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COMPONENTS OF DENSITY-DEPENDENT POPULATION DYNAMICS: MODELS AND TESTS WITH *DROSOPHILA*

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Abstract.—This study has tested a model of density-dependent population dynamics in food-limited environments. Parameters of the model were estimated using standard regression techniques and observations on viability and female size in eight populations of *Drosophila melanogaster*. The model was tested by comparing its predictions with observations of female size that had not been utilized in the estimation process. In general there was good agreement between observations and predictions of the mean size of females supplied with differing amounts of food. There were substantial deviations from the predicted and observed variance of female size. This difference may be attributed to certain simplifying assumptions of the model and factors other than food that contribute to mortality in these experimental systems. These results point to additional phenomena, such as tolerance to waste products, which may be important in the density-dependent population dynamics of *Drosophila* and should be incorporated in models describing this process.

The theory of density-dependent natural selection was in full bloom by the early 1970s with the appearance of a number of formal models (Anderson 1971; Charlesworth 1971; King and Anderson 1971; Roughgarden 1971; Clarke 1972). These models usually included general descriptions of density-regulated population growth, such as the logistic model. In addition, the specific evolutionary predictions concerned just one phenotype: density-dependent rates of population growth.

The predicted effects of natural selection on density-dependent rates of population growth have been observed in laboratory populations of *Drosophila melanogaster* (Mueller and Ayala 1981*a*). However, continued investigation of this phenomenon has been hampered by the lack of a more detailed theory of life-history evolution in density-regulated populations.

Recently, we have developed a model of density-dependent population growth and natural selection in food-limited environments (Mueller 1988*a*). This model includes ecological details of competition for food that are relevant to *Drosophila* populations. The effects of limited food on viability and fecundity are included. Evolutionary predictions emerge concerning traits such as competitive ability for food, minimum food necessary for successful pupation, and average female size. Current empirical studies indicate that natural selection at high densities has led to

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a substantial increase in competitive ability (Mueller 1988*b*) and that a correlated response may have been an increase in minimum food requirements (Mueller 1990).

The components of the limited-food model of population dynamics are supported by numerous empirical studies (see references in Mueller 1988*a*). However, the complete model has not been subject to rigorous tests. Nunney (1983) has shown that the viability component of the model can fit empirical data quite well. In this article, we test the viability and fecundity components of the model in a two-step process. The first step involves using certain experimental observations to estimate parameters of the model. The second step involves testing predictions of the model with data not used in the estimation procedure. If the same observations are used to estimate model parameters and assess goodness of fit, the results are liable to be overly optimistic. The ability to test this model with independent data will provide a rigorous test of the utility of this theory.

METHODS

Population-Dynamics Model

In a genetically variable population with allele frequencies at a single locus described by the vector $\mathbf{p}_t$, the number of eggs at time $t + 1$, n_{t+1}, is described by

$$n_{t+1} = \tfrac{1}{2}G(N_t)\bar{F}(n_t, \mathbf{p}_t)\bar{W}(n_t, \mathbf{p}_t)Vn_t, \tag{1}$$

where V is the probability of an egg's becoming a first instar larva, $\bar{W}$ is the frequency- and density-dependent function describing the viability of these first-instar larvae, $\bar{F}$ is the mean fecundity of adult females and reflects the effects of food limitation on female size, and $G(N_t)$ describes the effects of adult density, N_t, on female fecundity. In this article we examine the effects of limited food on viability and fecundity. As described elsewhere (Nunney 1983; Mueller 1988*a*), the viability of genotype A_iA_j in food-limited environments is

$$W_{ij}(n_t, \mathbf{p}_t) = \int_x^\infty \phi(y)\,dy, \tag{2}$$

where $\phi(y)$ is the standard normal density function and $x = (mVn_t\bar{\alpha}/B\alpha_{ij} - 1)/\sigma$, in which m is the minimum amount of food a larva must consume to successfully pupate, α_{ij} is the competitive ability of genotype A_iA_j, $\bar{\alpha}$ is the average competitive ability of the population, B is the total amount of food in the environment, and σ^2 is proportional to the variance in food consumed by the Vn_t larvae. This model assumes that in food-limited environments the amount of food consumed by different larvae, after all food is consumed, is described by a normal distribution. All larvae consuming more than m units of food survive to become adults; the rest die. Equation (2) is simply the fraction of the population that survives. The lower limit of integration equals m before it has been transformed to a standard normal deviate.

The effects of limited food on female fecundity are studied through the size of adult females. Since female size is highly correlated with fecundity (Chiang and Hodson 1950; Robertson 1957; Mueller 1987), we treat these traits as equivalent. The average size of females of genotype A_iA_j is given by

$$\overline{s_{ij}}(n_t, \mathbf{p}_t) = W_{ij}^{-1}(n_t, \mathbf{p}_t) \int_x^\infty s[B\alpha_{ij}(\sigma y + 1)/Vn_t\bar{\alpha}]\phi(y)dy, \quad (3)$$

and $s(k)$ describes the size of a single larva that has consumed k mg of food. To compute the size of any adult requires only knowledge of the amount of food that it consumed as a larva. Thus, equation (3) integrates the size function over all food levels that produced surviving larvae and is normalized by the fraction of the population that survives.

Experimental Populations

The experimental populations consisted of six independent populations initially derived from the same source population: three have been kept at low population density (50 adults) and are called *r*-selected, and three have been kept at high densities (~1,000 adults) by a serial transfer system (Mueller and Ayala 1981*b*) and are called *K*-selected. Each *r*- and *K*-population has been randomly assigned an index from one to three. At any one time, experiments were conducted on matched populations, for example, *r*-1 with *K*-1, *r*-2 with *K*-2, and so forth. In addition to these six populations, two other populations, called *r*-F_1 and *K*-F_1, which were F_1's of the three *r*- and the three *K*-populations, respectively, were studied. These populations were created by making all possible crosses; for example, for the *r*-F_1 population there were six crosses (male × female): *r*-1 × *r*-2, *r*-1 × *r*-3, *r*-2 × *r*-3, and the reciprocal crosses. At the time these experiments were initiated, the *r*- and *K*-populations had been in their respective environments for 125 generations. All experiments were conducted at 23°C on a schedule of 12 h of light and 12 h of darkness.

