

# Egg Size and Reproductive Allocation in the Pitcherplant Mosquito *Wyeomyia smithii* (Diptera: Culicidae)

WILLIAM E. BRADSHAW, CHRISTINA M. HOLZAPFEL, AND TIMOTHY O'NEILL

Department of Biology, University of Oregon, Eugene, OR 97403

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**ABSTRACT** Adult longevity and lifetime fecundity, but not fertility, of northern (Maine, USA) *Wyeomyia smithii* (Coquillett) increase with female pupal weight. Mean egg size does not vary with pupal weight, but the standard deviation in egg size shows a marginally significant increase with pupal weight. Egg sizes are not skewed but are leptokurtic in their distribution; neither skewness nor kurtosis changes with female pupal weight. Mean egg size is not correlated with weight-specific adult longevity or with weight- and longevity-specific lifetime fecundity. Reproductive effort early in adult life does not affect longevity, reproductive effort late in life, or reproductive rate late in life. Finally, there is no significant correlation late in adult life between weight-specific rate of egg production and the size of eggs being produced. Egg size does vary within females but is not a variable entered into the physiological allocation of resources among survivorship, fecundity, or rate of egg production.

**KEY WORDS** *Wyeomyia smithii*, fecundity, reproductive effort

THE REPRODUCTIVE STRATEGY of an organism first involves reproductive effort, the partitioning of total body mass or available energy between reproduction and the soma. Reproductive allocation then involves apportioning the mass or energy committed to reproduction among its various components. Questions surrounding reproductive allocation usually concern when and how often to reproduce and how many or how big to make the offspring. Each of these components of reproduction makes a direct contribution to fitness, but, given the constraints of parental time, size, and energy, not all of these components can be maximized at once. Therefore, reproductive strategies are expected to exhibit inverse relationships, or tradeoffs, among the components of reproduction.

As aptly pointed out by Reznick (1985), genetic and phenotypic (physiological) tradeoffs often are confounded. In this article, we specifically are not testing whether tradeoffs in reproductive allocation impose constraints to evolution; rather, we are concerned with physiological tradeoffs in the allocation to the components of reproduction. The existence or nonexistence of tradeoffs may be obscured by variation in resource acquisition so that one observes positive or no correlations among components of reproduction when tradeoffs (negative correlations) might exist (Capinera 1979, Reznick 1985, van Noordwijk & de Jong 1986). Because of differential resource acquisition, larger individuals may have been better competitors, developed faster, and metamorphosed at larger sizes. They then are able to produce more, larger offspring

earlier, faster, and longer than other, even genetically identical, individuals that because of chance, acquired fewer resources during development or even during embryogenesis. Thus, to be comparable even within populations of a single species, tradeoffs among the components of reproduction must be evaluated on the basis of resource acquisition, energy, size, or weight.

In mosquitoes, reduced larval resources or increased larval density, or both, lead to prolonged development, reduced adult size and fecundity, and, consequently, reduced per capita rates of increase (Hawley 1985, Hard et al. 1989, Fisher et al. 1990). Among different species of mosquitoes (Hawley 1985), as well as among different species of drosophilid and syrphid flies (Gilbert 1990), egg size is inversely proportional to weight-specific fecundity. Within species, a negative genetic correlation is predicted between propagule size and weight-specific propagule number (Smith & Fretwell 1974, Begon & Parker 1986). Individual energetic constraints also would predict a negative phenotypic correlation between egg size and weight-specific egg number. To our knowledge, only three studies have looked for even a phenotypic correlation between egg size and number in mosquitoes. In *Aedes aegypti*(L.), both egg size and number increased when female body mass and bloodmeal mass increased jointly (Steinwascher 1984). In *Aedes sierrensis* (Ludlow), egg weight was not correlated with pupal weight, but pupal weight was correlated closely with number of eggs laid per batch after blood feeding to repletion (Hawley 1985). Egg size, but not number, varied

among populations of *Ae. sierrensis*, and a trade-off between egg size and number occurred in only one of three populations examined (Hard & Bradshaw 1992). The correlation between egg size and number in *Ae. aegypti* is confounded by bloodmeal size and any production of eggs in *Ae. sierrensis* still requires a blood meal. This article circumvents the problem of blood feeding by considering phenotypic correlations between egg size and reproductive allocation in an obligately nonbiting population of the mosquito *Wyeomyia smithii* (Coquillett).

