Reproductive Consequences of Density-Dependent Size Variation in the Pitcherplant Mosquito, *Wyeomyia smithii* (Diptera: Culicidae)

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ABSTRACT   Cohort fitness and individual female pupal weight in a northern (40°N) U.S. population of *Wyeomyia smithii* (Coquillett) were inversely proportional to larval density on a fixed resource. Larger females lived longer and realized higher absolute and weight-specific fecundity than did smaller individuals. Females produced a large initial batch of eggs early during their reproductive period and several smaller batches later. Early fecundity was correlated with pupal weight but not longevity. Late fecundity increased with both pupal weight and longevity but there was no significant tradeoff between late and early weight-specific fecundity. Fertility (percent hatch) was higher in earlier than later batches of eggs but there were no significant trade-offs between late fertility and either early fertility or early weight-specific fecundity. Variation in larval density results in reduced weight at pupation which, in turn, results in reduced fecundity and longevity. Consequences of increased larval density thus persist into adulthood as unrealized reproductive potential.

KEY WORDS   Insecta, allocation, acquisition, tradeoff

WHEN RESOURCES ARE limited by increased density, decreased food levels, or both, individual organisms cannot simultaneously maximize all components of fitness. Reduced acquisition of resources should then result in reduced fitness and to variable allocation of acquired resources leading to tradeoffs or variable costs (sensu Bell 1984a) among fitness components. Even at a single combination of food and density, some individuals may acquire more resources than others because of variation in local microhabitat or maternal investment in yolk or parental care, and will be "better" than others (Capinera 1979, Tuomi et al. 1983, Reznick 1985, Reznick et al. 1986, Bell & Kofoupanou 1986, van Noordwijk & de Jong 1986, Lomnicki 1988). Environmental variation in resource acquisition can obscure underlying physiological or developmental trade-offs. These tradeoffs should increase as resource acquisition declines and should become more apparent when per-capita resource level, weight, or some other index of resource acquisition is taken into account (Bell & Kofoupanou 1986).

This article considers reproductive consequences of variation in larval density on female size and reproductive allocation in a nonbiting, northern population of the mosquito *Wyeomyia smithii* (Coquillett). We specifically are not testing the hypothesis that tradeoffs in reproductive allocation impose constraints on evolution. Rather, we ask to what extent mosquitoes respond as larvae to environmentally-imposed variation in resource acquisition by reallocating components of adult reproduction involving the timing, number, and viability of offspring.

Reduced per-capita resources in larval mosquitoes results in reduced pupation success and, among those individuals that do pupate, longer development time and smaller size at metamorphosis (see Hawley 1985a, Hard et al. 1989, Fisher et al. 1990, and references therein). Mosquito ovaries begin to develop late in the fourth stadium, soon after the onset of pupal development, so that the number of ovarioles and adult size and blood capacity have been determined by the time of the larval-to-pupal molt (Clements 1963). Consequently, pupal weight is a good predictor of adult size, survivorship, and eggs per batch (Hawley 1985a,b).

The pitcherplant mosquito, *W. smithii*, occurs with its host plant *Sarracenia purpurea* L. from the Gulf of Mexico to eastern and central Canada (30–54°N). Larval resources for *W. smithii* consist of prey captured by the host leaf, and fitness in nature depends upon the per-capita availability of these resources (Bradshaw & Holzapfel 1986). In northern *W. smithii*, egg size is not correlated with either female size, age, or weight-specific fecundity (W.E.B. et al., unpublished), so that costs of reproduction should be manifest as trade-offs in egg number. No trade-offs with egg number were observed in northern

W. smithii by Moeur & Istock (1980) among females reared at two food levels. The food levels used by Moeur & Istock resulted in different pupal weights and development times but the differences were subtle. Their food levels did not produce significant differences in individual gross lifetime fecundity or, unlike the majority of other studies (Hawley 1985a), a correlation between gross lifetime fecundity or eggs per batch and individual female size. Moeur and Istock predicted that a further reduction in food level should produce such a correlation. Other studies have shown clear correlations between per-capita fecundity and per-capita resources in *W. smithii* (Istock et al. 1975, Bradshaw & Holzapfel 1990). In the current study, northern *W. smithii* were reared at various densities that produced a 4-fold variation in female size (as measured by female pupal weight) and, concomitantly, a greater than 12-fold variation in gross lifetime fecundity.