Collection of Experimental Larvae

Experiments were initiated by removing adults from the running *r*- and *K*-populations of a matched pair (fig. 1). About 100 adults were placed in half-pint cultures with standard *Drosophila* medium and allowed to lay eggs for 24 h. Two weeks later adults were collected from these cultures to provide first-instar larvae for experimental measurements.

We used the following procedure to maximize egg production of these females. About 100 adults were placed in half-pint cultures with tissue paper and a large volume of live yeast paste. These adults were kept in these cultures for 3 d. The extra food increased egg production (Sang 1949); in addition, by the third day, the presence of larvae in these cultures inhibited egg laying by females (Chiang and Hodson 1950) until they were moved to a fresh culture. After this 3-d period, the adults were moved to empty 100-mL beakers that had a watch glass fastened to the top. The watch glass was filled with soft agar that had been painted with dilute vinegar and had a drop of yeast paste in the center. Egg laying was initiated

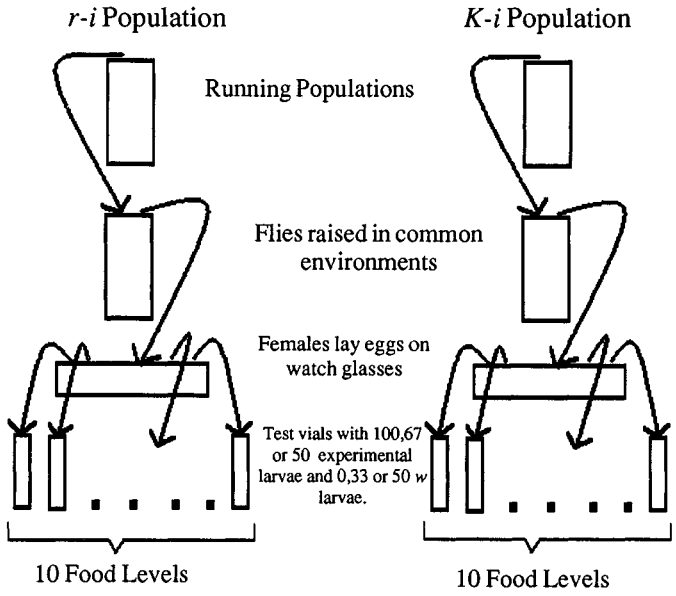

FIG. 1.—Experimental protocol for estimating viability and female thorax length as a function of food availability for a matched pair (*r-i* vs. *K-i*) of selected populations.

just before incubator "sunset," a time of increased egg-laying activity. Beakers were placed in the incubators with the watch glass on the bottom for 1 h. Eggs from the first half hour were discarded because they usually contained many fertilized eggs that had been developing for several hours before egg laying. Adults were transferred to new beakers for an additional hour of egg laying as needed. Usually enough eggs could be collected in just 2 h.

Viability and Female Size versus Food

The drop of yeast was removed from each watch glass 17 h after egg laying. At this time, early hatching larvae would be present in this yeast and were thus removed. Within 2 h of hatching, 100 first-instar larvae from each population were placed in 8-dram vials (22 × 95 mm) at each of 10 different food levels.

Each vial was filled with 10 mL of nonnutritive Kalmus medium: 11.3 g agar, 1.54 g KH_2PO_4, 2.06 g $(NH_4)_2SO_4$, 0.51 g $MgSO_4 \cdot 7H_2O$, and 5.1 mL propionic acid per 1,000 mL water. Live yeast and water (2.67 mL/g yeast) were added to each vial about 2 h before the larvae were added. Food levels varied from 25 mg to 158 mg per 100 larvae. As discussed by Bakker (1961), these cultures preclude growth of yeast, and thus the total amount of food available to the larval population is known. In addition, the larval densities can be kept relatively low, and other factors that influence viability and adult size in crowded environments can be diminished and controlled.

Depending on the food level, adults emerged 11–14 d after larvae were placed in the vials. At daily intervals, the number of newly emerged males and females from the *r*, *K*, and *white* monocultures were recorded. The thorax length of all

females was measured to the nearest 0.05 mm. Vials were checked for newly emerged adults for up to 12 d after the first adults appeared.

Measuring Competitive Ability for Food

In the first series of experiments, the 100 larvae added to each vial were all from the same population (monocultures). To estimate relative competitive ability, two additional types of experiments were conducted. The second type of experiment created a mixture of 50 larvae from either the *r* or *K* population, with 50 larvae from a population homozygous for the *white* (*w*) allele (even-mixture experiments). The third type of experiment created mixtures of 67 *r* or *K* larvae and 33 *w* larvae (uneven-mixture experiments).

Each experiment with monocultures was conducted on at least three separate dates. The even-mixture and uneven-mixture experiments were conducted on two separate dates for each population and each frequency of larvae. Thus, for instance, we performed two replicates of the experiments in which equal numbers of *K*-1 and *w* larvae competed at 10 food levels. Since data were collected over a long period of time (March 1985–January 1987), replicates of the pure and mixed populations were evenly distributed over this period. In this way, if there were temporal changes in the populations or techniques, replicates would be separated by a long time period and hence reflect the variance caused by such changes. During the course of the experiment, 60,000 first-instar larvae were counted, 29,200 adult survivors were censused, and the thorax lengths of 14,600 females were measured.

