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POPULATION DYNAMICS OF AEDES SIERRENSIS

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ABSTRACT

A three year field study of the western treehole mosquito, *Aedes sierrensis*, shows that though overall larval mortality and rate of larval parasitism by a ciliate, *Lambornella clarki*, are density-independent, pupal weight of either sex is inversely correlated with larval density. Larger pupae give rise to adults that lay more eggs per batch in the laboratory. In nature, a positive correlation is found between adult longevity and adult size. From these observations, expressions relating larval density to adult fecundity are derived and, in conjunction with estimates of egg and pupal mortality in nature, integrated with the population model of Hassell (1975) to predict that the population density will tend to damp exponentially to an equilibrium level of at least 1,219 larvae/liter. Density-dependent size at metamorphosis is therefore the basis of population regulation in this species. Factors affecting male fitness are briefly considered. Both size at metamorphosis and the time of metamorphosis are important in this regard: larger males can remain active over a wider temperature range than their smaller conspecifics, but early season males have greater opportunity to mate with large, early season, high fecundity females.

INTRODUCTION

Despite the medical importance of the Culicidae, quantitative analysis of the population dynamics of members of this group has been done for only a handful of species. Much discussion of 'population dynamics' of mosquitoes is based on laboratory studies or anecdotal accounts of field populations. Statistical inference based on data from natural populations of mosquitoes is rarely used to predict population behavior. In addition, workers tend to concentrate on either larval or, more commonly, adult populations. Elucidation of population dynamics requires that the appropriate field measurements be made on all stages of the life cycle. That this approach is rarely taken by medical entomologists is evident from the following statement from Varley *et al*.'s (1973) text on insect population ecology:

> "We have found few examples from medical entomology to illustrate the principles of population dynamics. Too often only the easy things have been measured, and the interpretation of the figures demands observations which have not yet been made." (p.1)

Medical entomologists are typically interested in predicting either (1) disease outbreaks due to an increase in the vector population or (2) effects of various control measures upon vector populations. Attainment of the first goal requires identification of the key environmental factors correlated with adult abundance. Many years of data may be necessary; understanding of the process of population regulation is not required. But to progress towards the second goal, an understanding of population regulation is essential. No more than a few years' census data may be necessary, but all of the appropriate parameters must be measured. These include (1) quantification of the response of the population to its own density, (2) estimation of the overall density independent mortality and (3) an estimate of the realized rate of increase of the population. A population which is strongly self-limiting, or is limited by predation or parasitism, may nevertheless exhibit extreme fluctuations in abundance due to the influence of environmental factors. Understanding of population regulation does not, therefore, allow one to predict fluctuations in abundance with great accuracy, but it can provide a rough indication of long term population behavior and abundance. More importantly, it allows realistic prediction of the effects of various control methods on the animal's vectorial capacity.

In this study, I report the results of an investigation of the population dynamics of the western treehole mosquito, *Aedes sierrensis* (Ludlow), in which the main question is: "How is the population regulated?"

STUDIES OF THE IMMATURE STAGES

The life cycle of *A. sierrensis* is adapted to the seasonal rainfall pattern of the west coast of the United States (Fig. 1):

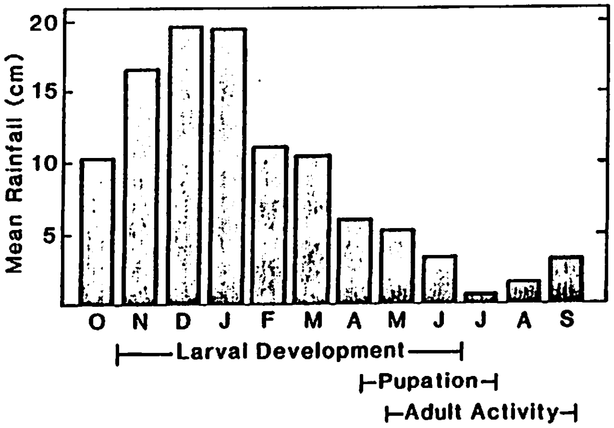

Fig. 1. Thirty year mean rainfall pattern at Eugene, Oregon and its relationship to the life cycle of *A. sierrensis*.

Eggs hatch when treeholes fill in October, November or December. Larval development continues throughout the winter, with pupation beginning in April and continuing until treeholes dry up in early summer. Adult activity occurs from May to September. One generation is produced each year.