**Reproductive Life-History of *W. smithii*.** *W. smithii* oviposits into and completes its entire preadult development only within the water-filled leaves of the purple pitcher-plant (*Sarracenia purpurea* L.) (Bradshaw 1983). Adult female weight is inversely proportional to density on a fixed resource, and both adult longevity and fecundity increase with pupal weight (Bradshaw & Holzapfel 1992). Northern (latitude of origin  $\geq 40^\circ\text{N}$ ) *W. smithii* produce an initial, large clutch of eggs and then several, smaller batches every few days thereafter (Lang 1978, Moeur & Istock 1980, O'Meara et al. 1981). Early fecundity is correlated with pupal weight but not longevity; late fecundity increases with both pupal weight and longevity, but there is no significant physiological tradeoff between late and early weight-specific fecundity (Bradshaw & Holzapfel 1992). Fertility (percentage hatch) is higher for earlier than later batches of eggs, but fertility is not correlated with pupal weight, either early or late in reproduction. Neither Bradshaw & Holzapfel (1992) nor Moeur & Istock (1980) were able to identify any physiological tradeoffs among adult traits involving egg number in northern *W. smithii*, even on a weight-specific basis that should have accounted for variation in resource acquisition (van Noordwijk & de Jong 1986, Begon & Parker 1986). Neither study accounted for variation in egg size.

### Materials and Methods

*W. smithii* were collected from eastern North America in Maine (Aroostook County, "KC" of Bradshaw & Holzapfel [1989];  $46^\circ\text{N}$ ,  $68^\circ\text{W}$ , 110 m elev.). Stocks were maintained as laboratory populations on a larval diet of mixed ground guinea pig chow and freeze-dried brine shrimp (Bradshaw 1986) for 2–10 generations before the start of experiments.

To generate pupae and adults of varying size, larvae were reared from the day of hatch at densities of 10, 20, or 40 larvae per 200 adult *Drosophila melanogaster* Meigen in 20 ml distilled water in petri dishes (100 by 25 mm). The resulting female pupae were weighed to the closest 0.1 mg. Single female pupae were allowed to eclose, and the resulting adult female was maintained from eclosion to death in a small (4.5 by 10 cm)

cylindrical butyrate plastic cage. The cages were friction fit to plastic jars (4.5 cm high, 4.5 cm diameter) with  $\approx 20$  ml distilled water for oviposition. At the same time, three large adult males having been reared at low densities on a mixed brine shrimp–guinea pig chow diet also were introduced into the cages. Each cage with a single female and her three male consorts was provided with a single pesticide-free raisin as a carbohydrate source. This raisin was changed whenever fungal mycelia or spores were observed. Individual cages were placed in a larger (48 by 40 by 23 cm) polystyrene box with moist vermiculite on the bottom to maintain high humidity. Larvae were reared and adults were maintained in an incubator providing a long-day photoperiod (17:7 [L:D] h) without twilight and on a 22–28°C (mean = 26°C) square-wave thermoperiod (warm:cool = 17:7) that lagged the photoperiod by 1 h.

Cages were checked and eggs counted three times per week for the life of the female. The eggs from each day and cage were examined for 7 d after collection, and number of larvae hatching was recorded. Dead adult males were replaced. The shape of *W. smithii*'s egg is that of an asymmetrical ellipsoid with a flattened ventral surface (Barr & Barr 1969, Frank et al. 1981). The mean egg volume for each female's lifetime egg production was approximated as the mean volume of prolate spheroid defined by each egg's length ( $a$ ) and width ( $b$ ): egg volume =  $\pi ab^2/6$ . The dimensions of each egg were measured to the nearest 0.01 mm with a dissecting microscope and an ocular micrometer. All of the eggs up to 20 were measured for each batch of eggs laid by a female over a 3–4-d period; when  $>20$  eggs were laid, the 20 to be measured were selected haphazardly.

**Definitions.** The following definition will be used: reproductive effort, (mean egg volume)(number of eggs)/(female pupal weight); reproductive rate, reproductive effort per day; reproductive allocation, partitioning of reproductive effort among egg size, egg number, and rate of oviposition; fecundity, egg production, number; fertility, percentage hatch arcsine transformed for statistical analyses. Means are provided  $\pm$  one standard deviation unless otherwise noted. Adult demographic symbols follow Moeur & Istock (1980):  $\alpha$ , day of first egg;  $\omega$ , day of last egg;  $R_g$ , gross lifetime fecundity which is the total eggs produced by a single female; reproductive period; days from  $\alpha$  to  $\omega$ ; early reproductive period,  $\alpha$  to  $\alpha + 5$ ; late reproductive period,  $\alpha + 6$  to  $\omega$ .

