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Density-dependent natural selection does not increase efficiency

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Summary

Populations of *Drosophila melanogaster* kept at high population density (*K*-selected) for 125 generations have higher larval viability than populations kept at low densities (*r*-selected) when both are raised under crowded conditions. In addition *K*-selected adults that emerge from crowded cultures are larger than their *r*-selected counterparts. These differences cannot be explained by differences in efficiency of food use. The minimum food required for successful pupation is actually greater in the *K*-selected populations. I conjecture that there may be a trade-off between minimum food requirements and competitive ability, which has changed substantially in the *K*-selected populations. The possibility that *K*-selected larvae can dig more more deeply and gain access to unused food is examined and rejected as a possible explanation of the viability differences. Evidence is provided supporting the hypothesis that the differences in viability may be due to an increased tendency of the *K*-selected larvae to pupate off the surface of the medium.

Keywords: *Drosophila melanogaster*; competitive ability; efficiency; *r*-selection; *K*-selection.

Introduction

MacArthur and Wilson (1967) produced the most influential exposition of the theory of density-dependent natural selection, or *r*- and *K*-selection, as it is often called (Boyce, 1984). Their discussion of selection in crowded environments concluded that '. . . genotypes which can at least replace themselves with a small family at the lowest food level will win . . . Evolution here favours *efficiency* of conversion of food into offspring . . .' (MacArthur and Wilson, 1967, p. 149). More formal theories of density-dependent natural selection have identified density-dependent rates of population growth as the phenotype that should respond to selection (Roughgarden, 1971).

The two most careful tests of the predictions of the formal theories have used organisms with quite different life histories (Luckinbill, 1978; Mueller and Ayala, 1981). The results of these studies have, not surprisingly, been contradictory. The studies with *Drosophila melanogaster* (Mueller and Ayala, 1981) showed that the populations that had evolved at high densities, called *K*-selected, had higher *per capita* rates of increase in crowded environments than did the populations that had evolved at low densities, called *r*-selected.

More recently Bierbaum *et al.* (1989) have shown that after 36 generations of selection larvae from these *K*-selected populations survive better under crowded conditions and are larger when they become adults than *r*-selected larvae. Thus, the higher *per capita* growth rates of the *K*-selected *Drosophila* populations at high densities is due to both increased viability and increased female fécundity (since larger females lay more eggs; Mueller, 1987).

In this paper, I examine possible mechanisms by which larval viability and adult size may have increased in the *K*-populations. First, *K*-populations may have increased efficiency. *Drosophila*

larvae must reach a critical minimum size and thus consume a minimum amount of food to pupate successfully (Chiang and Hodson, 1950; Bakker, 1961; Nunney, 1983). One way in which natural selection may increase efficiency is by lowering minimum food requirements (Mueller, 1988a).

Secondly, the digging behaviour of the *r*- and *K*-selected larvae may differ. When larvae were crowded in the studies of Bierbaum *et al.* (1989) there were portions of the food medium on the bottom of vials that were unused. This suggests that larvae that dig more deeply have access to unused food and could increase their chances of survival and adult size in crowded environments.

Finally, viability differences between the *r*- and *K*-selected populations at high densities may be due to increased mortality to pupae on the surface of the medium. Mueller and Sweet (1986) showed that under identical larval densities the *K*-selected larvae are less likely to pupate on the surface of the medium than are the *r*-selected larvae. This behaviour, unlike the previous two, cannot explain the size differences of larvae since adult size is fixed at the time of pupation.

Methods and materials

Population maintenance and inbreeding

The experimental populations consisted of six independent populations initially derived from the same source population: three have been kept at low population density (50 adults) and are called *r*-selected and three have been kept at high densities (at carrying capacity for these environments, ~ 1000 adults) and are called *K*-selected. The details of their maintenance are given in Mueller and Ayala (1981). At the time these experiments were conducted these populations had been maintained in their respective environments for a little over six years or 125 generations for the *r*-populations.

A confounding factor in these experiments is the differential effects of random genetic drift. Clearly, the effects of drift will be more pronounced in the *r*-populations. This implies that any observed phenotypic differences may not be due solely to natural selection, but that deleterious (with respect to their action on the trait under consideration) recessive alleles may have become fixed in the *r*-populations by chance alone. Since the three *r*-populations are maintained independently, it will be unlikely that all three will become fixed for the same sets of deleterious alleles by these random processes. Thus, F_1 progeny of the *r*-populations should be largely heterozygous at the relevant loci and hence 'cured' of these deleterious effects. This is the typical observation of hybrid vigour observed in the F_1's of inbred lines (Wright, 1977). In the experiments estimating minimum food requirements and digging behaviour, F_1 populations have been created for the *r*- and *K*-populations by making all possible crosses. For example in the *r*-F_1 population there were six crosses (male × female) *r*-1 × *r*-2, *r*-1 × *r*-3, *r*-2 × *r*-3 and the reciprocal crosses.

