Ecological determinants of life-history evolution

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SUMMARY

Density-dependent natural selection has been studied, empirically with laboratory populations of *Drosophila melanogaster*. Populations kept at very high and low population density have become differentiated with respect to important fitness-related traits. There is now some understanding of the behavioural and physiological basis of these differences. These studies have identified larval competitive ability and efficiency of food utilization as traits that are negatively correlated with respect to effects on fitness. Theory that illuminates and motivates additional research with this experimental system has been lacking. Current research has focused on models that incorporate many details of *Drosophila* ecology in laboratory environments.

1. INTRODUCTION

The importance of the natural environment in determining the evolution of species was obvious to Darwin. Despite this, the early synthesis of evolutionary biology largely ignored the interaction between ecology and evolution. The first important theoretical fusion of ecological theory and evolutionary theory came with MacArthur (1962) and MacArthur & Wilson (1967).

MacArthur & Wilson utilized the well developed theory of density-dependent population growth to study the outcome of adaptation to extreme population densities. This was a logical first step since population density is a predictable component of the environment and thus amenable to this sort of theoretical investigation. MacArthur & Wilson selected one general model of population growth, the logistic equation, to develop their theory. The great generality of the logistic was also a liability for the purposes of designing tests of the theory.

The two parameters of the logistic, r and K, were variously interpreted as measuring life-history traits that they had little connection to. The result of such a misapplication of theory was the general dismissal of r- and K-selection, as the MacArthur–Wilson theory is often called. In fact, it has become clear that population density can have a profound effect on aspects of life-history evolution. It is also evident that precise theoretical predictions about life-history evolution for any particular species will have to utilize theory that takes into account relevant ecological details of that species.

In the next section I describe a series of studies with laboratory populations of *Drosophila melanogaster* designed to investigate the effects of adaptation to extreme densities. This will be followed by a discussion of the interaction between theory and experiment in this field.

2. EXPERIMENTAL RESEARCH

The early 1970s saw numerous attempts to test the theory of density-dependent natural selection or r- and K-selection as it was sometimes called. These studies used natural populations of different species (McNaughton 1975), or different populations of the same species (Gadgil & Solbrig 1972), which were thought to have experienced different degrees of density regulation. A significant shortcoming of this type of research is that the study populations might differ with respect to environmental variables other than density in an unknown and uncontrolled fashion. Often the inferred differences in the density régimes were uncertain.

(a) Experimental Drosophila populations

To remedy these problems I undertook, in 1978, a study of laboratory populations of *Drosophila melanogaster*. With this organism, replicate samples could be taken from the same source population, thus insuring that initially the populations would be identical with respect to the studied characters. The replicate populations could then be subjected to different density regimes while keeping all other variables constant.

The creation of these populations and important historical events during their maintenance are shown in figure 1. Three replicates of the low density populations (r-populations) were created and maintained using a reproductive population of 50 adults. The high density, K-populations, were maintained at adult population sizes of approximately 1000. In the r-populations both adults and larvae were uncrowded whereas larval and adult crowding were severe in the K-populations. In addition to these density differences were differences in the timing of adult reproduction. In the r-populations adults were generally 3–6 days old at the time of egg laying. Adults in the K-populations
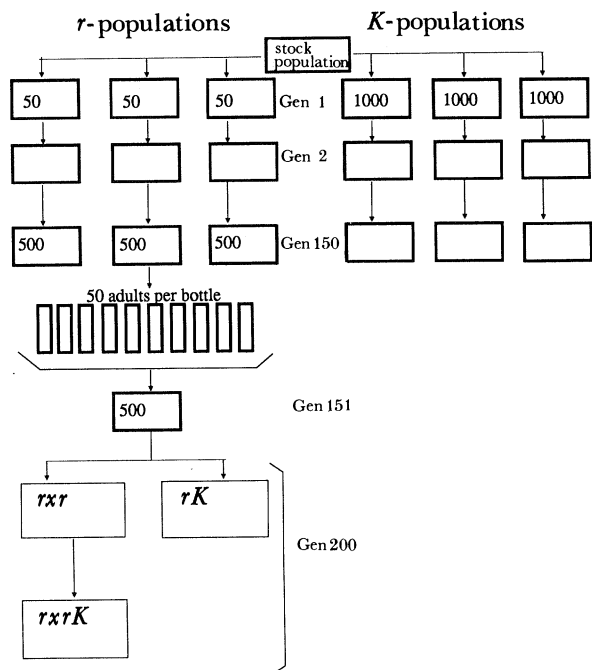
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r-populations   K-populations