Egg survivorship

Egg survivorship was estimated as follows: 20 ovitraps constructed according to the design of Mortenson *et al*. (1978) but equipped with maple paddles were placed in the field for one week in late June, 1983. After 10 days, the paddles were collected and eggs on each paddle counted. It was observed that eggs were oviposited only on the side of the paddle adjacent to the wall of the ovitrap. Ten paddles with eggs were then placed in two dry treeholes (five per treehole) with the paddles rotated so that the side with eggs faced towards the center of the hole. Further oviposition, if it occurred, would therefore be on the side of the paddle without the experimental eggs. The paddles were left undisturbed in the treeholes for four months, until November. One treehole had flooded by the time the paddles were retrieved; no unhatched eggs were visible on any of the five paddles, but many split, empty eggs were visible. Eggs on the other five paddles were recounted, then subjected to a strong hatching stimulus in the laboratory. No newly oviposited eggs were observed on the paddles. Two trends are evident in the data (Table 1):

Table 1. Egg survivorship of *A. sierrensis* on five ovitrap paddles, after four months in treeholes, and number and percent hatch after flooding with water of low O_2 tension in the laboratory.

No. eggs oviposited on paddles	865
No. eggs remaining on paddles after four months in treeholes	464
No. hatched	377
Percent hatch of remaining eggs	81.3
Percent hatch of original eggs	43.6

(1) after four months in the treehole the number of eggs on the paddles is reduced and (2) among the eggs still attached to the paddles, hatchability is very high. The reduction in number of eggs on the paddles could be due to predation, decomposition of infertile eggs, or a result of eggs simply dropping off the paddles into the treehole. I believe the last explanation to be the most probable, since some eggs still present on the paddles after four months were loosely attached. Nevertheless, both estimates of egg survivorship are used in subsequent calculations.

Larval survivorship

Two complications arise when studying larval populations of this species. Very large numbers of larvae can be found in single treeholes -- densities (defined as the cumulative number of first instars to appear during the season divided by the maximum observed treehole volume for that season) of several thousand larvae per liter of water are commonly encountered (Table 2):

Table 2. Numbers and first instar larval density of A. sierrensis in treeholes in Eugene, Oregon, for all censuses combined.

	1981-2		1982-3	
Treehole no.	No. first instar larvae	Log density (larvae/liter)	No. larvae	Log density
1	4,159	1.54	8,228	1.82
2	310	2.95	165	2.67
3	899	2.39	2.890	3.35
4	5,633	2.83	1,414	2.87
8	204	2.16	377	2.52
10	1,437	3.31	3,797	3.68
12	4,003	3.49	7,172	3.43
16	488	2.48	288	2.06
17	99	3.12	-	-
18	3,616	3.25	959	2.62
21	787	3.45	-	-
22	843	2.85	875	2.77
23	171	2.15	779	2.89

These numbers limit the number of treeholes that can be censused; results of censuses of four, 13 and 11 treeholes in each of three seasons are reported here. The second major complication is the occurrence of at least six different larval parasites (Clark & Fukuda 1967; Sanders 1972; Sanders & Poinar 1973; McClelland et al. 1982). Little is known of the biology of most organisms so their effect on the population dynamics of the mosquito is obscure. One of these parasites is, however, particularly suitable for study: the ciliate Lambornella clarki (Corliss). This parasite is visible within the haemocoel of infected larvae, so infection rates in larval populations can be measured without destructive sampling. Most infected larvae die before pupation while the few infected females which successfully ecdyse show reduced survivorship in the laboratory and fail to mature eggs after feeding (Hawley, unpublished data). The pathogenicity of this parasite is therefore extremely high: once infected, females invariably fail to reproduce.

During the winter, treeholes were censused by removing all water with a siphon or pipette at intervals of about six weeks. The number of individuals of each stage was counted by hand. The minimum duration of the first instar (fed a standard diet ad libitum) at winter and spring temperatures was determined in the laboratory; this information, along with the census data allowed me to estimate the number of first instars appearing in each hole during the season. Treehole volume and temperature were measured at each census, and the percentage of larvae parasitized with Lambornella determined for a sample of each stage. After the appearance of pupae in the spring, the census intervals were shortened to 6-14 days, depending upon the temperature, to allow collection of all pupae appearing in each treehole. Pupae were sexed, and samples of up to 20 of each sex were weighed live to the nearest 0.1 mg. All pupae were returned to the field within two days after collection so as not to adversely affect the adult population.

Data on larval populations were analyzed by regressing percent pupation, percent parasitism by Lambornella, and mean pupal weight of both males and females on log larval density. Only pupal weight (of either sex) was found to be significantly correlated with density (Fig. 2).

