Embryonic Diapause in Three Populations of the Western Tree Hole Mosquito, *Aedes sierrensis*[1,2]

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ABSTRACT

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Northern populations of *Aedes sierrensis* (Ludlow) (Diptera: Culicidae) undergo long-day induced embryonic diapause in the summer as well as short-day induced 4th instar diapause in winter. Photoperiod experienced by the parental generation has no effect on embryonic diapause. The duality of the photoperiodic response confers univoltinism on populations exhibiting both embryonic and larval diapause.

Many species of insects rely on the length of day to trigger the onset or termination of diapause, a state in which development or reproductive activity is suspended. Daylength is the most reliable indicator of season for such insects, enabling them through diapause to avoid annually recurring unfavorable conditions. Among mosquitoes, diapause has been found in every life history stage except the pupa (Clements 1963). We have described the geographic variation in short-day induced 4th-instar diapause in the western tree hole mosquito, *Aedes sierrensis* (Ludlow) (Jordan and Bradshaw 1978). Here I present evidence for an additional diapause in this species, one occurring in the embryo and induced by long daylengths.

Methods and Materials

I collected larvae of *A. sierrensis* in March 1979, from tree holes at Pala Mission, San Diego Co., California (33°21'N), Clear Lake, Lake Co., California (38°55'N), and Halsey, Linn Co., Oregon (44°21'N), and reared them to adulthood as described elsewhere (Jordan and Bradshaw 1978). I maintained the adults under either short-day (SD, light:dark 8:16) or long-day (LD, light:dark 16:8) photoperiods, and transferred newly deposited eggs to either LD or SD conditions. All experiments were carried out at 21°C. The Halsey population was subjected to both parental treatments, but there were only enough animals from California for one parental treatment per population. Thus Clear Lake parents experienced SD, Pala Mission parents LD. I removed replicate cohorts of 25 eggs from each treatment at 10, 20, 30, and 45 days after oviposition, further sampling at 60 and 90 days if eggs were available, and subjected the eggs to a hatching stimulus consisting of immersion in de-aerated (boiled), darkly stained tree hole water for 24 h. The viability of non-hatching eggs was determined by treatment in 2% hypochlorite solution, which dissolves the chorion to expose the embryo. I eliminated cohorts with less than 70% viability, and considered eggs which did not hatch to be in diapause.

To determine if development would resume after prolonged chilling, I transferred eggs from the Halsey population to SD at 5°C following 60 days on either SD or LD at 21°C. I applied the hatching stimulus after 100 days of chilling, and considered the response of the eggs originally on LD separately from the response of those never exposed to LD.

Results

Hatching response for each population and treatment is presented in Fig. 1. The proportional data were subjected to the arcsin transformation before treatments were compared using t-tests. The photoperiod to which the eggs were exposed greatly affected hatching in both the Halsey and Clear Lake populations, but was much less important for the Pala Mission animals, there being a significant difference between treatments only at day 45. Where the incidence of diapause differed significantly, eggs kept on LD were invariably the less likely to hatch. The differences were most pronounced 20 and 30 days after oviposition but decreased in significance in older eggs, most of which appeared to be in diapause. Similar comparisons between parental treatments for the Halsey population revealed a significant difference at only one point (day 30, eggs LD).

Eggs chilled for 100 days at 5°C after initial LD treatment showed a marked increase in hatching, but those originally on SD showed only a modest increase (Table 1). No non-chilled controls of similar age were tested, so chilling effects cannot be distinguished from the effects of age alone.

Discussion

Although photoperiodic control of embryonic diapause has been described in several species of mosquitoes, the stage sensitive to daylength is not the same in all of them. The photoperiod experienced by the parental generation is critical in *A. atropalpus* (Anderson 1968), but only that to which the eggs are exposed is important in the eastern tree hole mosquito, *A. triseriatus* (Kappus and Venard 1967). Pinger and Eldridge (1977) provide a table summarizing such data for a variety of aedines. The effect of parental photoperiod is negligible in the Halsey population of *A. sierrensis*.

The occurrence of diapause at more than one point in the life cycle of an insect has been documented in the carabid beetles *Nebria brevicollis* and *Patrobus atrorufus* (Thiele 1969), whose larvae overwinter and whose adults undergo LD-induced reproductive diapause in the summer. Larval diapause in these beetles is not, however, under photoperiodic control. Masaki (cited in Danilevskii 1965) found both LD and SD induced pupal