Methods

Experimental Design. *Wyeomyia smithii* used in this study originated in New Jersey (PB of Bradshaw & Holzapfel [1989]; 40°N 44°W, 10 m elevation). 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. Larvae were reared and adults maintained in a controlled-environment room providing an unambiguous long-day photoperiod of 17:7 (L:D), including two 0.5-h transitory twilights and a smooth sine-wave temperature cycle fluctuating from 12–28°C (mean, 21°C) with a period of 24 h that lagged the light cycle by 3 h (Bradshaw 1986).

Experiment 1. To examine the effect of larval density on fitness, 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 either intact pitcher-plant leaves or in 100 by 25 mm petri dishes. Nine replicates were run at each density in leaves and in dishes. Pitcher plants were placed in polystyrene terraria in the controlled-environment room. Pupae were counted and removed 3 times per week. Resulting adults were pooled from each density treatment in dishes or leaves and maintained in cylindrical cardboard cages (10 by 30 cm) with access to a raisin for carbohydrate and 50 ml water for oviposition. Individual cages were placed in a larger (48 by 40 by 23 cm deep) polystyrene box with moist vermiculite on the bottom to maintain high humidity. Eggs were removed and counted 3 times per week. Cohort fitness was then calculated as capacity for increase

$$r_c = \ln R_0/T$$

where

$R_0 = \Sigma E_x/N_0 =$ replacement rate
$T = \Sigma x E_x/\Sigma E_x =$ mean generation time
$E_x =$ number of eggs collected at time x, days since oviposition of the original cohort
$N_0 =$ number of first instars in the initial cohort, i.e., 90, 180, or 360 at densities of 10, 20, or 40 per leaf or dish, respectively.

Experiment 2. To generate pupae and adult females of various sizes, larvae were reared from the day of hatch at densities of 10, 20, or 40 larvae per 200 adult *D. melanogaster* in 20 ml distilled water in petri dishes (100 by 25 mm) and maintained in the controlled environment room as above. Resulting female pupae were weighed to the closest 0.1 mg and sorted into 0.2-mg intervals from 0.8 to 3.6 mg. About four adult females from each 0.2-mg size interval were placed individually into separate cylindrical butyrate plastic cages (3 by 10 cm) with a small leaf of *S. purpurea* for oviposition. A single organically grown raisin was provided as an adult carbohydrate source and was changed weekly for the lifetime of the female. At the same time, three large adult males that had been reared at low densities on the mixed brine shrimp–guinea-pig chow diet were also introduced into each cage.

Cages were checked and eggs were removed and counted 3 times per week. Eggs from each day and cage were examined for 7 d and number of larvae hatching was recorded. Dead adult males were replaced.

Definitions. *Lifespan* is the days from adult eclosion to death. *Fecundity* is the number of eggs produced. *Fertility* is percent hatch (arcsin transformed for statistical analyses). Means are provided ± 1 SD unless otherwise noted.

Adult demographic symbols follow Moeur & Istock (1980):

X_{ecl} is the days from oviposition to adult eclosion, α is the day of first egg, ω is the day of last egg, R_g is the gross lifetime fecundity (total eggs produced by a single female), and *reproductive period* is the days from α to ω.

The reproductive period in northern *W. smithii* can be divided into an early period of 3–5 d when the initial, large batch of eggs is produced and a later period when repeated, small batches are produced (Lang 1978, Moeur & Istock 1980, O'Meara et al. 1981). In our study, early fecundity is the eggs produced from α to $\alpha + 5$, and late fecundity is the eggs produced from $\alpha + 6$ to ω. The latter period comprised about two-thirds (10.3 ± 7.2 d) of the total reproductive period.

