

# Resource- and density-dependent development in tree-hole mosquitoes

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Populations of the tree-hole mosquitoes *Aedes geniculatus* and *A. triseriatus* were cultured at different food levels and larval densities to determine the fitness consequences of variation in these factors for each species. A composite fitness index and four fitness correlates were calculated for each population. Response-surface regression analysis of these indices indicated that the two species have fundamentally different responses to food and density: The interaction and quadratic effects of these factors had a strong influence on fitness in *A. triseriatus* but little impact in *A. geniculatus*. In both species, the composite fitness index was most sensitive to male and female pupal weight, less sensitive to sex ratio and development time, and least sensitive to pupation success. The response-surface model explained over 90% of the variation in fitness in *A. triseriatus*, but only two-thirds of that in *A. geniculatus*. We suggest that *A. triseriatus* is more homeostatic and *A. geniculatus* more polymorphic for fitness traits, and predict that life-history characters will have higher heritabilities in *A. geniculatus* than in *A. triseriatus*.

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## Introduction

In this paper, we examine the effects of food level and larval density on larval development and estimated population growth in laboratory cultures of two tree-hole mosquitoes, *Aedes geniculatus* (Olivier) from western Europe and *A. triseriatus* (Say) from eastern North America. These organisms are appropriate for this type of investigation because they characteristically occupy tree holes – discrete, highly circumscribed habitats – during larval development, frequently at very high densities in nature.

We address three central questions in this study. First, are the effects of food and density additive or do they interact so that response to constant per capita resource is density dependent? Second, what correlates of fitness most accurately reflect a composite index analogous to per capita rate of increase? Third, do the answers to these questions differ between two congeneric species that live in physically convergent but geographically disjunct habitats? Our intent is to determine

whether *A. geniculatus* and *A. triseriatus* respond to food and intraspecific density in fundamentally similar or different ways. Because the relationship of separate fitness correlates to overall population fitness is often obscure (Livdahl and Sugihara 1984, Jones 1987), we compare an estimate of each population's per capita rate of change to that of separate correlates of fitness, in assessing this response.

In mosquitoes, larval density limits population growth by reducing larval survivorship, slowing development, and reducing pupal size, which in turn restricts adult survivorship and fecundity (Steinwascher 1982, Hawley 1985a,b). Less is known of the relative effects of food and density on larval performance. Several studies have illustrated the restricting effects of larval density (e.g., Terzian and Stahler 1949, Surtees 1959, Greenough et al. 1971, Barbosa et al. 1972, Nekrasova 1976); fewer have considered the limits of food under controlled density (Keirans and Fay 1968, Wilton 1968) or both factors simultaneously (Wada 1965, Nayar 1969, Istock et al. 1975, Livdahl 1982, Carpenter 1983). In the

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most revealing of these experiments, Livdahl (1982) demonstrated that food and density could interact in affecting survivorship in a mixed-cohort population of *A. triseriatus* but that these interactions were not detectable in other correlates of fitness including female pupal weight and development time, or in a composite index of fitness analogous to per capita rate of population change.

Among animals, density may reduce fitness through territoriality or other interference mechanisms, as well as through depletion of resources. Direct interference (Shannon and Putnam 1934) and chemical inhibition by metabolites or growth retardants (Moore and Fisher 1969, Ikeshoji and Mulla 1970) may increase with larval density in some mosquitoes, regardless of food level (but see Dye 1982, 1984 for contrasting evidence). If all other resources are available in sufficient quantities, then unless competition for food increases linearly with a decline in per capita food availability, density must affect rates of development and population growth by means other than limited per capita food.

## Methods

### Experimental design

Eggs of *Aedes triseriatus* were collected in Lahaska, Bucks County, Pennsylvania, USA (40°20'N, 75° 4W, 180 m elevation) in summer 1984; eggs of *A. geniculatus* were collected from Silwood Park, Ascot, Berkshire, England (51°25'N, 0° 38'W, 60 m elevation) in summer 1986. Eggs laid on wooden slats in tree holes were stored in sealed plastic bags and refrigerated until the start of experiments; the experiments were conducted in different years for the two species but the eggs were approximately the same age (3–4 mo) when hatched. After exposure to long-day photoperiod and room temperature (20–25°C) for 4–7 d, eggs were flooded with foul water to stimulate hatching. Hatched larvae were immediately counted into 100 mm-diameter plastic Petri dishes filled with 75 ml (*A. triseriatus*) or 80 ml (*A. geniculatus*) distilled water. Larvae were cultured at one of 3 food levels and at one of 4 densities, so that the combination of treatments comprised a full factorial design. Food consisted of a mixture of ground, sifted guinea pig chow and dried brine shrimp in a 2:1 ratio by volume. Two kg of this food was ground and mixed in 1983 and serves as a laboratory standard. Food levels, to the nearest 0.1 mg, were 0.05 g per dish (low), 0.10 g per dish (intermediate), and 0.20 g per dish (high).