**Statistical Procedures.** Analyses of variance (ANOVA) were performed according to methods outlined in Sokal & Rohlf (1969); regressions and correlations were run with the REG procedure on SAS (SAS Institute 1985). If the relationships are curvilinear (allometric rather than isometric),

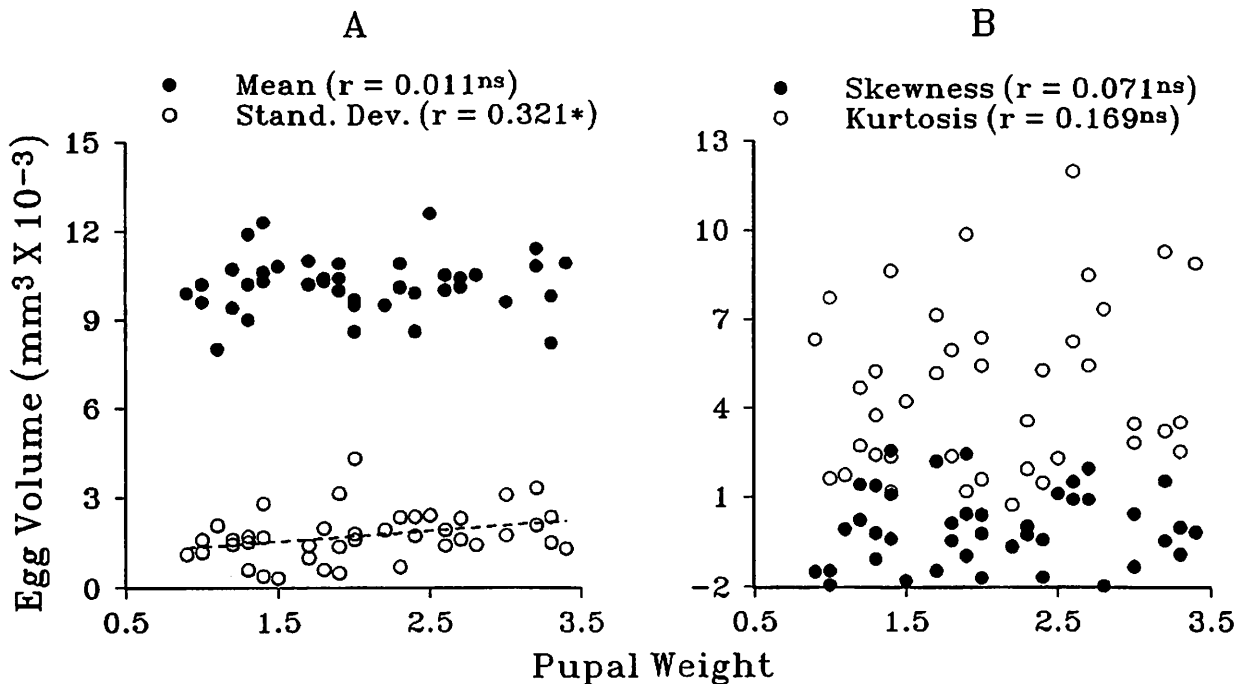


Fig. 1. Dependence of egg size (volume =  $\text{mm}^3 \times 10^{-3}$ ) and its variation on female pupal weight. (A), mean and standard deviation (Stand. Dev.); (B), skewness ( $g_1$ ) and kurtosis ( $g_2$ ). ns,  $P > 0.05$ ; \*,  $P < 0.05$ .

it is inappropriate to perform linear correlations or regressions. All relationships were first tested for allometry by regressing  $\log_{10}Y$  on  $\log_{10}X$  and testing for significant departure of the resulting regression coefficient ( $b$ ) from 1.0:  $t = |b - 1.0| / s_b$  where  $s_b$  is the standard error of the regression coefficient.

To partition variation in egg size among and within females, nested ANOVA was performed on egg size in all females that produced at least 10 eggs both early and late in their reproductive period. To achieve equal sample sizes, exactly 10 eggs were selected from the total produced early and from the total produced late by assigning a number to each egg and selecting eggs by turning cards. The deck of cards was shuffled three times between each selection of 10 eggs.