Statistical Analysis

The analysis of model parameters has been achieved by a two-step process. Using the viability data alone in conjunction with equation (2), estimates of m, α, and V were obtained for each population. These estimated parameters were then used in conjunction with equation (3) to estimate the three parameters of the adult-size model: a_0, a_1, and a_2. Several assumptions have been made in order to proceed with the statistical analysis of the data described in the preceding subsection. The first concerns the viability of eggs. In the experimental system used here, maximum viability was often between 70% and 85%; however, more than 90% of the input larvae would pupate when food was abundant. We have therefore assumed that $V = 1$ and that all mortality not caused by limited food occurs after competition for food is completed. This assumption is important for computing the average competitive ability of larvae in the experimental populations. Clearly, if many larvae died shortly after hatching because of density-independent causes, the number of larvae competing for food would be less than the assumed number of 100.

The next set of assumptions concerns the value of parameters for males and females. All parameters except α are allowed to differ between males and females. Our experimental data on cephalopharyngeal retraction rates (Joshi and Mueller 1988) show no consistent differences between males and females. These retraction rates seem to be useful behavioral indexes of competitive ability for limited food (Burnet et al. 1977; Joshi and Mueller 1988).

Viability and Competitive Ability

We use the linear-regression techniques of Nunney (1983) to estimate parameters of the viability component of population dynamics. Thus, if W_f is the observed viability of females in a pure population, and $\Phi^{-1}(\cdot)$ is the inverse of the cumulative normal distribution function, then

$$\Phi^{-1}(W_f) = \frac{1}{\sigma_f} - \left(\frac{m_f}{\sigma_f}\right)\left(\frac{100}{B}\right). \tag{4a}$$

From these data we can estimate σ_f and m_f/σ_f using standard linear-regression techniques (for more details on this technique, see Nunney 1983, table 3). If females from the same population have viability $\hat{W}_f$ when placed in competition with equal numbers of *white* larvae, then

$$\Phi^{-1}(\hat{W}_f) = \frac{1}{\sigma_f} - \left(\frac{m_f\bar{\alpha}}{\sigma_f\alpha}\right)\left(\frac{100}{B}\right), \tag{4b}$$

where $\bar{\alpha} = (\alpha + 1)/2$ since the *white* larvae are assumed to have a competitive ability of 1. Using the estimates of m_f/σ_f from the pure population experiment, α can be estimated from the slope of equation (4b) in the competition experiment. Similar results are obtained for males and from male and female viability of *w* larvae. Likewise, additional estimates of α are obtained from the experiments using different input frequencies of larvae.

Thorax-Length Model

To model the size of a female, $s(k)$, which has consumed k mg of food as a larva, we use

$$s(k) = a_0 + a_1\{1 - \exp[-a_2(k - m)]\}. \tag{5}$$

The maximum size, $a_0 + a_1$, is approached asymptotically as k approaches infinity, and the minimum size, a_0, is achieved when $k = m$. Since it is impossible to know the precise amount of food consumed by any individual larva, parameters of equation (5) are estimated using equation (3) and the average size of all females at a given food level.

Bootstrap Statistics

Statistical inference on m and α is complicated because these have been estimated using nonlinear functions of the regression parameters from equation (4). To circumvent these problems, the bootstrap technique has been used (Efron 1979*a*, 1979*b*). This method generates new data sets by recreating the sampling process inherent in the collection of these data and using the original data as an empirical estimate of the distribution function of the relevant random variables. This technique has been used to construct bias-corrected confidence intervals (Efron 1981) for α, m, and σ. Recent evidence indicates that bootstrap confidence intervals may be accurate in a wide variety of problems (Efron 1985). Statistics reported here are based on 1,000 independently generated samples.

The sampling process for the bootstrap required over 100 million random numbers. To maximize the speed of the program, random numbers were read directly into main memory. Sixty thousand single-precision, uniformly distributed random numbers and 60,000 normal random numbers were read into the main memory. Except for these numbers, all numerical work used double-precision real variables with about 15 significant digits and was programmed in Pascal. Clearly, if these random numbers were just read in order, the sequence would cycle every 60,000 numbers. To avoid any possible correlations in the numerical results from such cycles, the following process was used. A vector was filled with the first 1,000 random numbers. To generate one random number, the next number in the main sequence was taken and changed to an integer ϵ [1, 1000], with each integer having an equal chance of being chosen. This integer was used to specify the random number in the vector, which was then used in the bootstrap program. The chosen number was then replaced in the vector with the next number from the main sequence. Thus, for every random number used in the program, two numbers are read. The benefit of this process is that the cycle time of the resulting sequence of random numbers is the product of the two component sequences, which is approximately 10^9.

Nonlinear Regression

After the bootstrap yielded estimates of the parameters in equation (4), nonlinear regression was used to estimate parameters of the size equation (3). Nonlinear regression was performed with Marquardt's algorithm (Marquardt 1963). Romberg integration (Philips and Taylor 1973, p. 136) was used to evaluate equation (3). The implementation of Romberg integration used here successfully integrated the standard normal density function with an accuracy of more than nine significant digits. The systems of linear equations that are solved repeatedly in the nonlinear regression program were solved by the techniques of compact elimination with partial pivoting (Philips and Taylor 1973, p. 209). Iterative recovery (Philips and Taylor 1973, p. 248) did not improve the accuracy of these solutions substantially during trial runs and consequently was not used. The Marquardt routine was run from several different starting places in the vicinity of a final solution to explore for other local minima in the least-squares space. Statistics on the nonlinear least-squares parameters were derived from the standard large-sample theory (Gallant 1975).

