# DOES POPULATION STABILITY EVOLVE?

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*Abstract.* Population stability ultimately depends on the life-history characteristics of individuals; thus, it may be indirectly affected by natural selection acting on various life-history traits. This study investigates the efficacy of natural selection in molding the stability of populations living at an unstable equilibrium. The stability of laboratory populations of *Drosophila* is affected by the relative amount of food given to larvae and adults. Environments with high larval food levels and low adult food levels (HL environments) tend to have asymptotically stable carrying capacities. Environments with low larval food levels and high adult food levels (LH environments) tend to exhibit unstable dynamics, like population cycles. In this experiment, 20 populations were created from two different types of source populations. Five of the source populations had evolved for 71 generations under crowded larval conditions and uncrowded adult conditions (CU populations), while the other five source populations had evolved for a comparable time in uncrowded larval and uncrowded adult conditions (UU). In this study, five replicate CU and UU populations each were placed in both the HL and LH environments, and total adult population counts and adult biomass were recorded for 45 generations. Every five generations, we also estimated the density-dependent fecundity function in each population, since population stability depends critically on the shape of this function. While we could document phenotypic evolution in these populations for several characters due to density-dependent natural selection, there was no detectable change in the population stability characteristics of the unstable LH populations. This result is consistent with either no evolution of population stability, or very slow change. Thus, while evolution in these populations affects important life-history characteristics, these changes appear to have no detectable effects on population stability.

*Key words:   density-dependent population growth; density-dependent selection;* Drosophila; *experimental ecology; population cycles; population stability; time series.*

## INTRODUCTION

One of the earliest successes in the theory of population ecology was the development of models of density-dependent population growth (Pearl and Reed 1920). This theory provided a simple summary of the environment and its interaction with the basic processes of reproduction and survival. It is also of some historical interest for the present paper that much of the early research on population dynamics was carried out with laboratory populations of *Drosophila* by Pearl and his colleagues (Pearl 1927).

Despite the early development of this theory, many of the properties of models of density-dependent population growth were still being described in the 1970s. One of the most important developments here was the realization by May (1974) that internal density-regulating mechanisms in populations could generate population cycles or even aperiodic fluctuations called chaos. The stability of populations in these simple models depended on the parameters that affect density-depen-

dent rates of population growth. Thus, a natural theoretical question that arises is whether density-dependent natural selection may also cause population stability to evolve in a predictable manner, through its influence on growth rate parameters. While this theoretical question is easy to pose and a little less easy to answer, the more difficult problem is to determine if we expect population stability to evolve in real biological populations. We find evidence from natural history, theory, and estimates of standing genetic variation that suggest population stability can evolve.

### Natural history

Early studies (Hassell et al. 1976, Thomas et al. 1980, Mueller and Ayala 1981*a*) suggested that most populations seemed to have asymptotically stable equilibria. However, more recent studies with natural populations (Turchin and Taylor 1992, Turchin 1993, Stenseth et al. 1996) and laboratory populations (Mueller and Huynh 1994, Costantino et al. 1995, Dennis et al. 1995) lead to the conclusion that unstable dynamics may be more common than the early studies had suggested. Nevertheless, populations with stable equilibria appear to be common, perhaps due to natural selection favoring genotypes which give rise to such dynamics.

## Theory

A well-developed body of theory in density-dependent natural selection suggested that evolution might mold many of the important characteristics modulating a population's sensitivity to crowding (Charlesworth 1971, Roughgarden 1971, Anderson and Arnold 1983, Asmussen 1983, Mueller 1988a, Tanaka 1996). There have been several theoretical studies examining the role of natural selection in determining the ultimate stability of populations (Heckel and Roughgarden 1980, Turelli and Petry 1980, Mueller and Ayala 1981a, Stokes et al. 1988, Godfray et al. 1991, Hansen 1992, Gatto 1993, Ebenman et al. 1996, Gomulkiewicz et al. 1999). A common finding in this theoretical work is that there are broad conditions that favor the evolution of stable dynamics, when populations initially start out with stable dynamics. Several studies also investigated evolution in populations initially at an unstable equilibrium and have determined conditions necessary for the populations to evolve stable dynamics (Mueller and Ayala 1981a, Stokes et al. 1988, Godfray et al. 1991, Gatto 1993, Ebenman et al. 1996).

All of these studies have inevitably needed to invoke some life history trade-off to insure the evolution of stability. For instance Stokes et al. (1988) suggest that populations of blowflies may have evolved more stable dynamics over the course of a two-year experiment. They conjecture that this was accomplished by changes in three life history traits, with increased ability to lay eggs on low food levels, trading-off with adult survival and maximum fecundity. Decreases in the latter two traits, presumably, were then responsible for the increased stability of the dynamics. Whether these trade-offs generally exist is an open empirical question. The conditions required for populations to evolve unstable or chaotic dynamics are quite special (Gatto 1993, Doebeli and Koella 1995) and, we might presume, less likely to occur.

The theoretical debate over the evolution of population stability has been aired recently (Ferrière and Fox 1995, Doebeli and Koella 1996, Fox 1996). Ferrière and Fox have argued that there are no theoretical barriers to the evolution of chaos, and, therefore, this possibility needs to be considered seriously. Doebeli and Koella suggest that their own modeling efforts (Doebeli and Koella 1995) support the notion that natural selection is more likely to favor the evolution of stable dynamics. The theory of Ferrière and Fox (1995) and Doebeli and Koella (1995) has not really clarified any of the issues raised in the previous theory considered. For instance neither consider more than one functional form of population dynamics, despite Turelli and Petry's (1980) demonstration that predictions are sensitive to the structure of the model. Special assumptions about the relationship of population parameters are ultimately critical to the evolution of stability in both models (Doebeli and Koella 1995, Ferrière and Fox 1995).

In our view, population stability is the by-product of individual life history characteristics that are directly connected to genotypic fitness. Thus, for example, natural selection may affect the evolution of fecundity, either directly, or as a correlated response to selection on other life history traits that are genetically correlated with fecundity. A direct consequence of the evolution of female fecundity may, in turn, be to alter the stability characteristics of the population. This view contrasts with others that view the dynamical properties of a population as traits that evolution may mold directly. For instance, Ferrière and Fox speak about adaptive chaos and suggest that "chaos may be an easy way to generate variability and uncertainty" (Ferrière and Fox 1995). This suggests that population dynamical behavior drives evolution, whereas we think that it is the fitness-related traits of individuals that are the focus of evolution, and that stability characteristics can, in principle, be molded indirectly by such evolutionary change.

