GEOGRAPHIC DIFFERENTIATION IN THE DEVELOPMENT OF *AEDES SIERRENSIS* (DIPTERA: CULICIDAE) IN NATURE

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Abstract

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The critical photoperiod for fourth instar diapause of the western treehole mosquito, *Aedes sierrensis*, varies among geographic populations. When reared together in the field at different latitudes, larvae from northern (ca. 45°N), central (ca. 39°N), and southern (ca. 33°N) populations all develop more rapidly through the early instars at more southerly latitudes. The order of pupation dates among the populations, however, depends on their critical photoperiods, and can be predicted from laboratory data on photoperiodism.

The study of the seasonality of insect development may be approached from two different directions. Either development can be followed in the laboratory under controlled conditions in an attempt to isolate as much as possible the effects of different variables, or the progression of development in the field can be correlated with an array of environmental parameters in the search for useful relationships. These approaches are complementary because the former alone will rarely yield good predictions of actual developmental schedules in the field, while the latter by itself, overburdened with numerous uncontrolled and highly variable parameters, will often fail to clearly expose the causal factors involved. Where photoperiod plays a role in the timing of seasonal development, predictions made from laboratory data may be of more value, since daylength is both accurately measurable and invariate from year to year.

The literature on photoperiodism and its importance in the seasonal development of insects has been reviewed by Danilevskii (1965), who compared the developmental schedules of several lepidopteran species reared at non-native latitudes. These studies are of particular value because of their coupling of laboratory data with field experiments. A more recent discussion of insect photoperiodism is presented by Saunders (1976). Work with mosquitoes corroborates the general trends found in other groups, particularly the relationship of critical photoperiod to latitude or elevation of origin. Bradshaw (1976) has described this effect most precisely for *Wyeomyia smithii*, the pitcher plant mosquito, but geographical variation in critical photoperiod has also been documented in *Anopheles freeborni* (Depner and Harwood 1966) and *An. maculipennis* (Vinogradova 1960), in the rockhole mosquito *Aedes atropalpus* (Anderson 1968), and in the treehole mosquitoes *Ae. triseriatus* (Kappus and Venard 1967) and *Ae. sierrensis* (Jordan and Bradshaw 1978). Here I report the results of experiments in which larvae of northern, central, and southern populations of *Ae. sierrensis* were reared at different latitudes in the field, and I compare these data with the photoperiodic response of these same populations in the laboratory.

Materials and Methods

To determine photoperiod and temperature relationships in the laboratory, I exposed wild-caught or F_1 first instars of *Ae. sierrensis* collected in 1977 at Halsey, Oregon (44°35′ N), St Helena, California (38°35′ N), and Pala Mission, California (33°21′ N), to a variety of photoperiods at 12°, 16.5°, and 21°C (methods in Jordan and Bradshaw 1978), considering a larva to be in diapause if it spent more than 45, 30, or 15 days, respectively, in the fourth instar. Throughout this paper, these populations are referred to as northern, central, or southern, whereas the sites of the field experiments are referred to by name.

For the field experiments I obtained first instars of the three populations by flooding dry treehole debris collected in the fall of 1978. In early November I placed

Table I. Sites of the field experiments (all in California)

Site	Latitude	Elevation
Clear Lake, Lake County	38°55′ N	440 m
St Helena, Napa County	38°35′ N	110 m
Pala Creek, San Diego County	33°23′ N	208 m
Pala Mission, San Diego County	33°21′ N	125 m

two replicate cohorts ($n = 100$) of each population at each of four field sites (Table I). The larvae were in jars mounted in wooden boxes (Fig. 1), in 400 ml of natural treehole water (a uniform mixture from oak and maple) to which had been added 0.125 g of powdered rat chow as a food source. The jars were open and exposed to the weather, but were covered with mesh to protect the larvae from other disturbances and to prevent the escape of emerging adults. As a natural control, I flooded a treehole at St Helena (from which the central population had originated) at the same time the experiments were begun. I monitored the development of the larvae in this tree hole and in the jars at all four sites approximately every 6 weeks.

I analyzed the extent of development in late December, early February, and late March, using the average stage attained in each jar (assigning instars values of 1-4, pupa 5, and adult 6, discarding jars in which survival from the previous sampling fell below 50%). Analysis of variance can be used with such data since average stage attained is a continuous variable which estimates the progress of morphogenesis in each sample. Error variance in such an analysis is that between replicate samples at each site, not that within a sample jar. I therefore used 2-way ANOVA (Sokal and Rohlf 1969) to examine the differences among the samples by origin and by site of rearing. To estimate the temperatures the larvae experienced during their development, I used air temperature data from the weather station nearest each site (U.S. Environmental Data Service 1978, 1979).