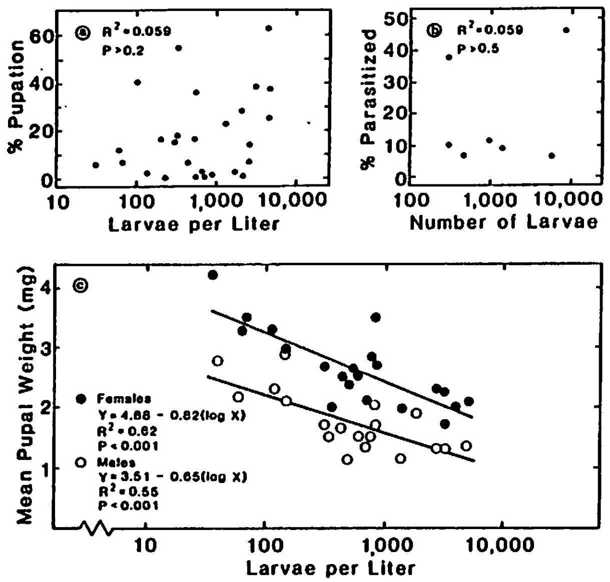

Fig. 2. (a) Relationship between percent pupation and larval density of A. sierrensis in Oregon. Three years of data are lumped. (b) Relationship between percent of larvae parasitized by L. clarki and number of larvae in the treeholes, for treeholes in which the parasite was present. (c) Mean pupal weight of male and female A. sierrensis as a function of larval density. For males, two years' data are lumped; for females, three years.

For females:

$$\text{PUPAL WEIGHT} = 4.88 - 0.82(\text{LOG DENSITY}) \qquad (1)$$

Pupal survivorship

Pupal survivorship was estimated by placing pupae from four different treeholes in restraining containers in the treeholes from which they originated. Containers were constructed of plastic tubing (3.5 cm diameter; 2 cm length; wall 0.5 mm thick) with 1 mm nylon mesh covering the bottom. Containers were attached to a steel rod that provided support at the appropriate depth in treeholes. After sufficient time had elapsed for ecdysis, adults and dead pupae within each container were counted. Of 644 pupae set out in these four holes, 618 or 96% successfully ecdysed.

PUPAL SIZE AND ADULT FITNESS

Pupal weight is inversely proportional to larval density (Fig. 2), but how does pupal size translate into adult fitness of males and females? To answer this question, I examined the relationship between pupal weight and (1) adult longevity, (2) number of eggs laid per batch, and (3) male mating success.

I first examined laboratory populations. Wild-caught pupae were weighed and single females kept with 1-3 males in 0.95 liter jars. Females were offered a blood source every two days and mortality of both sexes was tallied daily. Eggs laid per batch was positively correlated with pupal weight (Fig. 3), where

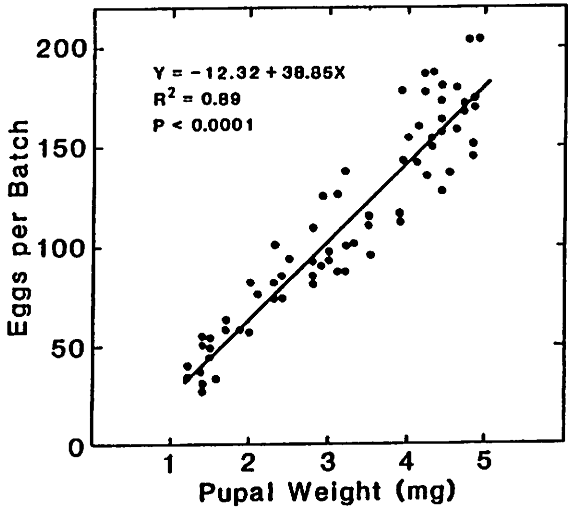

Fig. 3. Number of eggs laid per batch by A. sierrensis captured as pupae and fed to repletion in the laboratory as a function of pupal wet weight.

$$\text{NUMBER EGGS PER BATCH} = -12.32 + 38.85(\text{PUPAL WEIGHT}) \qquad (2)$$

but there was no relationship between adult survivorship and pupal weight for either sex (Fig. 4).

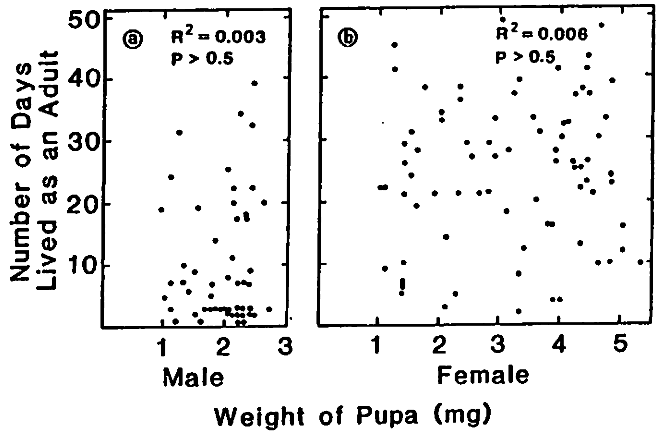

Fig. 4. Survival of adult A. sierrensis in the laboratory as a function of pupal weight.