### Standing genetic variation

It is now clear that density-dependent rates of population growth may be molded by natural selection over relatively short periods of time (Mueller and Ayala 1981b, Mueller et al. 1991), clearly indicating that populations harbor genetic variation that affects parameters determining stability, such as $r$ in the logistic equation (Mueller and Ayala 1981c). Since Mueller and Ayala (1981c) looked at different inbred lines of *Drosophila*, this genetic variation may all represent low-fitness genotypes that have been revealed by inbreeding. However, it is clear from this study that existing genetic variation may affect life-history traits that are important for determining population stability (Mueller and Ayala 1981c). Stokes et al. (1988), in their reanalysis of Nicholson's (1957) blowfly data, have suggested that there might be evidence for the evolution of increased stability in one of the experiments.

It is also now well established that genetically variable populations of *Drosophila* maintained at extreme densities (very high and very low) evolve different rates of population growth (Mueller and Ayala 1981b, Mueller et al. 1991). These differences in population growth rates are at least in part due to a number of life-history traits that have evolved in response to different densities. Egg-to-adult viability in crowded populations increased, due to changes in pupation height behavior, permitting those larvae adapted to high density to avoid an important source of mortality (Joshi and Mueller 1993). These same populations adapted to high densities also evolved increased competitive ability (Mueller 1988b), which, however, led to a decline in viability at low population densities (Borash et al. 1998). In general, we expect there to be a wide range of avenues for evolution to affect rates of population

growth. Even the examples given here for *Drosophila* can not be considered exhaustive. For all these reasons, we believe there is a good expectation that population stability can evolve. The general preponderance of stable populations and some theory (Turelli and Petry 1980) would suggest that evolution of stable dynamics would be more likely. However, there are conditions that can favor the evolution of unstable dynamics or even chaos (Ferrire and Fox 1995).

This paper extends our earlier work in density-dependent natural selection by specifically looking at the evolution of population stability. As with some of the theoretical work that we have described, we will study evolution by creating populations that do not have stable dynamics, and then observing their evolution over many generations.

### Dynamics of laboratory Drosophila populations

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

$$n_{t+1} = \tfrac{1}{2}G(N_t)F(n_t)W(n_t)Vn_t \qquad (1)$$

where $G(N_t)$ describes the effects of adult density, $N_t$, on female fecundity, $F$ 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, $W$ is the density-dependent function describing the viability of first instar larvae, and $V$ is the probability of an egg becoming a first instar larva (Mueller 1988a). Detailed descriptions of the precise functions used in these models can be found in Mueller (1988a). An important result from this model is that the stability of populations growing according to Eq. 1 depends critically on the parameters of the function $G(N_t)$. Specifically, if female fecundity does not decline at a sufficiently fast rate with increasing adult density, then population instability becomes more likely.

The obvious point to consider here is whether natural selection can be expected to change the slope of the function $G(N_t)$. All other things being equal, natural selection should favor increased fecundity at all densities. Indeed, if this were how selection worked, *Drosophila* populations would become less stable over time. However, suppose larval survival under extreme crowding trades off with female fecundity. Then selection may favor decreases in female fecundity, if it is accompanied by a sufficiently large increase in egg-to-adult viability. As suggested by theory, the ultimate course taken by natural selection will depend critically on the pattern of genetic correlations among life-history traits. We think the most direct way to address these empirical issues is to examine the outcome of natural selection under controlled conditions.

In assessing the predictions of the *Drosophila* model (Eq. 1) two qualitatively extreme environments have been investigated, both theoretically and experimen-tally (Mueller and Huynh 1994). High levels of nutrition to larvae and low levels for adults characterize the first environment, called HL. This is the environment most similar to traditional laboratory *Drosophila* cultures. The second environment, called LH, has low levels of nutrition for larvae, but high levels for adults. The theoretical predictions, which have been verified with experiments on both large and very small populations (Mueller and Huynh 1994, Sheeba and Joshi 1998), are that HL populations will typically have asymptotically stable carrying capacities, while LH environments will display a variety of unstable behaviors, ranging from cycles to chaos.

The observations from this model of *Drosophila* population dynamics are in accord with the heuristic framework developed by McNair (1995). McNair calls the life stage that is the dominant consumer of resources the controlled part of the life cycle, and the stage at which density dependence is most significant, the regulatory stage of the life cycle. If the regulatory stage is strong, and close to the controlled stage, then it is more likely that population dynamics will be stable. A useful analogy is the placement of a thermostat for the control of temperature in a room. If the heat vents are in the room, but the thermostat is some distance from the room, the temperature is expected to vary more widely than had we placed the thermostat right in the controlled room. In the *Drosophila* model (Eq. 1), a primary regulatory phase is density-dependent fecundity, which has an immediate effect on the number of primary consumers, the larvae. With strong density-dependent fecundity, we observe a stable population equilibrium. When the strength of density-dependent fecundity is weakened, by providing high nutrition levels to adults, unstable dynamics appear.

## METHODS

### Study populations

All populations used in this study were ultimately derived from the five B populations of Rose (1984). The B populations had been kept in the laboratory for ~200+ generations before their use in this study, with effective population sizes of ~1000 individuals (L. Mueller, A. Joshi, and M. Rose, *unpublished data*). Consequently, these populations have had adequate time to adapt to many of the unique features of the laboratory environment, such as food medium, temperature, humidity, and microflora. This makes it more likely that any genetic differentiation observed in this experiment will be due to the new alterations in the environment that we produce, and not due to continuing evolutionary change in response to the trivial aspects of the laboratory environment (Service and Rose 1985). From each of the five B populations, one new population was derived and thereafter cultured at very high larval densities (1000–1500/22-mL vial), but low adult densities (50/30-mL vial) (Mueller et al. 1993), giving

## Life Cycle of the LH and HL Population



Each population consists of eight 237-mL cultures.

Adult flies are collected from the cultures daily and added to a large population cage, until day 20 after eggs were first laid.

After two days of feeding, a fresh food plate is put in the cage, and flies are allowed to lay eggs for 24 h. These eggs are then divided evenly into the eight cultures, which have a total of either 15 mL food (LH) or 35 mL of food (HL) per culture.

