

A HIGH-FECUNDITY AEDINE: FACTORS AFFECTING EGG PRODUCTION OF THE WESTERN TREEHOLE MOSQUITO, *Aedes sierrensis* (DIPTERA: CULICIDAE)

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Abstract. *Aedes sierrensis* is typical of most mosquitoes in that larger females lay more eggs per batch and females blood fed to repletion lay more eggs than those not taking a complete meal. Neither mating nor gonotrophic age affects egg maturation, but mated mosquitoes oviposit more readily than unmated ones. Pupal weight does not correlate with egg weight, survivorship of either sex, number of clutches produced, mating success, day of 1st feeding, or 1st day of oviposition. *Aedes sierrensis* is unusual in its high weight-specific fecundity and small egg size relative to 5 other *Aedes* species. High fecundity may be an adaptation allowing individual females of this species to oviposit single egg batches in a greater number of tree holes.

A study of the factors affecting the fecundity of an organism can be approached from a physiological or evolutionary standpoint. Numerous studies have shown that the physiological, or proximate, factors affecting mosquito fecundity include adult size, gonotrophic age, blood meal size, and blood meal source (Table 1). However, none of these studies has addressed the fact that evolutionary, or ultimate, factors also affect fecundity. Any biological phenomenon, including the fecundity of a mosquito, is a result of both proximate and ultimate causes (Mayr 1961, 1982). The evolutionary forces affecting fecundity are difficult to define experimentally, but for a given species it is possible to determine if natural selection has resulted in allocation of resources to fewer, larger offspring or to many, smaller offspring. The hypothesis that such an inverse relationship exists for some organisms is at least several decades old (Lack 1954) and has been treated theoretically by Smith & Fretwell (1974). Though some data supporting this hypothesis exist for the Drosophilidae (Kambysellis & Heed 1971, Montague et al. 1981), none exist for the Culicidae. If it can be shown that such a relationship does hold for the Culicidae, a 1st step in elucidating the evolutionary forces affecting fecundity of a mosquito is to determine where on the continuum relating size to number of offspring that species has been placed by natural selection.

The purpose of the present study was 3-fold: (1) to experimentally investigate some of the proximate causes affecting fecundity in the western tree-hole mosquito, *Aedes sierrensis*; (2) to demonstrate that an inverse relationship between egg size and egg number exists within the Culicidae; and (3) to assess the position of *Ae. sierrensis* on this continuum. The results show that though *Ae. sierrensis* is typical of most mosquitoes in the proximate factors affecting its fecundity, it occupies an extreme position in the size/number-of-offspring continuum, laying large numbers of very small eggs.

This study departs from the traditional methodology of most mosquito workers in that pupal weight is the measure of size used, rather than wing length or adult weight. Wing length, though easy to obtain on dead specimens, is a linear measure and thus is not a direct measure of biomass; measurement of adult weight requires anesthetization of fragile specimens. Live pupal weight is easy to obtain and is a direct measure of biomass. Furthermore, pupal weight is a logical endpoint in the study of larval populations and thus provides a convenient bridge between studies of larval and adult populations.

MATERIALS AND METHODS

Pupae were collected from tree holes in Eugene, Oregon, USA (44°07'N), during the spring and summer of 1982 and weighed individually to the nearest 0.1 mg after blotting on a paper towel. One newly ecdysed female and 1-3 males were placed in 0.95-litre wide-mouthed jars and maintained at $24 \pm 2^\circ\text{C}$, L:D 16:8. Adults always had access to a fresh raisin. Two pieces of 5×10 -cm paper toweling moistened with tree-hole water, which adhered to the vertical surface of each jar, served as oviposition sites. A mouse anesthetized with sodium pentobarbital was placed on top of each screened jar every 2 days until feeding was observed. Blood meals were offered again only after oviposition occurred. Most animals were allowed to feed to repletion, but the feeding of several