Although the results displayed in Fig. 4 indicated no size-specific survivorship in the laboratory, it is still important to assess size-specific survivorship and potential fecundity in the field. I was unable to determine gonotrophic age using Polovodova's method (Beklemishev et al. 1959), but could reliably age-grade females into parous and nulliparous age classes. For a mosquito exhibiting gonotrophic concordance, parous rate is equivalent to survivorship per gonotrophic cycle only if recruitment into the population is constant (MacDonald 1957). Though A. sierrensis exhibits gonotrophic concordance, recruitment is clearly not constant. This problem can be overcome by sampling the adult population from the beginning of recruitment until the end, using a series of small samples (Birley et al. 1983). Under such circumstances, parous rate is again equivalent to survivorship per gonotrophic cycle.

I therefore sampled adults daily from their first appearance in May until activity ceased in September. Adults were collected with an aspirator and small net as they approached the bait (myself) for one-hour periods each afternoon from 9 May to 11 September, 1983. The first adult A. sierrensis was captured on 12 May; the last on 4 September. Both sexes were collected, as males of this species exhibit host attendance. Adults were taken to the laboratory and frozen. Females were usually dissected within three days to determine parity; the wing length of each individual of both sexes was also determined.

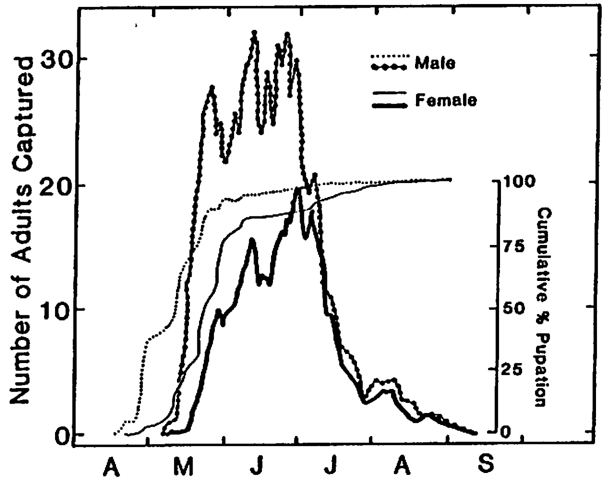

Fig. 5. Eleven day running mean of male and female *A. sierrensis* adults captured during 1983 and the cumulative percent pupation in treeholes at the study site during the same period.

Fig. 5 shows the relationship between number of adults captured (11 day running mean), cumulative percent pupation in treeholes, and date. The median date of pupation of males (11 May) is 12 days earlier than that for females (23 May). This extreme degree of protandry is reflected in the adult collections, also: the ratio of males to females is highest early in the season, gradually decreasing as the season progresses. The overall sex ratio of all pupae collected is not, however, significantly different from that of the total adult sample (Table 3):

Table 3. Sexes of *A. sierrensis* captured as pupae and adults during the spring and summer of 1983.

	No. males	No. females	% males
pupae	2,119	1,288	62.2
adults	1,589	883	64.3

Since both the phenology and sex ratio of the pupal and adult collections are remarkably consistent, it seems likely that the adult collections represent an unbiased sample of the adult population active during the 1983 season.

Female size, survivorship and fecundity

The 883 females captured during the course of the season were divided into ten approximately equal size categories. The median wing length of each size category was transformed to pupal wet weight using an equation derived from lab measurements of the wing length of 120 females of known pupal weight:

$$\text{PUPAL WEIGHT} = -0.12 + 0.075(\text{WING LENGTH})^3 \quad (3)$$
$$(r^2 = 0.95;\ P < 0.0001)$$

where pupal weight is measured in mg and wing length in mm. The relationship between calculated pupal weight of wild-caught adults and the parous rate of each size category is shown in Fig. 6:

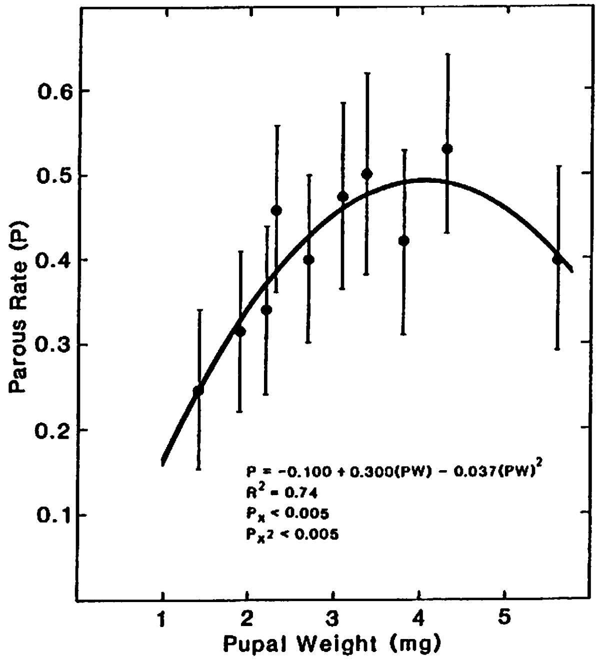

Fig. 6. Parous rate (mean and 95% C.I.) as a function of calculated pupal weight for 883 *A. sierrensis* collected in 1983.

$$\%\ \text{PAROUS} = -0.10 + 0.30(\text{PUPAL WEIGHT}) - 0.037(\text{PUPAL WEIGHT})^2 \quad (4)$$

The relationship is clearly curvilinear, but for 9 of the 10 size classes, an increase in size leads to increased survivorship.