After all adults are collected, the flies are given a petri dish with either excess live yeast (LH) or 1.5 mL of a 1.5% yeast solution (HL).
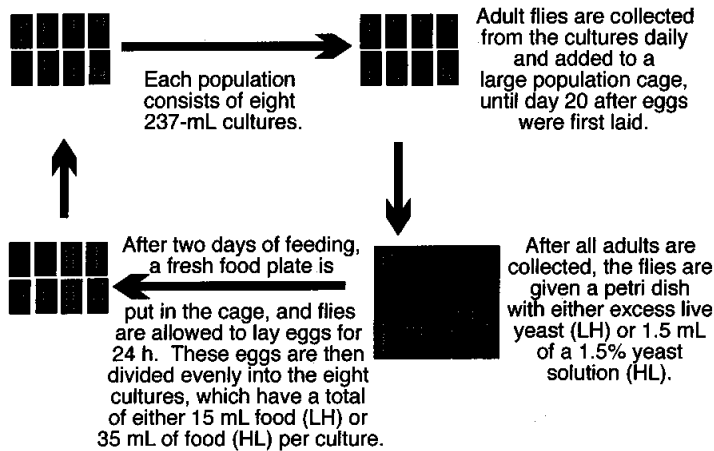
FIG. 1. The life cycle of the experimental LH and HL populations. The population represented by this figure is just one of the 20 experimental populations.

rise to a set of five populations, called CU. Similarly, another set of five populations, called UU, was derived from the B's that were handled the same as the CUs, except that they were kept at low (50–80/30-mL vial) larval densities. The UU and CU populations had completed ≥43 generations of maintenance under their respective density regimes when large samples (the range for all 20 populations was 893–5796) were taken from each of them to create the 20 experimental populations used in this study.

In the course of their maintenance at different larval densities, the CU and UU populations have become differentiated for a number of traits including the following: (1) viability under crowded larval conditions (CU > UU; Shiotsugu et al. 1997), (2) viability in cultures with urea (CU > UU/iotsugu et al. 1997), (3) larval feeding rates and growth rates (CU > UU; Santos et al. 1997), (3) minimum food requirements for pupation (UU > CU; Joshi and Mueller 1996), and (4) larval foraging path length (CU > UU; Sokolowski et al. 1997). Thus, the CU and UU populations represent different genetic starting points for the present experiments. From each CU and UU population, two populations were derived and subjected to an LH and HL maintenance regime, respectively (see *Introduction: Dynamics of laboratory Drosophila populations*; Fig. 1), thus giving rise to the four types of experimental populations, UU–HL, UU–LH, CU–HL, and CU–LH, each replicated five times. These five replicates were maintained independently of each other. Ultimately, they provide this study with the ability to differentiate between random genetic drift, founder events, or uncontrolled artifacts of the experiment vs. natural selection. Since selection in a large population is a deterministic process, we expect that each of the five replicate populations should show signs of any effects of selection. Processes like genetic drift cause random changes in allele frequencies that should not be exactly duplicated in each of the five replicate populations.

Thus, each replicate population can be considered a single observation of the evolutionary process and is treated as such in this study.

### Population maintenance

All populations were maintained in 25°C incubators with 24-h light. The details of the maintenance techniques are shown in Fig. 1. These methods differ from those used in Mueller and Huynh (1994), especially with regard to the cultures used per population and, therefore, total population size. The primary reason for the change in techniques was our desire to minimize the effects of random genetic drift. The culture techniques used by Mueller and Huynh (1994) caused populations to occasionally go through bottlenecks of ~60 breeding adults. In *Drosophila*, one of the by-products of inbreeding is a reduction in female fecundity (Marinkovic 1967). This would be a most unfortunate artifact for this experiment, because a primary force driving *Drosophila* population cycles is very high female fecundity. Clearly, anything, including inbreeding, that reduces female fecundity may also reduce the magnitude of the population cycles (inbreeding may have been the cause of a reduction in the severity of population cycles in Nicholson's blowfly experiments; Stokes et al. 1988). By using eight 237-mL cultures (Fig. 1) to raise larvae for each population, instead of the one used by Mueller and Huynh (1994), we were able to keep most valleys in our population cycles at numbers >1000 adults.

### Population assays

*Adult census and dry mass.*—Every generation following egg laying, all adults were counted in every population. The adults were then placed in an 80°C oven, to dry for ~12 hrs. After cooling, masses of the dried flies were measured to the nearest 0.1 mg. Since adult size is largely determined by larval density (Barker and Podger 1970, Prout and McChesney 1985), these

mass measurements provide insights into the larval densities every generation. As an example of the effects of larval crowding on adult size, we refer to Bierbaum et al. (1989). Larvae raised at densities of 30/22-mL vial produced adults with mean dry masses of 0.209 mg, with 95% of all flies falling within ±15% of this value. When raised at 320/22-mL vial, their mass dropped 32% (0.144 mg ± 10%). In the present experiment, the mean LH adult was 41% smaller than was the mean HL adult. Since this mean value is based on many observations, we interpret differences in this size range to be almost entirely due to larval-density differences. Over the entire experiment, a total of 3.3 × 10⁶ flies were counted.

*Feeding rates.*—This character has responded to density-dependent selection in other experiments (Joshi and Mueller 1988, 1996, Guo et al. 1991, Santos et al. 1997), and, thus, is used as an indicator of whether there is evolution taking place in these populations. The measurements were made every three generations for the first 15 generations and every five generations thereafter. The techniques used are described in Joshi and Mueller (1996). After raising larvae for two generations under standardized conditions, 48-h old larvae were placed, one at a time, in a pertri dish (9-cm diameter) containing agar coated with a thin layer of 10% yeast suspension (10 g dry yeast/100 mL water). After a 15-s acclimation period, the number of cephalopharyngeal sclerite retractions was recorded for one minute under a dissecting microscope. Twenty larvae per population were assayed.

*Female fecundity vs. adult density.*—Every five generations, the relationship between female fecundity and adult density was measured in all 20 experimental populations, as well as in the five CU and the five UU populations. All 30 populations were passed through two generations of common environments to eliminate environmental and maternally-based differences before the assays began. Young adults were then placed in 30-mL vials, with 5 mL of food and yeast paste, for three days. Daily transfers were made at densities of 2, 4, 8, 16, 32, and 64 adults (with equal numbers of males and females). After the conditioning period, flies were transferred to fresh vials with charcoal-laced sucrose–agar food and allowed to lay eggs for 24 h. Any adults that died during the three days in the yeasted conditioning vials were replaced with backup adults that had been similarly conditioned. Vials were placed in a refrigerator until the eggs could be counted. We typically tried to have seven replicates of the density 2 and 4 treatments, four replicates of the density 8 and 16 treatments, and three replicates of the density 32 and 64 treatments. The numbers varied from this, but usually by only one or two replicates. Over the entire experiment at total of ~1.9 × 10⁶ eggs were counted in 6300 vials.

