild-caught fourth instars, since they were unavailable at many latitudes. To obtain comparable cohorts from a variety of localities, we therefore collected the first instars resulting from the warming of tire contents, reared them from the first to the fourth instar on short days (8 h L : 16 h D) at 16.5°C in the laboratory, and exposed 10–20 fourth instars to each of eight photoperiods at 16.5°C. We examined the response of larvae from six localities (TT, AI, DU, SF, NF, BA) spanning 9° of latitude and 1100 m of elevation.

Figure 5A shows that geography has a dramatic influence on the maintenance of diapause in *A. triseriatus*. Percent development was significantly correlated with photoperiod ( $F_{1,24} = 41.2$ ,  $P < 0.001$ ), latitude ( $F_{1,24} = 18.5$ ,  $P < 0.001$ ), and altitude ( $F_{1,24} = 9.0$ ,  $P < 0.01$ ). The coefficients of the regression equation

$$[4] \hat{\phi}_{tr} = -16.8 + 1.28 \text{ latitude} \\ + 0.00503 \text{ altitude} - 2.99 \text{ photoperiod}$$

provide an altitude to latitude conversion factor of 254 m = 1° latitude, and the latitudinal axis in Fig. 5A is based on this conversion. The critical photoperiod for the maintenance of larval diapause is then given by

$$[5] \text{ Critical photoperiod} = -5.60 \\ + 0.427 \text{ latitude} + 0.00168 \text{ altitude}$$

Thus, critical photoperiod increases by 1 h for each increase in latitude of 2.34° or for each increase in elevation of 595 m (Fig. 6).

Figure 5B shows that geography has a similarly strong effect on rate of development in *A. triseriatus*. Rate of development was significantly correlated with photoperiod ( $F_{1,34} = 32.0$ ,  $P < 0.001$ ), latitude ( $F_{1,34} = 46.0$ ,  $P < 0.001$ ), and altitude ( $F_{1,34} = 17.6$ ,  $P < 0.001$ ). The coefficients of the regression equation

$$[6] \widehat{\log \text{ rate}}_{tr} = -3.42 + 0.331 \text{ latitude} \\ + 0.00125 \text{ altitude} - 0.685 \text{ photoperiod}$$

provide an altitude to latitude conversion factor of 266 m = 1° latitude. The critical photoperiod for rate of larval development at 16.5°C is given by

$$[7] \text{ Critical photoperiod} = -4.98 \\ + 0.486 \text{ latitude} + 0.00182 \text{ altitude}$$

Thus, critical photoperiod increases by 1 h for each increase in latitude of 2.06° or in altitude of 549 m (Fig. 6).

#### Discussion

Our observations of tire contents (Fig. 2) support earlier conclusions made in the laboratory (Clay and Venard 1972; Love and Whelchel 1955; Wright 1966; Wright and Venard 1971) that the incidence of *A. triseriatus* overwintering as diapausing fourth instars increases at lower latitudes. However, as evidenced by the abundant hatching of first instars upon warming tire contents, a substantial proportion of the population may