Larval densities were 10, 20, 40, and 80 larvae per dish for *A. triseriatus* (in 1984) and 10, 20, 40, and 60 larvae per dish for *A. geniculatus* (in 1986). As a result of our experiment with *A. triseriatus*, the lower maximal density was chosen for *A. geniculatus* to allow an increase in the absolute number of larvae surviving to pupation in this treatment while maintaining a density high enough to produce a strong reduction in fitness

beyond that observed at 40 larvae per dish. In order to minimize interpretational problems arising from the difference in densities, only those portions of the response surfaces common to both species are compared. Moreover, presentation of predicted values of the various indices is limited to values actually observed in the experimental treatments or to values interpolated among them.

Each combination of food and density was replicated three times for *A. triseriatus* and four times for *A. geniculatus*. All experimental treatments were conducted at  $21.0 \pm 0.5^\circ\text{C}$  and at a photoperiod of 16L:8D.

Individual pupae were removed from culture dishes every 1–2 d, sexed, blotted dry on a paper towel, and weighed live to the nearest 0.1 mg. For each culture-dish group of mosquitoes, several correlates of fitness were measured: pupation success (proportion of larvae surviving to pupation), pupal sex ratio (proportion of pupae that were female), sex-specific mean time to pupation (days since hatching) and mean pupal weight for each sex. After 30 d, the experiment involving *A. triseriatus* was terminated; at this time, 1132 larvae (83.9%) of the initial number) had not pupated and 241 (17.9%) remained alive. The experiment involving *A. geniculatus* was continued until all surviving larvae had pupated, but of 983 larvae (63.0%) that had not pupated within 30 d, only 4 (0.3%) subsequently pupated and the remainder died.

For comparison with the separate fitness correlates, a composite index of fitness described by Livdahl (1982), analogous to per capita rate of increase, was calculated for each group of mosquitoes in a culture dish:

$$r' = \frac{\ln [1/N_0 \sum_x (\bar{w}_x A_x f(\bar{w}_x))]}{D + [\sum_x x \bar{w}_x A_x f(\bar{w}_x)] / [\sum_x \bar{w}_x A_x f(\bar{w}_x)]} \quad (1)$$

where  $x$  is a given day of adult female emergence (days since hatching);  $\bar{w}_x$  is the mean female pupal weight on day  $x$ ;  $A_x$  is the number of females pupating on day  $x$ ;  $N_0$  is the initial number of female larvae in the culture dish (assumed to be half the initial total);  $D$  is a constant, in days, determined by the interval between adult emergence and oviposition; and  $f(\bar{w}_x)$  is a function converting female pupal weight to ovariole number.

For *A. geniculatus*, the value of  $x$  was calculated as the sum of the mean number of days to pupation and 6.5 d as a pupa,  $D$  was estimated to be 17 d from field data (Bradshaw and Holzapfel, unpubl.) and  $f(\bar{w}_x)$  was calculated by the equation (Bradshaw and Holzapfel, unpubl.):

$$f(\bar{w}_x) = -35.50 + 90.94 \ln(\bar{w}_x) \quad (2)$$

For *A. triseriatus* the same equation was used with two modifications. The constant  $D$  was assumed to be 7 d for all culture groups, and  $f(\bar{w}_x)$  was calculated by an equation that relates female pupal weight to expected

lifetime fecundity (McCombs 1980, Livdahl 1982, Bradshaw and Malarkey, unpubl.):

$$f(\bar{w}_x) = 7.13 + 45.85 e^{-1.82 + 0.42\bar{w}_x} \quad (3)$$

For each species, the calculation of  $r'$  assumes that all females lay one clutch and then die (Livdahl 1982); the calculation also assumes that fitness for day  $x$  is determined by mean pupal weight on that day.