Results

Development in the Laboratory

The results of the laboratory experiments are presented in Fig. 2. At 21°, only the shortest photoperiod (L:D 8:16) elicited a substantial diapause response in any of the three populations, but at the lower temperatures the critical photoperiod was generally much higher. At 12° and 16.5°, short days were effective in halting development of the northern population and of at least some individuals in the central and southern populations. Critical photoperiod for the initiation and main-

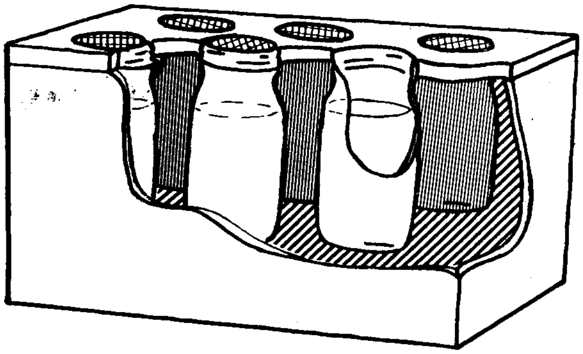

FIG. 1. Design of boxes in which larvae were reared in the field.

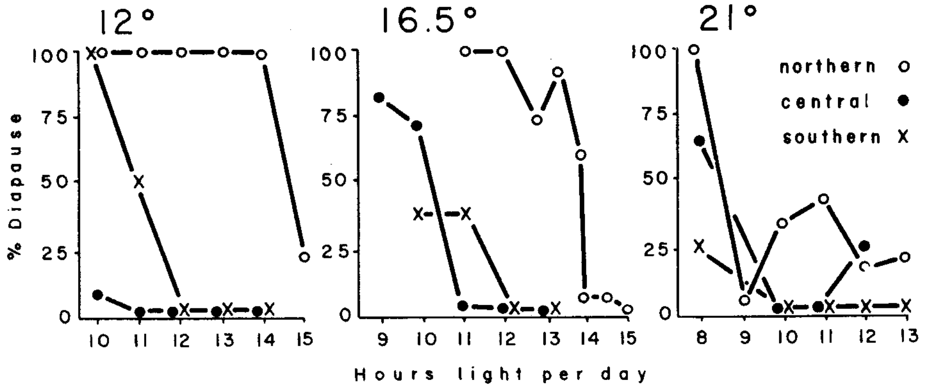

FIG. 2. Diapause in three populations of *Aedes sierrensis* as a function of photoperiod at three temperatures.

tenance of fourth instar diapause was clearly longest for the northern population, but the southern population required a longer photoperiod to sustain development than did the central. These data predict that the sequence of development among these populations should be central-southern-northern.

Development in Nature

There was high mortality at Clear Lake between the December and February samplings, but prior to that time survivorship had been high (averaging 84%). The larvae at St Helena, Pala Creek, and Pala Mission showed high survivorship throughout (85%).

Two-way analyses of variance of the average instar attained in each jar are presented in Table II for the late December, early February, and late March samples. In late December the among-sites component of variation was very significant. There were no significant differences among populations, though the interaction term was marginally significant. In early February there were again no significant differences among populations, and differences among sites were only marginally significant. I therefore pooled populations at each site to show the progress of development after 6 and 12 weeks (Fig. 3). In late December, animals at Pala Mission were the most developmentally advanced, and the age structures at the other sites were progressively younger with increasing latitude or elevation. By early February, most of the larvae had attained the fourth (diapause) instar at all the sites.

In late March (after 18 weeks), analysis of variance revealed significant differences in development both among populations and among field sites (Table II). In marked contrast to the earlier censuses, the among-population component was

Table II. Two-way analyses of variance of average instar attained in late December, early February, and late March for larvae hatched in November

	Late December		Early February		Late March	
Source of variation	d.f.	M.S.	d.f.	M.S.	d.f.	M.S.
Among populations	2	0.0093 ns	2	0.0007 ns	2	2.4927***
Among sites	3	0.8906***	2	0.0031*	2	0.2864***
Interaction	6	0.0325*	4	0.0021 ns	4	0.1941***
Error	12	0.0069	9	0.0007	9	0.0041
Total	23		17		17	