To assess the qualitative agreement between observations and model predictions, 95% regression-surface confidence bands (Miller 1966, p. 111) have been calculated for the nonlinear regression model. These upper and lower confidence bands are functions that bound the true regression surface with 95% confidence. The extension of the theory outlined by Miller (1966) to nonlinear models requires an estimate of the variance of predicted dependent variables. Let average female thorax length be $\bar{s}(B,\hat{\mathbf{a}})$, where the independent variable is total food, B, and $\hat{\mathbf{a}}$ is the estimated vector of parameters in equation (5). Then for the ith food level, B_i, the variance of average female size, can be approximated by the delta method (Bishop et al. 1975, pp. 486–488) as

$$\text{var}[\bar{s}(B_i,\hat{\mathbf{a}})] = \nabla'\Sigma\nabla$$

TABLE 1

ESTIMATED VALUES (±95% CONFIDENCE INTERVAL) FOR VIABILITY MODEL PARAMETERS FOR EACH POPULATION

		m		σ	
POPULATION	α	Male	Female	Male	Female
K-1	1.07	.45	.45	.30	.30
	(±.24)	(±.065)	(±.065)	(±.11)	(±.13)
r-1	.95	.52	.59	.61	.43
	(±.31)	(±.80)	(±.10)	(.30, .58)*	(.32, .61)*
K-2	1.17	.47	.47	.36	.48
	(±.33)	(±.13)	(±.15)	(±.13)	(.36, .73)*
r-2	.74	.34	.52	.43	.46
	(±.34)	(±.15)	(±.15)	(.33, .63)*	(.35, .67)*
K-3	1.19	.42	.51	.39	.39
	(±.26)	(±.082)	(±.046)	(.29, .52)*	(.30, .51)*
r-3	.47	.42	.47	.32	.33
	(±.28)	(±.092)	(±.067)	(±.14)	(.28, .44)*
K-F_1	1.16	.43	.45	.17	.23
	(±.20)	(±.12)	(±.081)	(±.22)	(±.10)
r-F_1	.77	.19	.24	.54	.43
	(±.25)	(±.084)	(±.13)	(.38, .88)*	(.34, .68)*

* Bias-adjusted confidence intervals.

TABLE 2

PARAMETER ESTIMATES FROM THE SIZE MODEL (EQUATION [5]) ± 95% CONFIDENCE INTERVALS

Line	a_0	a_1	a_2
K-1	.60 ± .06	.50 ± .06	2,500 ± 1,400
r-1	.69 ± .07	.44 ± .20	1,300 ± 1,600
K-2	.63 ± .11	.53 ± .15	1,400 ± 1,600
r-2	.64 ± .06	.54 ± .17	1,300 ± 1,100
K-3	.62 ± .05	.46 ± .05	2,200 ± 1,100
r-3	.72 ± .03	.39 ± .06	1,500 ± 820
K-F_1	.72 ± .03	.44 ± .10	1,500 ± 820
r-F_1	.64 ± .03	.65 ± .12	940 ± 430

where

$$\nabla' = \left[\frac{\partial \bar{s}(B_i,\hat{\mathbf{a}})}{\partial a_0}, \frac{\partial \bar{s}(B_i,\hat{\mathbf{a}})}{\partial a_1}, \frac{\partial \bar{s}(B_i,\hat{\mathbf{a}})}{\partial a_2}\right]$$

and Σ is the covariance matrix of $\hat{\mathbf{a}}$.

RESULTS

Model Predictions and Observations

The evolutionary implications of the differences in viability-parameter values (table 1) have been discussed previously (Mueller 1988*b*, 1990). The estimates of viability parameters were used in the process of nonlinear estimation of the size-model parameters (table 2). To assess the goodness of fit provided by these

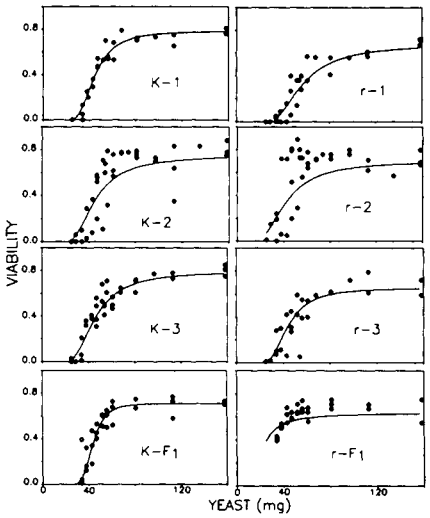

FIG. 2.—Viability of monocultures of the eight experimental populations with the predictions (*solid line*) from eq. (2).

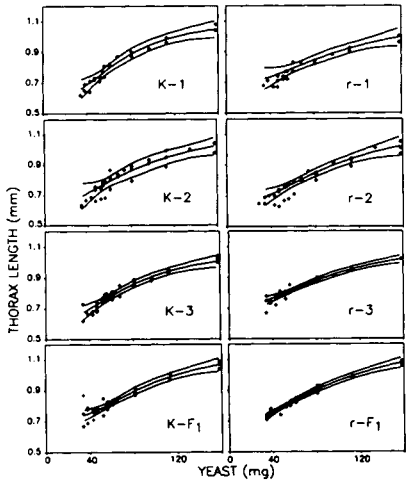

FIG. 3.—Thorax length of experimental females in the monoculture experiments. *Middle solid line,* the predicted value from eq. (3); *top and bottom lines,* the simultaneous 95% confidence limits.

models, the parameters in tables 1 and 2 have been used to construct the expected viability (fig. 2) and thorax length (fig. 3) for each population. These curves are displayed with the observed viabilities and thorax lengths from experiments with pure populations. Above and below the expected thorax length are upper and lower bounds of the simultaneous 95% confidence intervals.