The reason for the decline in survivorship of the largest size class is unknown; perhaps these animals suffer increased mortality due to predators which orient to their prey visually. Assuming that the mortality rate is constant for all age classes, the parous rate for a population sampled in the manner described is equal to the survival rate per gonotrophic cycle. For the purposes of the present analysis, however, we require an estimate of the number of eggs a female of a given size class is expected to produce. If P is the survivorship per gonotrophic cycle, then the number of egg batches laid per female is equal to (Miller *et al*. 1973):

$$\sum_{n=1}^{\infty} P^n = \frac{P}{1-P} \qquad (5)$$

It is now possible to calculate the expected fecundity of a female of a given size, as follows. For each pupal weight, the survival rate per gonotrophic cycle was estimated with equation (4) converted to expected number of egg batches laid with equation (5), and then multiplied by the expected number of eggs laid per batch estimated with equation (2). Fig. 7 illustrates this relationship.

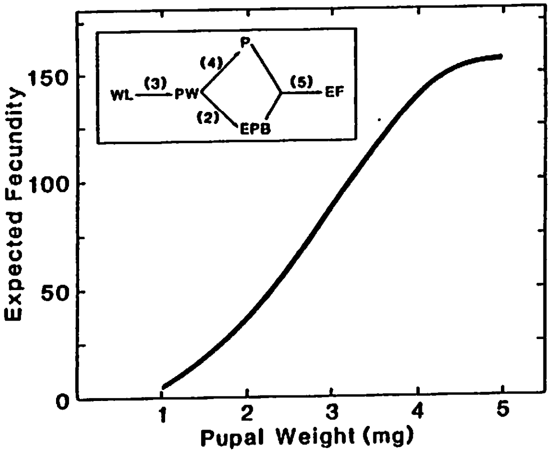

Fig. 7. Expected fecundity (EF) of *A. sierrensis* adults as function of their pupal weight. Inset: method of calculation of EF. Numbers refer to equations in the text (WL = wing length; PW = pupal weight; P = parous rate; EPB = eggs laid per batch).

While the observed variation in weight is only six-fold, the range of expected fecundities varies more than 30-fold. Qualitatively, at least, it therefore appears that density dependent size variation in pupal size could be a factor capable of regulating the population.

Size, temperature, activity and male fitness

Male abundance is maximal during the month of June, yet marked fluctuations are also evident. Much of the fluctuation is due to the fact that smaller males are apparently inactive when temperatures are low (Fig. 8b).

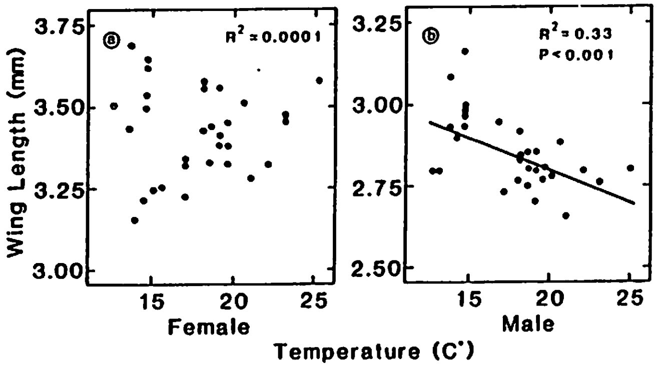

Fig. 8. Relationship between mean wing length of *A. sierrensis* adults and ambient temperature for females (a) and males (b) during the period of maximum abundance for either sex (females -- 10 June to 11 July; males -- 1 June to 30 June).

The same phenomenon does not occur for females (Fig. 8a), which are larger than all but the largest males. Larger males, which are able to remain active over a greater temperature range than their smaller conspecifics, will thus presumably realize greater reproductive success due to increased opportunities for mating. Nevertheless, the timing of male development is probably a more important determinant of male fitness. Fig. 9 shows the wing length of nulliparous females collected at each date. Parous females are not included since these are presumably mated, unavailable to males, and therefore unimportant from the standpoint of sexual selection. At the beginning of the season, the largest females are active. As shown by Fig. 7, these females will exhibit much higher fecundity than those ecdysing later in the season. It is therefore an advantage to males to be ready and waiting to mate with these large females. This advantage to the earliest males, I believe, is the selective force behind the observed high degree of protandry in *A. sierrensis*. This strategy will be effective, however, only if male survivorship is high. Examination of Fig. 5 shows that this is indeed the case: 90% of males have pupated by 26 May, yet the adult male population does not begin its decline until 1 July, indicating that males survive three to four weeks on the average (allowing 8-14 days spent as a pupa).

