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THE EFFECT OF LARVAL DENSITY ON ADULT LONGEVITY OF A MOSQUITO, *Aedes sierrensis*: EPIDEMIOLOGICAL CONSEQUENCES

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SUMMARY

(1) A 3-year field study of larval populations of *Aedes sierrensis*, a common North American tree-hole mosquito, produced no evidence for density-dependent larval mortality, but revealed that pupal weight of females was inversely correlated with larval density.

(2) Sampling of a wild adult population indicated that, in general, larger adults lived longer than smaller ones. The interval between blood meals in nature was estimated as 8 days.

(3) The total expectation of infective life (for transmission of a nematode, *Dirofilaria immitis*) for females was estimated within the range of larval densities observed in nature. As these estimates may be maximal at intermediate population densities, reduction of larval density may result in an increase in the capacity of the adult population to transmit disease.

INTRODUCTION

Accurate assessment of the longevity of adult female mosquitoes has long been recognized as prerequisite to quantification of the ability of a species to transmit disease (MacDonald 1957; Garrett-Jones & Grab 1964; Garrett-Jones 1964). In no case, however, has it been shown that intraspecific variation in adult longevity may be related in a simple fashion to larval density, and that this relationship has important epidemiological consequences.

The present study shows that for a wild mosquito population (i) pupal size is inversely related to larval density and (ii) adult longevity is positively correlated with adult size. Equations describing these relationships are linked by an equation relating pupal weight to adult size, then used in conjunction with MacDonald's (1957) equation describing adult survivorship to explore the relationship between the total expectation of infective life of females arising from a given population and the larval density of that population.

The treehole-breeding *Aedes sierrensis* (Ludlow) is an appropriate species for this kind of study because: (i) it is common and easily identified; (ii) as its larval habitat is confined, sampling is simplified; (iii) it is univoltine, allowing easy estimation of larval mortality; (iv) it is the only common mosquito inhabiting tree-holes throughout most of its range (Zavortink 1985); and (v) it is a vector of a nematode parasite of canids, *Dirofilaria immitis* (Leidy) (Weinmann & Garcia 1974; Walters & Lavoipierre 1982).

Life history of A. sierrensis

Aedes sierrensis is prevalent on the west coast of North America from southern California to British Columbia. Winters in this region are mild and wet, while summers are

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hot and dry (Steinhauser 1979). Eggs of *A. sierrensis* hatch when tree-holes fill in October, November or December. Larval development continues throughout the winter, with pupation beginning in April and continuing until tree-holes dry up in early summer. Adult activity occurs from May through September.

MATERIALS AND METHODS

Tree-hole censuses

These were performed in Alton Baker Park (123°04'W; 33°03'N) in Eugene, Oregon from 1980–83. Adults were sampled at the same site in 1983. Four, thirteen, and eleven tree-holes were censused in each of three successive seasons. Eleven tree-holes were found in *Acer macrophyllum* (Pursh); two others were located in *Populus trichocarpa* (Torr. & Gray). All were rot-holes, according to the classification of Kitching (1971).

Tree-holes were censused every 4–6 weeks, beginning in the autumn after the first egg hatch and continued until the first appearance of pupae in April. The interval between censuses was then shortened to 6–14 days, depending upon the temperature, to allow collection of all pupae appearing in each tree-hole. Censuses continued until pupal production stopped.

Censuses consisted of measurement of water temperature, removal of all standing water with siphon or pipette, and counting of numbers of each larval instar and pupae. Larvae were returned to the field on the same day. After determining the sex of all pupae present, randomly selected live female pupae were individually weighed to the nearest 0.1 mg after blotting on a paper towel. In 1981, a maximum of twelve pupae from each census was weighed; in 1982 and 1983 up to twenty pupae were weighed per census. Pupae were returned to the field within 2 days after weighing and allowed to ecdyse normally.