### Statistical analyses

*Time series.*—The primary analysis of the population census and mass data was accomplished by time series analysis. Autocorrelation functions were estimated for the number of adults, after removing any linear trend in the data. The mass data was first transformed by taking the inverse of the mass per fly each generation. This was done, since we are primarily interested in the mass as an indicator of the larval density, and the density of larvae will scale approximately as the inverse of individual mass. Linear trends were also removed from the inverse mass data prior to analysis.

*Fecundity vs. adult density.*—From the fecundity experiments, the number of eggs laid per female, $f(N)$, was regressed on adult density, $N$, using the hyperbolic function:

$$f(N) = F \, [1 + aN]^{-1}.$$

The parameters $a$ and $F$ were estimated with standard nonlinear regression techniques. $F$ represents the maximum fecundity achieved at low density, and $a$ is a measure of the sensitivity of fecundity to crowding. Small values of $a$, which reflect low sensitivity to crowding, are destabilizing. A primary interest of this study was to determine if there were any evolutionary changes in the value of $a$ in the LH populations, relative to the HL populations, or the ancestral UU or CU populations.

*Direct estimates of stability determining eigenvalues.*—Another method to estimate population stability is by estimating the parameters of a specific population growth model and then determining the stability of the resulting model via standard analytical techniques (e.g., Roughgarden 1979:574–599). We have chosen to use a class of models called the response surface method (RSM), used by Turchin and his colleagues for similar problems (Turchin 1991, Turchin and Taylor 1992, Ellner and Turchin 1995). Our analysis focused on two versions of the RSM models, a second-order model (e.g., $N_t$ depends on two previous population sizes),

$$\ln(N_{t+1}/N_t) = a_1 + a_2 N_t^\theta + a_3 N_t^{2\theta} + a_4 N_{t-1}^\theta + a_5 N_t^\theta N_{t-1}^\theta \tag{2}$$

and a third order model,

$$\ln(N_{t+1}/N_t) = a_1 + a_2 N_t^\theta + a_3 N_t^{2\theta} + a_4 N_{t-1}^\theta$$
$$+ a_5 N_t^\theta N_{t-1}^\theta + a_6 N_{t-2}^\theta + a_7 N_{t-1}^\theta N_{t-2}^\theta \tag{3}$$

where $\theta$ was set to either $-1.5, -1.0, -0.5, 0, 0.5, 1.0, 1.5, 2.0, 2.5,$ or $3.0$. When $\theta = 0$, $N^\theta$ is defined as $\ln(N)$. A preliminary analysis of these data showed that the models in Eqs. 2 and 3, with a $N_{t-1}^{2\theta}$ term added, performed poorly. This same preliminary analysis also indicated that the simpler models, with just the first-order linear and quadratic, terms did poorly. We did not examine more complicated models, due to the small number of observations. Standard linear regression techniques were used to estimate the parameters, $a_i$, in Eqs.
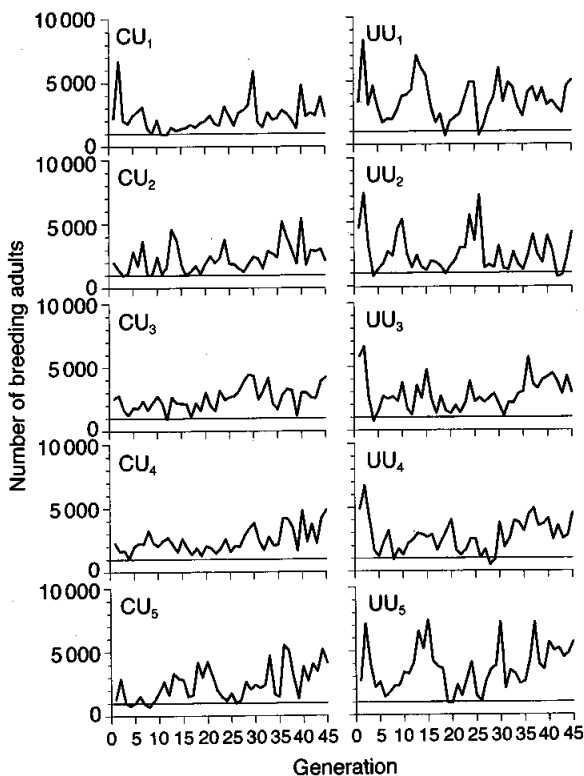
FIG. 2. The total adult population size in each of 10 HL experimental populations, over 45 generations. Each population was censused immediately after reproduction. A horizontal line in each figure shows how infrequently population size dipped below 1000 adults.
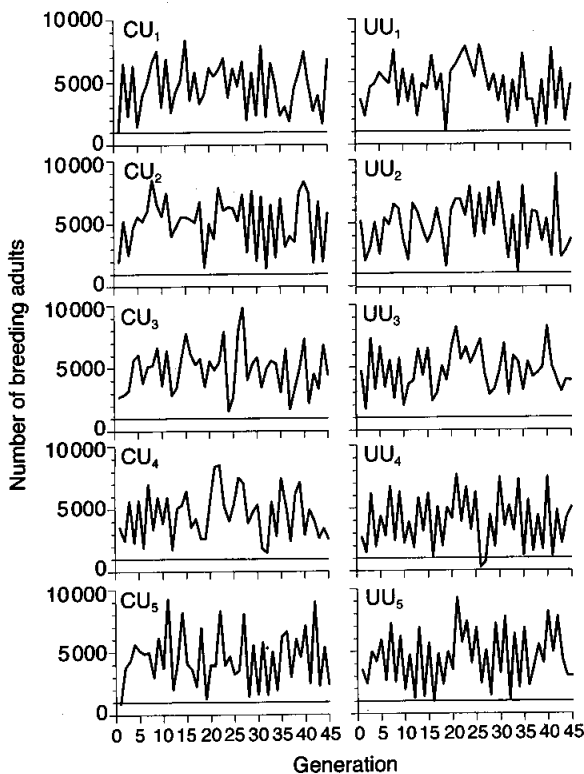
FIG. 3. The total adult population size in each of 10 LH experimental populations, over 45 generations. Each population was censused immediately after reproduction. A horizontal line in each figure shows how infrequently population size dipped below 1000 adults.