Figure 1. The derivation and maintenance of the r-, K-, rxr-, rK- and rxrK-populations.

were allowed to breed indefinitely, although the average lifespan was probably only 2–3 weeks. Although differences in adult age at reproduction are unlikely to affect the evolution of larval characters they are important for adult characters. Evidence that age-specific female fecundity has differentiated as a consequence of the timing of adult reproduction in the r- and K-populations is described in Mueller (1987). After approximately 150 generations the maintenance régime of the r-populations was altered such that the effective population size per population was closer to 500 rather than 50; future effects of random genetic drift could therefore be forestalled.

At about generation, 200, three new types of populations were created (figure 1). The rK-populations were derived from the three replicate r-populations. The rK-populations were kept in the K-environments and thus these populations represented a form of reverse selection. The rxr-populations were created by making all possible pairwise crosses between the three r-populations and taking equal numbers of progeny from each cross to initiate each rxr-population. These populations were maintained in the same way as the r-populations but had genetic variation from all the original populations combined into each constituent population, thus mitigating inbreeding effects that might have been present in the r-populations. Finally, from the rxr-populations three rxrK-populations were derived which were kept in a K-population maintenance regime (figure 1).

(b) Phenotypic differentiation of the experimental Drosophila populations

The first test of the r- and K-populations examined density-dependent rates of population growth at one low (10 adults) and two high (750, 1000) densities

(Mueller & Ayala 1981) after eight generations of selection. The results were that at high population density the K-populations showed rates of population growth that were significantly elevated relative to the r-populations. The opposite result was seen at the low density. These results do not allow us to infer the magnitude or even the direction of change in each individual population from its initial condition although, since the initial condition of these stocks is somewhat arbitrary, the most important result is the differentiation of the r- and K-populations from each other.

The differences in population growth rates of the r- and K-populations may be the result of differences in viability of adults or larvae, differences in female fecundity or some combination of these traits. After approximately 30 generations of selection age-specific fecundity and survival rates were estimated at low density and egg-to-adult viability was measured at several larval densities (Bierbaum *et al.* 1989). No differences were seen in the adult fitness components but the K-larvae had higher survival rates under crowded larval conditions and the adults which emerged from these crowded cultures and were larger than their r counterparts. These results suggest that the differences in population growth rates, at least at high densities, are due to increased survival of K-larvae and increased fecundity of K-females, as larger females lay more eggs (Robertson 1957; Mueller 1987).

One reason the K-larvae survive better under crowded conditions is because these larvae are less likely to pupate on the surface of the food (Mueller & Sweet 1986) where mortality is quite high (Joshi & Mueller 1991). The high densities of larvae used in the Bierbaum *et al.* study create several challenges. Certainly, food is limiting so that a larva that is more efficient at processing food should have a higher probability of survival and should be larger than a less efficient larva all other things being equal. These crowded larvae must also contend with high concentrations of waste products that they inevitably eat. It is known that this consumption of waste has effects on viability and development time (Botella *et al.* 1985) and may also have effects on adult size. Below, I describe experiments aimed at addressing the affects of limited food on viability and adult size. Studies of the effects of waste products on the r- and K-populations are currently in progress.

Larval food levels may be carefully controlled using techniques first described by Bakker (1961). By examining viability of r- and K-larvae at various food levels in pure populations and in competition with a genetically marked standard population, it is possible to estimate, for each population, the minimum food level necessary for successful pupation (m) and larval competitive ability for food (α), (Mueller 1988a). It is worth noting that although competitive ability should be under strong selection in crowded environments (Mueller 1988b), it will not lead to improvements in density-dependent viability and so cannot explain the observations of Bierbaum *et al.* However, reductions in the minimum food requirements will lead to increases in viability (Mueller 1988b). Competitive ability

showed consistent and large differences between the *r*- and *K*-populations (Mueller 1988a). The average competitive ability of the *K*-larvae was 1.14 and for the *r*-larvae 0.72. However, the minimum food requirements showed no consistent differences between the populations.