The total number of first instars to appear in each hole during each season was estimated from the census figures, tree-hole temperatures, and knowledge of the minimal duration of the first instar over the relevant temperature range (2.5–20 °C). Larval density for each tree-hole was calculated as the number of first instars to appear divided by the maximum observed tree-hole volume for the season. Since pupae were collected from individual tree-holes in cohorts which varied in number and mean weight, a weighted average pupal weight was calculated for each tree-hole.

Sampling of the adult population

The parous rate, or proportion of females that have laid at least one batch of eggs, is a commonly used measure of mosquito survivorship (Service 1976). The probability of surviving from one blood meal to the next (the survivorship per gonotrophic cycle) is equal to the parous rate when two assumptions are met (MacDonald 1957): (i) females bite only once per oviposition cycle and (ii) recruitment into the population is constant throughout the sampling interval. For *A. sierrensis*, both laboratory evidence (Hawley 1985a) and field evidence (see Results) support the first assumption, but the second is obviously false for this univoltine species. Under such circumstances, the population must be sampled from zero recruitment at the beginning of the season to zero recruitment at season's end for the parous rate to be equivalent to survivorship per gonotrophic cycle (Birley, Walsh & Davies 1983).

Adults were therefore sampled from their first appearance in spring until their late-summer disappearance. The first adult *A. sierrensis* was captured on 12 May, the last on 4 September. Females were collected daily with a small net and aspirator as they

approached the bait (myself) for 1 h periods each afternoon from 9 May to 11 September, 1983 (no collection was made on 27 July). Specimens were frozen, then dissected within 3 days to determine parity by examination of ovarian tracheation (Beklemishev, Detinova & Polovodova 1959). Wing length of each individual was measured with an ocular micrometer.

Estimation of the duration of the gonotrophic cycle (the interval between blood meals) was accomplished by methods described in detail in Birley & Rajagopalan (1981). In this method, a correlation index (R) is calculated for the relationship between total (parous + nulliparous) daily captures and total parous females captured using successive integer estimates of the duration of the gonotrophic cycle (U). The best estimate of the average oviposition period is obtained when the value of R is maximal (excluding $U = 0$).

RESULTS

Larval density, metamorphic success, and pupal weight

Pupation success of *A. sierrensis* did not depend on larval density (Fig. 1a), but mean pupal weight of females was inversely density dependent (Fig. 1b). Data for 3 years were included in Fig. 1; analysis of covariance indicated no difference between years for either relationship.

Adult longevity and the interval between blood meals

The total catch of 883 adult female *A. sierrensis* was sorted according to size, divided into ten categories with approximately equal numbers, and a parous rate was estimated for each size category. Median wing length of each size category was transformed to pupal weight using an equation derived from wing length measurements of 120 females of known pupal weight ($r^2 = 0.95$; $P < 0.0001$), where

$$\text{Pupal weight} = -0.12 + 0.075 (\text{wing length})^3. \quad (1)$$

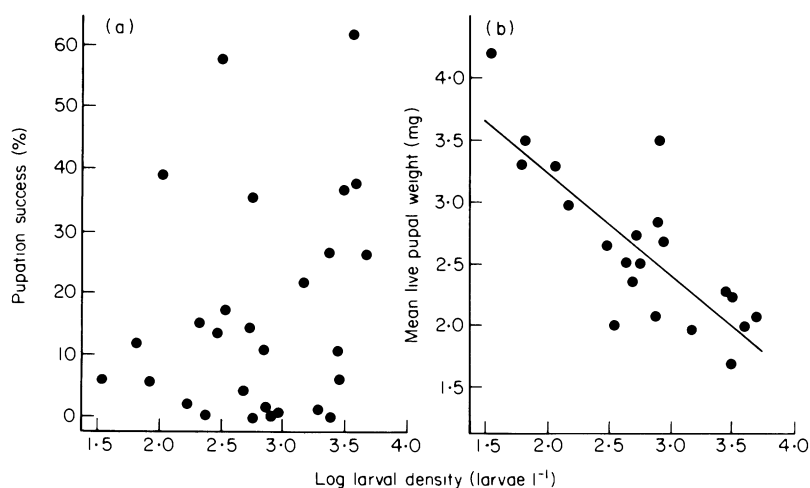


FIG. 1 (a) The relationship between per cent pupation and log larval density of *A. sierrensis* in nature ($r^2 = 0.059$; $P > 0.2$); (b) Mean live pupal weight of *A. sierrensis* females as a function of larval density ($r^2 = 0.62$; $P < 0.001$). The regression equation is: pupal weight = $4.882 - 0.817$ (log larval density).

