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THEORETICAL AND EMPIRICAL EXAMINATION OF DENSITY-DEPENDENT SELECTION

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ABSTRACT

The development of theory on density-dependent natural selection has seen a transition from very general, logistic growth-based models to theories that incorporate details of specific life histories. This transition has been justified by the need to make predictions that can then be tested experimentally with specific model systems like bacteria or *Drosophila*. The most general models predict that natural selection should increase density-dependent rates of population growth. When trade-offs exist, those genotypes favored in low-density environments will show reduced per capita growth rates under crowded conditions and vice versa for evolution in crowded environments. This central prediction has been verified twice in carefully controlled experiments with *Drosophila*. Empirical research in this field has also witnessed a major transition from field-based observations and conjecture to carefully controlled laboratory selection experiments. This change in approach has permitted crucial tests of theories of density-dependent natural selection and a deeper understanding of the mechanisms of adaptation to different levels of population crowding. Experimental research with *Drosophila* has identified several phenotypes important to adaptation, especially at high larval densities. This same research revealed that an important trade-off occurs between competitive ability and energetic efficiency.

INTRODUCTION

The idea that the natural environment plays an important and distinctive role in shaping the process of evolution has been understood since Darwin. Indeed,

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Charles Darwin declared that "The slightest advantage in one being, at any age or during any season, over those with which it comes into competition, or better adaptation in however slight a degree to the surrounding physical conditions, will turn the balance" (23, pg. 442). However, until the 1960s there was no formal theory of evolution and ecology that attempted to describe the consequences of this idea. Great advances had certainly been made in the separate fields of ecology and microevolution or population genetics. One stumbling block to the development of a united theory was the general impression that the ecological factors that mattered to the survival and reproduction of a species were many and complex. This idea was fostered in the late 1950s by concepts like Hutchinson's *n*-dimensional niche, which developed an abstract description of the ecological requirements of a species and suggested these requirements could not be simply enumerated (41).

Despite this attitude, in the early 1960s MacArthur (52) and later MacArthur & Wilson (53) initiated the development of the theory of density-dependent natural selection, which suggested that one aspect of the environment—density—could be isolated and studied. Further, they suggested that many aspects of an organism's life-history could be due to the population density it had experienced historically. These ideas prompted development of a body of theory (reviewed in the next sections) that would serve as a focus for continuing tension between theoreticians and field scientists both in ecology and evolutionary biology.

At the heart of this tension was the desire of the theoretician or the theoretically inclined to show that elegant theories could describe natural systems, with the hope that the many ecological details not considered by the theory would be unimportant. The field biologist, having accepted the Hutchinsonian reality of ecology, could not believe nature was so simple, and indeed, with little effort, many examples of natural populations could be found that apparently contradicted the expectations of this theory (56). What had been missed through much of the early work in the 1970s was the more sober conclusion that these simple theories might never or only rarely provide complete explanations of real populations. Thus, the only proper way to test these ideas was in controlled settings congruent with the assumptions of the simple models. In the meantime, it was unrealistic to expect the birth, de novo, of a theory in evolutionary ecology that could account for all aspects of the natural environment and their impact on evolutionary processes. Here the lessons from many other more-developed branches of science could be used to suggest that one should try first to understand how simple systems with few variables work and then build upon that to reach the complexity of the real world. Physics has frictionless hockey pucks, thermodynamics has Carnot engines, and evolutionary ecology has *r*- and *K*-selection.

THEORY

Verbal Theories

In the next two sections I separate the verbal theory of density-dependent natural selection from the mathematical theory for several reasons. First, the two types of theories have yielded very different predictions about the expected outcome of natural selection. I don't suggest that verbal and mathematical theories will never agree, but agreement is generally lacking in the theories considered here. Second, the assumptions and logic behind the mathematical theories are usually more transparent and easier to evaluate. This doesn't mean the assumptions made in mathematical theories will be better or more reasonable, but in general they are easier to identify.

One of the early discussions of evolution in environments with different levels of competition is given by Dobzhansky (29). Dobzhansky's ideas were known to MacArthur & Wilson (53). Many of the features of r-selected genotypes were outlined in Lewontin's discussion of colonizing species (50). Using an age-structured model, Lewontin provided examples emphasizing that exponential rates of increase are affected most by rapid development and early reproduction. These ideas were developed in a more general setting by Demetrius (27).