### Analysis

Data for pupation success, pupal sex ratio, mean time to pupation, mean pupal weight, and  $r'$  were analyzed with a response-surface regression model (SAS Institute 1985). Response-surface regression has the advantages that it allows both the determination of the relative sensitivity of a response variable to different factors over the spectrum of factor levels examined and the estimation of factor levels that produced maxima and minima in the response variable. Before analysis, pupation success and pupal sex ratio data were transformed by arcsin square root; data for mean time to pupation and mean pupal weight were transformed by the base-10 logarithm. The composite index  $r'$ , already a function of the natural logarithm, was not transformed. The response surface incorporating food and density effects on the various fitness correlates was modeled as:

$$y = B_0 + B_1F + B_2D + B_{11}F^2 + B_{22}D^2 + B_{12}FD + e \quad (4)$$

where  $y$  is the expected value of the response variable (pupation success, pupal sex ratio, mean development time, mean pupal weight, or  $r'$ );  $F$  is food level;  $D$  is larval density;  $B_0$ ,  $B_1$ ,  $B_2$ ,  $B_{11}$ ,  $B_{22}$ , and  $B_{12}$  are regression coefficients; and  $e$  is the residual error.

In this paper, we distinguish between the terms "fitness components" and "fitness correlates", since some confusion appears to exist in the literature over their appropriate use. We consider characters such as survivorship, sex ratio, development time and size to be fitness correlates, since changes in these variables affect indices of fitness such as per capita rate of change only indirectly. We restrict the term fitness components for parameters such as replacement rate ( $R_0$ ), equivalent to the numerator of Eq. 1, and generation time ( $\tau$ ), equivalent to the denominator of Eq. 1, because changes in these parameters result in predictable responses in the per capita rate of change.

## Results

### Linear, interaction, and quadratic effects of food level and larval density

Food level and larval density had significant linear effects on  $r'$  and on all fitness correlates except time to pupation of *Aedes geniculatus* males, which was not significantly affected by either treatment (Tab. 1). Species, but generally not sexes within them, varied in the contribution of food-density interaction and quadratic responses to the overall model (Tab. 1) and to the generated response surfaces (Figs 1–4); without exception, these terms were more important in determining the values of fitness correlates in *A. triseriatus* than in *A. geniculatus*. In general, the interaction and quadratic terms accounted for less of the total explained variance than linear effects except in days to pupation of female *A. triseriatus* (Tab. 1C) where the interaction and quadratic terms had greater impact than the linear effects.

Among *A. geniculatus*, significant interaction effects of food and density (Tab. 1) affected pupation success and sex ratio but not days to pupation, pupal weight of either sex, or the composite index of fitness  $r'$ . Among *A. triseriatus*, significant interaction effects of food and density affected pupation success, sex ratio, days to pupation of females, pupal weight of both sexes, and  $r'$  but not days to pupation of males.

Among *A. geniculatus*, significant quadratic effects of food and density (Tab. 1) affected sex ratio but not pupation success, days to pupation, pupal weight, or  $r'$ . Among *A. triseriatus*, significant quadratic effects of food and density affected pupation success, sex ratio, days to pupation of females, and  $r'$  but not days to pupation of males or pupal weight of either sex.

The above contributions of linear, interaction, and quadratic effects combined to produce response surfaces of fitness correlates that differed markedly between the two species.

### Pupation success

The proportion of *Aedes geniculatus* larvae surviving to pupation ranged from 0.76 at high food level and intermediate larval density to 0.00 at low food and higher density. The response-surface (Fig. 1A) showed a flat peak in pupation success at high food but over a broad range in larval density. The shapes of the contours indicated that pupation success was more sensitive to food than to density.

The proportion of *A. triseriatus* larvae surviving to pupation ranged from 0.70 at the lowest larval density (10 larvae/dish) but at intermediate food level, to 0.00 at low food and high density. Pupation success declined with increasing density, regardless of food level, until larval density exceeded 20 larvae/dish; pupation success was then sensitive to the effects of both food and density at higher density (Fig. 1B).

Tab. 1. Coefficients of determination of linear, interaction and quadratic terms in the response-surface regression model (Eq. 4) incorporating the effects of food and density on correlates of fitness (A–D) and on the composite index of fitness (E).

			Total	Linear	Interaction	Quadratic
A. Pupation Success	Ag		0.496***	0.394***	0.059*	0.043 <sup>ns</sup>
	At		0.796***	0.527***	0.106***	0.163***
B. Sex Ratio	Ag		0.401**	0.177*	0.090*	0.134*
	At		0.758***	0.408***	0.186***	0.163**
C. Days to Pupation	Ag-m		0.032 <sup>ns</sup>	0.016 <sup>ns</sup>	0.010 <sup>ns</sup>	0.007 <sup>ns</sup>
	Ag-f		0.322*	0.292**	0.015 <sup>ns</sup>	0.014 <sup>ns</sup>
	At-m		0.465*	0.387**	0.025 <sup>ns</sup>	0.052 <sup>ns</sup>
	At-f		0.607**	0.110 <sup>ns</sup>	0.184*	0.312*
D. Pupal Weight	Ag-m		0.612***	0.585***	0.004 <sup>ns</sup>	0.024 <sup>ns</sup>
	Ag-f		0.654***	0.595***	0.038 <sup>ns</sup>	0.020 <sup>ns</sup>
	At-m		0.893***	0.644***	0.231***	0.018 <sup>ns</sup>
	At-f		0.822***	0.551***	0.262***	0.009 <sup>ns</sup>
E. $r'$	Ag		0.661***	0.616***	0.007 <sup>ns</sup>	0.039 <sup>ns</sup>
	At		0.924***	0.738***	0.143***	0.043*