Adult longevity of a mosquito

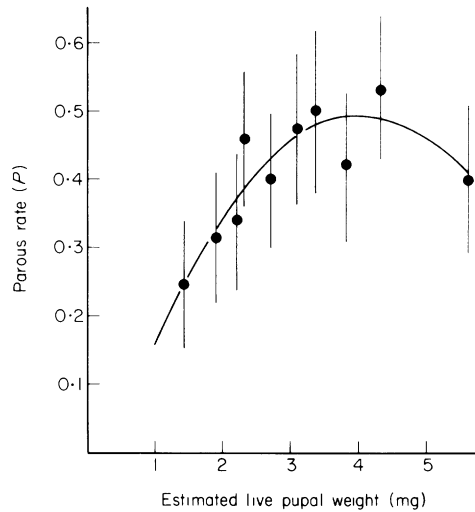


FIG. 2. Proportion parous (mean \pm 95% C.I.) as a function of estimated pupal weight for wild-caught *A. sierrensis* females ($r^2 = 0.74$; $P_x < 0.005$; $P_{x^2} < 0.005$). The regression equation is: parous rate = $-0.100 + 0.296$ (pupal weight) $- 0.0369$ (pupal weight) 2 . Under the sampling conditions used in this study, parous rate is equivalent to the probability of surviving from one blood meal to the next.

The relationship between adult parous rate and estimated pupal weight was curvilinear (Fig. 2) but, in general, groups of larger females had higher parous rates than smaller ones. Since only two of 883 blood-seeking females contained partially digested blood meals, indicating a very low level of multiple feeding per gonotrophic cycle, assumption (i), above, was met and parous rates shown in Fig. 2 were equivalent to the survivorship rate per gonotrophic cycle.

The correlation index (R) attained a clear maximum at $U = 8$; the best estimate of the average interval between blood meals in nature was therefore 8 days (Table 1).

TABLE 1. Estimates of the correlation index (R) obtained from the entire season's data for different estimates of the interval between blood meals (U). The best estimate of U in nature is that for which R is maximal (for $U \neq 0$)

Estimate of U (days)	Correlation index (R)
0	0.74
1	0.50
2	0.50
3	0.42
4	0.38
5	0.47
6	0.46
7	0.58
8	0.62
9	0.59
10	0.54
11	0.52
12	0.54

EXPECTATION OF INFECTIVE LIFE OF ADULTS

If the mortality rate is age independent, and the probability of surviving through 1 day is equal to p' , the expectation of life of an adult mosquito n days old is given by (MacDonald 1957)

$$\frac{p^n}{-\ln p} \quad (2)$$

p is equal to the U th root of P , where U is the interval between blood meals (in days) and P is the probability of surviving from one blood meal to the next. A female can transmit a particular parasite only if she has lived at least as long as the extrinsic incubation period of that parasite. Setting n equal to the parasite's extrinsic incubation period in eqn (2) allows, therefore, calculation of the expectation of infective life (E) of an individual mosquito whose daily survival rate is known. E is equivalent to the 'longevity factor' of Garrett-Jones & Grab (1964). The extrinsic incubation period of *D. immitis* in *A. sierrensis* was measured as 28 days in California (Walters & Lavoipierre 1982). Since temperatures during the period of that study were somewhat higher than those prevalent in Oregon when *A. sierrensis* is active, 30 days was used as an approximation of the duration of the extrinsic incubation period in the calculations presented here.