### Results

**Size, Fecundity, and Fertility.** The 41 females ranged in weight from 0.9 to 3.3 mg. No allometries were detected among significant regressions relating the length of the reproductive period  $\log_{10}(\alpha \text{ to } \omega)$  ( $b \pm s_b = 1.195 \pm 0.425$ ), gross lifetime fecundity  $\log_{10}(R_g)$  ( $b = 1.462 \pm 0.252$ ),  $\log_{10}$ [early ( $\alpha$  to  $\alpha + 5$ ) fecundity] ( $b = 1.091 \pm 0.291$ ),  $\log_{10}$ [late ( $\alpha + 6$  to  $\omega$ ) fecundity] ( $b = 1.889 \pm 0.640$ ), or  $\log_{10}$ [fertility ( $\sin^{-1}\sqrt{\% \text{ hatch}}$ )] ( $b = -0.366 \pm 0.185$ ) to  $\log_{10}$ (female pupal weight). Note that although the relationship between fertility and pupal weight appears allometric, the regression coefficient itself is not significantly different from zero. Consequently, all of the following relationships are based on linear

correlation of the untransformed variables or the residuals from the corresponding regressions, or both.

Length of the reproductive period ( $r = 0.333$ ,  $P < 0.05$ ) and gross lifetime fecundity ( $r = 0.766$ ,  $P < 0.001$ ) were positively correlated with female pupal weight. Similarly, from multiple linear regression, early fecundity was significantly correlated with pupal weight (partial  $r = 0.665$ ,  $P < 0.001$ ), but not length of the reproductive period (partial  $r = 0.055$ ,  $P > 0.05$ ); late fecundity was significantly correlated with both pupal weight (partial  $r = 0.338$ ,  $P < 0.01$ ) and length of the reproductive period (partial  $r = 0.736$ ,  $P < 0.001$ ). The relationships among the length of the reproductive period, fecundity, fertility, and pupal weight of Maine females are in accord with these same relationships among New Jersey females (Bradshaw & Holzapfel 1992) and will not be elaborated upon further in this article.

**Egg Size and Tradeoffs with Fecundity.** Mean egg size per female averaged  $10.2 \pm 1.9 \times 10^{-3} \text{ mm}^3$ . Over the reproductive lifetime of a female, neither the mean, skewness, nor kurtosis of egg size was correlated significantly with pupal weight, but the standard deviation in egg size was positively correlated with pupal weight (Fig. 1).

To determine if there was a tradeoff between egg size and female survivorship once the effects of size on survivorship had been taken into account, we examined the residuals from regression of length of the reproductive period on pupal weight. There was no significant correlation between these residuals and egg size (Fig. 2A).

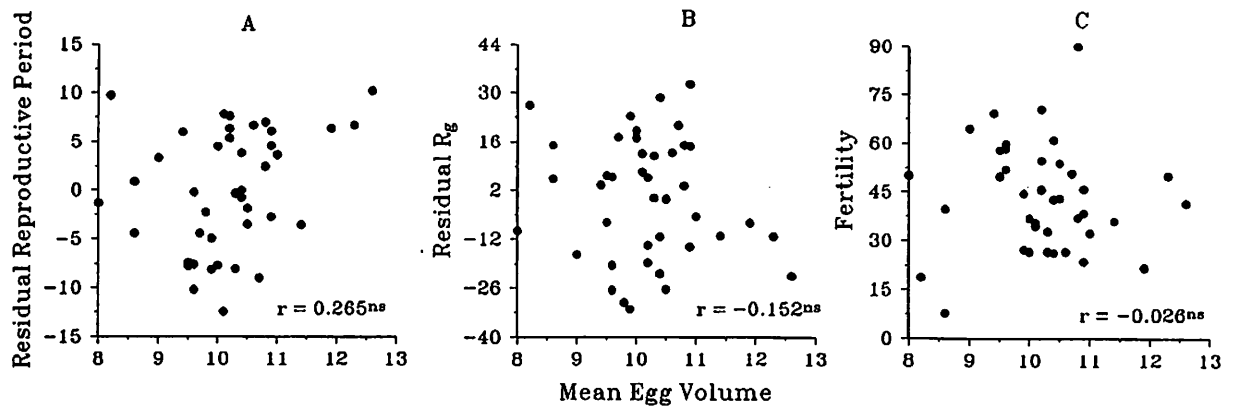


Fig. 2. Effect of mean egg volume ( $\text{mm}^3 \times 10^{-3}$ ) on (A), residuals from regression of the length of the reproductive period ( $\alpha$  to  $\omega$ ) on pupal weight; (B), residuals from gross lifetime fecundity ( $R_g$ ) regressed on both pupal weight and length of the reproductive period ( $\alpha$  to  $\omega$ ); and (C), fertility ( $\sin^{-1}\sqrt{\% \text{ hatch}}$ ).