Statistical Procedures. Analysis of variance (ANOVA) was performed according to methods outlined in Snedecor (1956); regressions and cor-
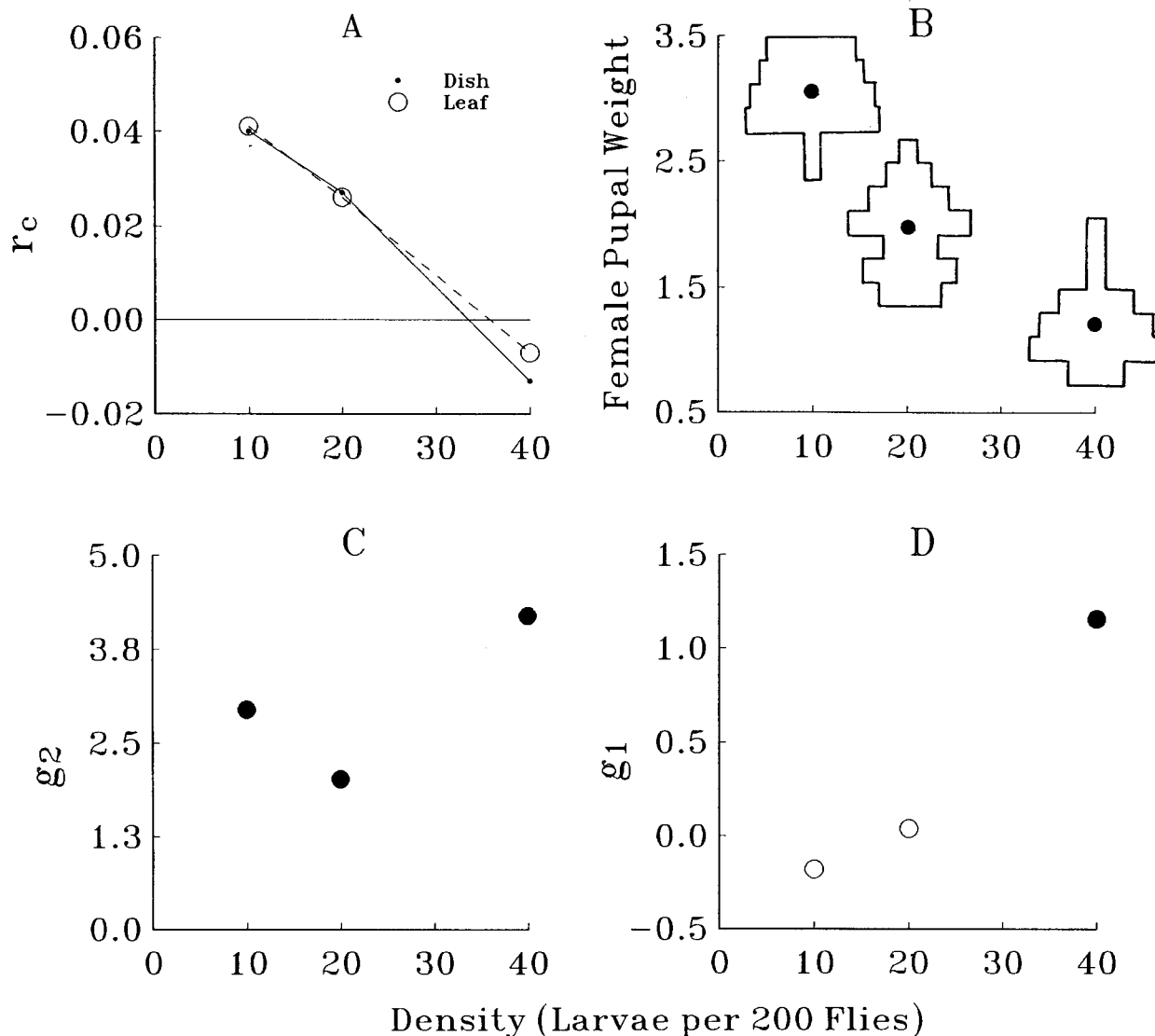
Fig. 1. Effect of larval density on (A) cohort fitness (r_c), (B) female pupal weight, (C) kurtosis (g_2) of female pupal weight, and (D) skewness (g_1) of female pupal weight (experiment 1). In C and D, open circles indicate skewness or kurtosis not significantly different from 0 $(P > 0.05)$; closed circles indicate significant deviation from 0 $(P < 0.05)$.

relations were run with the REG procedure (SAS Institute 1985). All correlations 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. Relationships with log-log regression coefficients that did not deviate significantly from 1.0 were analyzed with linear regression directly; relationships whose slopes deviated significantly from 1.0 were subjected to a $\log_{10}$ transform of the dependent variable if $b > 1.0$ and of the independent variable if $b < 1.0$, and then analyzed with linear regression. In the latter case, residuals were always calculated from the regression of appropriately transformed data.

