Vol. 128, No. 2 The American Naturalist August 1986

DENSITY-DEPENDENT RATES OF POPULATION GROWTH: ESTIMATION IN LABORATORY POPULATIONS

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Submitted September 3, 1985; Accepted January 16, 1986

A fundamental problem in population ecology has been the development of simple quantitative models of single-species population growth (Gilpin and Ayala 1973; Pomerantz et al. 1980; Hastings et al. 1981; Mueller and Ayala 1981*b*). In discrete time, these models take the general form

$$N_t = g(N_{t-1}), \tag{1}$$

where $g(N_t)$ is some nonlinear function and N_t is the number of individuals, usually adults, in the population at time t. With organisms such as *Escherichia coli* and *Paramecium* there is no ambiguity about which life stage equation (1) refers to. A population of *Drosophila*, on the other hand, may consist of eggs, larvae, pupae, and adults in a single generation, and their numbers may all be different. Since adults are the most conspicuous life stage of many organisms, including *Drosophila*, and the most easily manipulated, population ecologists have almost always let N_t represent adult numbers. Although natural populations of *Drosophila* usually exhibit overlapping generations with essentially continuous reproduction, it is possible to enforce a discrete regimen of reproduction on laboratory populations and, hence, to use models such as equation (1) to describe population dynamics in these laboratory environments.

Even though the adult life stage can be shortened to a day or less, it is impossible, even in the laboratory, to eliminate the preadult life stages of *Drosophila*. In a very interesting paper, Prout and McChesney (1985) examined the effect of these preadult life stages on population dynamics when adults were the usual census stage. Prout and McChesney noted that, for *Drosophila*, the fecundity of females depends on their preadult larval density and that empirical evidence indicates no one-to-one correspondence between adult density and the density these adults experienced in the larval stage. Under these conditions they arrived at the surprising result that population dynamics based on adult-to-adult observations are biased. In particular, estimates of the population's stability at carrying capacity can be severely biased when adult transitions have been used to estimate population dynamics. The determination of this bias requires the as-

Am. Nat. 1986. Vol. 128, pp. 282–293.

sumption that stock populations have been kept at carrying capacity. If this is not true, then the bias may not be calculated even in theory. Prout and McChesney's own data seem to indicate that the eigenvalues governing stability may indeed be less than -1. Thus, the considerable variation in the size of their running populations may be caused by the nature of the density-regulating mechanisms rather than by stochastic forces alone (May 1974; May and Oster 1976). Such results call into question the conclusions of Mueller and Ayala (1981*a*) and Thomas et al. (1980). They observed that the vast majority of *Drosophila* populations examined have stable population dynamics; these results, however, were based on observations of adult-to-adult transitions. In addition, deviations from logistic population growth (Ayala et al. 1973; Mueller and Ayala 1981*b*) may result from a bias in one particular method of observing adult-to-adult transitions.

It does not appear that the bias noted by Prout and McChesney can be "corrected" in the studies of Mueller and Ayala and of Thomas et al. Although the theoretical results of Prout and McChesney seem unassailable, it is the experimental procedures that are subject to criticism. In this note I hope to show that Prout and McChesney's own data support, most strongly, the conclusions of Mueller and Ayala and Thomas et al. An unambiguous resolution of this problem may require the unpleasant task of observing egg-to-egg transitions.

The analysis of Prout and McChesney (1985) considered only fully discrete populations. The studies of Mueller and Ayala (1981*a*) and Thomas et al. (1980) both used a modification of this procedure called the serial-transfer system (STS). It is likely that the generic problems discussed by Prout and McChesney also apply to the STS. Aside from these problems, two quite different methods have been used to analyze population stability in the STS. The method employed by Thomas et al. (1980) I call the intuitive method, and the technique I have proposed (Mueller and Ayala 1981*a*,*b*) may be called the *k*th-order difference-equation technique. Although similar qualitative results have been reached using both methods, this agreement may have been largely fortuitous. In the last section of this paper I show that these techniques need not agree and that the *k*th-order difference-equation technique should thus be favored.