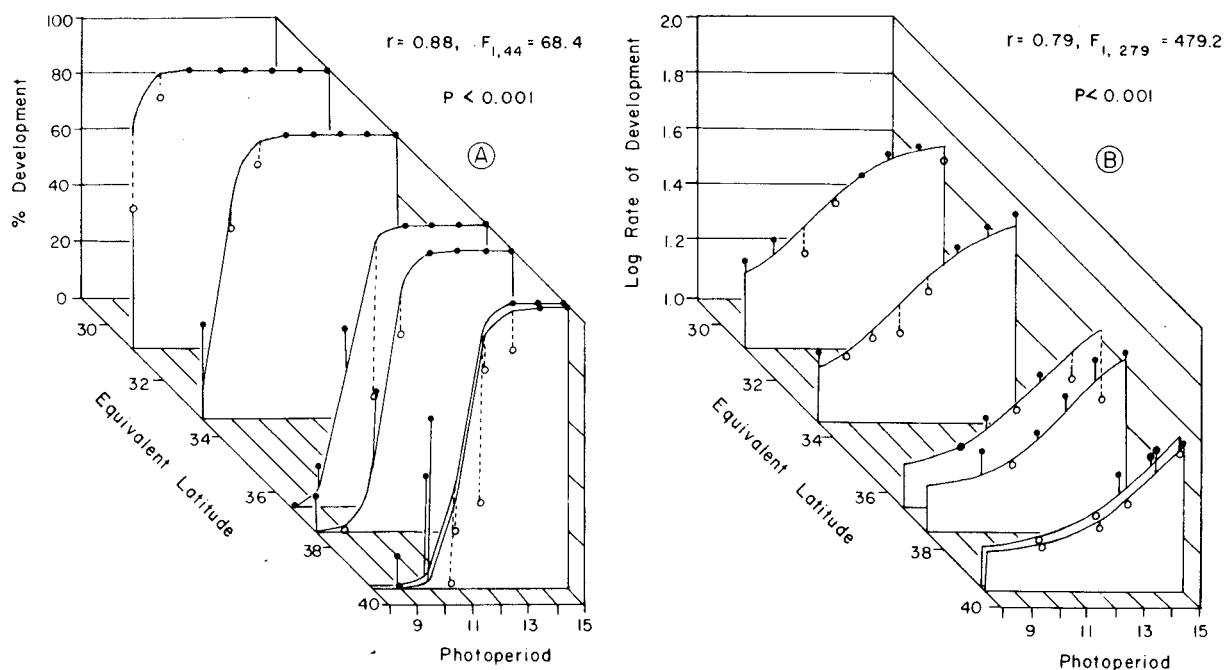


FIG. 5. Influence of geography of origin and photoperiod on (A) maintenance and termination of fourth instar diapause and (B) rate of development (log (1000/days)). Equivalent latitude is calculated by converting units of altitude to units of latitude with the conversion factors described in the text. The correlation coefficient in Fig. 5B was derived from regression of actual individual rates on mean log rate predicted by the backtransformation of equation 6.

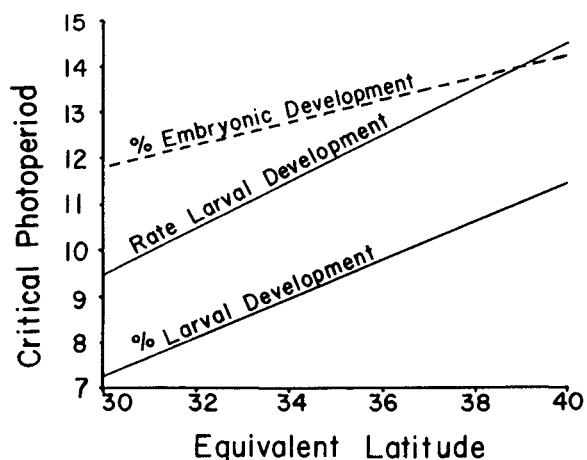


FIG. 6. Change of critical photoperiod with latitude. Percent larval development and rate of development are plots of equations 5 and 7, respectively; percent embryonic development is a plot derived from Shroyer (1979, Fig. 15).

overwinter as embryos at any locality and this proportion may vary considerably from year to year. Shroyer (1979) found that *A. triseriatus* from all latitudes in temperate North America (but not peninsular Florida) are capable of diapausing as embryos and that this diapause could be terminated by prolonged chilling as well as photoperiod. We expect that the first instars we recovered from thawed, warmed tire contents in January were individuals which had commenced overwintering as diapausing embryos, had undergone chilling, had terminated diapause, and lacked but the appropriate,

immediate stimulus to evoke hatching. This stimulus usually consists of anaerobic water (Novak and Shroyer 1978), conditions which exist in freshly thawed tires or tree holes. We therefore propose that individual *A. triseriatus* may potentially undergo diapause twice, once as an embryo and once again as a fourth instar.

Polymorphism for stage of dormancy is not unique among insects in general (Harvey 1961; Corbet 1956; Geispits 1965) or mosquitoes in particular (Lounibos and Bradshaw 1975; Jordan 1980). The present polymorphism in *A. triseriatus* may consist of both genetic and environmental components. Since individuals may undergo embryonic diapause, larval diapause, or both, or avert diapause altogether, the diapausing state itself is largely under environmental control among the populations considered: individual genomes produce the appropriate phenotype in response to environmental cues such as temperature and photoperiod.