The first extensive elaboration of a verbal theory of density-dependent natural selection is found in MacArthur & Wilson's (53) book, *The Theory of Island Biogeography*. MacArthur & Wilson wrote about the differences expected in populations that live at very low and high densities; they were interested in understanding the phenotypes most successful at colonizing new habitats. MacArthur & Wilson used the logistic equation as a backdrop for their discussion, although their predictions—such as evolution favoring productivity or efficiency—are not explicitly derived from any models based on the logistic equation. MacArthur & Wilson originated the terms r- and K-selection, to which the theory of density-dependent selection often refers. MacArthur & Wilson used them to describe the types of selection expected in either uncrowded environments or very crowded environments, respectively. They asserted that r was the appropriate measure of fitness at very low densities and K at very high densities. In fact, the formal theories of density-dependent selection equate per-capita rates of population growth to fitness. Only in the special case when population growth rates follow the logistic equation will fitness be approximated by r and K. Most of the ensuing verbal theories consistently fail to recognize this point. It is also important to recognize that r and K are just two of many phenotypes one could assume are surrogates of fitness, like foraging efficiency, predator avoidance, or clutch size. Later I discuss the theoretical limitations of this idea and the extent to which experimental evidence supports predictions from this theory.

The notion of trade-offs in life-history evolution was a prominent feature of the MacArthur-Wilson theory. The importance of trade-offs was emphasized by Cody (21) in his discussion of the evolution of clutch size. Cody suggested that birds must make the most effective allocation of limited energy to three major competing needs—predator avoidance, interspecific competition, and reproduction. These ideas were further developed by Gadgil & Bossert (30) in an age-structured model. They assumed that age-specific survival and fecundity are affected by reproductive effort and environmental quality. Reproductive effort was defined as the fraction of total energy devoted to reproduction. Gadgil & Bossert showed that in favorable environments reproductive effort increased at all ages. This result also became associated with other predictions about *r*-selection. Much subsequent work focused on examining energy budgets and the proportion devoted to reproduction vs other activities (104).

The major articulations of the verbal theory of *r*- and *K*-selection are found in two papers by Pianka (77, 78). These theories suggest that traits like long life-span, iteroparity, large size, and prolonged development will result from *K*-selection, whereas a suite of opposing traits would be expected under *r*-selection. Some of the logical fallacies of these claims have been discussed in previous reviews (11, 96, 97). Many problems stem from the overinterpretation of the parameters *r* and *K*. For instance, no logical relationship exists between the logistic equation and age-structured populations, but verbal theory makes specific predictions about phenotypes of age-structured populations. Despite these problems, the verbal theory of *r*- and *K*-selection is still influential and finds its way into many ecology textbooks (7).

Population Genetic Models Without Age-Structure

Shortly after the appearance of MacArthur & Wilson's book, several more formal models of density-dependent natural selection appeared (1–3, 16, 20, 90). These models showed explicitly which assumptions were required for density-dependent selection to result in phenotypic differentiation. The discussions in Roughgarden (90, 91) are particularly lucid and are followed here. The primary assumption in these models is that genotypic fitness is assumed equivalent to per-capita rates of population growth. In particular, if fitness varies with density according to the logistic equation, then at a single locus, with multiple alleles, $A_1, A_2, \ldots$ etc, the fitness of genotype A_iA_j is given by

$$W_{ij} = 1 + r_{ij} - r_{ij} N K_{ij}^{-1},$$

where N is the total population size, and r_{ij} and K_{ij} are genotypic-specific measures of sensitivity to density. It is clear that, as a general proposition, this formulation of fitness will not be correct. For instance, consider a species like *Drosophila melanogaster* in which females can store sperm and exert choice over the males they mate with. The rate at which a population of *Drosophila* grows may be limited by how many eggs a female can lay but is almost certainly not limited by male fertility. Nevertheless, in *Drosophila*, male mating success or virility can be an important component of fitness (14, 48) but would not be expected to affect rates of population growth (67). However, in some circumstances genetically based differences in fitness may be reflected in differences in per-capita rates of population growth. This assumption clearly must be tested.

The other major component of these theories is the assumption of some trade-off between the ability to do well under uncrowded conditions and under crowded conditions. Without this assumption, the same genotype would be favored in all environments, and there would be no phenotypic differentiation of populations evolving in environments of different densities. Only with some sort of trade-off does the interesting prediction of different evolutionary outcomes depending on the environment appear. The assumption of trade-offs is a ubiquitous and important one in the theory of life-history evolution (21; Ch. 4 of 98). The trade-off assumption appears most naturally in quantitative genetic models in which some phenotype jointly affects r and K in opposing directions in the logistic (100).

An important question is, then, does the theory of density-dependent natural selection make predictions about the evolution of any trait other than population growth rates? I contend the answer is “no.” Any particular organism may have many physiological, behavioral, and even morphological characters that may change and have an effect on rates of population growth. However, the types of characters that are important are likely to vary between organisms. Thus, evolution of population growth rates in an insect may be accomplished by altering the number of eggs laid per unit time by females. We would not expect to see this kind of change in bacteria (certainly the rate of division may change in bacteria, but typically bacteria do not have the option to divide into five daughter cells or 100 daughter cells).