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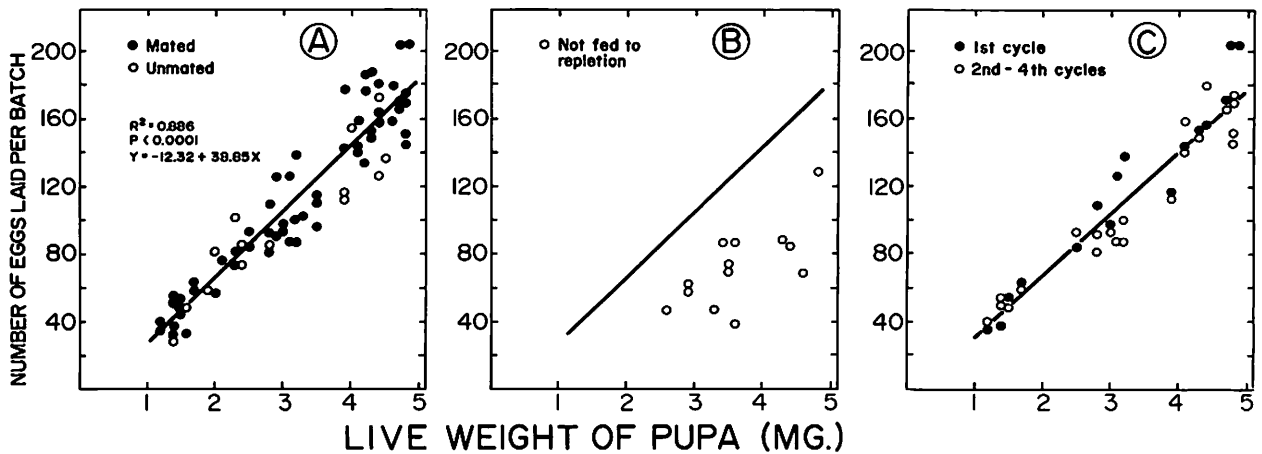


FIG. 1. A. Relationship between live weight of ♀ *Ae. sierrensis* pupae and number of eggs laid per batch as adults. B. Effect of failure to feed to repletion upon fecundity of *Ae. sierrensis*. The regression line for mosquitoes fed to repletion is shown for comparison. C. Relationship between fecundity and pupal weight for ♀♀ that laid more than 1 batch of eggs on replete meals.

females was interrupted to assess the effect upon fecundity of failure to feed to repletion. Mortality and egg production were monitored daily. Mating status was determined by direct examination of eggs (cleared with 2% sodium hypochlorite) for embryonation or spermathecae for sperm.

The relationship between pupal and adult weight was determined by keeping 36 weighed pupae individually in 5-cm petri dishes until ecdysis, then placing the dishes in a freezer for about 1 h to cold-immobilize adults for weighing (to the nearest 0.1 mg).

The relationship between pupal weight and weight of eggs produced was determined as follows: 20 eggs from each of 20 females of various sizes were placed on cover slips, dried on a hotplate for 5 min at 60 °C, and stored in a desiccator for 3 days before weighing to the nearest microgram.

Egg size was determined by measuring the maximum length and width of individual eggs with an ocular micrometer. Egg volumes were calculated assuming that egg shape approximates that of a prolate spheroid, where volume = $\frac{4}{3}\pi ab^2$ and a = length of the major radius and b = length of the minor radius.

To obtain further data on the relationship between egg size and number within the Culicidae, egg volumes of several species (for which measurements of adult size and fecundity were also available) were calculated using published egg measurements. Mean egg volumes were determined for those species for which more than 1 author pro-

vided measurements. In addition, the fecundity of several individual lab-reared *Aedes geniculatus* (originally from Sardinia, Italy) was determined in the manner described above. Cold-immobilized adults were weighed to the nearest 0.1 mg before dissection.

RESULTS

Of 1287 female pupae collected, 542 were weighed and 78 selected for the experiment. Of the 78 adult females, 61 took at least 1 blood meal and 52 laid eggs; of those that oviposited, 37 had mated. Feeding usually began 4 to 6 days after ecdysis (median = 5 days), and oviposition typically began 6 days after feeding. Most females were therefore 11 days old when they began to lay their 1st batch of eggs. Subsequent batches, however, were sometimes produced within 6 days of the 1st, as females often fed on the day that they completed oviposition. Though 72% of females completed oviposition within 2 days of laying their 1st eggs, some females laid single batches over periods as long as 14 days. Unmated females fed as readily as mated ones ($t = -1.646$; $P > 0.1$), but mated females oviposited more readily than unmated ones (Table 2).

Both pupal weight and blood meal size had marked effects on fecundity in *Ae. sierrensis*: larger females laid more eggs per batch (Fig. 1A), while females that fed to repletion laid larger egg batches than those that did not (Fig. 1B). Analysis of covariance, however, shows that neither physiologi-

cal age (Fig. 1C) [$F(1,34) = 3.557$; $P > 0.05$] nor mating status (Fig. 1A) [$F(1,68) = 2.538$; $P > 0.1$] affected fecundity.

Egg weight of *Ae. sierrensis* was not correlated with pupal weight [$F(1,18) = 0.249$; $P > 0.5$]. In addition, pupal weight had no effect on adult survivorship of males ($r = 0.055$; $P > 0.5$) or females ($r = 0.78$; $P > 0.5$), number of clutches produced [$F(4,34) = 0.34$; $P > 0.25$], mating success ($t = 0.604$; $P > 0.5$), day of 1st feeding ($r = -0.223$; $P > 0.1$), or day of beginning of oviposition ($r = 0.043$; $P > 0.5$).