IMPLICATION FOR POPULATION DYNAMICS

Various models of single species population dynamics have

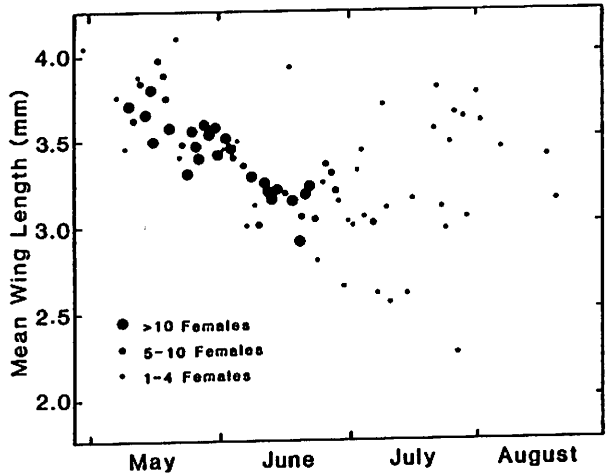

Fig. 9. Mean wing length of daily collections of nulliparous female *A. sierrensis* in 1983.

been proposed (see Bellows 1981, May 1981). Given the appropriate parameters, these models predict (1) long-term population behavior and (2) equilibrium population density (if appropriate). Four categories of population behavior are predicted by these models: (a) exponential damping, (b) damped oscillations, (c) stable limit cycles and (d) chaotic fluctuations. An equilibrium density can be calculated only if the population exhibits behaviors (a) or (b).

For any of the common models, one plots k-value (log mortality or log reduction in fecundity) as a function of log density and, using a least squares technique, fits these data to the appropriate one or two parameter model (Bellows 1981). For *A. sierrensis*, however, all the necessary curve fitting was done in producing equations (1), (2), (3) and (4); the value of k (in this case, log reduction in fecundity) at each log density can be computed directly (with the assistance of a programmable calculator) using these four equations and equation (5). Three such curves are shown in Fig. 10, based on the regression for equation (1) and its 95% confidence limits.

In order to assess the behavior of the population, these calculated relationships (Fig. 10) must be compared to those produced by an appropriate population model. I have chosen that of Hassell (1975) since it is meant to describe a single species population with discrete generations. This model is of the form:

$$k = b \log(1 + aN_t) \qquad (6)$$

where k is the log reduction in fecundity, N_t is the population size, and a and b are parameters describing the shape of the relationship. The parameter b is a measure of the strength of the density dependent effect; its value is equal to the maximum slope of the curve and is used to predict the stability of the population (Hassell 1975). Based on graphical analysis (Fig. 10), b for *A. sierrensis* lies between 0.26 and 0.80. The reduction in fecundity due to size variation is therefore undercompensating and the population necessarily exhibits exponential damping (Hassell 1975). An important assumption should be noted: the calculation of b is based on differences between treeholes, not on between-year overall population differences. Nonetheless, the use of b calculated in this manner will be invalid only if ovipositing mosquitoes can predict, for the year ahead, the amount of food that will be available per ml of treehole water.

The equilibrium density (D*) of the population depends upon the value of three parameters: a and b from equation (6) and F, the realized fecundity of an adult female, adjusted to include the effects of all density independent mortality and the sex ratio. For *A. sierrensis*,

$$F = EF \times S \qquad (7)$$

where S is equal to the product of the observed values for egg, larval and pupal survivorship and the sex ratio (Table 4),

Table 4. Survival rate of eggs, larvae and pupae of *A. sierrensis* in nature. Sample size is given under n; number of years of data in parentheses. Sex ratio is based on 6,525 pupae collected over two years. S is the product of egg to adult survivorship and the sex ratio. Upper (2) and lower (b) estimates of egg to adult survivorship and S are based on the respective estimates of egg survivorship.

	n	Survival rate
Eggs	865(1) 464(1)	(a) 0.436 (b) 0.813
Larvae	49,679(2)	0.128
Pupae	644(1)	0.960
Egg to adult		(a) 0.100 (b) 0.054
Sex ratio (females:males)		0.395
S		(a) 0.0395 (b) 0.0212

and EF is the expected fecundity of a female of given size (Fig. 7). Varley *et al.* (1973) determine D* graphically by finding the density at which k = logF on a plot of k versus log density.

However, in their examples, k is based on mortality and F is assumed to be a constant. For A. sierrensis, since EF is size-dependent (Fig. 7), F will also vary. What value of EF should be used in the calculation of F?