Another important issue with these populations is whether both populations have differentiated from their initial state or only one has with the second remaining unchanged. Ultimately, the most interesting contrast is simply that the two types of populations have become differentiated due to natural selection. However, it is reasonable to assume that the crowded environments experienced by the *K*-populations are novel for wild *Drosophila*. Earlier studies (Buzzati-Traverso, 1955; Ayala, 1965, 1968) documented increases in the carrying capacity of *Drosophila* populations upon being brought into the laboratory environment and crowded. This would imply the *Drosophila* populations rarely exist under high-density conditions outside the laboratory.

Estimates of minimum food requirements

Estimates of minimum food requirements were made using experimental techniques developed

by Bakker (1961) and statistical methods described by Nunney (1983). The three independent r-and K-populations have been randomly assigned indices from 1 to 3. Each r- and K-population has been matched by this index. All experiments reported here were conducted simultaneously on matched pairs of populations. Viability was determined by placing 100 newly hatched (within 2 h) first instar larvae in vials with measured amounts of yeast and water (2.67 ml g^{-1} yeast). This solution was placed on non-nutritive Kalmus medium which precluded growth of the yeast. The raw data consisted of the number of adults emerging from each vial. At any given time, viability was determined at 10 different yeast levels (25 mg – 158 mg/100 larvae) in each matched population. These experiments were conducted on at least two different occasions.

Using the techniques described by Nunney (1983), the viability data from a given population, s, can be used to estimate the minimum food required for successful pupation by males (m_{sm}) and females (m_{sf}). The derivation of these estimates and their sampling variance makes three important assumptions. First, the sex ratio of newly hatched larvae is assumed to be 1 with sampling variation following a binomial distribution. Second, mortality due to factors other than limited food is assumed to act after all the food has been consumed. This assumption is supported by the observation that at very high food levels almost all larvae placed in the vial pupate and therefore almost all larvae which fail to develop into adults have died as pupae. Last, this derivation assumes that male and female larvae from the experimental population have approximately the same competitive ability(α).

The latter assumption may seem suspect given Nunney's finding of differences between sexes in his competition studies. Nunney (1983) actually shows that in a given population the ratio $(m_m\alpha_f)/(m_f\,\alpha_m)$ may not be equal to one and is often less than one. This finding is consistent with my supposition that male and female competitive abilities are equal and $m_m < m_f$. This latter inequality is quite reasonable since at any given food level males are invariably smaller than females. A second line of support for this assumption comes from the analysis of cephalo-pharyngeal retractions. This feeding behaviour index appears to be highly correlated with measures of competitive ability (Burnet *et al*. 1977; Joshi and Mueller, 1988). Estimates of feeding rates of these r- and K-populations reveal no consistent differences between sexes of the same population (Joshi and Mueller, 1988). Consequently, I expect little or no difference in competitive ability of different sex larvae from the same population.

Statistical analysis of these data were performed with the bootstrap technique (Efron, 1979a, 1979b). The bootstrap generated new data sets by recreating the sampling process inherent in the collection of these data, using the original data as an empirical estimate of the distribution function of the relevant random variables. With this technique, bias-corrected confidence intervals (Efron, 1981) have been constructed for the minimum food requirements and the significance of differences between food requirements for the r- and K-populations has been calculated.

The minimum food requirements have been measured by a second, independent, yet more direct method. In these experiments a single larva was placed in an eight-dram vial with a measured amount of dry yeast and water (2.67 ml g^{-1} yeast). Populations were tested as matched pairs at five different food levels. For each population, 10 larvae were tested at each food level.

Digging behaviour

To quantify digging behaviour, the bottom was removed from standard eight-dram vials and replaced with tightly sealed plastic wrap. Standard food medium was placed in these vials along with 50 first instar larvae from the appropriate populations. Populations were tested as matched pairs as before. At 60, 72 and 96 h after the start of the experiment, the food plug of a particular vial would be pushed out and cut in thirds. The total number of larvae in each section was then recorded. Each experiment was conducted on two separate occasions.