2 and 3. To assess which of these models are best, we reviewed several criteria. Obviously, the model in Eq. 3 includes Eq. 2 as a special case. Thus, we expect the proportion of explained variance in Eq. 3 to be equal to or greater than that in Eq. 2 in every case. However, Eq. 3 may do a bad job predicting future observations. We used two criteria to evaluate each model: one technique determines the model's ability to predict future observations (by a statistic called PRESS, Allen 1974), the second is a form of cross-validation (by $V_2$, Ellner and Turchin 1995). For the rationale behind these statistics, either the original references or the general treatment by Miller (1990) may be consulted. These different techniques did not always identify the same "best" model. Thus, we compute the stability determining eigenvalues ($\lambda$) for a range of models identified as best by at least one of these criteria. Stability for real $\lambda$ require that $|\lambda| < 1$. In some cases, the stability determining eigenvalue is complex, ($\lambda = c_1 + ic_2$). Therefore, stability requires that, $\sqrt{c_1^2 + c_2^2} < 1$. It may seem anomalous for these populations to require second- or third-order models, since they were maintained on discrete, nonoverlapping generations, and hence should be adequately described by first-order models. However, since larval density af-

fects female fecundity, and the relationship between adult numbers and egg numbers is not one-to-one, adult numbers in *Drosophila* cultures may depend on several past population sizes (Prout and McChesney 1985).

## RESULTS

### Population census and masses

The population census data (Figs. 2 and 3) show that population sizes were generally appreciably >1000, and only in 26 out of 900 samples did the adult numbers fall below that value. The census data also show that the LH populations typically had a greater number of adults, but that they also varied more widely than did the HL populations (see *Introduction: Dynamics of laboratory* Drosophila *populations* for definitions of LH and HL). Thus, if we compare the variances of the five CU–LH populations to the five CU–HL populations (by the Wilcoxon signed-rank test), the variances of the CU–LH are significantly greater than the CU–HL populations. The same result is obtained in a comparison of the UU–LH to the UU–HL populations. However, if we scale the variance by the mean population size, the differences disappear; the mean coefficients of variation for the CU–HL, CU–LH, UU–HL, and UU–LH populations are 44, 41, 49, and 43%, respectively.
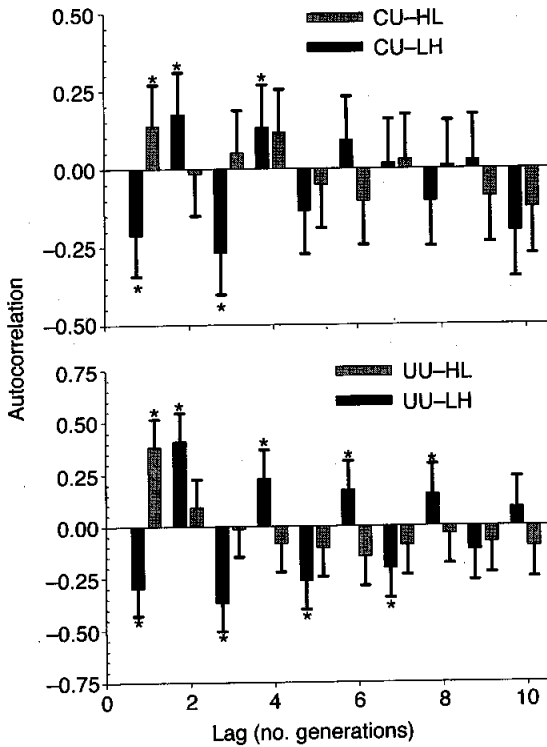
FIG. 4. The autocorrelation function for total adult numbers (with 95% confidence intervals indicated by whiskers), for the four different population–environment combinations. These estimates were based on all 45 generations of observations. The 95% confidence intervals were computed as $1.96/\sqrt{5} \times df$ where the factor of five comes from the number of replicate populations and df is the number of degrees of freedom, equal to the number of time intervals used minus the lag number. The asterisks indicate the correlations significantly different from zero ($P < 0.05$).

The mass per adult fly should be a rough indication of the larval densities (number of larvae per unit food) experienced by those adults, with smaller adults indicating higher larval densities. Although the LH treatments have less food than the HL environments, the effects of crowding on larval survival and size seem to depend primarily on the amount of food per larva. Whether one varies food level, keeping number of larvae constant, or vice versa, seems not to matter in *Drosophila* (Bakker 1961). The mass of the typical individual in the LH populations was 0.14 mg ($\pm 0.018$ mg, 95% CI), significantly lower than the HL populations (0.24 mg, $\pm 0.035$ mg), suggesting that the LH populations had much higher larval densities than the HL populations did. Of course we have no way of directly estimating the total number of larvae in these cultures.

### Time series analysis

The time series of the first 45 generations of adult populations sizes generally show striking differences between the LH and HL populations (Fig. 4). The CU–

HL and UU–HL populations show large positive correlations at a one-generation lag that rapidly become smaller, and not significantly different from zero, at higher lags. This type of pattern is consistent with a population at a stable equilibrium that is exhibiting small random perturbations from that equilibrium value every generation. By contrast, both types of LH populations show large negative correlations at a one-generation lag that become positive at even lags and negative at odd lags. These correlations in the LH populations are significantly different from zero for the first four to eight lags, although the alternating sign of these correlations is maintained for at least 10 lags. This type of pattern is consistent with a population undergoing cycles with an even number of equilibrium points (e.g., two-point cycles, four-point cycles, etc.). We note that many of the problems with the interpretation of time series from natural populations (Williams and Liebhold 1995), such as delayed density dependence and autocorrelated environmental fluctuations, are not present in these populations, due to the experimental design and controlled environment.

We have also estimated the cross correlation between adult population size and the inverse of per capita mass (Fig. 5). For each of the four population types, the only consistently significant cross correlation is at lag zero (Fig. 5). All of the lag-zero cross correlations are positive, suggesting that, within a generation, high adult population size is correlated with low adult mass or high larval density.

A crucial test for the evolution of population stability is an assessment of the dynamics in the LH populations
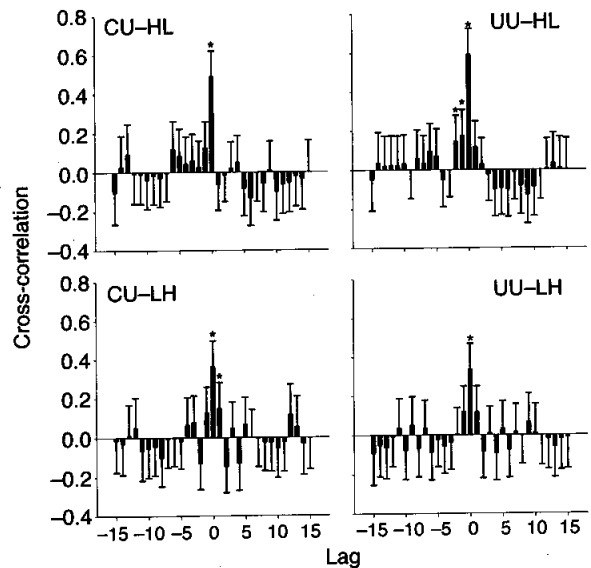