For *A. sierrensis*, adult longevity depended upon pupal size (Fig. 2), which depended upon larval density (Fig. 1b). Calculation of the E of individual adults arising from any initial density was based, therefore, on the regression equations fitted to data in Figs 1b and 2 (Table 2). A measure of the capability of a mosquito population to transmit disease is simply the sum of the E ($\sum E$) of all females constituting it, and this was calculated for each population density assuming 10% larval survivorship, tree-hole volume = 1 l, and a realized sex ratio of 50% at all densities. Thus,

$$\sum E = E \times \text{no. larvae} \times 0.1 \times 0.5. \quad (3)$$

TABLE 2. Equations used to calculate the expectation of infective life ($\sum E$) of female *A. sierrensis**

Slope**	Equation	Number
b_1	$PW = 4.882 - 0.817(\log D)$	(3)
$+b_1$	$PW = 5.734 - 1.121(\log D)$	(3a)
$-b_1$	$PW = 4.030 - 0.513(\log D)$	(3b)
b_2	$P = -0.100 + 0.296(PW) - 0.0369(PW)^2$	(4)
$+b_2$	$P = -0.346 + 0.449(PW) - 0.0584(PW)^2$	(4a)
$-b_2$	$P = 0.145 + 0.144(PW) - 0.0153(PW)^2$	(4b)

* PW = pupal weight; D = larval density; P = parous rate or survivorship per gonotrophic cycle.

** b , regression equation; $+b$, upper and lower 95% C.L., respectively.

Figure 3a shows the relationship between $\sum E$ and population density where pupal weights were calculated using either eqn (3), (3a) or (3b) from Table 2, but calculation of P was in each case based on eqn (4). p' was determined by taking the 8th root of P . Estimates of $\sum E$, assuming no size-dependent adult longevity, were included for comparison. At densities greater than about 1000 larvae l^{-1} , $\sum E$ calculated from these equations was always less than the estimates that assumed size-independent survivorship; the steeper the

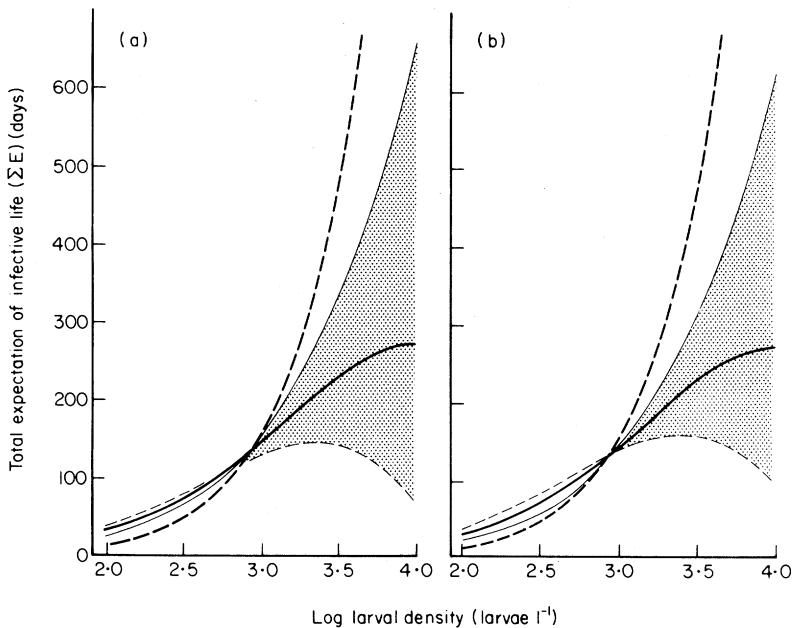


FIG. 3. The total expectation of infective life (ΣE) of *A. sierrensis* females arising from different population densities. (a) The effect of varying the slope of the relationship between pupal weight and log larval density is illustrated: (---), ΣE calculated using eqns (3a) and (4) or (—), eqns (3b) and (4) from Table 2. (b) Same as (a) but the slope of the relationship between the parous rate and pupal weight is varied: (---), ΣE calculated using eqns (3) and (4a) or (—), eqns (3) and (4b) from Table 2. (---), ΣE calculated assuming density-independent adult longevity; (—), E calculated using eqns (3) and (4) from Table 2.

slope relating pupal weight to density, the more pronounced the effect. When the slope was very steep, ΣE peaked at an intermediate population density.