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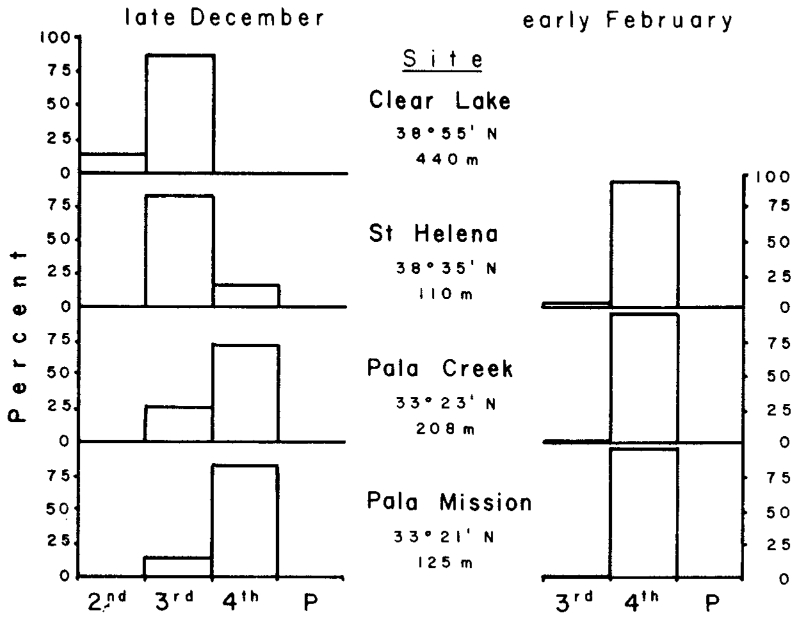
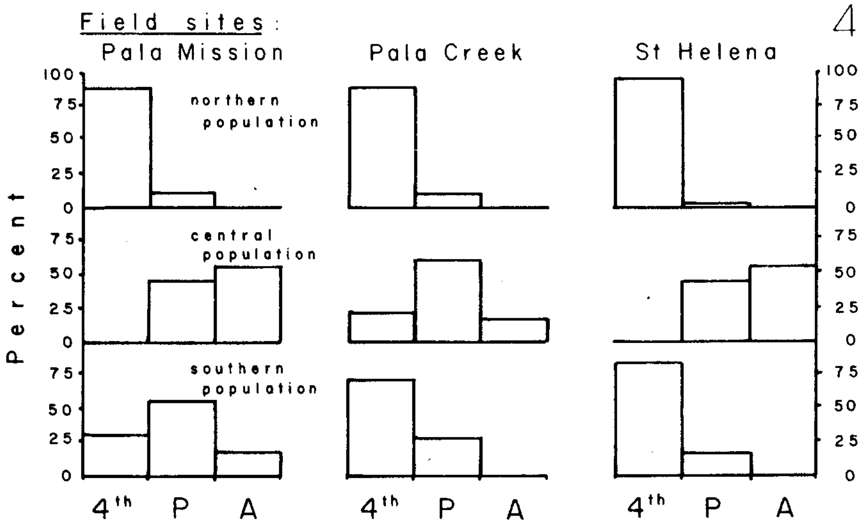
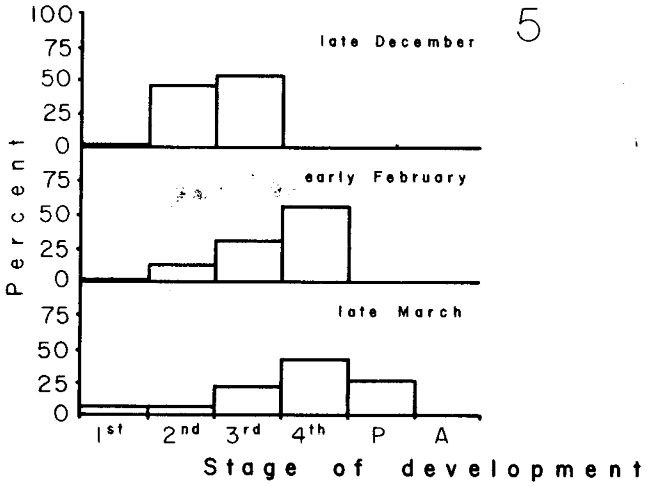

late December
early February
Site
Clear Lake
38°55' N
440 m
St Helena
38°35' N
110 m
Pala Creek
33°23' N
208 m
Pala Mission
33°21' N
125 m
Percent
100
75
50
25
0
2nd
3rd
4th
P

4


Field sites:
Pala Mission
Pala Creek
St Helena
northern population
central population
southern population
Percent
100
75
50
25
0
4th
P
A

5


late December
early February
late March
Percent
100
75
50
25
0
1st
2nd
3rd
4th
P
A
Stage of development

responsible for the majority of the observed variation in development. At all sites the central population had developed the furthest and the northern population the least (Fig. 4). The northern population exhibited little difference in development among the three sites, but a good deal of among-site heterogeneity was apparent in the development of the central and southern populations in late March.

