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ECOLOGICAL DETERMINANTS OF STABILITY IN MODEL POPULATIONS[1]

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Abstract. Detailed studies of the density-dependent interactions of larval and adult life stages of *Drosophila melanogaster* suggest that the stability of populations is dependent on environmental variables. Models of *Drosophila* population dynamics predict that the levels of food supplied to the adults and larvae will have important effects on population stability: stability is enhanced when adults are given low amounts of food and larvae are given high amounts of food. Experimental results presented here are consistent with these general predictions. These observations have implications for the management of biological populations and present an opportunity for studying the evolution of population stability.

Key words: *chaos;* Drosophila melanogaster; *fecundity; nutrition; population dynamics.*

INTRODUCTION

A long-standing problem in population biology has been understanding the factors in the environment and properties of organisms that affect the stability of population dynamics. Fluctuations in population size around an equilibrium may be due to the manner in which life history characters respond to population density, or they may reflect fluctuations in qualities of the environment that affect the numbers of organisms that can be supported. In this paper we describe how detailed life history components of *Drosophila melanogaster* are affected by density and how they, in turn, affect population stability.

The ability of biological populations to undergo dramatic and regular changes in population size was demonstrated by Nicholson (1957) in a classic series of experiments with sheep blowflies (*Lucilia cuprina*). In these studies Nicholson created populations with overlapping adult generations and independently manipulated the food supplied to adults and larvae. These populations generated regular cycles in adult numbers under a variety of conditions.

Interest in population stability was rekindled in 1974 by the important observation by May that populations with discrete generations may exhibit cyclical or even chaotic population dynamics as a result of nonlinearities in the organisms' response to population density (May 1974). These theoretical results stimulated several studies of natural and laboratory populations (Hassell et al. 1976, Thomas et al. 1980, Mueller and Ayala 1981). Although these studies used a wide variety of techniques, they shared the common goal of attempting to derive estimates of the dynamical characteristics of biological populations. The results of these studies were similar: most populations showed asymptotically stable dynamics.

A more recent analysis of data from natural populations suggests that complex dynamical behavior may be more common than suggested earlier (Turchin and Taylor 1992). Turchin and Taylor suggest that overly restrictive assumptions used in previous analyses of natural populations may account for their different conclusions. While these studies provided information on the gross dynamical properties of populations, they shed little light on the mechanisms responsible for these properties.

We consider the factors that affect the stability of a model population, *Drosophila melanogaster*, by studying the population dynamics of *Drosophila* in the well-defined environment of the laboratory. Although we are ultimately interested in the behavior of populations in their natural environment, the factors that affect population stability are complex. We feel that little progress will be made in understanding these factors unless experiments are carried out under carefully controlled conditions not possible in field environments.

METHODS

Population dynamic model

The effects of crowding on the life history of *Drosophila* are well known (Mueller 1985, 1988). Crowding will restrict food availability for larvae, and decrease survival and adult size (Bakker 1961, Nunney 1983, Mueller et al. 1991*a*). Crowding also increases the concentration of waste products, which will reduce larval viability (Botella et al. 1985) and adult size (L. D. Mueller, *unpublished data*). For populations of *Drosophila* kept on a discrete cycle of reproduction (e.g., reproduction takes place on a single day), effects of adult crowding on adult survival can safely be ignored. However, female fecundity is affected immediately by crowding in two ways. Larval crowding causes larvae to pupate at a smaller size, and these small adults lay fewer eggs than large adults, all other things being equal. Adult crowding will also decrease female fecundity. It

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was thought for some time that this effect was primarily mediated through increased behavioral interactions at higher densities (Mueller 1985). However, as we show in this paper, food availability (which decreases with increasing adult numbers) dramatically affects female fecundity.

In populations of *Drosophila* that are kept on fully discrete generations the number of eggs at time $t + 1$, n_{t+1}, can be described by

$$n_{t+1} = \frac{1}{2} G(N_t) F(n_t) W(n_t) V n_t, \qquad (1)$$

where V is the probability of an egg becoming a first instar larva, W is the density-dependent function describing the viability of first instar larvae, F is the mean fecundity of adult females and reflects the effects of food limitation (during the larval life stage) on female size and hence fecundity, and $G(N_t)$ describes the effects of adult density, N_t, on female fecundity (Mueller 1988). It is worth noting that the effects of adult crowding are assumed to be independent of the larval crowding effects. In fact, to our knowledge this assumption has never been tested, but testing could in principle be done by conducting experiments similar to the ones done in this paper with adults of different sizes.