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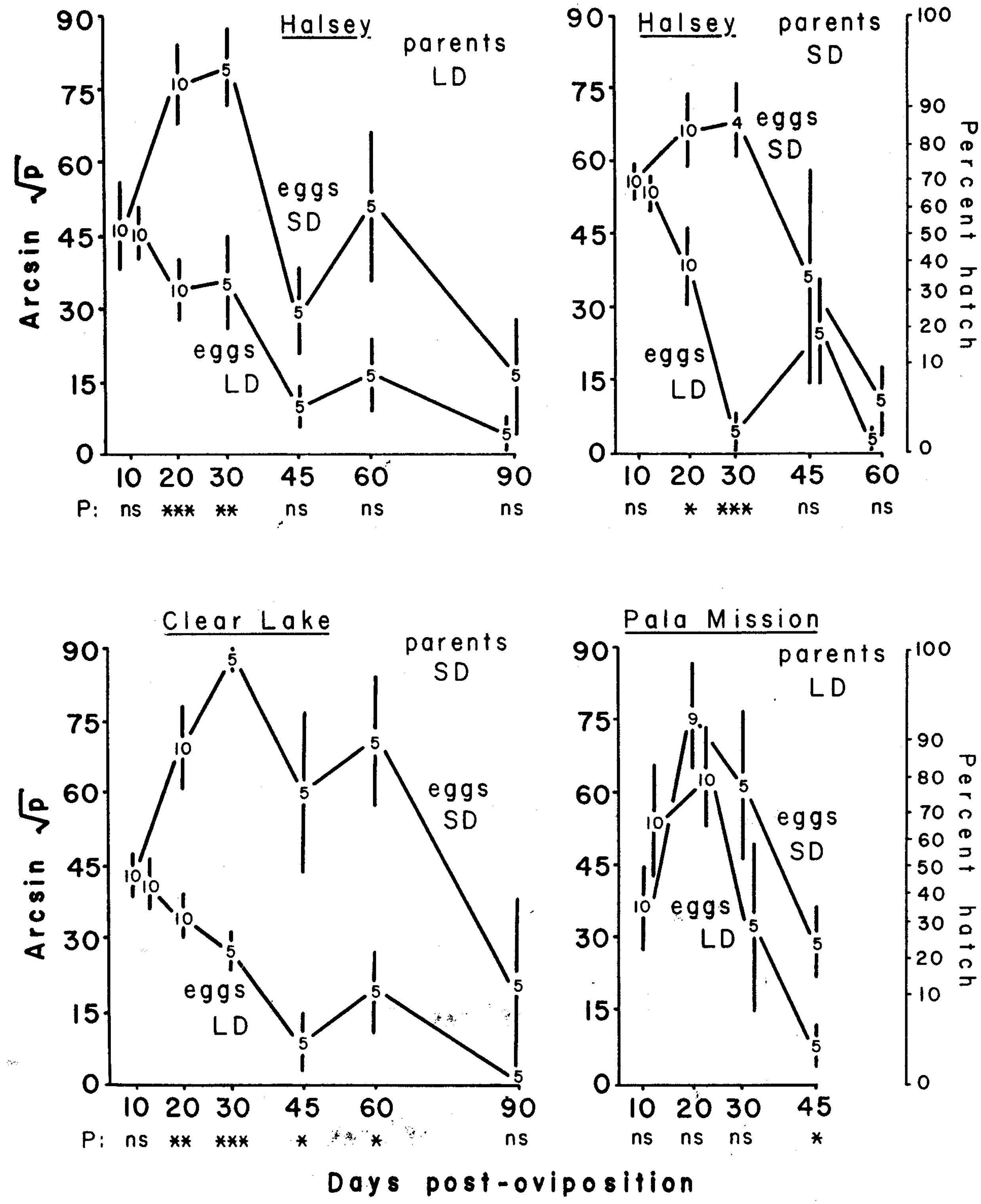

FIG. 1.—Effect of photoperiod on hatching of eggs of *Aedes sierrensis*. Proportions (p) transformed by arcsin $\sqrt{p}$, percent scale shown at right. Significance of differences between means at each interval determined by t-tests: *(P<0.05), **(P<0.01), ***(P<0.001), ns(P>0.05). Deviation of ± 1 S. E. and number of cohorts tested shown for each point.

diapause in some populations of the cabbage moth, *Mamestra brassicae*, but the insects were bivoltine and the diapauses occurred in the spring and summer generations, respectively, thus in different individuals. Diapause is known to occur in both the egg and larva of *A. triseriatus* (Clay and Venard 1972), although embryonic diapause predominates in more northerly areas, and both diapauses are of the SD type. In *A. sierrensis*, embryonic and larval diapauses are induced by opposite photoperiod regimes and both occur in single individuals.

Precipitation along the Pacific Coast is highly sea-

Table 1.—Hatching after 100 days chilling (Halsey population, parental generation on LD).

Egg treatments			
Days 1–60	Days 61–160	n	Hatch (%)
LD 21°C	SD 5°C	246	87.8
SD 21°C	SD 5°C	235	39.2

sonal, nearly all rainfall occurring in winter (Visher 1954). The dual response to photoperiod found in the northern populations of *A. sierrensis* adapts the insects to this climatic cycle. Following adult emergence in spring and early summer, eggs are laid above the water line in tree holes, which are drying out at this time. The eggs enter diapause under the influence of long days and are thus protected from hatching should late spring rains raise the water level temporarily. In the fall, whether through simple aging or the effects of chilling, diapause is terminated and the eggs hatch in response to the flooding of the tree hole by winter rains. The larvae experience short days, enter hibernal diapause in the 4th instar, and are thus protected from premature pupation and ecdysis which might otherwise be brought on by transient winter warming periods. In the spring, development resumes under the influence of long days and the first adults emerge within a few weeks to mate and complete the cycle.

Peyton (1956) believed egg estivation in *A. sierrensis* to be mere quiescence due to lack of summer rainfall. This may be the case for young eggs at Pala Mission, since they can hatch under either light regime in the laboratory, but is not true for eggs from the more northerly populations. As a result of the influence of photoperiod on their development, these populations are univoltine. This univoltinism contrasts with the multivoltinism displayed by *A. triseriatus* (Jenkins and Carpenter 1946), which is able to produce several summer generations in eastern North America, where tree holes can be better relied upon to hold water throughout the summer months.

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