Results

Density and Fitness (Experiment 1). As in previous studies (Bradshaw & Holzapfel 1989), r_c declined with increasing density (Fig. 1A). Fitness was positive at the two lower densities and negative at the higher density. Thus, the range of densities used in this study resulted in a wide range of fitness from positive to negative that was nearly identical for larvae reared in dishes and leaves. For convenience, dishes were used in subsequent experiments.

Density and Pupal Weight (Experiment 1). Female pupae ranged in weight from 0.8 to 3.5 mg (Fig. 1B). Mean female pupal weight was inversely proportional to the log of density. Mean pupal weight of larvae reared at a density of 10

Table 1. Egg production (x̄ ± SD) of *W. smithii* (experiment 2)

No. females	No. eggs		Pupal weight[a]	Adult lifespan[b]	α to ω[c]
	Oviposited	Hatched			
41	≥1	≥1	2.2 ± 0.7	23.1 ± 7.3	15.2 ± 7.4
7	≥1	0	2.5 ± 0.5	24.9 ± 10.2	12.1 ± 12.8
5	0	—	1.8 ± 0.6	8.2 ± 11.7	—

[a] ANOVA: $F = 1.62$; df = 2, 50; $P > 0.05$.
[b] ANOVA: $F = 7.99$; df = 2, 50; $P < 0.01$.
[c] ANOVA: $F = 0.83$; df = 1, 46; $P > 0.05$.

per dish exceeded the mean pupal weight of Moeur & Istock's (1980) larvae reared on high rations. Mean pupal weight of larvae reared at a density of 20 per dish was the same as their larvae reared on low rations. Mean pupal weight of larvae reared at 40 per dish was lower than the weight of any of their pupae reared on low rations. At all densities, weight distributions were peaked (Fig. 1C) but the weight distribution was skewed only at the highest density (Fig. 1D) and, in that case, toward higher weights. The generally high peakedness and low skewness indicate that individual female pupal weight is very tightly attuned to density. The analyses below therefore use female pupal weight as a reflection of microhabitat quality and assess reproductive allocation on a weight-specific basis.

Pupal Weight, Fecundity, Fertility, and Longevity (Experiment 2). Females that produced no eggs had about one-third the lifespan of females that produced at least one egg, but females that produced at least one fertile egg and those that produced only infertile eggs did not differ significantly in lifespan (Table 1). In addition, there was no significant difference in pupal weight among females that produced no eggs, that produced only infertile eggs, or that produced some fertile eggs. Finally (Table 2), there was no significant difference in the length of the reproductive period (α to ω) between females that produced fertile or infertile eggs. Thus, short-lived adults were more likely not to oviposit any eggs than long-lived adults but neither adult longevity, pupal weight, nor length of the reproductive period affected fertility. The results and analyses below consider only those females ($n = 41$) that oviposited at least one fertile egg, unless otherwise indicated.

Among adult females, neither the prereproductive period (X_{ecl} to α = 5.4 ± 2.5 d; $r^2 < 0.001$, $P > 0.05$) nor the postreproductive period (ω to

Table 2. Egg fertility (x̄ ± SD) of *W. smithii* (experiment 2)

Time in reproductive period	No. females	Fertility[a]
α to α + 5	41	71.6 ± 16.5
α + 6 to ω	35	58.3 ± 16.9

[a] ANOVA: $F = 12.06$; df = 1, 74; $P < 0.01$.

death = 2.6 ± 2.6 d; $r^2 < 0.001$, $P > 0.05$) was significantly correlated with pupal weight, but length of the reproductive period increased with the $\log_{10}$ of pupal weight (Fig. 2A). Gross lifetime fecundity increased exponentially with pupal weight (Fig. 2B), indicating that both absolute and weight-specific fecundity increased with female size. Fertility was not significantly correlated with pupal weight (Fig. 2C). In summary, larger females had a longer reproductive period and oviposited more over that period than did smaller females; fertility declined with age but was not related to female size.

Weight-dependent fecundity could be a simple consequence of size, or highly fecund females may achieve higher lifetime fecundity from increased longevity that is independent of size. To distinguish between these alternatives, residuals of $\log_{10}(R_g)$ regressed on pupal weight were correlated with residuals of the reproductive period regressed on $\log_{10}$ (pupal weight). The resultant correlation was not significant and the sign of the nonsignificant correlation was positive (Fig. 3). These results suggest that larger females produce more eggs during their lifetime than smaller females both through weight-dependent fecundity and weight-dependent prolongation of the reproductive period.