PROUT AND MCCHESNEY'S MODEL

Prout and McChesney (1985) assumed that egg-to-adult survival, $S(\cdot)$, and female fecundity, $F(\cdot)$, depend on the egg density in any generation. Thus, a recursion in the number of eggs at time $t + 1$, n_{t+1}, can be written

$$n_{t+1} = \tfrac{1}{2}F(n_t)\, S(n_t)\, n_t\ . \tag{2}$$

The evidence for such dependence is abundant (Chiang and Hodson 1950; Robertson 1957; Prout and McChesney 1985). The number of adults at time t, N_t, is $S(n_t)n_t$. It should be noted that with the population dynamics described by equation (2) it is impossible to express N_{t+1} as a function of N_t. If the equilibrium number of eggs is denoted by k, then the eigenvalue governing the stability of equation (2) given by Prout and McChesney (1985) is

$$\lambda = 1 + kF(k)S'(k) + kS(k)\,F'(k), \tag{3}$$

TABLE 1

SLOPES ($\times$ 10^{-4}) OF VARIOUS SURVIVAL FUNCTIONS FOR THREE EGG DENSITIES

	EGG DENSITY (PER ½-PINT CULTURE)		
MODEL	1600	2100	2600
Linear	−2.80	−2.80	−2.80
Exponential	−2.04	−1.54	−1.19
Hyperbolic	−1.42	−1.02	−0.77
Empirical estimate	−1.01	−1.01	−1.01

NOTE.—Data from Prout and McChesney 1985, figure 3*A*.

where the prime denotes differentiation with respect to n_t. If this eigenvalue has an absolute value greater than 1, the population may exhibit cyclic or chaotic dynamics.

Estimation of the Slope of the Fecundity and Survival Functions in the Vicinity of the Carrying Capacity

Linear, hyperbolic, and exponential functions were used to describe observations of survival and of female fecundity over a broad range of egg densities (Prout and McChesney 1985). Standard regression techniques were then used by Prout and McChesney to estimate the parameters of each function. The slopes, $S'(k)$ and $F'(k)$, can then be estimated by plugging in the appropriate parameters and k. If the underlying function is a poor mimic of the actual biological phenomenon and many data points are collected far from the carrying capacity, these predicted slopes may be quite inaccurate. This implies, of course, that the estimate of λ will be inaccurate.

This conjecture was tested as follows. From figure 3*A* in Prout and McChesney (1985), the last eight data points that covered egg densities of 1600–2600 per ½-pint culture were used to estimate the slope of the survival function empirically; that is, a straight line was fit to these data. This slope was then compared to the predicted slopes from the three functions fitted to the complete data set (table 1). Both the exponential and hyperbolic functions reasonably approximate the observed slope in this region, but the hyperbolic function is perhaps more accurate. The linear function is clearly the least accurate with a slope nearly three times too large in absolute magnitude.

The fecundity data were analyzed similarly using 16 points in the range of 1600–2000 eggs from Prout and McChesney's figure 5*A* (table 2). Again, the exponential and hyperbolic functions do an adequate job, with a slight edge to the exponential function. The linear function is quite bad, however, being greater than two times the observed value in absolute magnitude.

These results call into question the accuracy of any eigenvalue estimated from a linear survival or fecundity function. Since the slopes of these linear functions appear to be too large in absolute magnitude, at least at high egg densities, they are liable to produce eigenvalues from equation (3) that are too large in absolute

TABLE 2

SLOPES ($\times 10^{-3}$) OF VARIOUS FECUNDITY FUNCTIONS FOR THREE EGG DENSITIES

	EGG DENSITY (PER ½-PINT CULTURE)		
MODEL	1600	1800	2000
Linear	−5.70	−5.70	−5.70
Exponential	−3.32	−2.72	−2.22
Hyperbolic	−2.43	−2.10	−1.83
Empirical estimate	−2.42	−2.42	−2.42

NOTE.—Data from Prout and McChesney 1985, figure 5*A*.

magnitude. In fact, every function in Prout and McChesney's table 4 that yielded an eigenvalue less than -1 had at least one linear component. The worst function, which yielded $\lambda = -1.86$, consisted of a linear survival function and a linear fecundity function! It is entirely reasonable to discount the linear functions because of these inaccuracies and hence to conclude that their data do not appear to produce an $|\lambda| > 1$.