Adult weight of *Ae. sierrensis* was highly correlated with pupal weight ($r^2 = 0.989$; $P < 0.0001$); the regression equation is: adult weight = $-0.194 + 0.708(\text{pupal weight})$.

DISCUSSION

Proximate factors affecting fecundity. Fecundity is positively correlated with pupal or adult size in various autogenous and anautogenous species of mosquitoes (Table 1). In the 3 cases where no such relationship was found, the results were equivocal. In one instance (Shelton 1972), the correlation between female size and fecundity depended upon blood meal source, being positive when the animals were fed chicken blood, but not significant when fed turtle, guinea pig, or human blood. In another case (Miura & Takahashi 1972), there was no correlation between adult size and fecundity despite the simultaneous observations that blood meal size was positively correlated with both adult size and fecundity. In the one apparently unambiguous study where no correlation was found between pupal weight and fecundity (Moeur & Istock 1980), the authors themselves state that in nature "significant interrelations will appear . . . between pupal weight and lifetime fertility," owing to the greater food stress that occurs under natural conditions. Thus, including *Ae. sierrensis*, a clear, positive adult-size/fecundity relationship has been found in 13 of 16 mosquito species investigated, while for the 3 negative studies the results are equivocal. A positive size/fecundity relationship therefore appears to be a general phenomenon for mosquitoes.

Fecundity also depends upon blood meal size in *Ae. sierrensis* (Fig. 1B), in agreement with the results of other studies (Table 1). *Aedes sierrensis* is unusual, however, in that there is no apparent reduction in fecundity with increasing gonotrophic age (Fig. 1C). Most studies report such a decline (Table 1), though Gubler & Bhattacharya (1971) found no decline in

fecundity through 13 gonotrophic cycles in *Ae. albopictus*.

Unmated *Ae. sierrensis* females mature as many eggs as mated females but delay oviposition (Table 2). This result is similar to those of Lang (1956) and Wallis & Lang (1956) for *Ae. aegypti*. Jalil (1974) reported that virgin female *Ae. triseriatus* exhibit reduced fecundity (measured as number of eggs laid) and delayed oviposition. He does not, however, report checking for retained eggs, so it is unclear whether mating affects number of eggs matured in that species.

Trade-off between egg size and egg number. Mosquito fecundity is size-dependent (Table 1); therefore adult size as well as fecundity and egg size must be obtained to determine if an inverse relationship between egg size and number exists for the Culicidae. These 3 characteristics have been measured for 9 species, 7 from the literature and 2 from the present study. Measurements for *Ae. sierrensis* and *Ae. geniculatus*, a common European tree-hole-breeding species, are given in Table 3. Adult size and fecundity measurements for 4 additional *Aedes* species were found for the eastern treehole mosquito, *Ae. triseriatus* (Cochrane 1972), *Ae. nigromaculis* (Miura & Takahashi 1972), *Ae. aegypti* (Colless & Chellapah 1960), and *Ae. hexodontus* (Barlow 1955). Egg size data for these and 48 other North American aedines are provided by Craig (1956), Horsfall & Craig (1956), Craig & Horsfall (1960), Myers (1967) and Kalpage & Brust (1968). Adult size and fecundity data for *Anopheles stephensi* are from Reisen (1975); egg size data for the same strain of that species are from Rutledge et al. (1970). Lamb & Smith (1980) provide all 3 measurements for *Toxorhynchites rutilus septentrionalis* (Dyar & Knab) and *Tx. brevipalpis* (Theobald). Figure 2A shows the highly significant negative correlation between relative (weight-specific) fecundity and egg volume for these 9 species: more fecund mosquito species lay smaller eggs than less fecund species. Similar results were reported by Shannon & Hadjinalao (1941), who found that egg length and fecundity are inversely related in 4 anopheline species, while Lamb & Smith (1980) showed that though the fecundity of *Tx. brevipalpis* is double that of similarly sized *Tx. rutilus septentrionalis*, its eggs have 1/2 the biomass of that congener. Though Shannon & Hadjinalao (1941) measured only egg length and Lamb & Smith (1980) worked with only 2 species, results of these studies, taken with the results reported here (Fig. 2A), in-

TABLE 1. Physiological (proximate) factors affecting fecundity in mosquitoes.