FIG. 5. The cross-correlation between adult numbers and the inverse of per capita mass with 95% confidence intervals. A lag of $m$ positive units means that a correlation of adult numbers at time $t$ is computed with (i.e., lagged with) the inverse mass at time $t + m$. Confidence intervals were estimated as in Fig. 4, from the replicate populations.
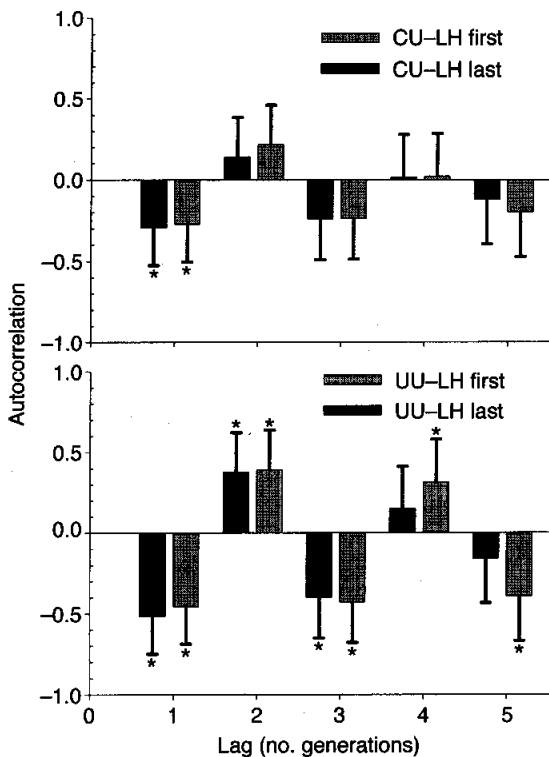
FIG. 6. The autocorrelation function for total adult numbers with 95% confidence intervals for the LH populations. These estimates were based on either the first 15 generations or the last 15 generations of observations. Confidence intervals were estimated as in Fig. 4.

at the start of the experiment vs. the end of the experiment. We have made such an assessment by estimating the autocorrelation function for each LH population, using only the first 15 generations of adult census and the last 15 generations (Fig. 6). The results (Fig. 6) are striking for the high degree of similarity between the first 15 and last 15 generations. There appear to be no detectable differences in the population dynamics at this level, over the 45 generations of observations.

To test this result more formally, we have examined in detail the autocorrelation at a lag of one generation. In LH populations, this correlation is negative. Furthermore, if evolution is causing the stability-determining eigenvalue to become less negative and approach either zero or positive values, we expect the magnitude of this correlation to decline over time and eventually become positive (see HL autocorrelation Fig. 4). We have examined this problem by taking the difference between the correlation at lag one for the first 15 generations and the last 15 generations of each CU–LH population, resulting in five paired comparisons. The sign of these differences were compared by the nonparametric Wilcoxon signed-rank tests. These tests were also done on the UU–LH populations. Neither test indicated a significant decline in the magnitude

of these correlations over the 45 generations of observations.

Significance by the Wilcoxon-signed rank test requires all five later correlations to be larger than the early correlations. Consequently, this test is not particularly powerful. For instance, if the correlations had been reduced to $-0.1$ in both the CU–LH and UU–LH populations by selection, the probability that the Wilcoxon-signed rank test would have given a significant result in at least one population is only 49% (assuming a normal distribution of the correlation coefficient). We can be less conservative and not require consistent results across all five replicate populations. For instance, our previous arguments about the possible action of natural selection also suggest that the mean value of the correlation coefficient should increase towards the end of the experiment. The power to detect a change in the mean, from the observed values in the first 15 generations to $-0.1$ in the CU–LH and UU–LH populations, would be close to 95%. In fact the mean value of the correlation is smaller at the end of the experiment in both populations. In short, the observed correlations at the beginning and end of the 45 generations of observations give no support to the idea that the LH populations have become more stable.

### Direct estimates of stability determining eigenvalues

For directly estimating values of the stability-determining eigenvalues, we must first determine which models to use. The answer to this question varies between the 20 populations, as well as between the two test criteria ($V_2$ and PRESS). Once the best model for each population was determined, we found that using the $V_2$ criteria, the second-order model, was best 15 out of 20 times. However, using PRESS, the second-order models were best only 11 out of 19 times. Several values of $\theta$ were judged best by these methods. However, for the vast majority of populations the best value of $\theta$ fell within $-1$ to 0.5. Consequently, we have estimated eight different stability-determining eigenvalues for the eight different models (four values of $\theta$, in the second- and third-order models). The largest eigenvalue for each model is plotted in the complex plane (Fig. 7). Only the top half of the plane is shown, since complex eigenvalues always come as complex conjugates, and we have chosen to display the eigenvalue with the positive imaginary part (e.g., the top half of the y-axis). Eigenvalues within the semicircle are consistent with stable equilibria. The HL populations typically have small positive eigenvalues (e.g., $\sim 0.5$), which is consistent with a rapid approach to equilibrium. The LH populations typically have negative eigenvalues that are invariably greater than or $\sim -1$. These large negative eigenvalues would typically produce either an oscillatory approach to equilibrium, or possibly a multipoint stable cycle (in the case that $\lambda < -1$).

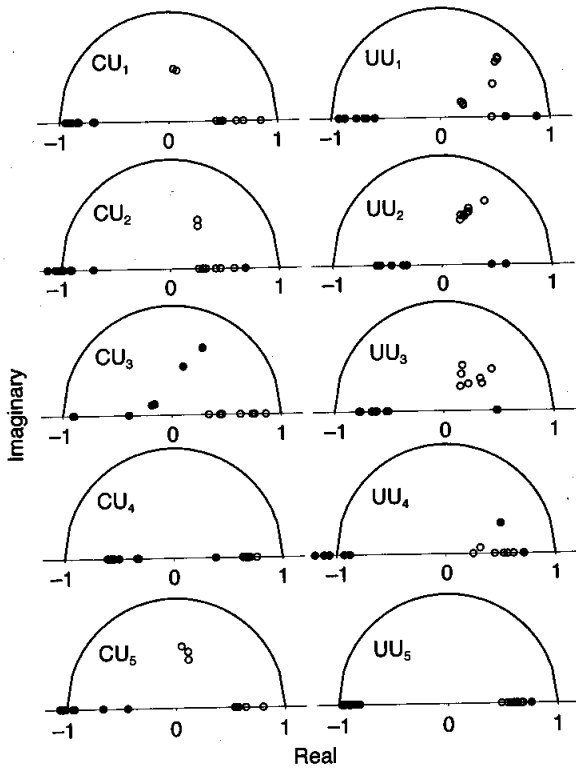To evaluate whether evolution has altered the mag-

FIG. 7. The estimated eigenvalues from the response surface method (RSM) second- and third-order models (Eqs. 1 and 2) in the complex plane. The x-axis is the real part of the complex number, and the y-axis is the imaginary part. Open circles are the HL populations; closed circles are the LH populations. For each population, there are eight points, corresponding to the eigenvalue for each of eight different models.