Components of this model have been tested and shown to account adequately for the effects of crowding on viability (Nunney 1983, Mueller et al. 1991*a*) and reduction of adult size (Mueller et al. 1991*a*), which ultimately reduces female fecundity (Mueller 1987). The stability properties of Eq. 1 have also been examined (Mueller 1988). This previous study showed that population stability was especially sensitive to changes in parameters of the function $G(N_t)$. Stability was enhanced in this theoretical study when female fecundity declined rapidly with increasing adult density. If this rate of decline was only modest, then cyclic and chaotic population dynamics were observed.

The functions used in Eq. 1 are summarized below. The viability function is,

$$W(n_t) = \int_x^\infty \phi(y)\, dy,$$

(Mueller 1988) where $\phi(y)$ is the standard normal density function, y is the amount of food consumed by the larval life stage, and $x = (mVn_tK^{-1} - 1)\sigma^{-1}$. In this model m is the minimum amount of food a larva must consume to successfully pupate, K is the total amount of food available for larvae, and σ^2 is the variance in food consumption. The effects of larval crowding on female fecundity are described by,

$$\ln[F(n_t)] = c_0 + c_1 \ln(\bar{s}),$$

where $\bar{s}$ is the mean adult size of females that have experienced larval crowding (n_t) and is equal to

$$\bar{s} = W(n_t)^{-1} \int_x^\infty s[K(\sigma y + 1)V^{-1}n_t^{-1}]\varphi(y)\, dy,$$

(Mueller 1988) and,

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

(Mueller et al. 1991*a*), a_0, a_1, and a_2 are empirically determined constants. Lastly, the effects of adult density on female fecundity are modeled by a hyperbolic function,

$$G(N_t) = f(1 + aN_t)^{-1},$$

where f is the maximum fecundity achieved at low adult densities and a measures the sensitivity of female fecundity to increasing density. Rodriguez (1989) used an exponential model for this function and obtained a good empirical fit to his data. Mechanistic models of egg-laying and intraspecific interactions can be developed that lead to the hyperbolic model (Pearl 1932) or the exponential model (Rodriguez 1989). We do not attempt to resolve the issue of which of these two functions is best. Nor do we feel the qualitative predictions made here will be sensitive to changes in this particular function, although this is certainly an interesting area for further research. In the numerical iteration of Eq. 1 three environmental conditions were simulated: high larval food and high adult food (HH), high larval food and low adult food (HL), and low larval food and high adult food (LH).

The viability component of Eq. 1 utilized these parameter estimates for the K_2 population (Mueller et al. 1991*a*): $m = 0.47$, $\sigma = 0.48$, $V = 0.817$ and $K = 230$ (for the HH and HL curves) or 180 (for the LH curve). The adult size vs. food level curve was estimated with parameter values $a_0 = 0.63$, $a_1 = 0.53$, and $a_2 = 1400$. The relationship between size and fecundity was determined from $c_1 = 3.056$ and $c_0 = 6.107$. Adult effects on fecundity were simulated with $f = 70$ (for HH and LH) or 75 (for HL) and $a = 0.014$ (for HH and LH) or 0.14 (for HL). The large change in the value of a reflects the effects of adult nutrition on female fecundity.

Female fecundity vs. adult density

Given the important role the function $G(N_t)$ plays in determining population stability, we have undertaken a more detailed examination of the relationship between female fecundity and adult density in *D. melanogaster*. There have been several studies that examined the form of the $G(N_t)$ function in *Drosophila* (Rodriguez 1988, 1989, Mueller et al. 1991*a*). In this study we have examined the relationship between fecundity and density at two different food levels.