To determine if there was a tradeoff between egg size and gross lifetime fecundity once the effects of both size and length of the reproductive period had been taken into account, we examined the residuals from multiple regression of  $R_g$  on pupal weight and  $\alpha$  to  $\omega$ . There was no significant correlation between these residuals and egg size (Fig. 2B). Finally, there was no significant correlation between fertility and egg size (Fig. 2C).

Of the total eggs produced by females, neither the mean, standard deviation, skewness, nor kurtosis of egg size differed significantly among 1) eggs laid early ( $\alpha$  to  $\alpha + 5$ ) when no eggs were laid later ( $\alpha + 6$  to  $\omega$ ); 2) eggs laid early when additional eggs were laid later; and 3) eggs laid later (Table 1). Of the 41 females producing fertile eggs, 20 possessed mature (stage V of Christophers [Clements 1963]) oöcytes when they died. There was no significant difference in the size of eggs already laid between females dying with (mean  $\pm$  SD =  $10.4 \pm 1.1$ ,  $n = 20$ ) or without ( $9.9 \pm 0.6$ ,  $n = 18$ ) mature oöcytes (ANOVA:  $F = 2.36$ ;  $df = 1,36$ ;  $P > 0.05$ ). For the 24 females that oviposited at least 10 eggs early and late in their reproductive period, a nested ANOVA revealed no significant differences among females ( $F = 1.25$ ;  $df = 23,24$ ;  $P > 0.05$ ) but very highly significant differences between egg sizes ovipos-

ited early and late within females ( $F = 3.38$ ;  $df = 24,432$ ;  $P < 0.001$ ).

**Reproductive Effort and Rate.** Reproductive effort early in the reproductive period had no significant effect on length of the reproductive period (Fig. 3A) and subsequent reproductive effort (Fig. 3B) or reproductive rate (Fig. 3C) late in the reproductive period. The number of eggs produced per milligram of pupal weight per day late in the reproductive period similarly was not correlated with egg size late in the reproductive period (Fig. 4).

Discussion

Within the population of *W. smithii* from Maine, pupal weight has a direct influence on length of the reproductive period and gross lifetime fecundity but not fertility or egg size. The Maine population of *W. smithii* therefore differs from Steinwascher's (1984) *Ae. aegypti* from southern Florida that showed a positive correlation between pupal weight and both egg size and egg number. In *Ae. aegypti*, bloodmeal mass had a greater effect on egg size than did female body size, but bloodmeal mass of females fed to repletion also was positively correlated with female size. The relationship between female body size

Table 1. Variation in egg size (mean  $\pm$  SD volume =  $\text{mm}^3 \times 10^{-3}$ ) and fecundity among female *W. smithii* early and late in the reproductive period

Mean of eggs laid	When late fecundity	No. of females <sup>a</sup>	Mean egg size <sup>b</sup>	Mean SD <sup>c</sup>	Mean $g_1^{d,f}$	Mean $g_2^{e,f}$
Early	$\geq 1$	27	$10.1 \pm 1.1$	$2.0 \pm 2.1$	$-0.3 \pm 1.7^*$	$5.4 \pm 17.1^{***}$
Late	$\geq 1$	27	$10.0 \pm 1.0$	$1.5 \pm 0.8$	$-0.3 \pm 2.8_{ns}$	$4.5 \pm 6.5^{***}$
Early	0	14	$10.5 \pm 1.4$	$1.4 \pm 0.8$	$0.0 \pm 2.7_{ns}$	$4.1 \pm 4.7^{***}$