TABLE 1. The estimated stability-determining eigenvalue for the 10 CU–LH and UU–LH populations, during the first and last 15 generations of the experiment.

| Population | Early (generations 1–15) | Late (generations 31–45) |
|---|---|---|
| CU$_1$ | −1.29 | −1.19 |
| CU$_2$ | −0.80 | −0.71 |
| CU$_3$ | −0.54 | −1.26 |
| CU$_4$ | −0.93 | −1.33 |
| CU$_5$ | −0.95 | −0.93 |
| UU$_1$ | −1.43‡ | −0.99‡ |
| UU$_2$ | 0.66† | −0.69 |
| UU$_3$ | −0.79 | 0.16† |
| UU$_4$ | −0.85 | −1.30 |
| UU$_5$ | −1.02 | −0.51 |

*Note*: In each case, the second-order model (Eq. 2) was used with $\theta = 0$ (except as noted).
 † Modulus of a complex eigenvalue.
 ‡ Estimated from $\theta = 0.5$.

LH and UU–LH populations had significantly higher feeding rates than the corresponding HL populations. All five CU–LH populations had higher feeding rates than the five CU–HL populations, and all five UU–LH populations were greater than the five UU–HL populations ($P = 0.0312$, Wilcoxon test). This differentiation reflects the fact that the larval densities were much higher in the LH populations than in the HL populations, and that evolution was occurring in response to the larval density.

### Evolution of density-dependent fecundity

We have estimated the two parameters of the hyperbolic model for each of the 20 experimental populations, as well as the 10 CU and UU populations, at five-generation intervals. All of these data have been combined (Fig. 8) to show that the hyperbolic model

nitude of these eigenvalues, we have also used the first 15 and last 15 generations of data in the LH populations to estimate the stability-determining eigenvalue. We expect these eigenvalues to become larger if the populations are becoming more stable. As with the analysis of the autocorrelation function, there is no consistent change across populations: six populations show an increase in magnitude of the eigenvalue, and four show a decrease (Table 1).

### Evolution of feeding rates

Initially, there were differences in feeding rates, with the CU–LH and CU–HL populations having higher feeding rates than the UU–LH and UU–HL. These differences were due to the history of the CU and UU populations (Joshi and Mueller 1996, Santos et al. 1997). The prolonged selection in crowded larval environments had increased feeding rates of the CU populations, relative to the low-density UU populations. Over the next 20 generations, the history of the populations became less important, and the current environment determined the feeding-rate characteristics of the population. Thus, by generation 20, both the CU–
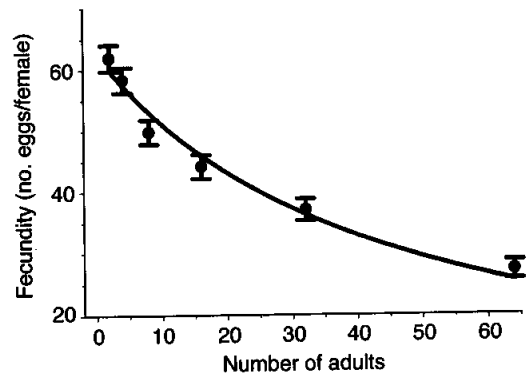


FIG. 8. Per capita fecundity vs. no. adults (density) for females raised on high levels of yeast. These results are based on the mean observed in each population at each density, taken over all samples in this study. Thus, each data point is the mean of ~220 observations. The intervals represent the 95% confidence interval on the mean. The solid line is the predicted value from the hyperbolic model fit to these data by nonlinear least-squares techniques. The estimated values of the parameters from the hyperbolic model were: $F = 62.6$, $a = 0.0227$.

TABLE 2. Analysis of variance of the slope, which reflects the degree of density dependence in female fecundity.

| Source | df | Sum of squares | Mean square | F | P |
|---|---|---|---|---|---|
| **CU** | | | | | |
| Population | 2 | 0.00548 | 0.00274 | 0.98 | 0.38 |
| Generation | 7 | 0.0264 | 0.00377 | 1.36 | 0.23 |
| Population × Generation | 14 | 0.0843 | 0.00602 | 2.17 | 0.015 |
| Error | 92 | 0.256 | 0.00278 | ... | ... |
| **UU** | | | | | |
| Population | 2 | 0.00129 | 0.000647 | 0.33 | 0.72 |
| Generation | 7 | 0.0215 | 0.00307 | 1.54 | 0.16 |
| Population × Generation | 14 | 0.0206 | 0.00147 | 0.74 | 0.73 |
| Error | 94 | 0.187 | 0.00199 | ... | ... |

*Notes:* UU populations (UU, UU–LH, and UU–HL) were analyzed separately from the CU populations (CU, CU–LH, and CU–HL). The slopes were determined at generations 5, 10, 15, 20, 25, 30, 35, and 41.

does indeed capture many of the features of density-dependent fecundity. Examination of the parameter $a$, which affects population stability, over 41 generations of evolution shows no consistent differences, either among the populations, or over time (Table 2). The analysis of the CU populations does reveal a significant population × generation interaction (Table 2). However, this is due to a significant difference among populations at generation five and, thus, is not an indication of an evolving difference in the slope. These results are in accord with the previous result showing no differences in the dynamics of the LH populations in the first and last 15 generations of the experiment.