Effect of Adult Density on Female Fecundity

Although Prout and McChesney's theoretical results demonstrate that eggs are the natural census stage, they chose not to observe egg-to-egg transitions because of the inherent difficulties of such a procedure with *Drosophila*. Instead, they attempted to examine in detail the parts of the life cycle that show density dependence and then to reconstruct the entire life cycle from these components. At least two serious problems seem to arise with this technique.

The first problem lies with the estimation of the carrying capacity. When egg-to-egg or adult-to-adult transitions are used, a direct empirical estimate of the carrying capacity is possible, for example, the density at which egg (or adult) numbers stay constant. The estimation of population stability depends critically on the population's behavior in the vicinity of the carrying capacity. From the components technique, the carrying capacity is estimated indirectly by iterating equation (2).

If one looks at figures 1*A* and 1*B* in Prout and McChesney (1985), the average adult carrying capacity of these running populations is apparently in the range of 360–370. However, their models predict adult carrying capacities, K, in the range of 538–637. Prout and McChesney suggested that for certain models K approaches the maximum population size. If the population is cycling, it spends most of the time below K and hence gives rise to the observed discrepancy. Other possible reasons for this discrepancy are discussed below.

The second problem with the components technique is that it may be incomplete. That is, a particular life stage showing density dependence may be overlooked. I now consider the effects of ignoring one seemingly innocuous life stage on the estimate of population stability.

TABLE 3

EQUILIBRIUM EGG NUMBER (k), EQUILIBRIUM ADULT NUMBER (K), AND EIGENVALUE (λ') FOR THREE SLOPES OF THE FECUNDITY-VERSUS-ADULT-DENSITY FUNCTION, $\tilde{F}'[kS(k)]$

SLOPE	k	K	λ'
0.0	1282	577	−0.82
-1.927×10^{-4}	1226.2	564.5	−0.79
-9.000×10^{-4}	914.6	483.0	0.014

NOTE.—Values calculated from equations (4) and (5) in the text.

Many workers (Pearl 1932; Bodenheimer 1938; Robertson and Sang 1944; Chiang and Hodson 1950) have shown that adult density exerts a strong influence on female fecundity at low densities and that this effect is greatly diminished at moderate and high adult densities. Prout and McChesney's (1985) own data on female fecundity at densities of 50–600 adults per ½-pint culture are entirely consistent with these previous findings. That is, at these moderate to high densities, per capita fecundity hardly changes at all and density certainly exerts no statistically significant effect. In fact, their data indicate a slight decline in female fecundity with increasing adult density. Even these very small effects can have a significant impact on the estimated stability eigenvalue.

First consider a new model of population dynamics that incorporates the effect of adult density on female fecundity,

$$n_{t+1} = \tilde{F}(N_t)\, \tfrac{1}{2}F(n_t)\, S(n_t)\, n_t\, . \tag{4}$$

Since Prout and McChesney's data on female fecundity were recorded at densities of 50 adults, $\tilde{F}(N_t)$ indicates the effect of adult density on female fecundity relative to that value at $N_t = 50$. For this analysis, let $\tilde{F}(N_t)$ be a linear function. Using the observations from figure 4 of Prout and McChesney (1985), the slope of $\tilde{F}(N_t)$ is -0.00019 ($\pm$ 0.00078, 95% confidence interval). The eigenvalue for equation (4) is

$$\begin{aligned} \lambda' = 1 + k\{F'(k)\tilde{F}[kS(k)]S(k) + S'(k)F(k)\tilde{F}[kS(k)] \\ + F(k)S(k)\tilde{F}'[kS(k)][S(k) + kS'(k)]\}\, . \end{aligned} \tag{5}$$