In general, the curves fitted the observed values quite well. In some cases, for

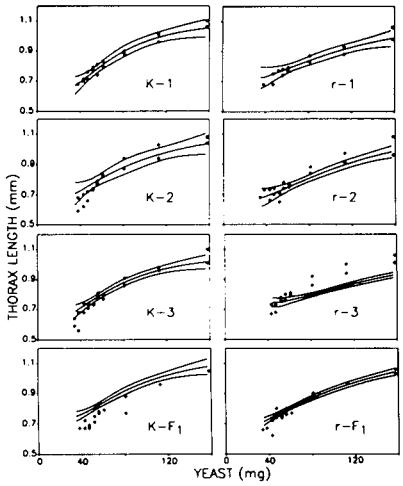

FIG. 4.—The same information as fig. 3 for the even-mixture experiments

example *r*-2 in figure 2, the observed viability at intermediate food levels was greater than at the highest food level. Maximum viability was estimated from the observed viability at the highest yeast level; consequently, the predicted viability is substantially less than the observed viability at these intermediate values, since the maximum viability is approached asymptotically.

The high survival rate of the r-F_1 larvae (fig. 2) at low food levels is due to their low minimum food requirement (see table 1). The points in figure 3 are mean thorax lengths; consequently, the values at higher food levels are based on larger sample sizes than the averages obtained at low food levels. Since the least-squares estimates weighted the sample size of each point, the final curves are most influenced by observations at high food levels. Thus, the expected curves in figure 3 are more likely to deviate from the observations at low food levels.

Thus far our confidence in models (3) and (4) is due to the incorporation of important empirical phenomena in these models (de Jong 1976; Nunney 1983; Mueller 1988*a*) and relatively good agreement between model predictions and observations (figs. 2, 3; Nunney 1983). Confidence that these models incorporate important features of viability and size in food-limited environments would be increased if the models made accurate predictions of new observations. In the experiments described above, the thorax lengths of females in the mixed populations were measured but not used in the estimation procedure. Thus, we can use equation (3) to predict the average thorax length of females in these experiments. These predictions will test not only the utility of equation (5) but the estimates of α that are derived solely from the viability studies.

To aid in the assessment of the model predictions for the even (fig. 4) and uneven (fig. 5) mixture experiments, simultaneous 95% confidence intervals have been placed on these values. As a cautionary note, it should be remembered that these confidence intervals would apply only to the data used to estimate the

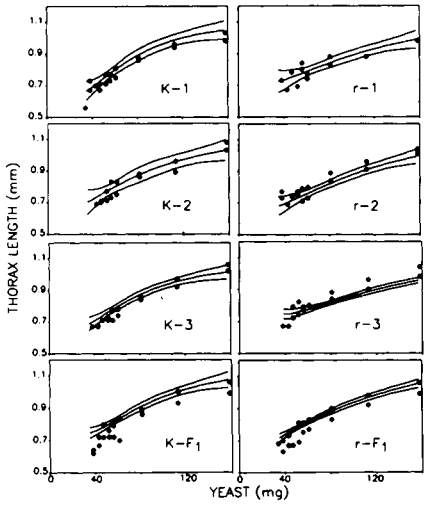

FIG. 5.—The same information as fig. 3 for the uneven-mixture experiments

model parameters. Even in these cases (fig. 3) it appears that greater than 5% of the observations lie outside the intervals, especially at low food levels. Recall that each point in figures 3–5 is the mean size of females and thus the observations at low food levels are due to very small numbers relative to the observations at high food levels. Since the regression weighted these means, we expect more observations to fall outside the intervals at the low food levels. Thus, if greater than 5% of the observations from these new experiments lie outside the interval that does not necessarily mean the model should be discarded. The intervals do allow a qualitative assessment of how close the observations are to the predicted values.

At this point, the reader may wonder whether there is not a test that will tell us whether this regression function equals $E[s(k)|n_t, \mathbf{p}_t]$. Despite our desire to develop physics-like precision in theories of ecological processes, we consider this an unlikely achievement even in these simplified laboratory environments. In this study, we are working under the assumption that equation (3), or any model we might design, is wrong to some degree and given a sufficient sample size this would ultimately be demonstrated. Consequently, the interesting question about models then becomes, How accurate are they? The confidence intervals aid our assessment of the data when answering this question. If there were some competing class of models, then we might make some comparison of the mean-squared error of prediction for each model. For the present study, as is discussed below, the deficiencies of the model are obvious when present and thus do not require a fine-tuned statistical hypothesis test to reveal.

For two populations the model predictions are consistently biased: the model predictions are too small for the K-F_1 population and too large for the r-3 population (figs. 4, 5). For the remaining six populations, the model predictions are quite

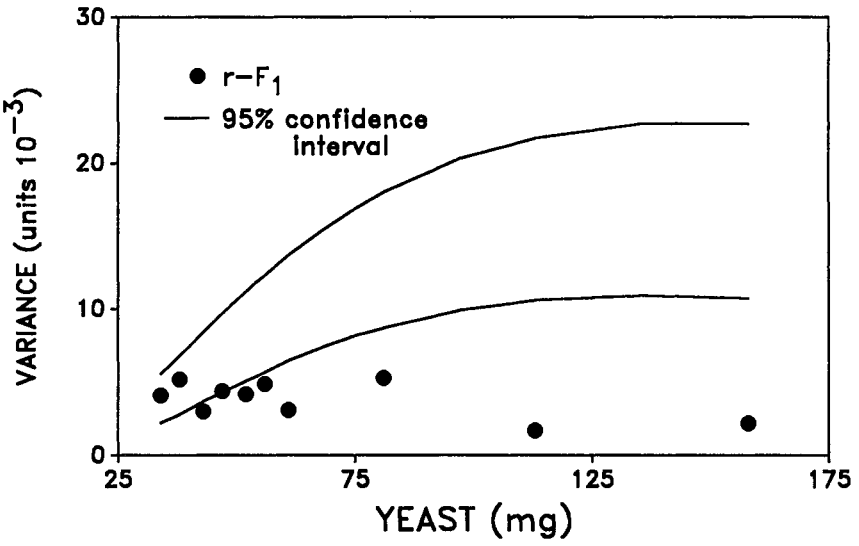

FIG. 6.—The observed variance of female thorax length for the r-F_1 population. *Solid curves*, approximate 95% confidence intervals on the predicted variance from eq. (6) that were computed as described in the text.

reasonable. Since the even-mixture experiments present environmental conditions that deviate the most from the pure populations from which the estimates of the size model emanate, these experiments are expected to be the most stringent test. The model predictions, in these even mixtures (fig. 4), are as good as or better than the uneven mixtures (fig. 5).