Models with Age-Structure

The major development of this theory of density-dependent selection in age-structured populations is found in Charlesworth (17). Consequent to this theory, some of the predictions of the verbal theory could be formalized. For instance, it is often suggested that low population density would favor semelparous life histories, whereas high density would favor iteroparous life histories. The simplest result from density-independent models of selection in age-structured populations is that improvements in survival or fertility will be most strongly favored by natural selection early in life. The addition of density-dependence to either survival or fertility functions does not alter this conclusion (17). Thus, there is no support for the idea that density-dependent selection will explain the evolution of iteroparity vs semelparity.

Charlesworth (17) showed that natural selection will maximize the equilibrium size of the age-class that is subject to density-dependence. This result extends the earlier work by Roughgarden (91) on populations without age-structure and is consistent with the results of Prout (82) and Iwasa & Teramoto (42) on stage-structured populations.

General vs. Specific Models

The most common life history assumed in both population genetics and population ecology is one that posits discrete generations and populations without stage or age structure. Problems arise when these theories are tested with organisms that depart from these assumptions. For instance, organisms like *Drosophila* can be made to reproduce on a discrete schedule and adult age-classes can be essentially eliminated, but the prereproductive stages of *Drosophila* cannot be removed. In the late 1960s and early 1970s, it was recognized that attempts to estimate fitness coefficients from simple population genetic models with organisms like *Drosophila* could be thwarted by selection acting on the various components of the life cycle (79–81). This, coupled with the necessity to assay adults rather than eggs, meant that the most general models of selection were inappropriate for providing a framework for observations in the simplest of *Drosophila* populations.

Prout (82, 84, 85) recognized that similar problems will occur in simple models of population dynamics. For instance, the simplified life cycle of *Drosophila* in the laboratory can have three census stages (Figure 1), each of which could be the population size in standard models of density-dependent population growth. If selection acts in a density-independent fashion, it is possible for evolution to increase, decrease, or have no effect on equilibrium numbers of particular census stages. In some numerical examples (82) all three results can be observed in the three different census stages (see Figure 1). Consequently, a general claim that selection will maximize population size is not true, just as the claim that mean fitness is always maximized by natural selection is false.

Utilizing the life cycle shown in Figure 1, Prout (83–85) noted that in many organisms fertility depends on pre-adult density. Crowding during these stages often has lasting effects on adult size that in turn affect fertility. This biological phenomenon poses some difficult problems for estimating the underlying population dynamics from data on adult numbers only.

The issues discussed above raise the general question of the most appropriate type of model to use when developing theory in life-history evolution in general. Christiansen (19) distinguishes between phenomenological and explanatory models. The phenomenological models are simple and attempt to

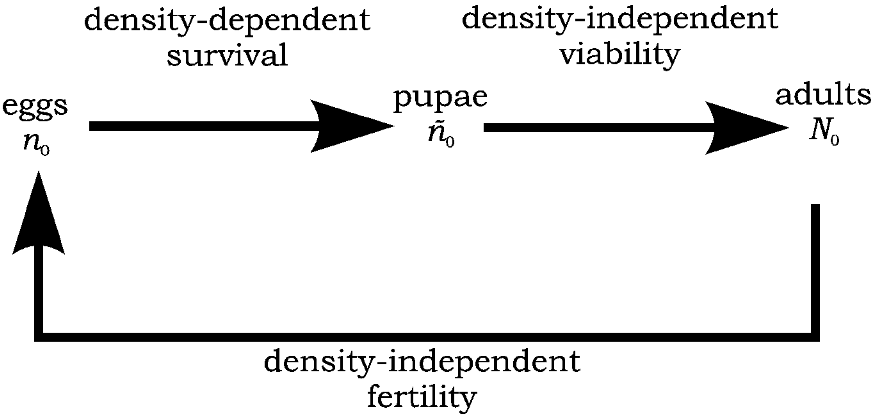

Figure 1 The life cycle of an organism with discrete generations but several pre-reproductive life stages. Selection may act at several places along the life cycle. The interaction of density-dependent survival (egg-to-pupa) and density-independent selection can have complicated outcomes on the equilibrium number of adults (82).

summarize the totality of density-dependence with a single simple function (e.g. the logistic). For these reasons the phenomenological models are thought to have greater generality (49). Explanatory models explicitly take into account specific components of the life cycle of some organism or group of organisms and try to model the response of these life-history components to density. Christiansen argued that this is the more appropriate way to develop theory for the study of life-history evolution in variable environments. Certainly, if theory is being used to make specific predictions about the evolution of a particular population, one cannot use a model that ignores crucial life-history details. Due to Prout's argument, this lesson cannot be overemphasized.