In Fig. 3b, pupal weight was calculated from eqn (3), while P was calculated using either eqn (4), (4a) or (4b). As the slope relating P to estimated pupal weight was increased, the greater was the departure from size-independent ΣE at high densities.

Some key assumptions

Equation (2) is valid only if the rate of adult mortality was age independent. For some species, mortality rate increases with age (Clements & Paterson 1981); for *A. sierrensis*, the nature of the relationship between age and mortality rate in nature is unknown.

Equation (3) is based upon within-year differences between tree-holes, but calculation of ΣE at different densities assumes that this equation is applicable to between-year differences in mean population density. If eggs are oviposited in tree-holes independently of their quality, this assumption will be valid. Female *A. sierrensis* oviposit in tree-holes before the input of nutrients for their offspring; this may make it unlikely that ovipositing females have evolved the capacity to predict the future quality of tree-holes. Nevertheless, it should be noted that if female *A. sierrensis* do preferentially oviposit in high quality tree-holes, the slope of eqn (3) will be shallower than the real between-year slope, resulting in overestimation of ΣE at high population densities.

The assumption of an invariable gonotrophic cycle of 8 days was, of course, false. Eight days was merely the best estimate of the average interval between blood meals; the method

of estimation of this parameter did not yield a measure of its variance. A related assumption, that the interval between blood meals was independent of adult size, was substantiated by laboratory data (Hawley 1985a).

DISCUSSION

The total expectation of infective life calculated from equations in Table 2 differs greatly from that predicted on the assumption of size-independent adult survivorship only when larval densities are in excess of about 1000 larvae l^{-1} (Fig. 2). If natural densities of *A. sierrensis* are less than this value, then the results of this study might be dismissed as an oddity irrelevant to the biology of this species. In fact, densities of *A. sierrensis* commonly exceed that figure, both in Oregon (Hawley 1985b) and in the southern parts of its range. Density-dependent adult survivorship is therefore of real epidemiological significance, and should be considered when designing control measures for this species.

Though Hawley (1985b) estimates the equilibrium population density of *A. sierrensis* in Oregon to be at least 1200 larvae l^{-1} the maximum value in that study is biologically unreasonable. For the present analysis, the equilibrium population density is assumed to be 1000–10 000 larvae l^{-1} . If reduction of pupal size at high densities is due to competition for food, the effect of control measures causing mortality late in larval development cannot be assessed from data presented here. If, however, control is attempted by release of sterile males or introduction of an agent which kills early larval instars, the following analysis is appropriate. Inspection of Fig. 3 shows that the effect upon $\sum E$ of reducing population density is dependent upon (i) the initial population density and (ii) the degree to which the population is decreased. If slopes of either eqn (2) or (3) have been underestimated, $\sum E$ may actually increase, though numbers of active females be reduced. In the worse case, where the slopes of both equations are underestimated, a 90% reduction in density (from 10000 to 1000 larvae l^{-1}) would result in a more than 16-fold increase in the capacity of the population to transmit *D. immitis* (Fig. 4).