To evaluate λ' numerically, the hyperbolic survival function and exponential fecundity function are used. The results of this analysis are shown in table 3. Table 3 also records Prout and McChesney's results for the version of equation (2) using hyperbolic survival and exponential fecundity. First note that the addition of adult effects on female fecundity has reduced the adult carrying capacity, which, although still higher than it should be, has been corrected in the right direction. Likewise, the magnitude of the eigenvalue has decreased somewhat. Both of these changes are rather small; thus, ignoring them would seem justified. However, if the slope of the $\tilde{F}(N_t)$ were actually -9×10^{-4}, still within the 95% confidence limits, substantial differences appear. The resulting equilibrium population size and eigenvalue are shown in table 3. It is clear from this example that biological significance and statistical significance do not go hand in hand. The uncertainty in the slope of $\tilde{F}(N_t)$ translates into a fairly large uncertainty in λ', and setting this slope equal to 0 just obscures the problem.

Bias in Methods 1 and 2

Incorporating the adult effects on female fecundity generally decreases, in absolute magnitude, the eigenvalue governing population stability. This assumes, of course, that the slope of $\tilde{F}(N_t)$ is more likely negative than positive. This result and the poor performance of the linear survival and fecundity functions force one to conclude that Prout and McChesney's experimental results are most consistent with $|\lambda| < 1$. However, the incorporation of adult density effects on female fecundity does not remove the problems inherent in observing adult-to-adult transitions.

Prout and McChesney discussed the bias inherent in two experimental methods. Method 1 takes N_t adults from a shelf population, presumably at carrying capacity, and records the number of offspring produced in one generation, N_{t+1}. These values of N_t and N_{t+1} are then used to estimate population dynamics. Method 2 follows the same steps as method 1 except that from the N_{t+1} progeny, N_t adults are again chosen and the process is repeated. In this way an attempt is made to remove the effects of the variable fecundity of shelf flies. At least in theory, a single generation does not remove the effects of the shelf flies, and an infinite number of generations is required. Prout and McChesney actually determined the bias in estimates of λ produced by methods 1 and 2. Numerical calculations (not shown) of this bias show in general that the bias of method 2 is less than that of method 1.

It is of some interest to know how these biases are affected by the incorporation of adult effects on female fecundity. For instance, if the population's dynamics are governed by equation (4), then eigenvalues estimated from data collected by method 1 have a bias of $kS(k)\tilde{F}[kS(k)]|F'(k)|$, whereas this bias is $kS(k)|F'(k)|$ when equation (2) describes the population dynamics. Since $\tilde{F}(N_t)$ is less than one for $N_t > 50$, incorporating the adult effects on female fecundity clearly reduces the bias for method 1 although certainly without eliminating it. Similar expressions for method 2 have been derived; however, they are not as readily interpreted. Suffice it to say that bias is still present in methods 1 and 2 and may be of substantial magnitude.

One problem not explicitly examined by Prout and McChesney is the degree to which the bias in methods 1 and 2 may have affected growth curves fitted to such data. These studies (Ayala et al. 1973; Pomerantz et al. 1980; Hastings et al. 1981; Mueller and Ayala 1981*b*) have generally observed per capita rates of population growth that decline, with increasing density, at rates much faster than linear. This problem can be examined numerically by using equation (4). For these examples, the hyperbolic survival and exponential fecundity functions are used. A starting egg number is specified, and then the adult numbers in that generation, N_t, and the next generation, N_{t+1}, are calculated from equation (4). These two adult numbers are then used to calculate per capita rates of population growth. Similar rates of population growth are calculated by methods 1 and 2, assuming that the population dynamics are actually described by equation (4) (see Prout and McChesney 1985, Appendix A). These results are shown in figure 1.