The estimates of minimum food requirements obtained in the preceding experiments were rather imprecise because this value was inferred from observations made on groups (100) of larvae. These results were checked by a second independent experiment. In this experiment a single larva was placed in a vial with measured quantities of food. With sufficient replication of various food levels this experimental design provides a direct estimate of the minimum amount of food necessary for pupation. This experiment showed that the *K*-populations consistently required more food to pupate successfully than did the *r*-populations (Mueller 1990). These results may show an antagonistic relation between competitive ability and efficiency. Several lines of evidence suggest such a relation.

The feeding rates (measured by rate of cephalopharyngeal contractions) of third instar *K*-larvae are significantly greater than *r*-larvae (Joshi & Mueller 1989). Previous research on this larval behaviour has shown that larvae artificially selected for high feeding rates are better competitors than slow feeders (Burnet *et al.* 1977). Thus it would appear that natural selection for high competitive ability in the *K*-populations has resulted in increasing the feeding rates of larvae. In addition, Sewell *et al.* (1975) have shown that larvae artificially selected for fast feeding are generally more active than slow feeders and that food passes through their alimentary tract more rapidly.

These observations suggest that the fast-feeding *K*-larvae spend more of their energy budget on activity than the slower-feeding *r*-larvae. In addition, the fast rate at which food is processed may prevent larvae from extracting all the available energy (Slansky & Feeny 1977). If these assumptions are correct than a logical consequence of selection for increased competitive ability would be reduced efficiency. Future research should allow us to collect direct evidence on the nature of any physiological differences between the *r*- and *K*-larvae.

(c) Selection versus genetic drift

One extreme viewpoint of the *r–K* differentiation is that in fact density has no effect on life history and the only cause of the differences observed between the populations is because of the small size (during the first 150 generations) of the *r*-populations and the consequent fixation of deleterious mutations. This possibility has been studied by examining the phenotypes of *r*–F_1 populations. If the inbreeding hypothesis were correct than the *r*–F_1 offspring should show elevated (near *K*-values) values of the phenotype relative to the depressed values of the parental *r*-populations. For the pupation height, competitive ability and feeding rate phenotypes the *r*–F_1 progeny showed intermediate values relative to the parental values.

Recently, I have addressed this question from a

different perspective. By placing the *r*- and *rxr*-populations in the *K*-environments their response to high densities can be observed. If the *K*-environment places no new selective pressures on the population or if the *r*-populations have been completely depleted of genetic variation then the expectation is that there will be no differences between the *rK*- and *rxrK*-populations and their controls, which are *r* and *rxr* respectively. Pupation height and larval feeding rates appear to have increased in the *rK*- and *rxrK*-populations relative to their controls (P. Z. Guo, L. D. Mueller and F. J. Ayala, unpublished observations). In addition, population growth rates appear to have increased, at high densities, in the *rK*- and *rxrK*-populations relative to controls and decreased at low densities relative to controls. Thus, the initial trade-off in population growth rates noted by Mueller & Ayala (1981) has been confirmed by this reverse selection experiment.

3. THEORY OF DENSITY-DEPENDENT NATURAL SELECTION

(a) Verbal theory

The ideas of *r*- and *K*-selection developed by MacArthur (1962) and MacArthur & Wilson (1967) contained a mixture of quantitative and verbal theory. This verbal theory was greatly expanded by Pianka (1970, 1972). Although the asset of verbal theory is the ability to pose theory in a simple, intuitive form, the logic behind the verbal theory of *r*- and *K*-selection has often been faulty. One major prediction of the verbal theory of *r*- and *K*-selection is that *K*-selection should favour repeated episodes of breeding or iteroparity. However, the most detailed studies of density-dependent selection in age-structured populations shows that early reproduction will be continually favoured at high population densities (Charlesworth 1980). For instance, assume density dependence results in each female producing only two net progeny. A genotype that has these progeny early in life will, over any fixed time-period, leave more descendants than a genotype that has her two progeny late in life, assuming identical mortality patterns, and thus will become more common even if the total population size is constant.