Adults used in these experiments had been raised for two generations in a common environment. Adults that were 1–2 d old were placed in 30-mL vials at one of six adult densities (2, 4, 8, 16, 32, or 64 adults) with an equal number of males and females. These adults

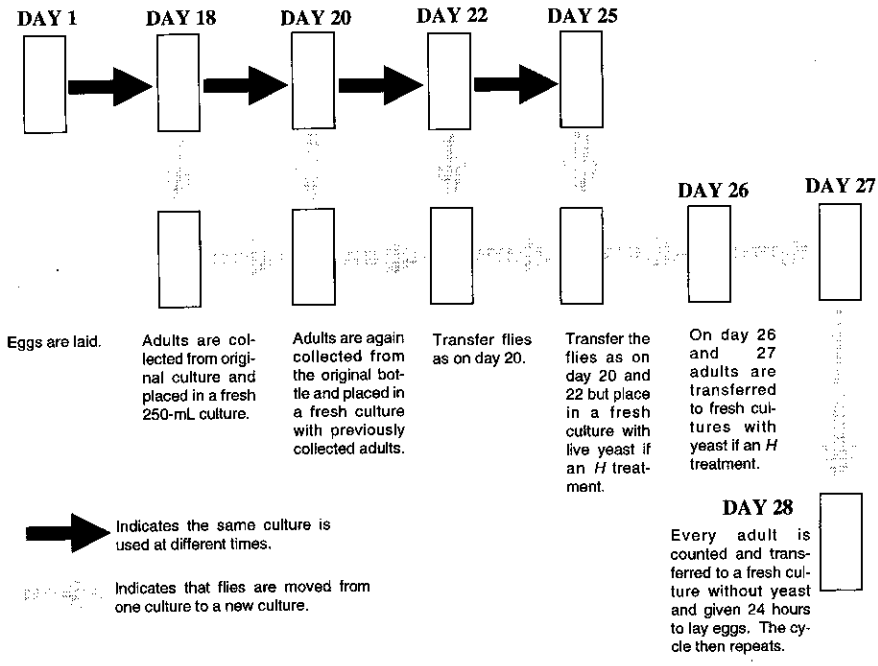

FIG. 1. The maintenance cycle for the experimental populations. The difference between the H and L treatments among adults occurred at days 25–27. Yeast was added to the cultures in the H treatments but not in the L treatments. The difference between the H and L treatments for the larvae occurred at day 28. The H treatments laid eggs in cultures with 40 mL of food and the L treatments in cultures with 20 mL of food.

were transferred daily for 4 d and then placed in egg-laying vials for 24 h. Any deaths during the 4 d of transfers were replaced with adults that had been kept at identical densities during this period. The high food treatment consisted of a small dab of concentrated yeast paste that was never fully consumed by the flies. The low food treatment consisted of 100 μL of a dilute yeast solution (0.015 g/mL water) added to the food surface.

Experimental populations

To test the theoretical predictions, 15 experimental populations were created. Five independent replicate populations were placed in one of three environmental treatments: high larval and high adult food levels (HH), high larval and low adult food (HL), and low larval and high adult food (LH). These populations were kept on a fully discrete generation of reproduction and the total population size was recorded each generation. The maintenance cycle these populations were kept on is shown in Fig. 1.

The LH populations were started 3 mo after the HH and HL populations. The HH and HL populations were initiated with samples from all three $r \times r$ populations (Mueller et al. 1991*b*). The LH populations were initiated with a sample of 100 adults from each HH population. The high adult food treatment received an excess of live yeast paste for 3 d prior to egg-laying. The low adult food treatment consisted of daily transfers to fresh cornmeal-flour-sugar medium with no added yeast. The high larval food treatment contained 40 mL of cornmeal–flour–sugar food in a 250-mL culture, while the low larval food treatment consisted of 20 mL of food. A generation was completed in 4 wk.

RESULTS

Female fecundity vs. adult density

In our study (Fig. 2), adult density, adult food level, and type of population (populations that had evolved at low adult density, $r \times r$, and high adult density, K [Mueller et al. 1991*b*]) were varied. These results (Fig. 2) show very little difference between the populations but a large difference between the food treatments. When females are supplied an excess of food their fecundity drops very slowly with increasing adult density. These results suggest that population stability will be adversely affected by high levels of adult nutrition.