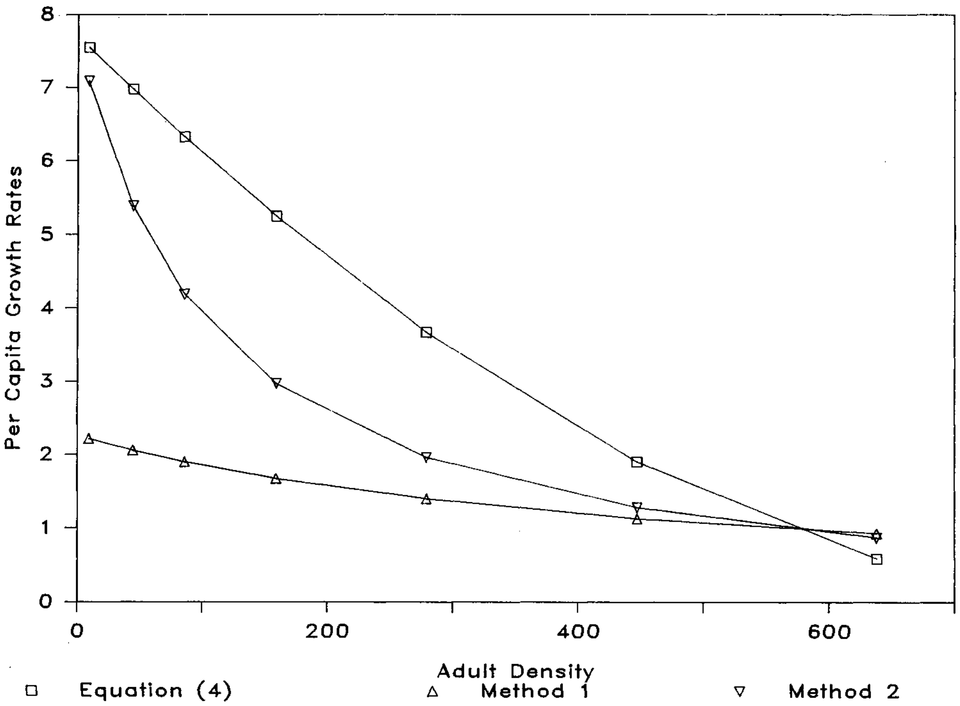

FIG. 1.—Rates of population growth estimated by three different methods. Numerical values were derived from the hyperbolic survival and exponential fecundity functions of Prout and McChesney (1985) and the linear fecundity function described in the text.

It is clear from figure 1 that the bias in method 1 is greater than that in method 2. Because all the adult flies used in method 1 were kept at high densities, their fecundity is quite low, and hence their rates of population growth are kept low even at low densities. Although Thomas et al. (1980) and Pomerantz et al. (1980) have used method 1, their data differ greatly from the results shown in figure 1. This turns out to be wholly a consequence of their method for estimating the rates of population growth in the serial-transfer system (STS, discussed below).

Method 2 appears to have little bias for very low and very high densities but appreciable bias for intermediate densities. The resulting curve departs substantially from a straight line. Observations of this sort have been made when method 2 has been applied to the STS (Ayala et al. 1973; Mueller and Ayala 1981*b*). A third parameter, θ, is used in these studies to account for these deviations from logistic population growth. If the bias exemplified in figure 1 is also present in the STS, then the observed deviations from logistic population growth may not be nearly so large as suspected. The only obvious way to clarify this problem is to repeat the experiments using egg-to-egg transitions.

Egg-to-Egg Recursions

Although it is reasonable to conclude that Prout and McChesney's data are consistent with $|\lambda| < 1$, the only unambiguous way to estimate λ and population dynamics is to observe changes in the number of eggs in a single generation. For at least three reasons, this procedure must be considered seriously.

1. Such a procedure implicitly takes into account all density effects; thus, no assumption about which life stages are affected by density is necessary.
2. Even if the recursion (4) were exactly true, determining precisely the slope of the curve describing fecundity versus adult density requires much work, perhaps more than egg-to-egg transitions require.
3. The equilibrium egg numbers can be determined by direct observation rather than by relying on predicted values from recursions such as (2) and (4). Furthermore, the stability eigenvalue can be estimated directly from linearized rates of population growth in the vicinity of k without reference to any particular model (Mueller and Ayala 1981*a*).