Three observations suggest a genetic component. First, populations vary geographically in the incidence of overwintering fourth instars (Fig. 2). Second, cold winters are correlated with changes in the incidence of overwintering fourth instars at a given locality. These changes are in the same direction as indicated by latitude, i.e., cold winters at a given locality reduce the number of *A. triseriatus* overwintering in the fourth instar. Third, as shown by the variation about the regression lines in Fig. 5A, there is considerable variability in the incidence of fourth instar diapause, especially among larvae from northern latitudes or

higher elevations in North Carolina. This same variability is reflected by the rate of development as well. In Fig. 5B, the reduction in sums of squares due to regression is 0.85 for mean rates alone but 0.63 for individual rates on rate predicted from regression of means.

Even though there is a correlation between changes in the incidence of overwintering fourth instars with geography and weather, these changes may be the direct result of weather itself and not changes in gene frequency. The initiation and maintenance of embryonic diapause has both a higher temperature threshold and longer critical photoperiod (Shroyer 1979) than the initiation or maintenance of larval diapause (Fig. 6). Thus, during the late summer and early fall, as both temperature and photoperiod decline, embryonic diapause will be induced at earlier dates than larval diapause. Given the rapid rate of development of larval *A. triseriatus* (Figs. 5B and 3) at higher temperature and longer photoperiods, one could well ask under what conditions they would ever overwinter as diapausing fourth instars. We can envision at least two situations. First, at the end of the growing season, *A. triseriatus* may have depleted resources in their tree holes or tires such that there are not sufficient resources for the completion of development. In that event, larvae may persist until daylengths are short enough and (or) temperatures are low enough to induce diapause in the fourth instar. Second, many of the larvae we observed (Fig. 2) may not represent individuals which originally attempted to overwinter as larvae. Rather, they may have resulted from overwintering embryos which, having undergone chilling, terminated diapause and hatched in response to one or more transient thaws or warming periods. Evidence for the latter interpretation is derived from two observations. First, apart from northern Florida in 1977, the bulk of the larvae found overwintering in tires are in a variety of instars, not just the fourth. Second, the frequency of males among fourth instars in winter tires (Table 2) is greater than among younger instars (Table 2, 1975) or embryos (Table 2, 1977). Shroyer (1979) observed that the sex ratio among the first *A. triseriatus* to hatch in Indiana was distorted towards males, while subsequent batches were increasingly biased towards females. Thus, in northern Florida (Table 2), the first overwintering embryos to hatch would be expected to consist mainly of males; subsequent batches hatching will be increasingly rich in females. At some later time, the tires are sampled and the first batch to have hatched will be represented by the older instars, the later batches by younger instars or, as in 1977, by embryos. Hence, if the overwintering larvae are the result of embryos which hatch in response to one or several transient warming periods, the frequency of males should be proportional to the developmental age of the cohorts, as is observed. Both nutrient depletion and transient warming periods are more likely at lower latitudes where growing seasons

are longer and transient thaws are more likely to be warm enough to stimulate hatching.

The adaptive significance of fourth instar diapause in *A. triseriatus* may relate to the modulation of late winter and spring development rather than overwintering. The responses to temperature and photoperiod discussed above suggest that embryonic dormancy is the primary state in which *A. triseriatus* enter winter. During the winter, they undergo chilling and may either terminate diapause or become more responsive to diapause terminating stimuli similarly to *Toxorhynchites rutilus* (Bradshaw and Holzapfel 1977). Development of larvae which hatch during the winter or spring then becomes dependent on temperature and photoperiod. If they hatch during the winter, days may be short enough and temperatures low enough to induce dormancy in the fourth instar. Longer daylengths would permit continued development, but at a rate which is modulated by photoperiod as well as temperature. Under short-day conditions, the influence of photoperiod prevails and rate of development is little affected by temperature (Figs. 3 and 4). As daylengths increase, temperature becomes increasingly important in governing rate of development. This process is not abrupt as in a more classical photoperiodic response, but proceeds over a photoperiodic range of several hours (Fig. 4B). Vernal development thus represents a gradual change in environmental controlling influences from an evolutionarily consistent factor (photoperiod) to one which tracks the prevailing weather of individual springs (temperature).

The above discussion suggests that embryonic and larval diapause are not discrete, adaptive, developmental strategies, but part of an integrated, finely tuned developmental continuum. Changes in the expression of genes controlling any one aspect would affect the fitness of genes controlling the others. We therefore suspect polygenic control of dormancy and development with diverse pleiotropy underlies the initiation, maintenance, and termination of both embryonic and larval dormancies in *A. triseriatus*.

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