Population dynamic model

To investigate this conjecture theoretically, we have iterated Eq. 1 to study the stability properties of populations at two extremes: (1) when fecundity vs. density curves resemble the high food curves in Fig. 2, and (2) when fecundity vs. density curves resemble the low food curves in Fig. 2. Some representative results from more extensive computer simulations are shown in Fig. 3. These results and others (not shown) suggest that population stability will be enhanced by combinations of low adult food and high larval food levels. The op-

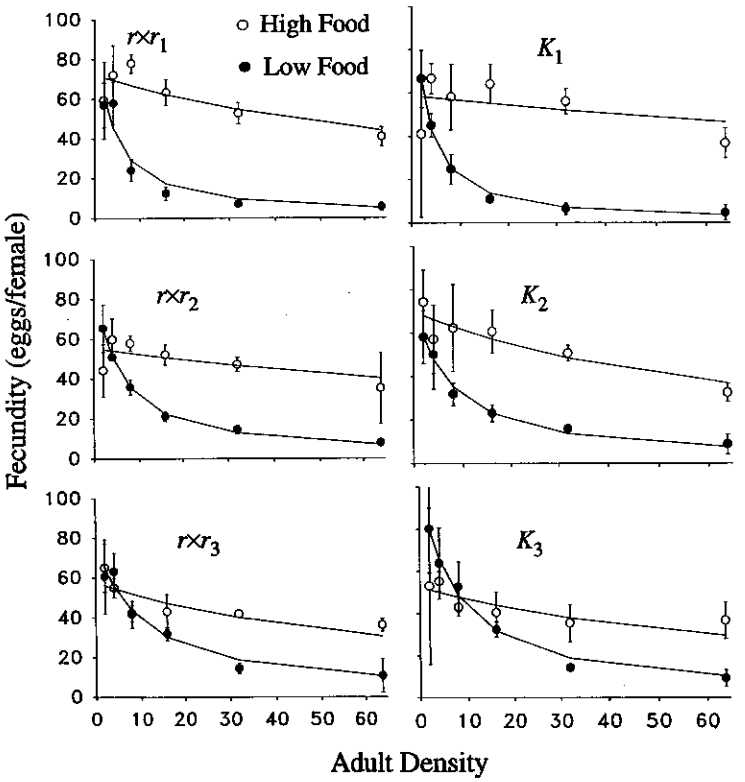

FIG. 2. Female fecundity is shown for six populations at two adult food levels (means and 95% CI). The curves show the fit to the hyperbolic model, which is fecundity $= \frac{f}{1 + aN}$.

posite combination (high adult food and low larval food) should destabilize population dynamics. This last result may be understood by recalling that when adults are given high food they continue to lay a large number of eggs even when the population is crowded (Fig. 2). As the population approaches carrying capacity the adult population will easily lay many more eggs than can possibly survive, especially when larval resources are low, and hence the adult population crashes in the next generation. However, since well-fed females lay up to 80 eggs per day the population recovers quickly from the crash and the cycle repeats.

It is worth emphasizing that even the detailed model used here involves numerous assumptions that will not be true even in the carefully controlled laboratory environment. For instance, the model described here considers only the effects of crowding on the limiting food availability. Especially in crowded larval cultures the accumulation of waste products is another hazard that affects survival, adult size, and female fecundity. The experiments used to calibrate parameter values in Fig. 3 were done in environments where the amount of yeast provided to larvae was carefully controlled and measured. In the population experiments done here, larvae and adults feed on standard *Drosophila* medium that has its own growing yeast and bacteria popula-