Ag, *A. geniculatus*; At, *A. triseriatus*; m, males; f, females <sup>ns</sup> = not significant; \* =  $P < 0.05$ ; \*\* =  $P < 0.01$ ; \*\*\* =  $P < 0.001$

#### Pupal sex ratio

In *Aedes geniculatus*, the proportion of female pupae varied from 0.00–0.66; this proportion was lowest at low food and high density, and highest at intermediate food and low density. The expected proportion female was maximal at the lowest larval density, and initially declined rapidly with increasing density. However, the

model predicted a ridge of 0.40 female at high food and intermediate-to-high density (Fig. 1C). As food declined at higher density, the proportion of female pupae decreased rapidly. In *A. triseriatus* the proportion of pupae that were female varied from 0 at low food level and high larval density to 0.85 at higher food and low density. The predicted maximum occurred at low density and intermediate food level. This proportion de-

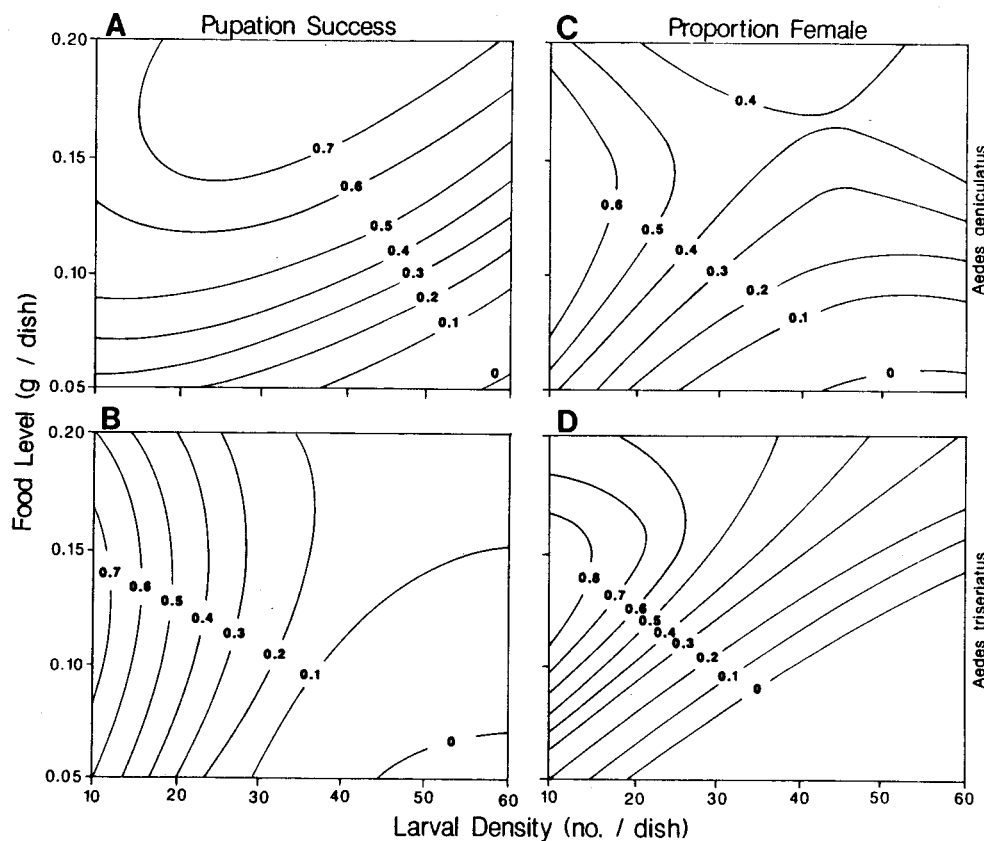


Fig. 1. Contour surfaces, calculated from the response surface regression model (Eq. 4), illustrating the effects of food level and larval density on pupation success (A, B) and proportion female (C, D).

