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# The evolution of population stability as a by-product of life-history evolution

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**Proposed mechanisms for the evolution of population stability include group selection through long-term persistence, individual selection acting directly on stability determining the demographic parameters, and the evolution of stability as a by-product of life-history evolution. None of these hypotheses currently has clear empirical support. Using two sets of *Drosophila melanogaster* populations, we provide experimental evidence of stability evolving as a correlated response to selection on traits not directly related to demography. Four populations (FEJs) were selected for faster development and early reproduction for 125 generations, and the other four (JBs) were ancestral controls. All FEJ and JB populations have been maintained on discrete generations at moderate density, thus eliminating differential selection on stability determining demographic parameters. We derived eight small populations from each FEJ and JB population, and subjected four small populations each to either stabilizing or destabilizing food regimes. Census data on these 64 small populations over 20 generations clearly showed that the FEJ populations have significantly less temporal fluctuations in their numbers in both food regimes compared to their controls. This greater stability of the FEJ populations is probably a by-product of the evolution of reduced fecundity and pre-adult survivorship, as a correlated response to selection for rapid development.**

**Keywords:** population dynamics; population stability; life-history evolution; *Drosophila melanogaster*

## 1. INTRODUCTION

Since the demonstration that simple population growth models yield complex dynamics (May 1974) there have been many reviews of population dynamics data, and relatively stable dynamics seem to be quite common (Turchin & Taylor 1992; Ellner & Turchin 1995). Why most populations show stable dynamics remains an open question, and there is no consensus on the mechanism(s) by which population stability may evolve through natural selection (Mueller & Joshi 2000). Theoretical explanations for the evolution of population stability include group selection acting through long-term persistence (Thomas *et al.* 1980; Berryman & Millstein 1989), individual selection acting on stability determining demographic parameters (Hansen 1992; Ebenman *et al.* 1996) and the evolution of stability as a correlated response to life-history evolution (Mueller *et al.* 2000). However, none of these hypotheses yet has clear empirical support.

In the group selectionist view, unstable populations undergo more frequent extinction than relatively stable populations (Thomas *et al.* 1980; Berryman & Millstein 1989). Consequently, the patches formerly occupied by unstable populations would probably be recolonized from nearby stable populations, and if the stability differences between populations were primarily genetic, population stability would evolve via group selection. This mechanism, however, will work only under very restrictive conditions (Mueller & Joshi 2000). It has also been suggested that population stability can evolve through direct selection on stability determining demographic parameters, such as growth rate components or their sensitivity to density (Hansen 1992; Ebenman *et al.* 1996). However, it is difficult to imagine scenarios where selection favours stabilizing traits such as lowered fecundity, and there is no experimental evidence for selection directly affecting the response of important demographic parameters to population density. In a rigorous test of this hypothesis, Mueller *et al.* (2000) subjected 20 populations of *Drosophila melanogaster* to an environmental regime that leads to large and regular fluctuations in population numbers. However, even after 65 generations, stability characteristics of these populations did not evolve, nor did traits important to stability, such as the sensitivity of female fecundity to increasing adult density (Mueller & Joshi 2000). Yet, rapid evolution of traits such as larval feeding rate did occur during the first 20 generations of this experiment, thereby suggesting that the lack of response in stability characteristics was not due to a general absence of evolutionary change in the course of the experiment (Mueller *et al.* 2000).

Earlier theoretical studies suggested that trade-offs among demographic parameters were crucial to the evolution of population stability (Turelli & Petry 1980; Mueller & Ayala 1981; Stokes *et al.* 1988; Gatto 1993; Ebenman *et al.* 1996). It was also shown that a pattern of apparent stabilization over time of the dynamics of laboratory populations of blowflies (Nicholson 1957) was consistent with an explanation involving selection for the ability of females to lay eggs even when malnourished coupled with a trade-off between this ability and both survivorship and maximal fecundity (Stokes *et al.* 1988). The results from all these studies, together with the ubiquity of life-history trade-offs, suggest that it may be most likely that population stability evolves indirectly, as a consequence of the correlated response of traits such as lower fecundity to selection on life-history traits not directly related to demography (Mueller *et al.* 2000). We provide, to our knowledge, the first clear evidence supporting this hypothesis by showing that populations of *D. melanogaster* selected for rapid development in the laboratory have evolved more stable dynamics than their ancestral control populations. This result can be understood in terms of a divergence in their life-history traits as a correlated response to the imposed selection pressure.