Another prediction of the verbal theory is that *K*-selection will favour large body size (Pianka 1972). However, density-dependent selection may either lead to increases or decreases in average body size depending on detailed assumptions about the organisms life history (Mueller 1988b). An unfortunate consequence of ill-posed verbal theory has been the abandonment of density-dependent selection as an important factor in life-history evolution (Boyce 1984).

(b) Quantitative theories

(i) *General formulations*

The first models of density-dependent natural selection utilized the logistic model of population growth and assumed that the two parameters of the model, *r* and *K*, were controlled by allelic variation at a single locus (Roughgarden 1971). In practical terms the most useful prediction to come from this model is

that density-dependent rates of population growth should respond to natural selection. If there is not a single genotype capable of maximum growth rates at all densities (e.g. a trade-off exists between high r and high K) then the outcome of evolution depends on the environment. This very general prediction has been observed for *D. melanogaster* as described earlier (Mueller & Ayala 1981).

The difficulty with this theory is that its very general nature precludes more detailed predictions concerning the evolution of life-history traits. For instance, even though K should increase in populations kept at high densities, it is difficult to predict precisely which life-histories will be most useful for effecting such an increase without a more detailed specification of the organisms ecology. This does not mean that the general models of density-dependent selection, or any other general model for that matter, are unless, Such models allow one to explore a variety of phenomena and determine whether certain lines of intuition are reasonable. In addition, the components of the model which are important for guiding the process of interest may be identified. However, when tests of such theories are made using a specific organism, it must be kept in mind that this specific creature may have attributes that violate key assumptions of the general model.

The discrete logistic assumes that the effects of density-dependence are influenced by the numbers of individuals as some unspecified point in the life cycle. Even organisms that reproduce at discrete time intervals, either naturally or through artificial manipulation in the laboratory, will often have different life stages in which the effects of density are different. The impact on population dynamics of density-dependence in preadult life stages has been carefully described by Prout (1980) and Prout & McChesney (1985). In population genetics, the application of simple models for the estimation of fitness need to take account of the preadult life stages if meaningful estimates are desired (Prout 1965, 1971 a, b). The lesson from these studies is that the application of simple models, even to relatively simple laboratory populations, may ignore certain important life-historical details of the organism which will compromise the ability to test the theory.

(ii) *Organism-specific models*

Recently, theoretical work in population biology has focussed on models that take into account species-specific details. Models of plant population dynamics have been developed to take into account close neighbour competition, which is a peculiar feature of sessile plants (Pacala & Silander 1985). Likewise, populations of intertidal invertebrates are often space limited, and their population dynamics require different sorts of models (Roughgarden *et al.* 1985).

I have attempted to develop models of *Drosophila* population dynamics which take into account the action of density on the various life stages of *Drosophila* (Mueller 1988 b). This theory is outlined in figure 2. High larval density affects the amount of food available to the larval population and the amount of food consumed by each larva is assumed to have a normal
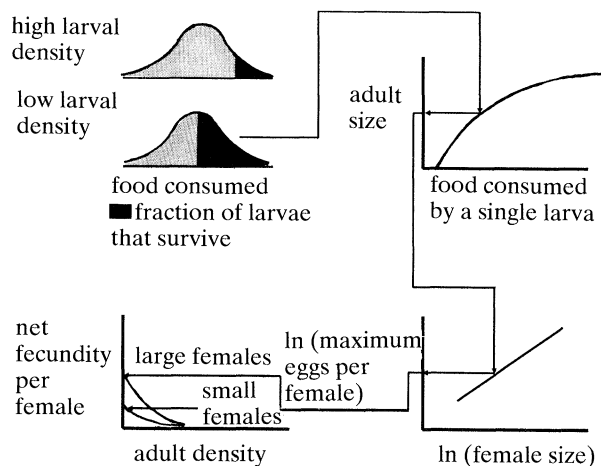
Figure 2. A graphical summary of the population dynamic model of Mueller (1988 b). See text for details.