Fig. 2. Contour surfaces, calculated from the response-surface regression model (Eq. 4), illustrating the effects of food level and larval density on male (A, C) and female (B, D) development time (days).

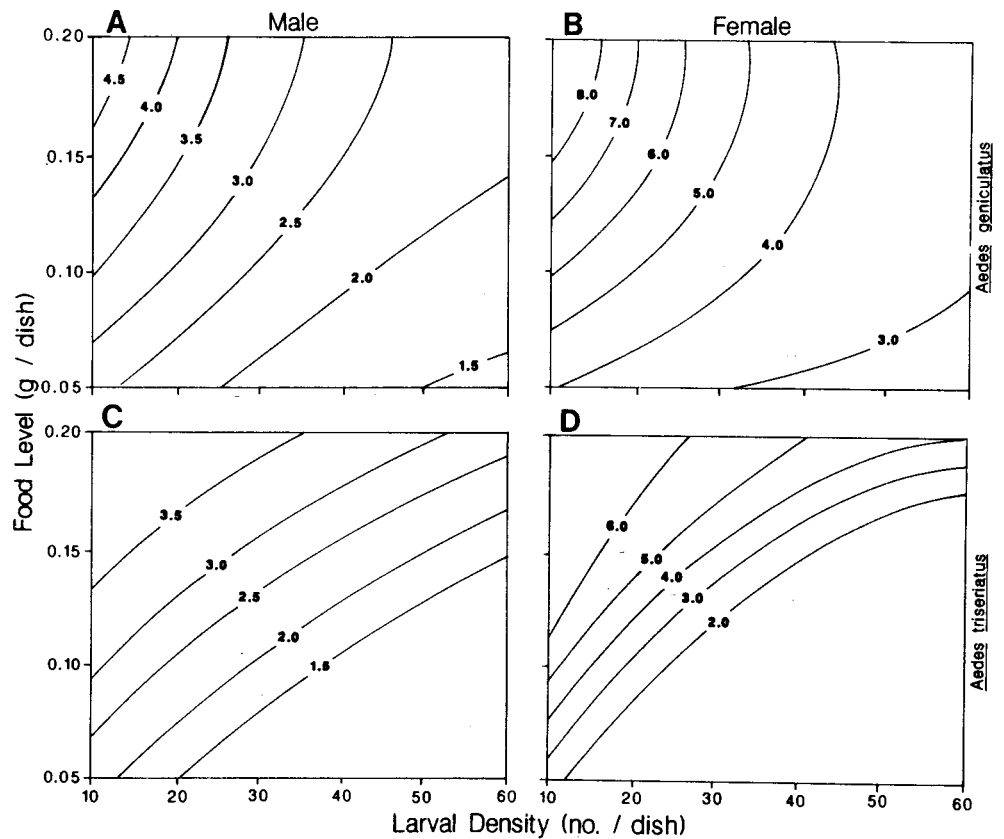
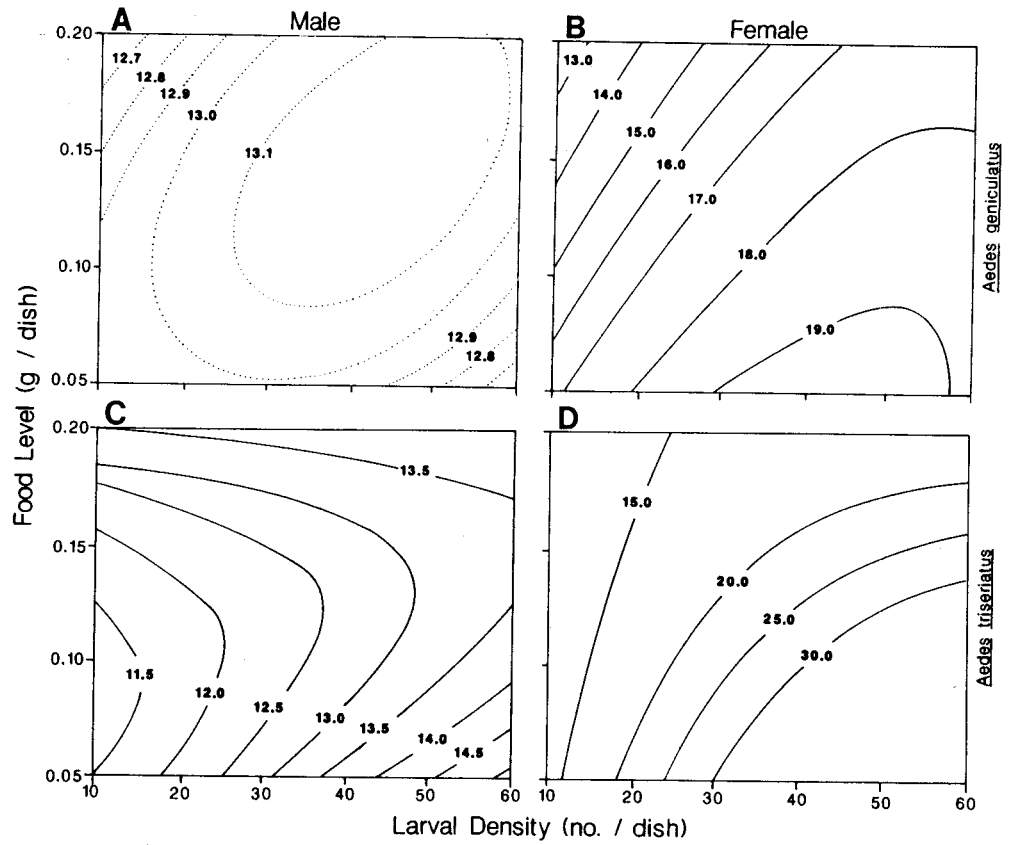