Larval development in the natural tree hole at St. Helena (Fig. 5) consistently lagged behind that in the jars at the same site, and the distribution of life history stages in the treehole was much broader than in the jars.

Temperatures in Nature

The differences in temperature experienced by the larvae among the sites can be estimated from the weekly average weather station temperatures in Fig. 6. The southern California sites were warmer throughout the sampling period. Of the central California sites, that at Clear Lake was cooler than the lower elevation site at St. Helena. All the larvae were continually exposed to lower temperatures in the field than those used in the laboratory experiments.

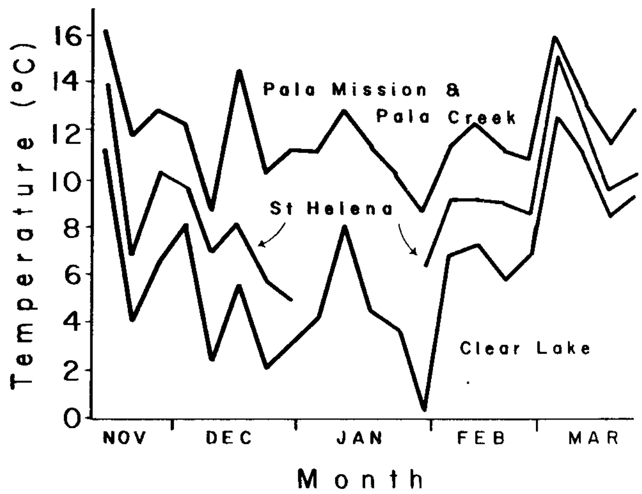


FIG. 6. Weekly average air temperatures from November 1978 to March 1979. Weather station data from Clearlake Highlands, St Helena, and Vista (Pala sites), California. No data available for St Helena in January 1979.

Discussion

The present laboratory findings are not consistent with our earlier work (Jordan and Bradshaw 1978) in that the southern population here exhibited a longer critical photoperiod than did the central population. Neither of these particular populations had been examined at that time, however. Though the correlation of critical photoperiod to latitude is a convenient one for the investigator (since latitude can serve as a rough indicator variable for seasonality at a given locality), the selective factors giving rise to a particular developmental schedule are in reality much more complex, being partly dependent on such local factors as topography and exposure. Gene flow among populations may also influence the critical photoperiod found at any locality.

FIG. 3. Instar distributions in the field experiments in late December (6 weeks) and early February (12 weeks), northern, central, and southern populations pooled at each site.

FIG. 4. Distributions of life history stages for each population at each site in late March (18 weeks).

FIG. 5. Distributions of life history stages in a natural tree hole at St Helena.

In the field, larval development proceeded most rapidly at Pala Mission and Pala Creek (as would be expected due to the warmer temperatures there), and was slowest at Clear Lake, which though only about 50 km from St Helena is some 300 m higher and is colder in the winter months.

In late March, the central population at each site had the most advanced development, followed by the southern and northern populations, consecutively, as the laboratory data predict. Larval growth rates, though they were highly subject to such factors as prevailing temperatures, were of less importance in determining seasonality of ecdysis in these insects than was fourth instar diapause. This conclusion must be tempered by the observation that the natural treehole at St Helena exhibited a broader distribution of instars at any given date than did the experimental jars, and larvae in it lagged behind the experimental animals in development. This result could be due to additional hatching in the treehole after the initial flooding in November (dependent in part on rainfall patterns), to differences in food quality or quantity, and perhaps to differences in temperature, since the more exposed jars undoubtedly warmed up more in the daytime than did the treehole.

The present study is of most value in its confirmation of the differentiation in seasonal development schedules of these insects in nature as predicted by laboratory work on the effects of temperature and photoperiod. The fact that animals from one locality will molt earlier than those from another, even when reared together in the field, suggests a genetic divergence among populations that not only makes the survival of immigrants less likely than that of natives, but probably lessens to some degree the amount of hybridization occurring between them.

Acknowledgments

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