Temporal Allocation of Reproductive Effort (Experiment 2). To examine the effects of adult size and longevity on the initial, large batch of eggs and the subsequent, repeated small batches, we subjected early and late fecundity to stepwise regression entering as the independent variables pupal weight first and length of the reproductive period second. Early fecundity (Fig. 4) increased exponentially with pupal weight ($r^2 = 0.487$, $P < 0.001$) but not longevity (increase in $R^2 < 0.001$). However, late fecundity increased with both pupal weight ($r^2 = 0.281$, $P < 0.001$) and length of the reproductive period (increase in $R^2 = 0.119$, $P < 0.05$). Larger females produced more eggs per batch both early and late during their reproductive period and, independently of size, females that lived longer continued to produce more eggs late in the reproductive period.

The residuals from regression of late egg production on pupal weight were not significantly correlated with residuals from regression of $\log_{10}$
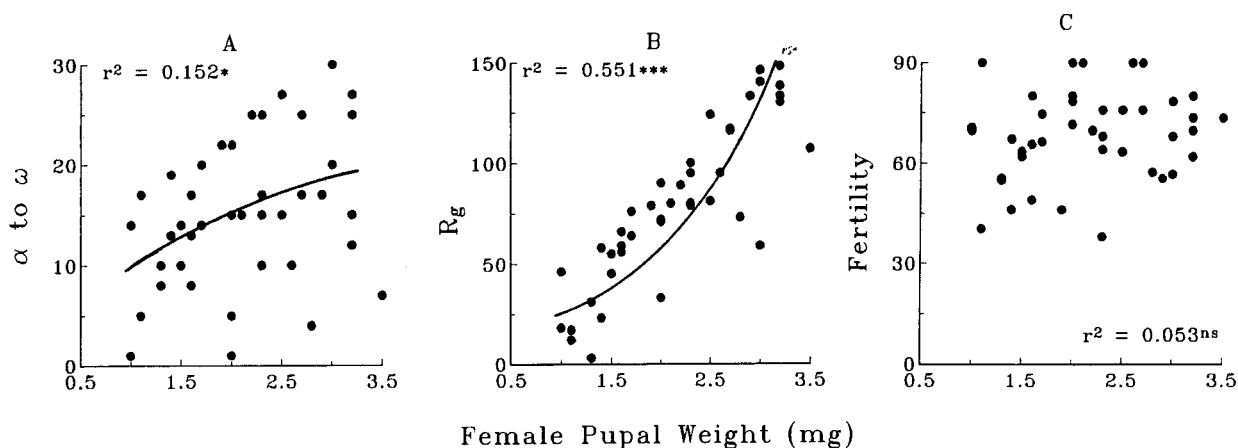
Fig. 2. Dependency of (A) length of the reproductive period (days), (B) gross lifetime fecundity, and (C) fertility (percent hatch) on pupal weight.

(early egg production) on pupal weight (Fig. 5). High weight-specific fecundity during the early reproductive period does not therefore adversely affect weight-specific fecundity later in the reproductive period.

Fertility was higher among earlier eggs (Table 2). Deviation from mean fertility among later eggs was not significantly correlated either with deviation from mean fertility among earlier eggs (Fig. 6A) or with residuals from regression of $\log_{10}$ (early egg production) on pupal weight (Fig. 6B). Later eggs were therefore less fertile than earlier eggs, and there was no significant trade-off between later fertility and either early fertility or early weight-specific fecundity.

Discussion

Physiological Trade-offs in Components of Reproduction. Moeur & Istock (1980) concluded
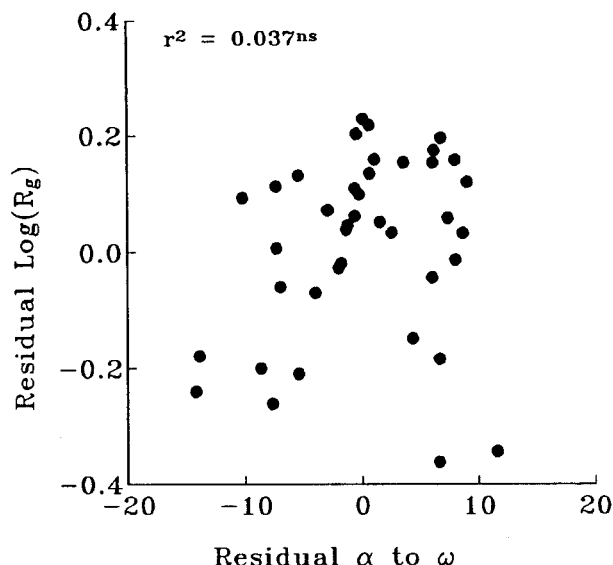