Fig. 3. Contour surfaces, calculated from the response-surface regression model (Eq. 4), illustrating the effects of food level and larval density on male (A, C) and female (B, D) pupal weight (g).

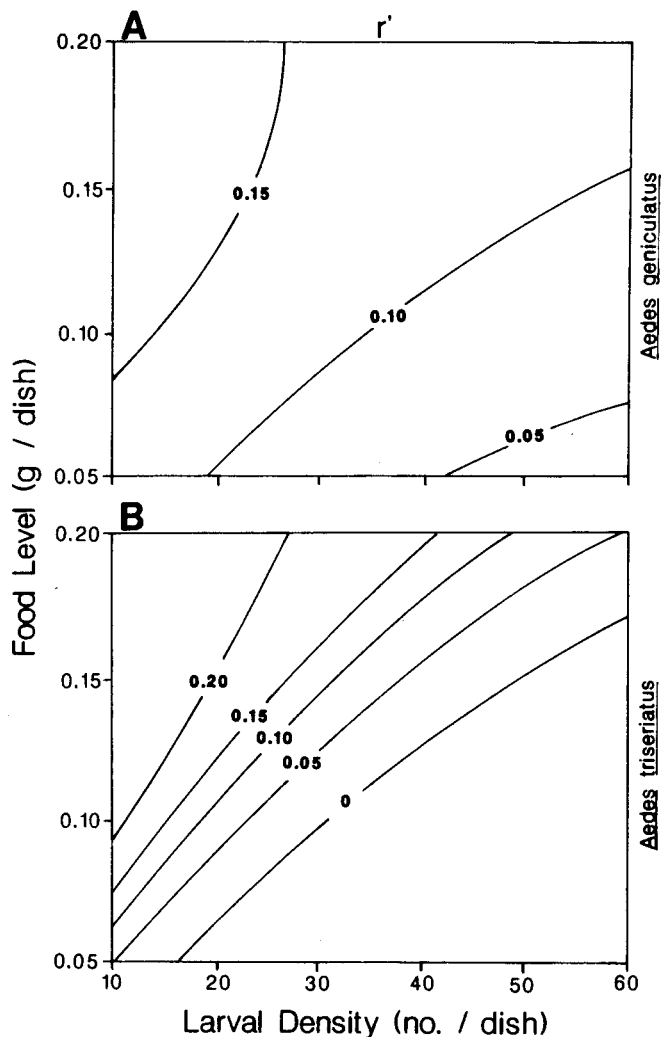


Fig. 4. Contour surfaces, calculated from the response-surface regression model (Eq. 4), illustrating the effects of food level and larval density on the composite index of fitness,  $r'$ .

clined rapidly with both food and density, although sex ratio appeared to be slightly more sensitive to food, based on the contour slopes (Fig. 1D).

In both species, this shift in sex ratio appears to result from sex-specific trade-offs between pupal weight and development time when per capita food is limited (Steinwascher 1982, Fisher 1988). Female mosquitoes respond to declining per capita food by increasing time to pupation; males pupate at lower weights under these conditions. Since these mosquitoes are protandrous and males require fewer resources to reach the size required for pupation, increased density acts to shift the sex ratio toward a higher proportion of males at pupation.