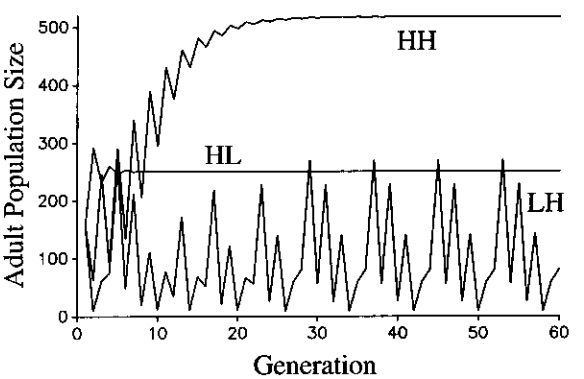

FIG. 3. The predicted adult population size from Eq. 1. Three types of populations are modeled, which differ by the amounts of food received in the larval and adult life stages. The first letter refers to the food level during the larval stage (either high (H) or low (L)) and the second letter of the population name refers to the food level supplied to adults. The relationship between adult population size and fecundity is given in Fig. 1. The HH and HL populations both attain a stable equilibrium adult population size, but the fluctuations prior to reaching the equilibrium are greater in HH, as is the final equilibrium size. The LH population does not approach an equilibrium point but appears to have settled into an 8-point cycle.

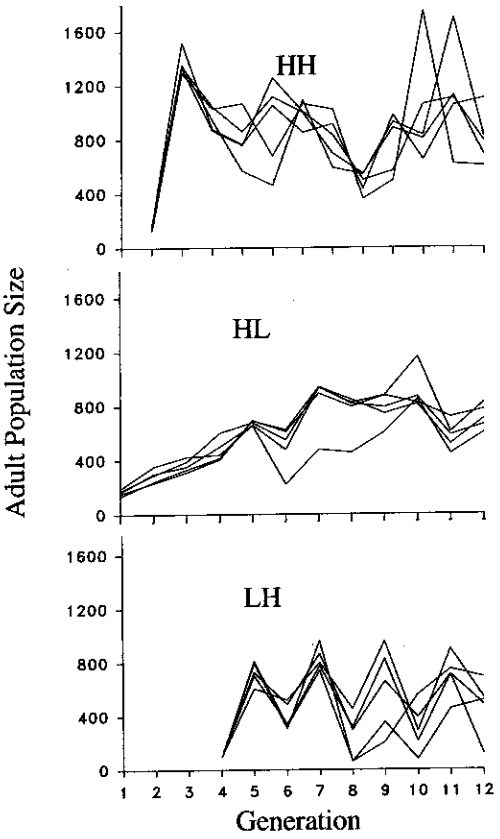

FIG. 4. The adult census just prior to reproduction for populations maintained at different larval and adult food levels. The population names reflect the same qualitative differences in larval and adult food levels as described in Fig. 3.

tions. Nevertheless, these models have provided qualitative predictions concerning population stability and food levels that would not have been possible with other, more simple models. These qualitative predictions must be tested experimentally. However, it is probably unrealistic to expect accurate quantitative agreement between this theory and our experiments given the number of assumptions that have been required to achieve this theory.

Experimental populations

The HH population shows a rapid increase in its carrying capacity and large but irregular fluctuations after the first few generations (Fig. 4). The HL populations show a slow but regular increase in population size until about the seventh generation; after this time the numbers fluctuate about the equilibrium less wildly than the HH populations. The differences between these populations can be attributed to the large differences in number of eggs laid. In the HL populations the number of eggs produced was very low for each female, and hence changes in the total population size were never very spectacular. Finally, the LH populations give the appearance of a regular two-point cycle: large adult numbers invariably followed by very small population size. In these populations the adults are well fed, and hence the females laid large numbers of eggs, but since the amount of food that is available for the larvae is limited, there are few surviving adults after a large pulse of eggs. Small numbers of adults are capable of increasing their numbers rapidly, however, so the population recovers from its "crashes" with an overexplosion of adults, and the cycle continues.

One qualitative prediction that follows from the models considered previously is that the carrying capacity of the HH populations should be greater than the HL populations as a consequence of the additional food provided to the adults. The average carrying capacity of the five HH populations is 913 (this excludes the first point, which was set by the experimenters). The HL populations do not appear to reach their carrying capacity until generation 7, and even at that time population HL_5 is lagging behind the other four populations. The average population size of HL_{1-4} after generation 6 is 805. The HH average population size is significantly greater than the HL average ($t_7 = 4.91$, $P < .005$, one-tailed test).