	CONDITIONS*	EFFECT**	REFERENCE
Pupal or adult size			
<i>Aedes aegypti</i> L.	L/L	+	Colless & Chellapah 1960, Steinwascher 1982
<i>Ae. cantans</i> Meig.	F/L	+	Service 1977
<i>Ae. dorsalis</i> Meig.	L/L	+	Parker 1982
<i>Ae. geniculatus</i> Oliver	F/L	+	Yates 1979
<i>Ae. hexodontus</i> Dyar	F/L	+	Barlow 1955
<i>Ae. nigromaculis</i> Ludlow	F/L	0	Miura & Takahashi 1972
<i>Ae. sierrensis</i> Ludlow	F/L	+	Fig. 1A
<i>Ae. triseriatus</i> Say	L/L	+	Cochrane 1972, Jalil 1974
<i>Anopheles sacharovi</i> Favr.	F/F	+	Shannon & Hadjinalao 1941
<i>An. stephensi</i> Liston	L/L	+	Reisen 1975
<i>An. subalpinus</i> Hackett & Lewis	F/F	+	Shannon & Hadjinalao 1941
<i>An. superpictus</i> Grassi	F/F	+	Shannon & Hadjinalao 1941
<i>An. typicus</i> Meig.	F/F	+	Shannon & Hadjinalao 1941
<i>Culex pipiens</i> L.	L/A	+	Spielman 1957
<i>Cx. salinarius</i> Coq.	L/L	+ / 0	Shelton 1972
<i>Wyeomyia smithii</i> Coq.	L/A	0	Moeur & Istock 1980
Gonotrophic age			
<i>Ae. aegypti</i>	L/L	-	Putnam & Shannon 1934
<i>Ae. albopictus</i> Skuse	L/L	0	Gubler & Bhattacharya 1971
<i>Ae. sierrensis</i>	F/L	0	Fig. 1C
<i>Cx. p. quinquefasciatus</i> Say	L/L	-	Walter & Hacker 1974
<i>Cx. salinarius</i>	L/L	-	Andreadis & Hall 1980
Blood meal size			
<i>Ae. aegypti</i>	L/L	+	Colless & Chellapah 1960, Hien 1976
<i>Ae. albopictus</i>	L/L	+	Hien 1976
<i>Ae. hexodontus</i>	F/L	+	Barlow 1955
<i>Ae. nigromaculis</i>	F/L	+	Miura & Takahashi 1972
<i>Ae. sierrensis</i>	F/L	+	Fig. 1B
<i>Ae. triseriatus</i>	L/L	+	Cochrane 1972, Jalil 1974
<i>An. stephensi</i>	L/L	+	Reisen 1975
<i>Cx. salinarius</i>	L/L	+	Shelton 1972
Blood meal source			
<i>Ae. aegypti</i>	L/L	+	Bennett 1970
<i>Ae. triseriatus</i>	F/L	+	Mather & DeFoliart 1983
<i>Cx. p. pipiens</i> L.	L/L	+	Shroyer & Siverly 1972
<i>Cx. p. quinquefasciatus</i>	L/L	+	McCray & Schoof 1970
<i>Cx. salinarius</i>	L/L	+	Shelton 1972

* Rearing/feeding conditions: F = field collected or field fed; L = lab reared or lab fed; A = autogenous.

** Effect: + = positive correlation; - = negative correlation; 0 = no correlation.

dicates that an inverse relationship between egg size and egg number exists for the Culicidae.

Aedes sierrensis occupies an extreme position on the egg-size/egg-number continuum compared to the 6 *Aedes* species that have been studied: it exhibits the highest relative fecundity but lays the smallest eggs. The latter point is valid even when the egg volume of *Ae. sierrensis* is compared to egg volumes of 52 of the 78 North American aedines (Fig. 2B); eggs of *Ae. sierrensis* are in the smallest size class. This situation is not a result of tree-hole

TABLE 2. Percentage of total eggs laid by mated and unmated *Ae. sierrensis* at different intervals after feeding. Egg batch sizes are normalized to 100. The 2 distributions are significantly different ($\chi^2 = 22.04$; $P < 0.001$).

	DAYS AFTER FEEDING						
	6	7	8	9-10	11-12	13-19	20-35
Unmated (17 batches)	14.6	28.1	20.8	11.9	5.4	5.9	13.3
Mated (68 batches)	34.9*	17.6	9.2	10.3	9.6	12.7	5.7

* Includes 1.5% laid after 5 days.

TABLE 3. Adult or pupal weight, fecundity, and egg size of *Ae. sierrensis* and *Ae. geniculatus* [mean \pm SE (sample size)].