Fig. 3. Correlation between residuals from $\log_{10}$ (gross lifetime fecundity) regressed on pupal weight with residuals from the length of the reproductive period regressed on $\log_{10}$ (pupal weight).

that there was no physiological cost of reproduction in *W. smithii*. The two food rations used by Moeur & Istock resulted in different pupal weights and development times but were not sufficiently different to impose significant reduction in R_g (gross lifetime fecundity) or in length of the reproductive period, or to reveal significant covariation between R_g and length of the reproductive period. Larval densities used in our study produced pupae over a wider range of weights (Fig. 1) than those observed by Moeur & Istock and produced positive correlations between pupal weight and R_g and length of the reproductive period. Still, there was no correlation between R_g and length of the reproductive period after the effects of weight were removed (Fig. 2 and 3).

Moeur & Istock (1980) did not consider temporal allocation of reproductive effort or fertility. The present study found that weight-specific fecundity increases with female size early but not late during the reproductive period (Fig. 4A) as predicted by the models of Begon & Parker (1986). However, a larger reproductive effort early in adult life does not condemn a female to a lower reproductive effort late in adult life (Fig. 5). Fertility declines during adult life (Table 2), but this decline is not affected by disproportionate fecundity or fertility early in adult life (Fig. 6). Lack of an inverse relationship in Fig. 6A suggests further that a reduction in egg viability per se (not sperm depletion) leads to the decline in fertility. The decline in female fertility may therefore indicate individual senescence as observed in *D. melanogaster* (Parsons 1962) but does not reveal whether this senescence might be the result of antagonistic pleiotropy (Rose & Charlesworth 1981a,b), deleterious alleles with delayed expression (Mueller 1987), or a combination of both.

Reproductive determinism (Bell 1984b) applies when the total number of germ cells or ovarioles is fixed (determined). A large earlier production of offspring necessarily results in a
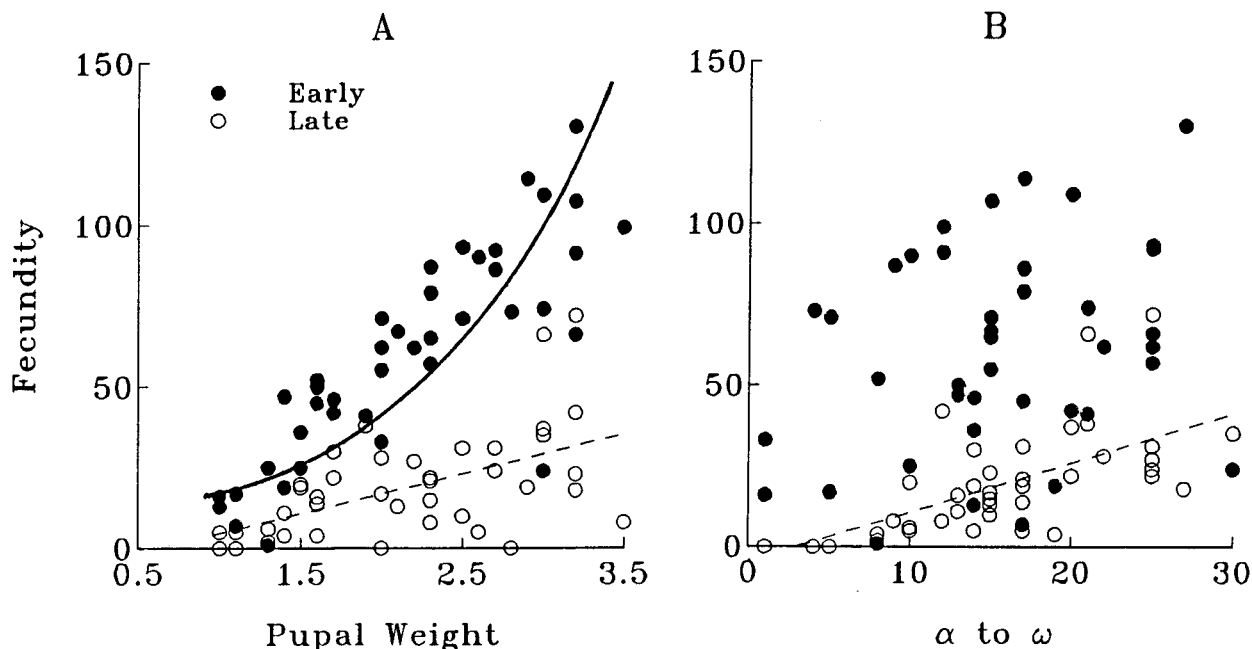
Fig. 4. Dependence of fecundity early (α to $\alpha + 5$) and late ($\alpha + 6$ to ω) during the reproductive period on (A) female pupal weight and (B) length of the reproductive period. Only significant correlations have fitted lines.