If D_t = larval density at generation t, then

$$\log D_{t+1} = \log D_t + \log EF + \log S \qquad (8)$$

By definition,

$$k = \log EF_{max} - \log EF \qquad (9)$$

where EF_{max} is a female's maximum expected fecundity. Substituting,

$$\log D_{t+1} = \log D_t + \log EF max - k + \log S \qquad (10)$$

At equilibrium $\log D_{t+1} = \log D_t$ and

$$k = \log EF_{max} + \log S \qquad (11)$$

EF_{max} can be estimated graphically from Fig. 7; a more precise iterative estimate is 155.73 eggs, attained at a pupal weight of 4.78 mg. Two estimates of S are used, based on upper and lower measures of egg survivorship (Table 4), allowing two graphical estimates of D* for each plot of k versus log density (Figure 10). A calculator program was then used to find iteratively a more precise value for each D*; these values are shown in Table 5.

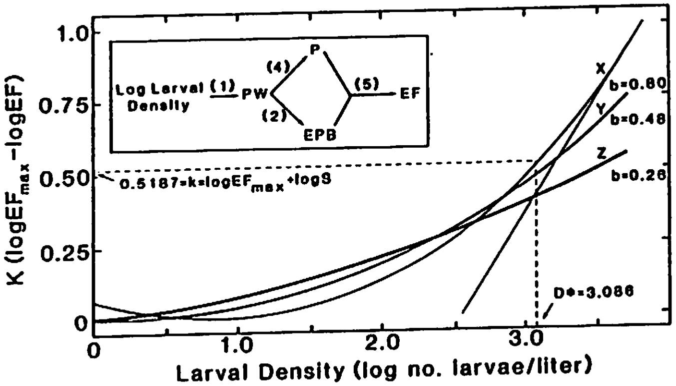

Fig. 10. Plot of k versus log larval density for A. sierrensis. The inset shows the method of calculation of the expected fecundity (EF) of adults produced at each density. Numbers in parentheses refer to equations in the text (PW = pupal weight, P = parous rate; EPB = eggs laid per batch). Plot Y is based on equation (1); plots X and Z are based on the 95% C.I. of equation (1). Slopes (b) of X, Y and Z at maximum density (= the highest density observed in the field) were estimated graphically; such an estimate is shown for X only. The graphical method of estimation of D* is also illustrated, based on X and S = 0.212 (Table 4). Other estimates of D* are listed in Table 5.

Table 5. Estimates of D* (equilibrium density) of A. sierrensis in Oregon, as number of first instars appearing per liter of treehole water during the course of a season. A separate estimate of D* is obtained for each estimate of S (Table 4); two estimates of D* are therefore obtained for each of the three plots (X, Y and Z) of k versus log density shown in Fig. 10. See text for the method of calculation of D*.

	S = 0.0212	S = 0.0395
(X)	1,219	3,412
(Y)	1,552	6,383
(Z)	2,636	25,003

The lowest estimate of D* is 1,219 larvae/liter, indicating that the observed high densities of A. sierrensis in Oregon (Table 2) and in the southern parts of its range (W. H. Hawley, personal obervation) are not transient, but are a consequence of the underlying dynamics of the population.

Analysis of life table data of the sort presented here has been done for only two other mosquito species. Based on reanalysis of data of Southwood et al. (1972) and Sheppard et al. (1969), Dye (1984a) predicted that a population of Aedes aegypti (L.) in Bangkok will exhibit exponential damping to equilibrium; mortality of immatures in this species is undercompensating [b<1 in equation (6)]. Chubachi (1979) also found undercompensating density dependent mortality among larvae of a population of Culex tritaeniorhynchus summorosus Dyar in Japan; exponential damping to equilibrium is therefore expected of this population, also.

Such predicted behavior is typical for insects: Hassell et al. (1976) collated field data on 24 species; most were predicted to exhibit exponential damping. These predictions must nonetheless be viewed with caution, as several forest insects for which many decades of census data are available exhibit long term cyclic changes in abundance, a result, quite possibly, of interaction with viral pathogens (Anderson & May 1981).

DIFFICULTIES WITH THE ANALYSIS: PARASITES

A key assumption in the foregoing analysis is that there is no density dependent mortality due to predation or parasitism. If there is, both the long term behavior and equilibrium level of the population could be altered. In fact, if more than one density dependent factor acts on a population (e.g., a pathogen and intraspecific competition) the order in which the factors affect the population will affect the results of the analysis (Wang & Gutierrez 1980; May *et al*. 1981). In such a case, a simulation model of the population should be developed.

Of the six parasites that have been found in *A. sierrensis*, infection rates as a function of density have been determined only for *L. clarki* which did not exert any density dependent effects (Fig. 2). Of the other five parasites, only one other, *Ascogregarina clarki* (Sanders & Poinar), has been the object of a careful laboratory study (Sanders & Poinar 1973). The pathogenicity of this parasite appears to be negligible, however, indicating that it cannot regulate the mosquito population. The other four parasites have yet to be the subject of a careful laboratory, much less field, investigation. The conclusions reached in this paper regarding the behavior and equilibrium level of *A. sierrensis* populations should therefore be regarded as tentative.