distribution. To survive successfully, a larva must consume a minimum amount of food. Survivors are shown as the dark portion of the normal distribution in figure 2. Adult size is determined by the amount of food consumed as a larva (figure 2). This is important for population dynamics of *Drosophila* because larger females lay more eggs than smaller females. Even very small females may lay 20–30 eggs per day (Mueller 1987) which is incompatible with stable population dynamics (Mueller 1988 b). Net female fecundity is also modulated by adult density and may decline dramatically with increasing adult numbers (figure 2). The form of the response of female fecundity to adult density is crucial for the ultimate stabilization of population dynamics about the carrying capacity. Recently, we have seen that the shape of these curves is quite sensitive to the nutritional state of the adults and, consequently, the stability characteristics of the population may be sensitive to the levels of food available to adults (L. D. Mueller, unpublished results).

The ability to understand the evolution of life history, even in carefully controlled environments, will depend not only on carefully controlled experiments but also on the development of theory that incorporates the relevant ecological details of the experimental organism in the study environments.

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Discussion

T. R. E. SOUTHWOOD (*University of Oxford, Oxford OX1 3PS, U.K.*). Professor Mueller's results on the food requirement for larvae did not show any clear picture between the different régimes. Has he corrected the amounts eaten per larva to allow for the different masses of the adults, those in the *K* régime being larger? If he did this he might find that the *K* régime individuals produced more milligrams of adult per milligram of food, that is, they would be more efficient, which intuitively one might expect.

L. D. MUELLER. The question is well posed and its answer requires some clarification of terms and experiments. The definition of efficiency in my studies has been the minimum amount of food a larva must consume to successfully pupate. By studying the survival of larvae placed individually in vials with measured amounts of food it was shown (Mueller 1990) that the *r*-populations were in fact more efficient than the *K*-populations. At these very low levels of food the adults that survive are very small and there is no indication that the minimum size of adults differs between the *r*- or *K*-populations. However, as Professor Southwood has suggested, if a *K*-larva consumes slightly more than the minimum amount of food it may be more efficient at turning the food into biomass.

From the experiments I have done on groups of larvae that have been given measured amounts of food the growth curves of individual larvae can be estimated. Figure d1 illustrates these sorts of curves for the K_1 population and its control (r_1), and the K_3 population and its control (r_3). It appears that a K_1 larva can become a larger adult at most intermediate food levels. However, this apparent advantage is not seen with the K_3 and r_3 data. The curves for the K_2 and r_2 populations are, likewise, nearly identical. Thus, analysis of these data give no indication of an increase in efficiency (as this term is used by Professor Southwood) of the *K*-larvae.

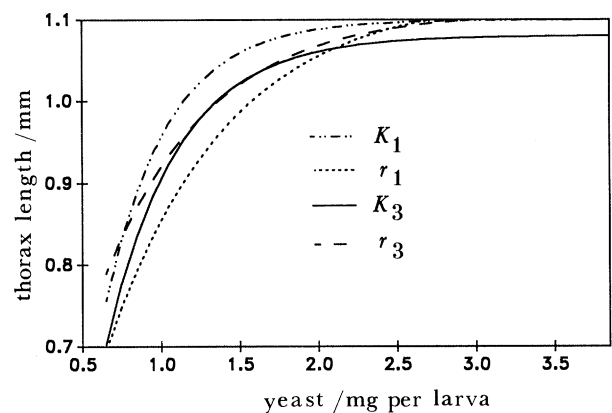It is also true that when many larvae are crowded in cultures with standard food that the viability and average

Figure d1. Growth curves of *r*-larvae and *K*-larvae given measured amounts of food. See text for details.

adult size of the surviving K-adults is greater that the r-adults (Bierbaum *et al.* 1989). However, in these crowded cultures it is difficult to say that the size differences observed show differences in efficiency. In these crowded cultures survival and growth is also affected by waste products that are consumed by the larvae (this is not a problem in the experiments that gave rise to figure 1 as the total numbers of larvae were low and constant). Some recent studies in my laboratory have shown that the K-populations tolerate high urea levels much better than do the r-populations. Consequently, it remains a possibility that the size differences observed by Bierbaum *et al.* are a result of differential tolerance to wastes and not efficiency of food conversion.