#### Time to pupation

In *Aedes geniculatus*, mean time to pupation of males did not respond to food or density (Fig. 2A), but these factors produced detectable variation in females (Fig. 2B). Mean times to pupation in males ranged from 12.7 d at high food level and low larval density to 13.1 d at

intermediate food and higher density. Mean times to pupation for females varied between 13.0 d (high food, low density) and 19.2 d (low food, high density). Density was more important than food in extending development time in female *A. geniculatus*, except at the highest density.

In *A. triseriatus*, mean male development time ranged from 11.5 d at low food level and density to 15.0 d at low food and high density (Fig. 2C). Mean female development time ranged from a minimum of 13.1 d at low density to 30.0 d at intermediate food and density. Mean female development time of *A. geniculatus* varied less than in *A. triseriatus*, and the response surface showed that at low food level and high density female *A. triseriatus* take longer to develop (Fig. 2D).

#### Pupal weight

Male *Aedes geniculatus* pupae varied in mean weight from 1.5 mg at low food and high density to 4.5 mg at high food and low density. Food and density appeared to be equally important overall in determining mean pupal weight, although the response to food was slightly greater at lower food and higher density and that to density greater in the converse case (Fig. 3A). Female *A. geniculatus* pupae varied in mean weight from 2.6 to 8.3 mg; the fitted model showed that mean female pupal weight was sensitive to both food and density (Fig. 3B). The overall pattern was very similar to the male response, and female weight was as sensitive to density as was male weight.

Female *A. triseriatus* pupae were smaller than female *A. geniculatus* pupae at comparable food and density treatments (Fig. 3B, D). Male *A. geniculatus* and *A. triseriatus* pupae were similar in size at intermediate food levels and larval densities, but the size of male *A. geniculatus* responded more rapidly to food and density as levels of these factors varied (Fig. 3A, C). Even more than *A. geniculatus*, female weight in *A. triseriatus* was more sensitive to density than was male weight. Generally, *A. triseriatus* showed greater sensitivity than *A. geniculatus* to food at higher densities.

#### Composite index of fitness

The composite index,  $r'$ , for *Aedes geniculatus* (Fig. 4A) was sensitive to both food level and density. The predicted maximum  $r'$  occurred at high food and low density, and declined steadily with decreasing food and increasing density. At even the highest density and lowest food level, however,  $r'$  remained positive. In contrast,  $r'$  for *A. triseriatus* (Fig. 4B), while also maximal at lower density and high food level, was much more sensitive to these factors. Maximal  $r'$  for *A. triseriatus* was greater than for *A. geniculatus* but declined rapidly to zero at moderate density and intermediate food level.

Tab. 2. Sensitivity and correlation of separate fitness correlates to the composite index  $r'$ . Sample sizes: *A. geniculatus*,  $n = 33$ ; *A. triseriatus*,  $n = 18$ .

		Percent change over range in $r'$	Correlation with $r'$
A. Pupation Success	Ag	4.8	0.357*
	At	19.9	0.144 <sup>ns</sup>
B. Sex Ratio	Ag	138.8	0.611***
	At	158.6	0.447 <sup>ns</sup>
C. Days to Pupation	Ag-m	11.2	-0.487**
	Ag-f	79.3	-0.496**
	At-m	3.8	0.214 <sup>ns</sup>
	At-f	9.2	-0.562*
D. Pupal Weight	Ag-m	133.9	0.764***
	Ag-f	223.6	0.718***
	At-m	49.6	0.758***
	At-f	93.2	0.867***

Ag, *A. geniculatus*; At, *A. triseriatus*; m, males; f, females  
<sup>ns</sup> = not significant; \* =  $P < 0.05$ ; \*\* =  $P < 0.01$ ; \*\*\* =  $P < 0.001$

#### Relationships between fitness correlates and the composite fitness index

The correlates of fitness examined varied widely in their sensitivity to and correlation with the value of the composite index  $r'$ . Survivorship, measured as pupation success, varied little over the range observed in  $r'$  in both species and was positively correlated with this index in *Aedes geniculatus* but not in *A. triseriatus* (Tab. 2A). Sex ratio was highly sensitive to and positively correlated with  $r'$  in *A. geniculatus* but not in *A. triseriatus* (Tab. 2B). Except in female *A. geniculatus*, development time (Days to pupation, Tab. 2C) changed relatively little over the range in  $r'$ ; the negative correlation between development time and  $r'$  was significant in all cases except in male *A. triseriatus*. Male and female pupal weight in both species were highly sensitive to  $r'$  and positively correlated with this index (Tab. 2D).