Variance of Female Thorax Length

Equation (3) predicts the mean thorax length of females at a given food level. Estimates of the parameters in this model used the observed mean thorax length in the pure populations. In addition to the mean, the model can be used to predict the variance in female size as

$$\operatorname{var} s(k) = W_{ij}^{-1}(n_t, \mathbf{p}_t) \int_x^\infty [sB\alpha_{ij}(\sigma y + 1)/Vn_t\bar{\alpha} - \bar{s}(n_t, \mathbf{p}_t)]^2 \, \phi(y)\, dy . \qquad (6)$$

These predicted values can be compared to the observed variance. Since the parameters in equation (6) have been estimated from viability data and mean thorax length, they are independent of the variance of thorax length. This constitutes a second independent test of the models.

The variance of thorax length of females from the pure populations has uncovered a substantial and consistent deviation from the model expectations (fig. 6). The predicted variance from equation (6) is quite sensitive to the estimate of σ. In figure 6, upper and lower bounds of the predicted variance have been calculated by using the upper and lower 95% confidence intervals on σ. Despite this large resulting interval, the observed variance of female thorax length is consistently smaller than predicted, especially at the highest food levels.

Mortality not Caused by Limited Food

Clearly, one reason for the deviations observed in figure 6 could be that limited food is not the only source of mortality in this experimental system. In these experimental vials it is difficult to census the dead larval population, but we can observe and measure pupae that survive and those that die. If limited food is the only density-dependent source of mortality, then the pupal population should fall into two nonoverlapping classes: small, dead pupae and large, live pupae. Occasionally the population of large pupae will have an individual that died from some density-independent cause. However, the population of small pupae should all be dead. The presence of numerous live pupae in the small class indicates that size and therefore food consumption is not the only cause of mortality. For the K-1 population, we have measured the length and height above the food surface of all dead and live pupae at 10 food levels. Two replicates were performed for each experiment.

The lowest three food levels in figure 7 show a fairly large class of exclusively small, dead pupae. However, when 56 mg of yeast are provided, this population of small, dead pupae is contaminated by a few live pupae. This trend continues in the next four highest yeast levels (fig. 8). It must be remembered that at many of these food levels there are dead larvae in addition to the dead pupae. These dead larvae account for the difference in total number of pupae between the high and low food levels. Many of these larvae died because of insufficient food. Nevertheless, these data indicate that at moderate to high food levels there are additional sources of mortality that are not simply due to insufficient food consumption. The mechanism by which this sort of biological phenomenon may lead to the discrepancy observed in figure 6 is presented in the discussion.

A secondary phenomenon is evident in figures 7 and 8. First, there is a gradual increase in pupation height with increasing food level. It is well-known that pupation height increases dramatically with larval density. In these experiments the input number of larvae was constant. However, the number of larvae that survive to pupate increases with increasing food level, as does the size of these surviving larvae. In the highest three food levels the number of total pupae is constant (observed number of pupae ranged from an average of 97.5–102 per vial), yet pupation height continues to increase. These results suggest that pupation height is influenced not only by the numbers of larvae present shortly before pupation but also by the relative size of these larvae.

The first five food levels in figures 7–8 show no evidence of a correlation between pupation height and death. However, the three highest food levels show a segregation of dead pupae to very low or high pupation heights. At the highest food level, the only pupae on the surface are dead.

DISCUSSION

Prediction of population dynamics with equation (1) requires accurate knowledge of the mean population fecundity and viability. The ability of this model to predict these mean values is quite good. This conclusion is based on model predictions of experimental data that were not used in the parameter-estimation process.