	WEIGHT (mg)	NO. EGGS PER BATCH	EGG LENGTH (μ m)	EGG WIDTH (μ m)
<i>Ae. geniculatus</i>	4.8 \pm 0.1 (4)*	90 \pm 3 (4)	684 \pm 5 (10)	218 \pm 4 (10)
<i>Ae. sierrensis</i>	3.2 \pm 0.2 (52)**	111 \pm 6 (72)	535 \pm 8 (10)	173 \pm 4 (10)

* Adult weight.

** Pupal weight (equivalent to adult weight of 2.1 mg).

breeding per se, as the tree-hole breeders *Ae. triseriatus* and *Ae. geniculatus* both exhibit much lower fecundity but lay larger eggs than *Ae. sierrensis* (Fig. 2A).

The apportioning of resources between number and size of offspring can result from a number of selective forces (Williams 1966, Wilbur 1977). Intense competition for resources among juveniles can lead to larger offspring, lower fecundity, and increased competitive ability. Unpredictability of habitat quality can lead to smaller offspring, higher fecundity, and greater dispersive ability. In this context, the extreme position of *Ae. sierrensis* in the egg-size/egg-number continuum may reflect either minimal competition for resources or great habitat unpredictability. In fact, *Ae. sierrensis* larvae experience intense competition for resources, but tree-hole quality is highly unpredictable (Hawley 1985). Wild adult *Ae. sierrensis* usually do not survive long enough to oviposit more than 1 batch of eggs (Hawley 1985). The inability of ovipositing

females to accurately predict which tree holes are likely to sustain larval development the following spring thus constitutes a strong selective force favoring the distribution of eggs in each batch in as many different tree holes as possible. Some container-breeding *Aedes* do have such a behavioral capability (Rozeboom et al. 1973); it seems likely that *Ae. sierrensis* does, also. High fecundity in *Ae. sierrensis* is thus seen as an adaptation allowing oviposition in a greater number of tree holes; the resultant small egg represents the price paid for this ability.

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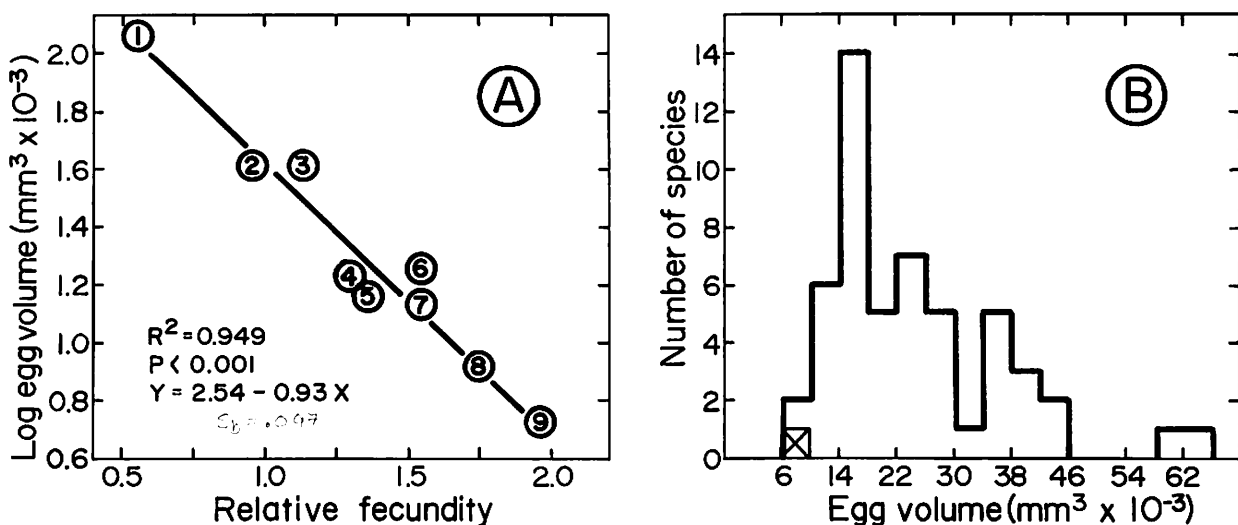


FIG. 2. A. Relationship between egg volume and relative fecundity [=log(no. eggs laid per batch/mg adult weight)] for 9 mosquito species (1 = *Tx. rutilus septentrionalis*; 2 = *Tx. brevipalpis*; 3 = *Ae. hexodontus*; 4 = *Ae. geniculatus*; 5 = *Ae. triseriatus*; 6 = *Ae. nigromaculis*; 7 = *Ae. aegypti*; 8 = *Ae. sierrensis*; 9 = *An. stephensi*). B. Calculated egg volumes of 52 North American aedines. The position of *Ae. sierrensis* is marked with an "X."

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