The autocorrelation functions of these 15 populations have been computed and the average value over the five replicate populations plotted in Fig. 5. The HH and HL populations show no evidence that fluctuations about their equilibria are due to a process that is correlated over time. Thus, the variation in these populations might be due to uncontrolled variation in handling flies and experimental technique. However, the LH populations show autocorrelations that are both large and that alternate in sign. This is the sort of autocorrelation one expects from a two-point cycle. Further, the fact that the magnitude of these correlations decreases over time is more consistent with the cycle being generated from endogenous factors (density dependence) than an environmental factor that fluctuates cyclically (Turchin and Taylor 1992). Given the controls that are placed on the laboratory environment, the likelihood that uncontrolled factors would oscillate in a regular fashion is further reduced.

The autospectrum (Fig. 5) shows that there is a high-frequency component to the variation in the LH population, which is expected if the population is in a regular short-period cycle. Neither of the two other types of populations shows a pronounced high-frequency component.

As an alternative method of investigating population stability the following analysis was conducted on the population size data. After the population has reached its equilibrium number the transitions in population size can be used to estimate the slope of the nonlinear density function from these N_t vs. N_{t+1} transitions (Table 1). Since the same data points are used twice it is difficult to assess confidence limits for the slopes computed from a single population. However, since five replicates are available for each environmental treat-

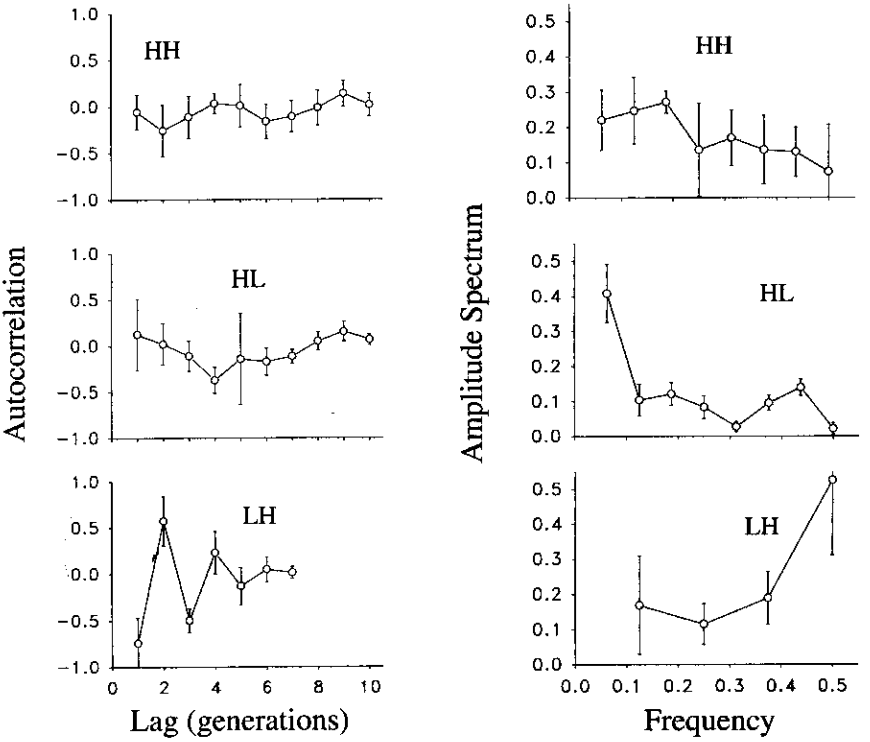

FIG. 5. The autocorrelation and amplitude spectrum for population sizes (both with 95% confidence interval) in the three environmental treatments in Fig. 3. This analysis excluded the first generation data, and linear trends were removed. The autocorrelation function and amplitude spectrum were estimated for each replicate population and the confidence interval computed from these five independent estimates.

ment the standard error of the average of these five populations can be computed (Table 1). The HH and HL populations have similar average eigenvalues that are small and negative. The LH eigenvalue is close to -1. The LH eigenvalues are significantly greater than the HL eigenvalues (Wilcoxon two-sample test, $P = .01$) but not significantly different from the HH eigenvalue. To generate a two-point cycle the eigenvalue of the LH populations should be < -1. The confidence interval of the average includes a range of values that would predict an unstable equilibrium ($-0.56, -1.32$).