One may wonder how a population can persist at such high densities with so many types of parasites infecting it. I believe that *A. sierrensis* is able to support a diverse array of pathogens because its population density is so persistently high. The concept of a transmission threshold, as postulated by MacDonald (1957) for malaria is also applicable to parasites of vectors -- there exists a threshold density necessary for the persistence of each parasite (Anderson & May 1981). It is therefore not surprising to find many species of pathogens infecting a mosquito, such as *A. sierrensis*, which regulates itself at a high, stable equilibrium density.

CONCLUSIONS

Though weights of *A. sierrensis* females vary only six-fold, the relationships between size, fecundity and survivorship augment each other to produce a more than 30-fold variation in expected fecundity. Since size at metamorphosis in nature is density dependent, size variation is the basis of population regulation in this species. The intensity of the density dependent effect produced by this mechanism is similar to that observed for other mosquito species where mortality was found to be density dependent. Density dependent size variation is a well-known phenomenon among laboratory populations of mosquitoes, but is little studied in nature. It may have been overlooked in other systems where, as for *A. sierrensis*, all observed mortality is density independent. Failure to find density dependent mortality does not, therefore, justify concluding that a mosquito population is not limited by intraspecific competition.

From an epidemiological standpoint, the relationship between adult size and survivorship is of particular importance. Such a relationship has been reported for only two other natural mosquito populations: *Culex pipiens pallens* Coq. (Makiya & Taguchi 1981) and *Aedes triseriatus* (Say) (Haramis 1983, this volume). Both of these species, like *A. sierrensis*, are

relatively long-lived; whether similar results will be obtained for short-lived tropical species remains to be determined.

Since males cannot be age-graded, I was unable to show that larger males live longer than smaller ones, though this possibility cannot be excluded. Larger males are active over a wider temperature range; presumably this ability leads to increased opportunity for mating. Since weight of males at metamorphosis is density dependent, I conclude that male fitness is affected by intraspecific competition. Nonetheless, the timing of male metamorphosis is probably more important than size at metamorphosis in this species; early flying males will have opportunity to mate with large, high fecundity early season females.

LIMITATIONS OF THE STUDY AND IMPLICATIONS FOR CONTROL

The preceding analysis, though it predicts a range of equilibrium densities for *A. sierrensis*, is of no use in predicting year to year changes in adult abundance that inevitably will occur due to variations in weather. I have observed that between year productivity of particular treeholes depends on rainfall; year to year variation in adult abundance should therefore be correlated with some measure of the amount and distribution of winter and spring rainfall.

The analysis is, however, very useful in assessing which means of control are likely to be most effective. The control method used should take advantage of the fact that intraspecific competition is occurring among the larvae. Genetic control measures, such as release of sterile males, will be of limited use since they affect the population before competition occurs.

Habitat destruction (filling of treeholes) is an appropriate control method for this animal. In the long run, the adult population would be reduced in proportion to the percentage of treeholes destroyed. Furthermore, the emerging adults will be the same reduced size as those emerging from an unperturbed population. Of course, treeholes are often cryptic. The cost of locating and filling a significant percentage of the available treeholes is likely to be high. However, it should be remembered that such control will be long-lasting and environmentally sound.

Alternatively, a pathogen causing mortality in the last larval instar, or even better, the pupal stage could be developed. Release of such a pathogen would not result in the amelioration of any of the density dependent constraints acting on the population. The ciliate *L. clarki*, shows variability in its effect on *A. sierrensis*: most infected mosquitoes die as larvae but a few animals die as pupae or young adults. It may be possible to select for a strain of *Lambornella* of reduced pathogenicity which could lower the equilibrium level of the mosquito population; the naturally occurring form is probably too pathogenic to act as an effective population regulator. However, the problem of getting the pathogen into the treeholes remains. Though infected adults could presumably fly to a treehole, die there and so spread the infection, this method of dispersal is likely very inefficient as infected females cannot become gravid and thus many not go near treeholes. So even if a strain of *Lambornella* with the appropriate characteristics could be developed, introduction into treeholes would still depend on the ability of humans to locate them. A transovarially transmitted parasite of sufficient pathogenicity would be ideal, but no such pathogen is known to infect *A. sierrensis*.

What would cost more: (1) an intensive, sustained program of locating and destroying treeholes or (2) a program to identify, develop and release a pathogen appropriate to the task? To answer this question, a field experiment, with appropriate controls, should be performed to assess the effectiveness of a treehole filling program; such an experiment has been done for *A. triseriatus*, with encouraging results (Garry & DeFoliart 1975). That being said, it is nonetheless true that *A. sierrensis* and its suite of pathogens represents a marvelous community in which to study parasite-host interactions in nature. Whether such basic research will lead to more effective control of this mosquito is possible, but by no means certain.

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