STABILITY IN THE SERIAL-TRANSFER SYSTEM

The serial-transfer system (STS) consists of m cultures, which can be ordered by age: 1 wk old, 2 wk old, . . . , m wk old. The youngest culture always contains the egg-laying adult population. The older cultures contain eggs, larvae, pupae, and newly emerged adults that resulted from a week of egg laying by the adult population 2, 3, . . . , and m wk ago. At weekly intervals additions to a fresh culture are made from the surviving adults from the 1-wk-old population and from the newly emerged adults from the 2-, 3-, . . . , m-wk-old culture. The oldest culture is discarded at this time. m is chosen to be small enough to exclude second-generation flies but large enough to include most of the first-generation flies; m is typically set at 4 (Mueller and Ayala 1981*a–d*), 5 (Ayala et al. 1973), or 6 (Pomerantz et al. 1980; Thomas et al. 1980). It seems reasonable to expect the rates of population growth in the STS to depend on the number of egg-laying adults, the total number of progeny produced from each week's egg laying, and the time at which these progeny emerge. The STS has the advantage of maintaining an adult population with overlapping generations, and thus perhaps of being more similar to the natural environment, but it suffers from being rather difficult to model.

In the studies of Thomas et al. (1980), Pomerantz et al. (1980), and Hastings et al. (1981), estimated rates of population growth were obtained by assuming that the surviving adults and all emerging progeny are available simultaneously to begin the next generation of population growth. This approximation clearly ignores the time structure of the STS and leads to inflated rates of population growth, especially at very low densities. In figure 2, data from a single population (Mueller and Ayala 1981*c*) are used to estimate rates of population growth by the methods of Thomas et al., Pomerantz et al., and Mueller and Ayala (1981*b*). Obviously, ignoring the time structure of the STS can lead to substantial differences in the estimated rates of population growth. Thus, although Thomas et al. and Pomerantz et al. used method 1 to collect their data and although the results from the section *Bias in Methods 1 and 2* suggest that the resulting growth rates should be too small, just the opposite is seen because of their method of analyzing the STS.