DISCUSSION

Nicholson's blowflies revisited

A natural question is whether the population dynamics of other species will be affected in a similar fashion with changing food levels. In one experiment performed by Nicholson, the adult ration of ground liver was changed from ad lib to 1 g/d. The pronounced cycles that were present when the adults were given unlimited food were significantly attenuated by restricting the adult food ration. While many other fac-

TABLE 1. The stability-determining eigenvalue for the HH, HL, and LH populations.*

Treatment	Replicate 1	2	3	4	5	Mean	95% confidence interval
HH	0.085	−1.09	0.021	0.15	−0.16	−0.20	±0.63
HL	−0.19	−0.0088	−0.50	−0.22	−0.18	−0.22	±0.22
LH	−0.47	−1.29	−1.12	−0.92	−0.88	−0.94	±0.38

* These estimates are determined from the N_t vs. N_{t+1} transitions for each population after the population had reached equilibrium. For the HH population the first data point was not used, for the HL populations only the data from generation 7-12 were used, and for the LH populations all the data were used. The eigenvalue was estimated by first fitting a quadratic equation to the N_t vs. N_{t+1} data. The first derivative of this quadratic is then taken and evaluated at the empirically determined equilibrium population size. The confidence intervals are calculated from the five independent population eigenvalues. It has been shown that eigenvalues estimated from adult-to-adult transitions may be biased (Prout and McChesney 1985). However, numerical studies (Mueller 1986) indicate the estimated eigenvalue is liable to be too small in absolute value.

tors in Nicholson's experiments differ from ours, there is the suggestion that the stability of the blowfly populations may depend on adult nutrition, presumably due to the effects of nutrition on female fecundity. Generally, the phenomena described here should be more likely to occur in species with distinct life stages that may have relatively independent food sources and experience different levels of crowding with respect to these food resources.

These experiments suggest some general ecological themes. Attempts to manage populations may consider supplementing food resources as a means of increasing population size. The results of this study suggest that if food is supplied to only one life stage (e.g., adults) the population may become destabilized, increasing the probability of extinction rather than increasing the total number of individuals. A similar type of problem has been noted in predator–prey systems some time ago. It was recognized that enriching the food available for prey, in an attempt to increase their numbers, and hence the numbers of some predator species, could cause the predator populations to become destabilized (Rosenzweig 1972).

Several previous studies with *D. melanogaster* have generally concluded that population dynamics are asymptotically stable (Thomas et al. 1980, Mueller and Ayala 1981). However, one feature of all these studies is that they were carried out under a standard set of conditions that most closely resembles the HL type of environment used in this study. Hence, the prior studies would not be expected to reveal the types of dynamics shown by the LH populations, since the LH environment is quite different from the standard "laboratory" environment.

Evolution of population stability

To what extent is population stability a phenotype that is under the influence of natural selection? Experimental work on this topic has been almost nonexistent until recently (Stokes at al. 1988). An analysis of a long-running population studied by Nicholson showed a reduction in the extent of population cycles late in the experiment. Stokes et al. argued that this reduction is consistent with a change in the demographic parameters of the population by natural selection. The observed demographic changes predicted stable dynamics around the equilibrium point.

Others (Thomas et al. 1980) have argued that group selection would prevent populations from evolving demographic properties that result in severe oscillations or chaotic population dynamics. Theoretical arguments based on individual selection produced a variety of predictions concerning the evolution of population stability that depended critically on certain assumptions and models used in the analysis (Heckel and Roughgarden 1980, Turelli and Petry 1980, Mueller and Ayala 1981, Hansen 1992). In models where trade-offs in certain parameter values were allowed, the outcome of evolution depended critically on the type of trade-offs permitted (Mueller and Ayala 1981, Gatto 1993). These studies were initially motivated by the pervasive observation of populations with stable dynamics. Although the occurrence of populations with cyclic or chaotic dynamics may be more common than previously thought (Turchin and Taylor 1992), the evolution of population stability is still an unsettled area. The ability to generate cyclic dynamics in *Drosophila* offers the possibility of doing more detailed studies of the evolution of this phenomenon. Such studies would benefit greatly from the many features of *Drosophila* that make them such a useful model system in evolutionary biology (Rose 1984).

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