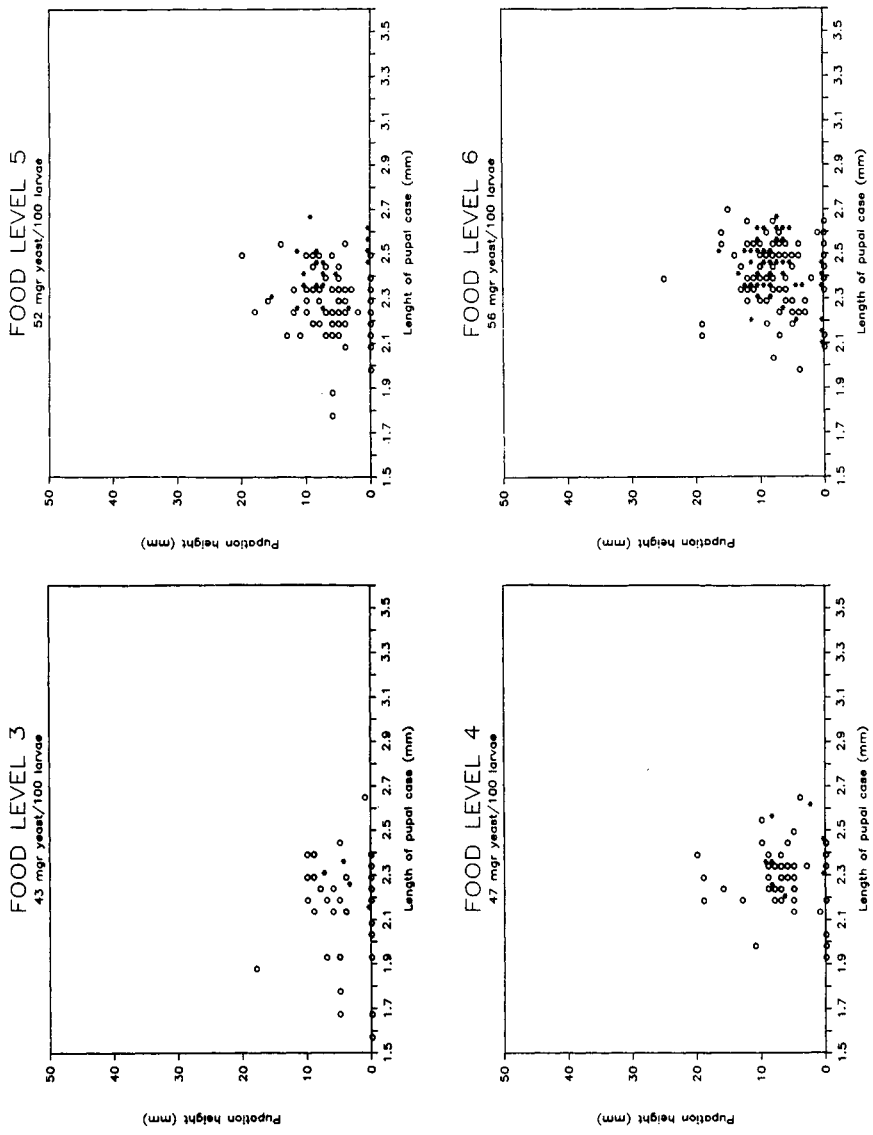

FIG. 7.—The mean length and height above the food surface for the *K*-1 pupae that died (*open circle*) or survived (*asterisk*) at four food levels.

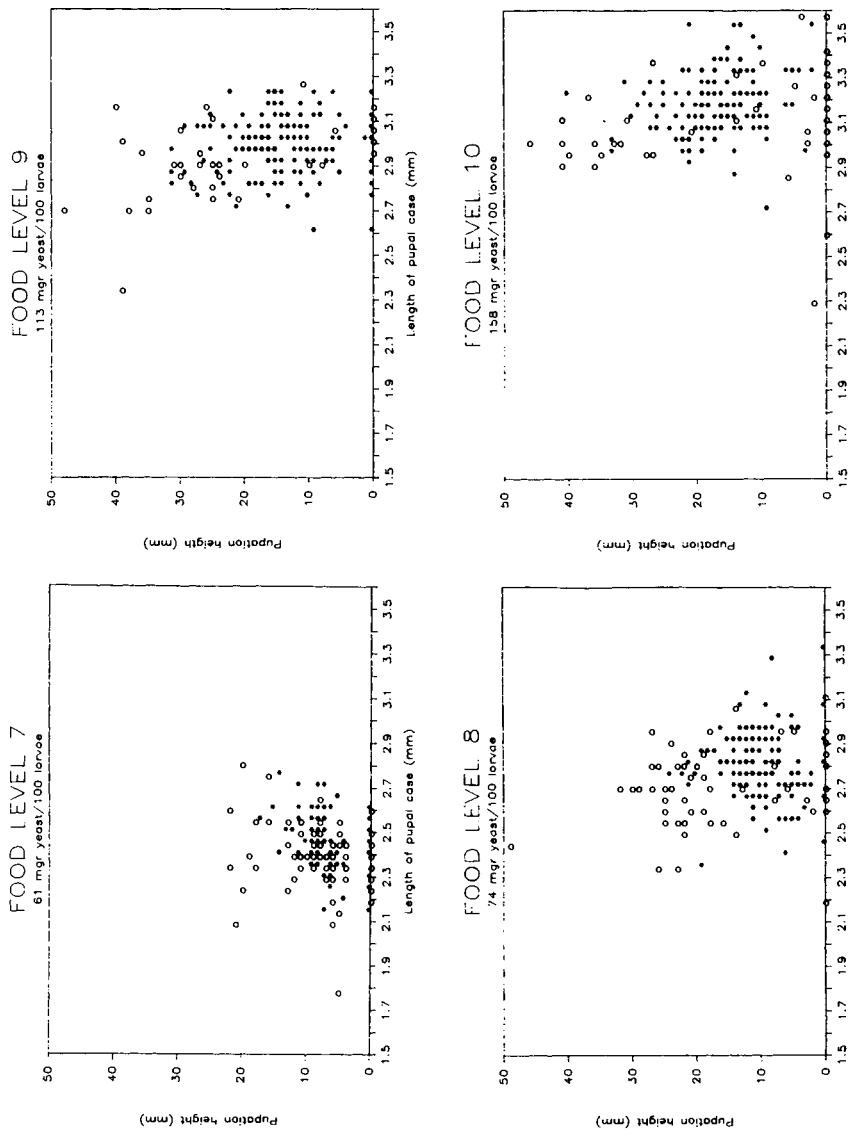

FIG. 8.—The mean length and height above the food surface for the *K*-1 pupae that died (*open circle*) or survived (*asterisk*) at four food levels.

As discussed elsewhere (Mueller 1988*a*), the development of such detailed population-dynamic models is necessary to derive realistic predictions concerning life-history evolution in *Drosophila*. To the extent that empirical research will focus on this genus, details of its ecology should be part of any formal theory that makes predictions about *Drosophila* life-history evolution.

The model does not accurately predict the variance of female size. Although it is not necessary to know this variance to predict population dynamics, this weakness highlights additional biological phenomena that might be relevant to density-dependent dynamics of *Drosophila* populations.

Alternative Models

Before discussing which biological phenomena might account for the observed deviations, we should consider whether the model might be altered in some meaningful way. One assumption made by this model (Mueller 1988*a*) is that the population may contain larvae that consume infinite amounts of food. Clearly, no single larva can consume more food than exists in the environment (B). More significantly, when food is relatively abundant, larvae may cease feeding when they have consumed some maximum amount (b_{max}). Both of these possibilities suggest that the distribution of food consumed by larvae should be truncated at high food levels at either B or b_{max}, whichever is less. The effect of such an alteration is to reduce the variance of the size of adults, especially at high food levels, that is exactly the bias seen in these data.