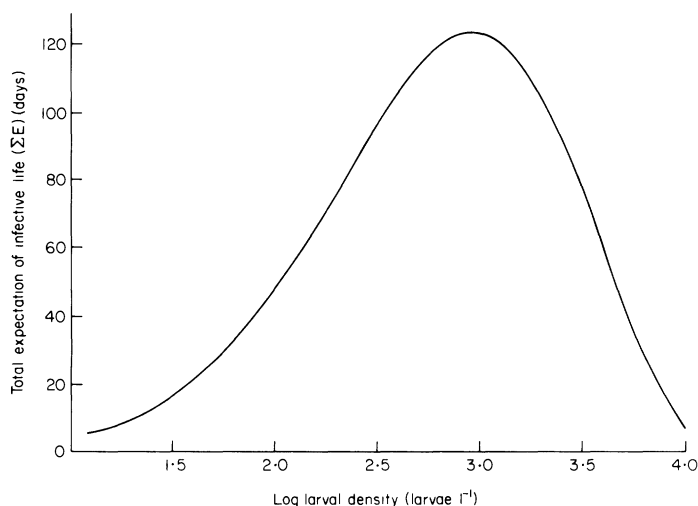


FIG. 4. The worst case of the relationship between total expectation of infective life ($\sum E$) and population density, eqns (3a) and (4a) from Table 2 were used in the calculation of $\sum E$ at each density.

The theoretical possibility that release of sterile males might increase the number of active females has been recognized, but egg to adult mortality must be overcompensating (Berryman, Bogyo & Dickmann 1973). This result probably has little relevance to natural mosquito populations: mortality in these populations is either undercompensating (Chubachi 1979; Dye 1984) or not density dependent (Nikolaeva 1979; Seifert 1980; Bradshaw & Holzapfel 1983; Mogi, Miyage & Cabrera 1984). In contrast, the effect of reducing density upon $\sum E$ in *A. sierrensis* depends upon the coexistence, in a single species, of two phenomena known to occur in mosquitoes: density-dependent size variation and size-dependent adult survivorship.

Density-dependent size variation occurs in mosquito populations in nature (Mogi 1984) and is repeatedly observed in the laboratory (Terzian & Stahler 1949; Wada 1965; Nayar 1969; Greenough, Peters & Barbosa 1971; Barbosa, Peters & Greenough 1972; Reisen 1975; Nekrasova 1976; Mori 1979; Gilpin & McClelland 1979; Carpenter 1983). Instances of failure to find density-dependent larval development rate or survivorship in nature are known, but these studies did not consider size at metamorphosis as a possible variable. Results from the present study show that pupal size may be density dependent even though larval survivorship is not, indicating that size at metamorphosis is more sensitive to increased density than larval survivorship. I know of no case of failure to find density-dependent size at metamorphosis in a mosquito population where the study has been designed to look for such an effect.

The ubiquity of size-dependent survivorship of adult female mosquitoes is less certain. The phenomenon has been reported for wild populations of *Aedes triseriatus* (Haramis 1983) and overwintering *Culex pipiens pallens* (Makiya & Taguchi 1981), but results for laboratory populations are mixed (Makiya & Sakurai 1975; Reisen 1975; Moeur & Istock 1980; Steinwascher 1982). Negative results from laboratory studies should not, however, be extrapolated to nature: survival of *A. sierrensis* adults is not size dependent in the laboratory (Hawley 1985b).

As both phenomena have been commonly observed separately, it is predicted that they will co-occur for many mosquito species in nature. In such instances, the epidemiological significance of density-dependent adult survivorship will depend upon not only the quantitative nature of the relationship, but also upon estimation of: (i) the population's equilibrium density; (ii) the degree to which pre-adult mortality is density dependent; (iii) the extrinsic incubation period of the parasite in question; and (iv) the interval between blood meals. Estimates of (iii) and (iv) are available for many mosquito-borne diseases and their vectors while (i) and (ii) are available for a few mosquito species (Chubachi 1979; Dye 1984). The degree to which adult survivorship is affected by larval density is not known for vectors of any major mosquito-borne disease. While it is recognized that study of a vector's larval population ecology is essential to the development of effective biological control agents (Service 1981, 1983), such analysis is usually limited to patterns of density-dependent larval mortality. The present study illustrates that the effect of larval density upon adult longevity may be, epidemiologically, the more important phenomenon.

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