Viability and pupation site

The effects of pupation site choice on viability have been examined in the r-F_1 population. One hundred larvae were added to vials with non-nutritive Kalmus medium and 0.081 g, 0.1125 g or 0.1575 g yeast. After the larvae pupated and the adults emerged, each pupal case was scored according to its location: on the surface of the medium or on the side of the vial; and its status: either dead or alive. At the two lowest yeast levels, almost all the food was consumed and the surface was relatively dry and hard. At the highest yeast level, there was excess food and the surface became soft and moist. These conditions resemble the conditions of the medium in crowded cultures and are thought to increase the chances of mortality.

Results

There is no indication that larvae from the K-populations require less food to pupate successfully (Table 1). The probability that differences in m for a matched pair of like sex was less than 5% was calculated during the bootstrap simulations. There are two populations in which m_m is significantly less than m_f (r-2 and K-3). This general tendency for males to require less food is reasonable since males are usually smaller than females.

There results were confirmed in the second experiment on survivorship of single larvae (Table

Table 1. Minimum food required (mg per larva, ±95% confidence interval).

Populations	Males		Females	
K-1	0.45 (±0.065)		0.45 (±0.065)	*
r-1	0.52 (±0.080)		0.59 (±0.10)	
K-2	0.47 (±0.13)	*	0.47 (±0.15)	
r-2	0.34 (±0.15)		0.52 (±0.52)	
K-3	0.42 (±0.082)		0.51 (±0.046)	
r-3	0.42 (±0.092)		0.47 (±0.067)	
K-F_1	0.43 (±0.12)	*	0.45 (±0.081)	*
r-F_1	0.19 (±0.084)		0.24 (±0.13)	

* Significantly different at $P < 0.05$.

Table 2. Number of surviving larvae (10 total) when each is given the indicated amount of yeast. Experiments were run as matched pairs.

Population	Food level (mg per larva)				
	3.5	4.0	4.5	5.0	5.5
K-1	0	0	0	1	0
r-1	0	3	4	6	4
K-2	0	2	2	4	3
r-2	8	3	5	9	8
K-3	0	2	3	4	7
r-3	3	7	9	7	8

2). A log-linear analysis of the data in Table 2 for each matched pair showed that survivorship is not independent of population of origin. Indeed, at the lowest yeast levels larvae from the *r*-populations survived better than larvae from *K*-populations.

The results from these first two experiments indicated substantial differences in the absolute amount of yeast needed for successful pupation (compare Tables 1 and 2). This difference is almost certainly due to the differences in experimental techniques. When a single larva is placed in a vial with small amounts of yeast much of the food is rendered unusable by the physical movement of the larva. Consequently, much more yeast must be supplied to a single larva (Table 2) for it to consume its minimum requirement.

Larvae from the *K*-populations show no tendency to dig more deeply than the *r*-larvae (Table 3). In fact, very few larvae ever dig into the bottom third of the medium column where most of the unused food is found.

Table 3.   Average number (50 total) of larvae found in the top (T), middle (M) and bottom (B) section of the food column taken at three different times. Each number is the mean of two replicates.

| Time | 60 h | | | 72 h | | | 96 h | | |
Food Section	T	M	B	T	M	B	T	M	B
Population									
K-1	41.0	8.0	0.0	34.5	14.5	0.0	45.0	4.5	0.0
r-1	33.5	14.5	0.5	31.5	16.5	0.0	45.5	3.0	0.0
K-2	24.5	22.0	3.0	38.5	9.5	0.5	48.0	1.5	0.0
r-2	38.5	10.5	0.5	42.5	8.5	0.0	42.0	7.5	0.0
K-3	21.5	24.5	1.5	34.5	13.0	1.5	47.5	1.5	0.0
r-3	29.0	16.5	1.5	15.0	28.0	2.0	28.5	18.5	2.0
K-F_1	29.0	19.5	0.5	39.0	11.5	0.0	46.0	3.0	0.0
r-F_1	35.0	15.5	0.0	45.0	5.0	0.0	46.5	3.0	0.0

A log-linear analysis was performed on the pupal mortality data (Table 4). If the excess yeast in the 0.1575 g treatment increases the mortality of pupae on the surface of the medium, then there should be a three-way interaction between treatment, location and status. This interaction is significant ($G^2 = 6.28$, $p < 0.05$; Bishop *et al.* 1975, chpt. 4).