### Temporal changes in total population size

We have fit straight lines to the 45 generations of adult population size results and the per capita mass

TABLE 3. The slopes from the regressions of adult numbers and per capita adult mass on generations.

| | Regression | | | |
|---|---|---|---|---|
| | Adult numbers | | Adult mass | |
| Population | Slope | P† | Slope | P† |
| CU$_1$–HL | 15.4 | 0.25 | −0.00035 | 0.54 |
| CU$_2$–HL | 31.0 | 0.01 | −0.00030 | 0.60 |
| CU$_3$–HL | 32.9 | 0.0005 | −0.0012 | 0.008 |
| CU$_4$–HL | 39.6 | 0.00008 | −0.0011 | 0.02 |
| CU$_5$–HL | 53.2 | 0.0001 | −0.0019 | 0.0008 |
| CU$_1$–LH | −4.2 | 0.85 | 0.000020 | 0.97 |
| CU$_2$–LH | −2.3 | 0.92 | 0.00036 | 0.59 |
| CU$_3$–LH | 1.2 | 0.95 | −0.00094 | 0.04 |
| CU$_4$–LH | −1.7 | 0.94 | −0.000034 | 0.96 |
| CU$_5$–LH | 5.0 | 0.84 | −0.0012 | 0.01 |
| UU$_1$–HL | −1.2 | 0.95 | −0.00062 | 0.08 |
| UU$_2$–HL | −17.8 | 0.32 | 0.0012 | 0.23 |
| UU$_3$–HL | 14.2 | 0.34 | 0.000082 | 0.87 |
| UU$_4$–HL | 13.9 | 0.35 | −0.00085 | 0.12 |
| UU$_5$–HL | 32.5 | 0.11 | −0.0011 | 0.09 |
| UU$_1$–LH | −15.7 | 0.47 | 0.00053 | 0.32 |
| UU$_2$–LH | 5.0 | 0.83 | −0.00024 | 0.68 |
| UU$_3$–LH | 7.8 | 0.68 | −0.0010 | 0.01 |
| UU$_4$–LH | 4.9 | 0.84 | −0.00020 | 0.70 |
| UU$_5$–LH | 20.7 | 0.41 | −0.00044 | 0.29 |

† Probability of the slope being significantly different from zero.

data (Table 3). Only the CU–HL populations show a consistent trend across the five replicates. All five CU–HL populations have a positive slope for the regression of adult numbers, and all five have a negative slope for the regression of per capita mass on time. Four of the five slopes are significantly different from zero in the former case, as are three out of five in the latter case. Thus, in addition to the decline in feeding rates experienced by the CU–HL populations, the equilibrium adult population size has also increased, and the size of the adults decreased over 45 generations of selection.

### DISCUSSION

#### Population stability remains unchanged

There were three important indicators of the stability of these *Drosophila* populations in this study: the autocorrelation of adult population size, the estimated eigenvalues, and the slope of the fecundity vs. density curve. From our analysis of the LH and HL populations, it is clear that small positive eigenvalues are associated with autocorrelation functions that display positive values, which decay exponentially with increasing lag. Large negative eigenvalues are associated with autocorrelation functions that alternate in sign; odd lags are negative, while even lags are positive. For the populations kept in the unstable LH environment, there were no indications that any measures of population stability had been altered over the course of 45 generations. However, over a much shorter time period, there was evidence of phenotypic differentiation, due to density-dependent natural selection. The feeding rates of the UU–LH populations increased relative to the UU–HL populations, and the feeding rates of the CU–HL populations decreased relative to the CU–LH populations. Thus, the absence of any change in the stability properties of the LH populations cannot be explained as simply being due to the absence of any evolutionary change in the populations.

Recall that the ancestral CU population had evolved in environments with very high larval densities, and that adults were raised on yeast for several days prior to egg laying. Thus, the CU environment is very similar

to the LH environment. We know from past work (Mueller et al. 1993, Joshi and Mueller 1996, Santos et al. 1997) that feeding rates increased in the CU populations relative to the UU populations. The present results suggest that feeding rates changed little, or not at all, in the CU–LH populations. However, feeding rates actually decreased in the low larval density CU–HL populations, due to the trade-off between feeding rates and other fitness components (Joshi and Mueller 1996, Borash et al. 1998). In the UU populations, the opposite forces are at work. The HL environment is most similar to the UU (due to the low larval densities), so the UU–LH populations are evolving higher feeding rates in response to the strong density-dependent selection.

In a similar fashion, we see the total adult population size in the CU–HL population increase over time as they become increasingly adapted to this novel environment, which is a result reminiscent of some of the very early work on population size evolution in *Drosophila* (Buzzati-Traverso 1955, Ayala 1965, 1968). One would have expected a similar observation in the UU–LH population, yet no consistent change in population size was observed (Table 3). In all likelihood, any genetically based changes that increase equilibrium numbers in these populations are probably obscured by the large population size fluctuations induced by the LH environment.

Of course, there may be changes in population stability occurring in the LH populations, but at a rate slow enough for the changes to still not be detectable after 45 generations of selection. To some extent, the CU populations may have experienced selection similar to that found in the LH populations, prior to the start of this experiment. This may have occurred because the CU environment is not unlike the LH environment: adults are given yeast prior to egg laying, and larvae are severely crowded. The magnitude of the autocorrelations in the CU–LH populations are always smaller than the magnitude in the UU–LH populations. One possible explanation is that the 71 generations of evolution in the CU environment, prior to the start of the present experiment, initiated the slow change in stability properties of the CU-derived populations, and that evolution is evident in a slight weakening of the magnitude of the correlations (and, hence, the population cycles). If we look at the mean eigenvalue (second order model, $\theta = 0$) for the CU–LH populations, it is $-0.67$ (95% CI, $\pm 0.46$); for the UU–LH populations, it is $-0.71$ ($\pm 0.37$). Thus, the eigenvalues are consistent with the idea that the UU–LH populations are less stable than the CU–LH populations, but the magnitude of the effect is quite weak. This is clearly, a fairly speculative interpretation of our experimental results and could only be confirmed by continued maintenance of the LH populations.

## Why can't population stability evolve?

At this time we have no direct evidence that may be used to answer this question, but several possibilities come to mind. As discussed earlier, one means of stabilizing population dynamics in the LH environments would be to reduce female fecundity, at least under crowded conditions. All other things being equal, natural selection, at the individual level, would not simply reduce fecundity. However, fecundity may decline due to natural selection, if it is correlated with some other fitness component that would increase (in a fitness sense). Such a correlated trait, for example, might be larval survival under crowded conditions. It may simply be that no such trade-off exists. Alternatively, such a trade-off may exist but, in these experiments, the net fitness benefit was very small; thus, selection proceeded at a very slow rate. This rate could be sufficiently slow that no measurable change in population dynamics was observable after only 45 generations. A related explanation could be that the net fitness advantage could be so small that it could not overcome the random effects of genetic drift in these populations (Mueller and Rose 1996).

Clearly, more empirical work is necessary before we can generally answer the question of whether population stability can evolve. At this time these results would suggest that population stability may be viewed as a property that will vary systematically over environments to a far greater degree than over time.

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