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Table 1. Results from ANOVA on the coefficient of variation of population size in the 64 small populations.

| effect | d.f. | mean square | *F*-value | *p*-value |
|---|---|---|---|---|
| selection regime | 1 | 0.4493 | 32.77 | 0.0106 |
| block | 3 | 0.0430 | 6.37 | 0.0010 |
| food regime | 1 | 3.6314 | 489.40 | 0.0002 |
| selection regime × block | 3 | 0.0137 | 2.03 | 0.1220 |
| block × food regime | 3 | 0.0074 | 1.10 | 0.3585 |
| selection regime × food regime | 1 | 0.0051 | 0.51 | 0.5273 |
| block × selection regime × food regime | 3 | 0.0100 | 1.48 | 0.2323 |
| error | 48 | 0.0067 | | |

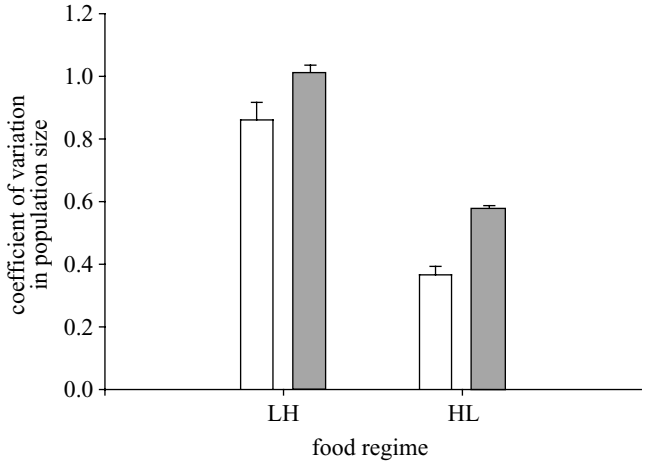


Figure 1. Mean (+ s.e.) coefficient of variation of population size in FEJ (open bars) and JB (filled bars) derived small populations, averaged over 16 replicates per selection regime × food regime combination.

## 2. MATERIAL AND METHODS

### (a) *Experimental populations*

This study used eight laboratory populations of *D. melanogaster*, whose derivation and maintenance has previously been described in detail (Prasad *et al.* 2000, 2001) and is outlined here. Four of these populations ($FEJ_{1–4}$; faster development, early reproduction, JB derived) had been subjected to selection for faster pre-adult development and early reproduction for *ca*. 125 generations at the time of this study, whereas the other four populations ($JB_{1–4}$) were ancestral controls. The JBs had been maintained in the laboratory for *ca*. 450 generations on a 21-day discrete generation cycle at large population size (*ca*. 1800) and a moderate larval density of 60–80 larvae per vial containing *ca*. 6 ml of food medium. On the 18th day after egg laying, all eclosed adults were collected into a Plexiglas cage, and eggs initiating the next generation were collected from these adults 3 days later. The FEJs were maintained in a manner similar to the JBs except that only the first 20% of the flies that eclosed in each vial were transferred to the cage to form the breeding population, and eggs were collected on the third day after eclosion. The number of breeding adults in the FEJ populations was *ca*. 1400. Each FEJ population was derived from one JB population. Thus, $JB_i$ and $FEJ_i$ were treated as random blocks in the analysis. Since these populations were on a discrete generation cycle, and both adult and larval densities were controlled at a moderate level there was no differential selection directly on stability determining demographic parameters or their sensitivity to density. In the maintenance regimes used in the experiments reported here development time is unlikely to have a major effect on population dynamics.

### (b) *Population dynamics experiment*

We derived eight small populations from each FEJ and JB population, and studied their dynamics under either a stabilizing or a destabilizing food regime, as in Sheeba & Joshi (1998). Each small population was maintained as a single vial culture, and was initiated by keeping eight males and eight females from the parent FEJ or JB population in a vial for 24 h. The adults were then discarded, and the eggs laid during those 24 h started generation zero of the population dynamics experiment. Once eclosion began, adults were collected into adult collection vials with 6 ml of food medium. Any new eclosing flies from the egg vials were added to these collection vials daily. Every alternate day, all adult flies eclosed in each small population until that day were transferred to a fresh vial. On the 18th day after egg collection, the egg vials were discarded, and all adult flies of each small population were transferred to a fresh food vial with or without yeast paste (depending upon food regime) for 3 days of conditioning. The next generation was started by allowing the adults to oviposit for 24 h into a new egg vial, after which they were censused and discarded. In this manner, we collected census data from all 64 small populations for 20 generations. Population sizes varied between *ca*. 2 and 250 adults.