<sup>a</sup> Of the 41 females, 27 laid eggs both early and late; 14 laid eggs early only.  
<sup>b</sup> ANOVA:  $F = 1.11$ ;  $df = 2,65$ ;  $P > 0.05$ ; reduction total sums of squares = 3.3%.  
<sup>c</sup> SD, standard deviation of egg size within females; ANOVA:  $F = 1.08$ ;  $df = 2,65$ ;  $P > 0.05$ ; reduction total sum of squares = 3.2%.  
<sup>d</sup> ANOVA:  $F = 0.26$ ;  $df = 2,65$ ;  $P > 0.05$ ; reduction total sum of squares = 0.8%.  
<sup>e</sup> ANOVA:  $F = 0.28$ ;  $df = 2,65$ ;  $P > 0.05$ ; reduction total sum of squares = 0.8%.  
<sup>f</sup> Probability individual  $g_1$  (skewness) or  $g_2$  (kurtosis) equal to zero: ns,  $P > 0.05$ ; \*,  $P < 0.05$ ; \*\*\*,  $P < 0.001$ .

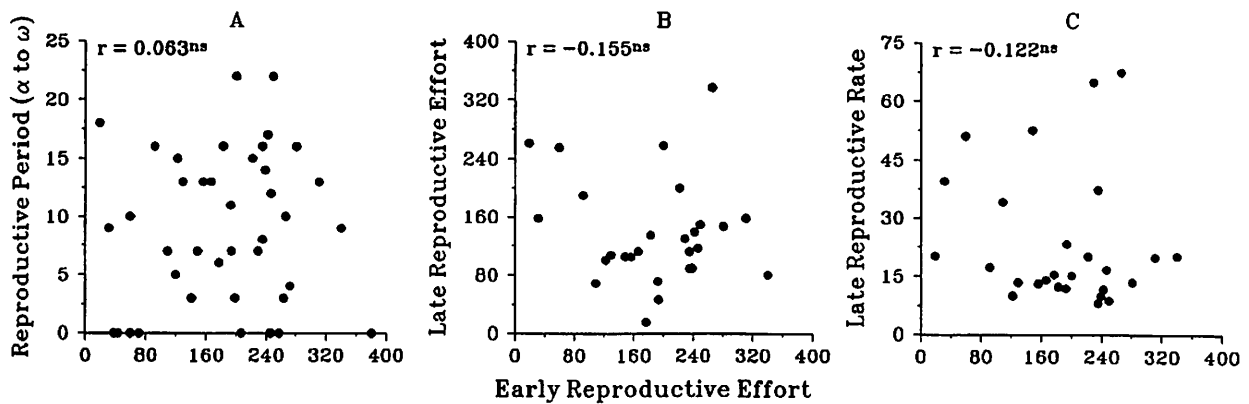


Fig. 3. Effect of early ( $\alpha$  to  $\alpha + 5$ ) reproductive effort (A) on length of the reproductive period ( $\alpha$  to  $\omega$ ); (B) on late ( $\alpha + 6$  to  $\omega$ ) reproductive effort; and (C) on late reproductive rate (number\*vol/mg\*da).

and bloodmeal mass is not known in *Ae. sierrensis*, but females that are prevented from feeding to repletion lay fewer eggs (Hawley 1985). In the Maine population of *W. smithii*, blood feeding is not a concern as northern populations of this species are autogenous for the first large and all subsequent small ovarian cycles (Lang 1978, Moeur & Istock 1980, O'Meara, et al. 1981). Mean egg volume does not affect a female's deviation from weight-specific length of the reproductive period, her lifetime fecundity, her deviation from weight-specific lifetime fecundity, or her deviation from lifetime fecundity adjusted for length of the reproductive period. Northern *W. smithii* emerge as adults with ovaries in an advanced stage of maturation (O'Meara & Lounibos 1981), and early fecundity is the direct man-

ifestation of "larval reserves" (Moeur & Istock 1980) modulated through size at pupation. Adult costs to reproduction might be averted for the first ovarian cycle, but subsequent batches are smaller. The size, number, or frequency, or all three, of later eggs are more likely to depend upon the allocation of resources garnered by the adults themselves. Mean egg size differed between eggs produced early and late in the reproductive period within, but not among, females. Still, egg size does not affect the weight-specific rate of egg production late in the reproductive period. Finally, reproductive effort early in life does not affect the duration of the adult reproductive period, reproductive effort late in the reproductive period, or reproductive rate late in the reproductive period. Thus, egg size does vary within females but is not a variable entered into the physiological allocation of resources among survivorship, fecundity, or rate of egg production.