Other Important Biological Phenomena Affected by Population Density

The results on pupal survival suggest that at moderate to high food levels there may be some additional sources of mortality not present at the low food levels. The input number of larvae is constant; as the food levels increase, more larvae survive for greater lengths of time and they become larger. Waste production, which should be proportional to the size of a larva, would increase as food levels increased as a result of the two previously mentioned trends. Larvae invariably ingest their own waste products and, if these become concentrated, there can be significant effects on viability and developmental time (Botella et al. 1985; Moya and Botella 1985). We conjecture that with increasing food levels larvae ingest more wastes and some die from ingestion of toxic levels. The result is that these additional deaths slow the achievement of maximum survival.

Figure 9 shows two viability curves that differ only in their value of σ. Large values of σ clearly retard the approach to maximum viability. We believe that the result of additional mortality in our experiments from waste ingestion has led to estimates of σ that are larger than they should be. For example, the data look more like the curve with the large σ in figure 9, although, if mortality due to waste ingestion were removed, the data would resemble the small σ curve.

It is clear from figure 6 that larger values of σ result in larger predicted variance of female thorax length. We conclude that the model prediction of higher variances than were observed can be attributed to an unrealistic assumption of the model (that larvae may consume infinite amounts of food) and an experimental system that includes density-dependent factors other than food limitation (waste concentration).

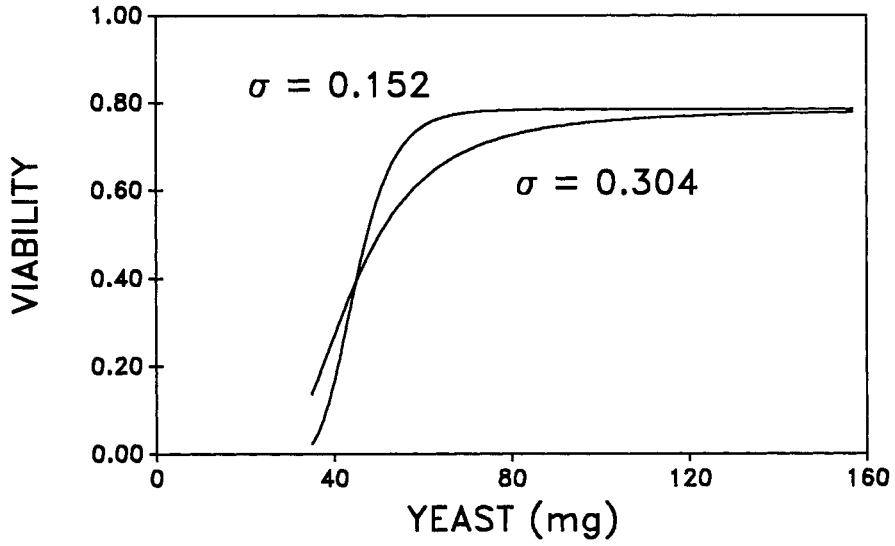

FIG. 9.—The predicted viability from eq. (2) for two populations that differ only in σ. The remaining parameter values were taken from the estimates for the K-1 population.

Our conclusions suggest that future work on population dynamics should attempt to include the effects of waste products on both viability and adult size. It will also be important to determine whether there is a maximum level of food consumed at which all larvae cease eating and pupate.

Enormous differences with respect to pupation height have been described for r- and K-populations (Mueller and Sweet 1986): at a fixed larval density and food level, the K larvae pupate much higher than do the r larvae. When the surface of the medium is soft and moist, as it is in crowded cultures, the chances of pupae on the surface dying increases dramatically (Mueller 1990). Thus, natural selection could be viewed as an agent responsible for increasing the tendency of K larvae to pupate off the surface.

Although there seemed to be no obvious advantage for the r larvae to travel large distances from the food surface to pupate in the r environments, there also appeared to be no disadvantage to such behavior. This study has uncovered such a disadvantage. Larvae that pupate very high appear to substantially increase their chances of dying. Thus, in the r environments where the surface of the food is entirely suitable for pupation, natural selection probably acts against individuals that pupate high. In crowded environments, there appears to be a classic case of stabilizing selection, with individuals that pupate very high or low having significantly higher mortality.

It is not clear what causes the increased mortality of the individuals that pupate near the tops of the vials. Humidity may affect survival and may be too low at the top of these vials. However, inspection of figure 8 shows that pupae that are dying at food level 74 (15–30 mm) survive at food level 158. Thus, if humidity is important, it is not a simple function of distance from the food surface.

Relevance for the Field Ecologist

This study has attempted to initiate the development of a coherent description of density-dependent population dynamics by examining the detailed mechanisms by which crowding affects life-history components in *Drosophila*. Crowding in these simplified environments probably limits reproductive capacity by limiting food and space and increasing waste concentration. The effects of crowding are almost certainly more complicated in the "real" world. Despite these complications, population dynamics of laboratory *Drosophila* populations can be summarized by fairly simple functions that ignore many of these details (Ayala et al. 1973; Pomerantz et al. 1980; Mueller and Ayala 1981*b*).

The obvious question is, when do these complications matter? Prout and McChesney (1985) have outlined conditions under which estimates of population growth rates from certain types of census data give biased results when density acts differentially on various life stages. This clearly means that population growth rates estimated from census data taken in the field must be viewed cautiously (Fowler 1988). The nature of density-dependence may also be important for evolutionary predictions. For instance, the evolution of body size may depend critically on the details of how crowding affects body size in *Drosophila* (Mueller 1988*a*).

Although our understanding of the action of density-dependent population dynamics in *Drosophila* is good, there is still more to be learned. One of the ultimate goals of this research program is to achieve a complete understanding of the nature of density-regulating mechanisms so that we can assess which details must be understood to make useful predictions about population-level phenomena.

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