Table 4.   Location and status of pupae from the *r*-F_1 population at three different yeast levels. The numbers in each column do not sum to 100 since a few larvae die before they pupate.

| Location | Status | Yeast (g per 100 larvae) | | |
		0.0810	0.1125	0.1575
Surface	Alive	16	12	2
	Dead	21	10	24
Side	Alive	52	60	56
	Dead	7	8	12

Discussion

Density-dependent viability

The verbal conjectures of MacArthur and Wilson (1967) and the predictions from the formal model of Mueller (1988a) that efficiency should increase in crowded environments have not been realized in this experimental system. The ability of larvae from the low and high density environments to successfully pupate on limited amounts of food has been determined by two independent methods. Each yielded the same results: larvae from the *K*-populations need as much or more food to successfully pupate than their *r* counterparts.

Larvae from the *K*-populations do not appear to have an increased propensity to dig more deeply in the food than do larvae from the *r*-populations. Thus, the differences in viability exhibited by these populations under crowded conditions cannot be attributed to this behaviour. This result may have been anticipated by the work of Godoy-Herrera (1979). He applied artificial selection for increased and decreased digging behaviour on a population of *D. melanogaster*. The selection for decreased digging was successful while the selection for increased digging was not. The failure of natural selection to increase digging behaviour is less surprising in light of these results.

The results from the pupation study show that viability may be substantially decreased for larvae which pupate on the surface of wet, soft medium. The propensity of *K*-larvae to pupate less often on the surface than the *r*-larvae (Mueller and Sweet, 1986) may account for differences in viability of these populations at high densities. Since the adult size is fixed at the time of pupation, it does not seem likely that this process can explain the observed size differences, unless large larvae are more likely to pupate on the surface. My own observations show no correlation between size of a pupa and its pupation height (Mueller, unpublished results).

Competitive ability vs minimum food requirements

The decrease in efficiency of larvae from the *K*-populations is contrary to theoretical expectations (Mueller, 1988a). Although MacArthur and Wilson (1967) make a claim similar to Mueller (1988a), earlier work by MacArthur (1962) recognizes that some traits may yield a competitive advantage without a concomitant increase in efficiency. If genetic variation at a single locus affects only the minimum food necessary for successful pupation, then natural selection favours genotypes with the smallest requirements in crowded environments. However, if this genetic variation has pleiotropic effects on minimum food requirements and competitive ability, then minimum food requirements may actually increase due to natural selection if compensated for by sufficiently large gains in competitive ability (Mueller, 1988a).

It appears that larvae of *D. melanogaster* which are superior competitors for food are characterized by high rates of the cephalopharyngeal retractions which accompany feeding (Sewell *et al.* 1975; Burnet *et al.* 1977). This means that competition for food by *Drosophila* larvae occurs by exploitative mechanisms rather than interference mechanisms common to many other species (Rosenzweig, 1987). The *K*-populations are superior competitors (Mueller, 1988b) and have higher retraction rates (Joshi and Mueller, 1988) than the *r*-populations. Higher feeding rates are accompanied by increased activity (Sewell *et al.* 1975), metabolic rates (McEvoy, 1984) and faster food passage (Burnet *et al.*, 1977). In some insects, assimilation of energy may decline with very high feeding rates (Slansky and Feeny, 1977). In crowded populations of *Drosophila*, natural selection for increased competitive ability may be accompanied by a decline in efficiency due to a physiological trade-off between these phenotypes.

Other factors affecting viability

This present study was initially motivated by the observations of Bierbaum *et al.* (1989) that *K*-

populations exhibited higher survival and produced larger adults under crowded larval conditions that did the *r*-populations. This study has identified pupation site choice as a behaviour which may account for part of the viability differences, but not the size differences. There are environmental factors that are affected by population density that have not been investigated. One of these factors is waste concentrations (Botella, *et al.* 1985). In crowded environments, *Drosophila* larvae may ingest substantial quantities of wastes prior to pupation. These wastes have been shown profoundly to affect survivorship and development time (Ménsua and Moya, 1983; Moya and Botella, 1985). Future work on the *r*- and *K*-populations will attempt to identify any differential effects of wastes on the survivorship or adult size of these populations.

Generality of results

The research described here is an attempt to develop a coherent description of density-dependent natural selection in a simple environment. I feel a detailed understanding of one system is better than a superficial understanding of many. The extent to which density-dependent selection will fail to increase efficiency in other organisms or indeed other species of *Drosophila* is unclear. Our ability to generalize the observations made here will depend on the replication of these results with other experimental organisms as well as a more detailed understanding of the processes at work in *D. melanogaster*.

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