small later production of offspring and a declining size-specific rate of offspring production with increasing age. In the case of mosquitoes, the number of ovarioles may be fixed at the time of metamorphosis, but each ovariole can potentially produce many eggs in succeeding ovarian cycles (Clements 1963). In northern *W. smithii*, after a high weight-specific production of eggs early in adult life, females do not exhibit reduced weight-specific total production (Fig. 5) or rate of

Fig. 5. Tradeoffs with fertility. Deviation of individual from mean fertility during the late reproductive period correlated with (A) deviation of individual from mean fertility during the early reproductive period and (B) weight-specific early fecundity (residuals from regression of $\log_{10}$ [early fecundity] on pupal weight).

production (W.E.B. et al., unpublished) late in life. Northern *W. smithii* do not, therefore, appear to be physiologically constrained by reproductive determinism.

Factors that affect gross lifetime fecundity in northern *W. smithii* are summarized as follows: per-capita larval resources directly affect female pupal weight; pupal weight determines both early and late fecundity directly and influences late fecundity indirectly through its effect on adult longevity; early and late fecundity then combine to produce gross lifetime fecundity; and pupal weight has no significant effect on fertility, and there are no significant correlations among the components of fecundity and fertility.

The above discussion provides no support for the variable allocation of acquired resources among the adult components of reproduction, as predicted by Bell (1984a). Bell & Kofoupanou (1986) suggested that such trade-offs should become more apparent when resource acquisition is taken into account. In our study, variable larval density leads to a 4-fold variation in female pupal weight and, subsequently, to a 12-fold variation in gross lifetime fecundity. Even using pupal weight as an index of resource acquisition, we still failed to identify weight-specific, physiological trade-offs in adult reproductive allocation in northern *W. smithii*.