For mathematical convenience in the following discussion, let $m = 2$, although

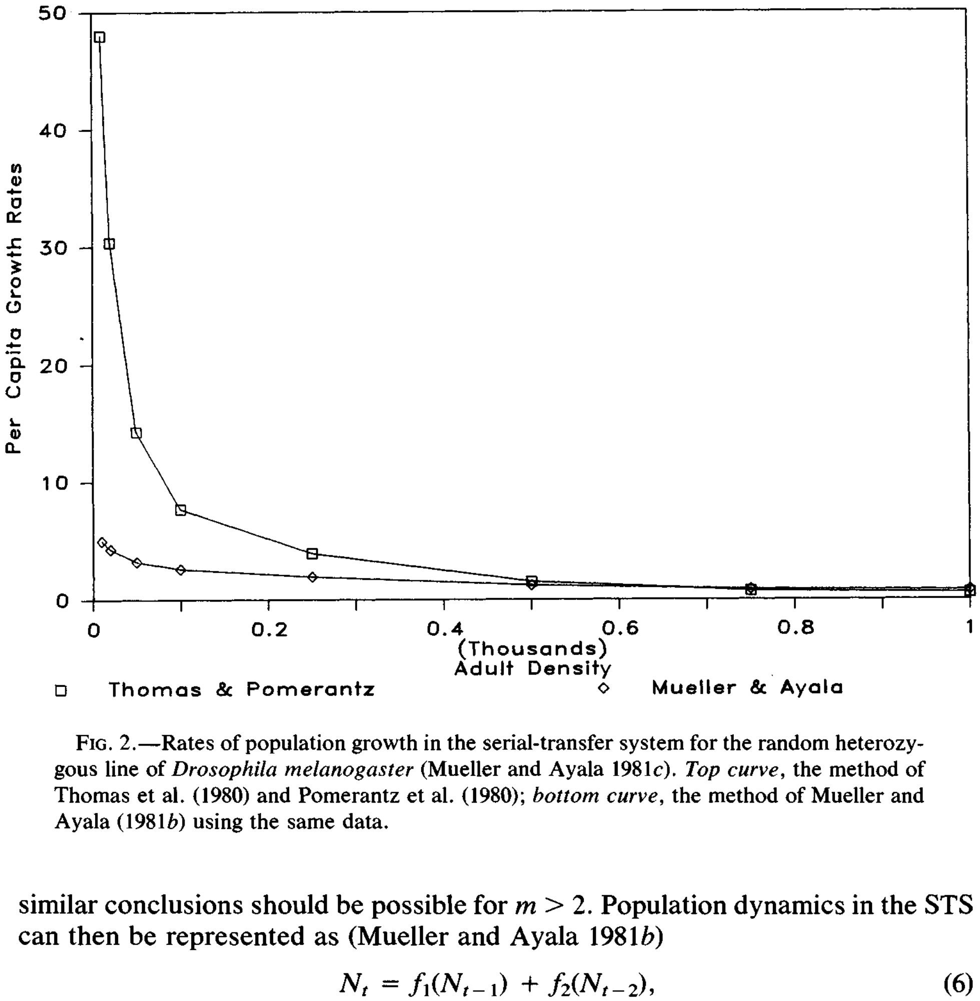

FIG. 2.—Rates of population growth in the serial-transfer system for the random heterozygous line of *Drosophila melanogaster* (Mueller and Ayala 1981*c*). *Top curve*, the method of Thomas et al. (1980) and Pomerantz et al. (1980); *bottom curve*, the method of Mueller and Ayala (1981*b*) using the same data.

similar conclusions should be possible for $m > 2$. Population dynamics in the STS can then be represented as (Mueller and Ayala 1981*b*)

$$N_t = f_1(N_{t-1}) + f_2(N_{t-2}), \tag{6}$$

where $f_1(N_{t-1})$ is some nonlinear function that describes adult survival over 1 wk as a function of density and $f_2(N_{t-2})$ is a nonlinear function that relates the number of emerging progeny from a 2-wk culture to the original number of egg-laying adults. Higher-order versions of this model have been used by Mueller and Ayala (1981*a*–*d*). Note that equation (6) is a second-order nonlinear difference equation. The "intuitive" method of modeling the STS (Pomerantz et al. 1980; Thomas et al. 1980) ignores the time structure of the STS and simply uses equation (1). As discussed in Mueller and Ayala (1981*a*), the linear population dynamics of equation (6) can be written as