#### Discussion

Correlates of fitness should be sensitive to changing per capita resource levels. Therefore, it is not surprising that fitness correlates in these mosquitoes respond to changing food and larval density; what is unexpected is the complexity of the responses and their marked differences between the two species. In *Aedes triseriatus*, survivorship (Wilton 1968) and development time (Keirans and Fay 1968, Barbosa et al. 1972) are affected by food, larval density, or temperature. Livdahl (1982) showed that the responses of separate fitness correlates in *A. triseriatus* to food and larval density may be quite complex, but that some of these interactions appear to counteract one another so that overall population growth may change with food and density in a simple

linear fashion. Thus, the behavior of separate fitness correlates is not a reliable indicator of the population response in per capita rate of change.

While we agree with Livdahl's (1982) general conclusion, our results with *A. triseriatus* indicate that population growth, measured as per capita rate of change, may also be a complex function of food and density (Fig. 4B). Nearly 15% of the variation in the composite fitness index  $r'$  is accounted for by the interaction terms. Thus, the effect of food on  $r'$  depends on the density, and vice versa.

Three differences between Livdahl's (1982) study and this one should be recognized. First, densities used by Livdahl (1982) ranged from 66–264 larvae per liter. The densities in this study ranged from 133–800 larvae per liter but are representative of some northern populations of *A. triseriatus*. For example, densities of first-instar *A. triseriatus* larvae at Ithaca, New York, USA (42° 27'N, 76° 30'W), may exceed 3500 larvae per liter in late spring (Bradshaw and Holzapfel, unpubl.). The densities and food levels that Livdahl (1982) tested were representative of those experienced by local populations sampled in a New Jersey woodlot but may have been too low to elicit an effect of food-density interaction on per capita rate of change. Second, the relationship between the tree-hole detritus used by Livdahl (1982) and the laboratory diet used in the present study is unknown. Third, larvae in this experiment developed under constant temperature (21°C), while those manipulated by Livdahl (1982) developed under a variable temperature regime. All three differences in experimental design may have contributed to this disparity in the responses of *A. triseriatus* to food and density.

To examine the effects of food and density interaction on the composite index of fitness  $r'$ , we compared values of  $r'$  obtained at different densities but at the same level of food per individual (Tab. 3). In *A. geniculatus*, there was no detectable interaction between food level and larval density that affected  $r'$  (Tab. 1E). At the same time,  $r'$  varied little with density at a constant level

Tab. 3. Variation in the mean composite index  $r'$  when per capita resource (food density) is held constant while larval density is varied.

Food density (mg ind <sup>-1</sup> )	Larval density (number per dish)		
	10	20	40
A. <i>Aedes geniculatus</i>			
10.0	0.163	0.173	nd
5.0	0.130	0.152	0.138
2.5	nf	0.063	0.066
B. <i>Aedes triseriatus</i>			
10.0	0.221	0.189	nd
5.0	0.118	0.123	0.180

nd, not determined

nf, no females survived to pupation

of food per individual (Tab. 3A). By contrast, in *A. triseriatus*, there was a highly significant ( $P < 0.001$ ) interaction between food and density under the same conditions (Tab. 1E) and  $r'$  at 5 mg per individual exhibited facilitative effects of density (Tab 3B).

*Aedes geniculatus* and *Aedes triseriatus* belong to the same subgenus (*Finlaya*) of *Aedes* and both are exclusively tree-hole mosquitoes. Their composite indices of fitness are qualitatively similar (Fig. 4) but similar patterns of  $r'$  are underlain by strikingly different patterns of fitness correlates (Figs 1–3). Differences in correlates of fitness (Figs 1–3) may be attributable to the independent evolution of *A. geniculatus* in Europe and *A. triseriatus* in North America.

Although  $r'$  is qualitatively similar in *A. triseriatus* and *A. geniculatus* (Fig. 4), quantitative differences exist. *Aedes geniculatus* is able to achieve a positive fitness over a greater range of food levels and densities than is *A. triseriatus*. Yet, *A. triseriatus* tracks food level and larval density more closely than *A. geniculatus*. Variation in these two parameters explained over 90% of variation in per capita fitness in *A. triseriatus* but only 66% in *A. geniculatus* (Tab. 1E). In each correlate of fitness, the total reduction in sum of squares attributable to food and density is consistently greater for *A. triseriatus* than for *A. geniculatus* (Tab. 1A–D). *Aedes triseriatus* thus appears to be more homeostatic, *A. geniculatus* more polymorphic for fitness correlates. If so, it may be this greater genetic repertoire that enables *A. geniculatus* to maintain a positive fitness over a greater range of environments than *A. triseriatus*.

Finally, because of the greater potential for genetic polymorphism in *A. geniculatus* than in *A. triseriatus* we predict that the heritabilities of life-history traits may be higher in the former species than in the latter.

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