The two food regimes used were as follows: (i) a stabilizing (HL) regime in which egg vials contained excess (6 ml) food medium, and adults were not provided with any supplementary live yeast for the 3-day conditioning period before egg collection; and (ii) a destabilizing (LH) regime in which egg vials contained only 2 ml of food medium, and adults were provided with supplementary live yeast paste during the conditioning period. The HL and LH regimes have been shown to have stabilizing and destabilizing effects, respectively, on the dynamics of *D. melanogaster* cultures, with the LH regime tending to induce large-amplitude two-point cycles in population size (Mueller & Huynh 1994; Sheeba & Joshi 1998; Mueller *et al.* 2000). Four out of the eight small populations derived from each FEJ and JB population were subjected to the LH regime, and four to the HL regime.

The coefficient of variation (CV) of population size of the FEJ- and JB-derived small populations was used to assess stability: a smaller CV being considered indicative of relatively stable dynamics. The CV data were subjected to analysis of variance (ANOVA), treating selection regime (FEJ, JB) and food regime (LH, HL) as fixed factors, crossed with each other and with block (1–4, representing ancestry of the FEJ and JB populations). CV values from the four small populations within each block × selection regime × food regime combination were treated as replicate within-cell observations.

## 3. RESULTS

As expected, the mean CV of population size in the LH food regime was significantly greater than that in the HL food regime (table 1; figure 1). More importantly, the mean CV of population size in the FEJ-derived populations was significantly smaller than that in the JB-derived populations (table 1; figure 1). There was no significant interaction between selection regime and food regime in the ANOVA (table 1). The results clearly indicate that the four FEJ populations have evolved more stable dynamics than their JB ancestors over 125 generations of selection for faster development and early reproduction.

## 4. DISCUSSION

The greater stability of the FEJs compared to the JB controls can be traced back to their respective life histories. As a correlated response to selection for faster development, the FEJs are known to have evolved reduced

fecundity (*ca*. 35%) (Joshi *et al.* 2001), as well as reduced body weight (*ca*. 45%) and pre-adult survivorship at moderate larval density (*ca*. 22%) (Prasad *et al.* 2000, 2001) compared to the JBs. These are clear correlated responses to selection for rapid development, which reduces the time available for the larvae to feed and accumulate lipid reserves and exacts a survivorship cost (Prasad *et al.* 2001). Adult lifespan did not differ between FEJ and JB populations at the time of the study (M. Shakarad, N. G. Prasad and A. Joshi, unpublished data).

The higher larval density in the small populations, compared to the parent FEJs and JBs in their controlled density cultures tends to prolong development in both FEJ- and JB-derived populations. Thus, all other factors being equal, the faster developing FEJ individuals have a greater chance of reaching adulthood before the 18-day deadline, compared to their JB counterparts. This potentially destabilizing survival advantage, however, appears to be offset by the intrinsically lower survivorship of FEJ larvae. Survivorship and fecundity in small populations could also be reduced over generations due to inbreeding, and this could have a stabilizing effect (Mueller & Joshi 2000). However, in our experiment, the JB-derived populations had a lower effective (harmonic mean) population size, on average (83 and 11 in HL and LH food regimes, respectively), than the FEJ-derived populations (115 and 16 in HL and LH food regimes, respectively). Thus, if anything, the JB-derived populations would be expected to have experienced greater inbreeding. Our results are, therefore, conservative.

We do not yet know if the sensitivity of fecundity or survivorship to density has also changed in the FEJs, although we cannot imagine why such changes in sensitivity might be expected given that the larval and adult densities in both JBs and FEJs are controlled at a very moderate level. However, both reduced pre-adult survivorship and fecundity are, in themselves, likely to play a stabilizing role in the dynamics of the FEJ-derived small populations by contributing to a reduction in their intrinsic growth rate, a parameter observed to be the main determinant of stability or instability in most population growth models (Mueller & Joshi 2000). Thus, our experimental results clearly show that population stability can evolve as a by-product of selection on life-history traits not directly related to population dynamics.

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