$$N_t = a_1 + b_1N_{t-1} + a_2 + b_2N_{t-2}. \tag{7}$$

The local stability of equation (7) is determined by the roots of the quadratic

$$-\lambda^2 + b_1\lambda + b_2 = 0. \tag{8}$$

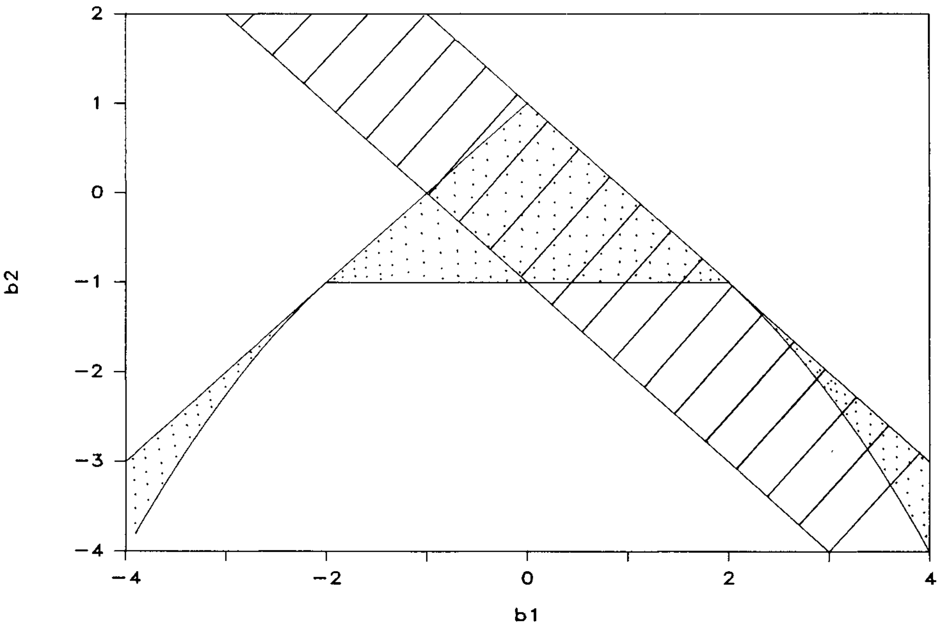

FIG. 3.—Regions of stability for models of the serial-transfer system in terms of the parameters b_1 and b_2: *hatched area*, by the intuitive method, equation (1); *dotted area*, by the second-order difference equation, equation (6).

To compare the stability predictions of equation (6) to equation (1), we note that the intuitive method implicitly assumes that $N_t = f_1(N_{t-1}) + f_2(N_{t-1}) = g(N_{t-1})$. This is a reasonable approximation to the population dynamics in the STS when $N_{t-1} = N_{t-2}$ (e.g., at carrying capacity), but it deteriorates as the population moves away from carrying capacity. Thus, in figure 2 the two curves become coincident as per capita growth rates approach 1. The linear dynamics of equation (1) can be written in terms of the parameters of equation (7) as $N_t = (a_1 + a_2) + (b_1 + b_2)N_{t-1}$. The local stability of equation (1) is guaranteed if

$$|b_1 + b_2| < 1. \tag{9}$$

The conditions for a local stability of equation (6) are (Goldberg 1958, pp. 171–172) $1 - b_1 - b_2 > 0$ and $1 + b_1 - b_2 > 0$, if $b_1^2 + 4b_2 \geq 0$. If $b_1^2 + 4b_2 < 0$, the stability conditions are the same as above plus $1 + b_2 > 0$. Thus, for both equations (1) and (6) the conditions for local stability can be expressed in terms of b_1 and b_2. Figure 3 shows the range of values that b_1 and b_2 may take while remaining consistent with a local stability of either equations (1) or (6). It is clearly possible for the intuitive method to predict stability while the difference-equation approach predicts instability, or vice versa. In addition, over large areas of the parameter space both methods yield similar results. Unfortunately, unless special restrictions are placed on the range of b_1 and b_2, the two methods can yield contrary results concerning the stability of the same population. Since equation

(6) represents a more detailed accounting of the STS, it seems reasonable to place more confidence in it when analyzing the stability of the STS.

SUMMARY

The fecundity of *Drosophila* in the laboratory depends on the level of crowding during the larval stage. In addition, the function describing the number of adults produced by an initial number of eggs is not one-to-one. Consequently, the population dynamics determined from adult-to-adult transitions are likely to be biased (Prout and McChesney 1985). This result has called into question the general conclusion that laboratory populations of *Drosophila* have asymptotically stable population dynamics, since these observations were based on adult-to-adult transitions. Prout and McChesney's own data seem to indicate that eigenvalues less than -1 may occur in laboratory populations of *Drosophila*.

A reexamination of their data actually supports the notion that laboratory populations of *Drosophila* have stable dynamics. However, a thorough resolution of this question will require a determination of the population dynamics by observing changes in the number of eggs. For populations of *Drosophila* kept in the serial-transfer system, it is shown that the two currently practiced methods for determining population stability are not equivalent. Since the method employing the *m*th-order difference equation (Mueller and Ayala 1981*a*) takes into account the complicated features of the serial-transfer system, it should be the preferred method.

ACKNOWLEDGMENTS

I thank T. Prout for his insightful discussion and for sending me his unpublished manuscripts. This research was supported by funds provided by the Washington State University Research and Arts Committee and National Institutes of Health grant GM34303.

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