The mean propagule size is not the only consideration in potential physiological tradeoffs. Rather, the variation and distribution of egg sizes can, themselves, be components of accommodation to variable environments (Gillespie 1974, Slatkin 1974, Capinera 1979, Kaplan 1980, Crump 1981, Cooper & Kaplan 1982). Among *W. smithii* from Maine, the standard deviation, but not the mean of egg size, increases with pupal weight. The implication is that females are able to regulate variation in egg size independently of the mean and, in so doing, larger females are "bet hedging" against temporally variable environments (Lacey et al. 1983, Orzack 1985). However appealing this interpretation, we believe the present evidence for it is weak. First, the increase in the standard deviation of egg size with pupal weight is hardly dramatic ( $r^2 \approx 10\%$ ) and barely significant ( $P = 0.041$ ). Second, a bet-hedging reallocation of resources to larger eggs alone or to more, smaller eggs alone should lead to increased skewness in egg size; but, skewness does not change with pupal weight. Third, a re-

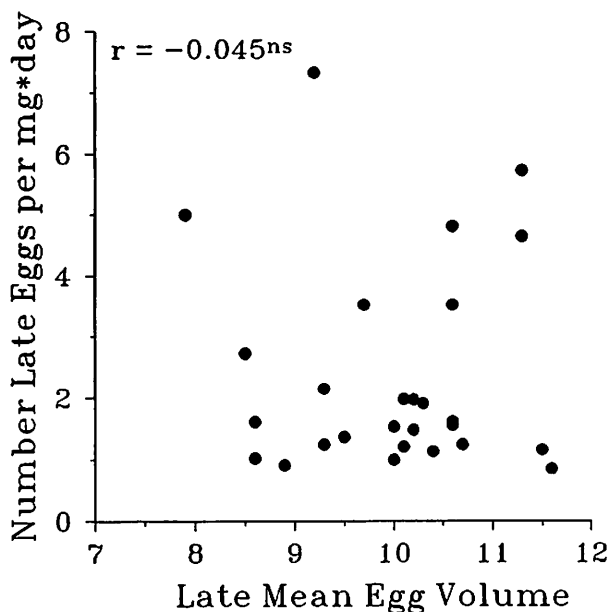


Fig. 4. Dependence of weight-specific rate of egg production late ( $\alpha + 6$  to  $\omega$ ) in the reproductive period on egg volume late in the reproductive period. Data are limited to the 27 females that produced eggs at  $\alpha + 6$  or later.

allocation of resources to larger eggs and, simultaneously to more, smaller eggs should lead to platykurtosis (as recognized by Crump [1981]); but, kurtosis does not change with pupal weight and, indeed, across all females is significantly leptokurtic.

Fewer late eggs hatch than early eggs (Bradshaw & Holzapfel 1992), but the mean, standard deviation, skewness, and kurtosis of egg size do not differ between early and late eggs. These observations indicate that egg size is tightly regulated during each ovarian cycle, that this regulation is well buffered against environmental variation producing a broad range of per capita rates of increase, and that egg size does not enter into considerations of senescence or into physiological tradeoffs with other components of adult reproductive allocation in northern *W. smithii*.

Bradshaw & Holzapfel (1992) proposed that costs to reproduction exist but are incurred in the larval stage. Under conditions of larval crowding or decreased per capita resources, or both, *W. smithii* maintain high pupation success over a wide range of conditions, whereas both larval development time and pupal weight are more sensitive to larval resources and density (Istock et al. 1975, Bradshaw & Holzapfel 1990). Similar patterns have been observed among the Amphibia (Wilbur 1977), but, unlike amphibians (Wilbur 1980), mosquitoes have determinate growth. Pre-reproductive or interclutch growth of mosquitoes cannot, therefore, compensate for an impoverished juvenile environment. The timing of pupation makes the largest contribution to generation time, and pupal weight-dependent fecundity makes the largest contribution to the replacement rate (Istock et al. 1975, Moeur & Istock 1980, Bradshaw & Holzapfel 1990). By pupating later and at lower weights, *W. smithii* may be able to increase the likelihood of surviving to adulthood but, in so doing, condemn the adult to a proportionally reduced per capita rate of increase.

Among a variety of insects, egg size may decrease with age (Harvey 1977, Begon & Parker 1986), may increase with age (Solbreck et al. 1990), or, as in *W. smithii* from Maine, may not change with age. Insects therefore may exhibit physiological tradeoffs among the components of reproductive allocation because of proximal energetic constraints, but the particular tradeoffs involved are likely to vary among populations, species, or higher taxa.

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