Where Are the Costs? Despite the lack of apparent physiological trade-offs in adult reproductive allocation, *W. smithii* cannot produce an indefinite number of offspring. Size at pupation does tightly constrain gross lifetime fecundity (Fig. 2 and 4). But, components of size- and longevity-specific reproduction show no trade-
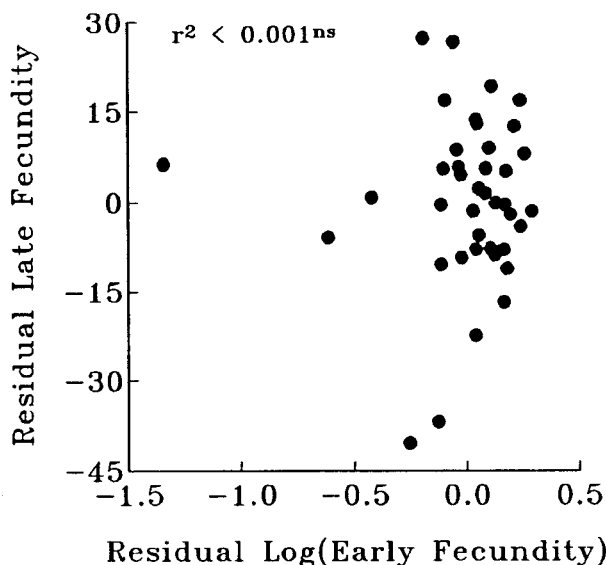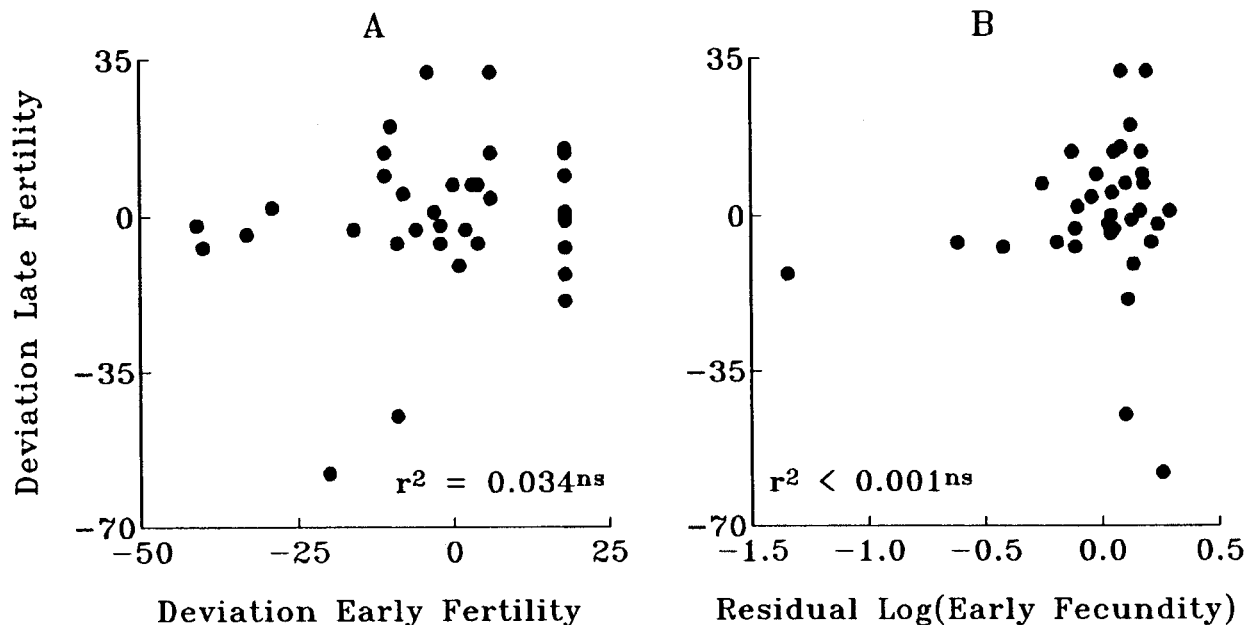
Fig. 6. Weight-specific fecundity during the early and late reproductive period assessed by residuals from $\log_{10}$ (early) and late fecundity regressed on female pupal weight.

offs (Fig. 3 and 5). Theories of reproductive allocation have long recognized a potentially reciprocal relationship between offspring size and number (Lack 1954, Price 1974, Smith & Fretwell 1974, Capinera 1979, Parker & Begon 1986). But, in another northern population of *W. smithii* from Maine, there is no correlation between female pupal weight or weight-specific fecundity and the size of eggs she produces (W.E.B. et al., unpublished).

Tamarina & Georgiyeva (1987) have proposed that the ultimate cost of reduced larval resources in mosquitoes is larval mortality; but, individuals are buffered from this mortality by prolonging development, metamorphosing at reduced weights, or both. When faced with reduced per-capita resources through lower rations or higher density, *W. smithii* does not die but does prolong development (Istock et al. 1975; Moeur & Istock 1980; Bradshaw & Holzapfel 1989, 1990), metamorphose at lower pupal weights (Fig. 1A), and realize lower gross lifetime fecundity (Fig. 2B) and lower per-capita rate of increase (Fig. 1A) (Istock et al. 1975; Bradshaw & Holzapfel 1989, 1990). These homeostatic responses protect the individual from failing to survive and therefore failing to reproduce (fitness of zero), but they incur a proportional cost to fitness from unrealized potential in rate of development and fecundity.

The peaked distributions in pupal weight (Fig. 1C) at each density indicate that pupal weight is a tightly regulated function of per-capita resource availability. The lack of apparent trade-offs in components of adult reproduction then reflects the fact that trade-offs have already been made at the time of pupation. Individual mosqui-

toes pupate with a fixed level of resources and a fixed number of ovarioles, so the cost of larval survival is carried through to the adult stage as unrealized reproductive potential.

Acknowledgment

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