Accordingly, some recent models of density-dependent selection have focused on more explanatory or specific models for organisms that are the current focus of evolutionary research. One model (61, 68) has been employed to develop ecological recursions and single-locus genetic models for *Drosophila* in food-limited environments. This model permits specific examination of the evolution of competitive ability, adult size, efficiency, and equilibrium population size. An interesting theoretical prediction is that density-dependent selection can lead to increased competitive ability, but this will have no lasting impact on the adult equilibrium population size. Thus, verbal theories that attempt to link K of the logistic equation and competitive ability are not sound, at least for the class of organisms modeled by this theory. Second, although adult size may be affected by density-dependent selection, it may either increase or decrease depending on the assumptions made about larval growth and adult size. Thus, this theory yields no single or simple prediction about the evolution of body size due to density-dependent selection. Finally, *Drosophila* populations that follow the life history described by this model are stable only if there is some form of adult density-dependence on female fecundity. This interesting prediction is discussed in more detail later.

Population Stability

A property of discrete time equations of population growth is their ability to exhibit deterministically generated chaos (39, 54, 55). In several surveys of natural (38) and laboratory populations (58, 66, 102, but see 73, 74), most populations appear to have asymptotically stable carrying capacities. However, recent evidence (22, 28, 71, 98a, 105) suggests that unstable dynamics may be more common than previously thought.

These results have stimulated several theoretical investigations of the evolution of population stability. Some (8, 102) have suggested that population stability may evolve by group selection. Those populations that become unstable also become more likely to go extinct, leaving only populations with stable dynamics. There is no empirical evidence to suggest the widespread existence of a population structure that would permit this type of evolution, and thus group selection can hardly be considered a general explanation for the existence of stable population dynamics.

Others (32, 37, 40, 66, 99, 106) have considered individual selection models with some form of density dependence. Details of the particular model (e.g. logistic vs. hyperbolic equations, environmental noise in r vs K) have qualitatively different effects on the outcome of evolution (40, 106). In some cases selection favors increases in population stability, in others stability decreases. Some models that produce the evolution of stable dynamics could do so only by assuming some sort of trade-off in life-history traits (29a, 32, 66, 99). However, the belief in the ubiquity of trade-offs has led some (33a) to suggest that natural selection should typically tend to stabilize populations dynamics.

Several specific theories have identified the biologically important characters that affect population stability. For instance, theoretical predictions that the rate of adult cannibalism of immature stages affects population stability have been verified in laboratory populations of *Tribolium* (22). In *Drosophila*, it appears that the relative amounts of food supplied to adults and larvae determine population stability (61, 71). The theoretical prediction that high levels of food to adults and low amounts to larvae tend to destabilize the population have been verified in experimental populations of *Drosophila* (71). This may be a fairly general mechanism for organisms with distinct life stages in which female fecundity varies with nutritional level of the adult. The characteristic cycles of blowflies (73) may be generated in part by the differing levels of food provided to adults and larvae (71).

A recent analysis of data from Nicholson's classic work (73) has suggested that evolution in the course of a 2-yr experiment may have resulted in the attenuation of population cycles (99). This conclusion must be tempered with the following observations. The experiment involved only a single population, and thus it is unclear if it is a replicable phenomenon. Since the adult population of blowflies went through severe fluctuations and thus bottlenecks, random genetic drift and inbreeding may have caused a reduction in female fecundity, which in turn could have attenuated the cycles. Obviously, these problems could be easily rectified in an experimental system with *Tribolium* or *Drosophila*.

EMPIRICAL RESEARCH

Translation of Theory to Experimental Predictions

The integration of theory and experiments is not easy when dealing with complex biological systems. Generally, scientific research guided by a body of theory will ultimately reach a point at which some theoretical prediction is compared to a set of observations. It is important to realize that agreement between the observations and theoretical expectations does not necessarily mean the theory is correct, nor does a lack of agreement mean the theory is wrong. In an unusually lucid and informative discussion of this issue, Royama (92) notes that the components and structure of a model may be a correct description of a biological system, but because the test systems depart, unintentionally, in substantial ways from the model components, observations and model predictions will disagree.

This point is especially important for models in evolutionary biology, including density-dependent natural selection, because many of our models are quite simple, ignoring many ecological details and thus needing to be tested under conditions that match these simple assumptions as well as possible. Consequently, natural populations are unlikely to be good systems to test theories that make very simple assumptions. Laboratory systems will be more likely to conform to the assumptions of simple models (89), and thus they are more appropriate for testing these models. To say theories that don't explain events in a "real" environment are useless misses an important intellectual thread about how theories of the real world are constructed. These theories are constructed in gradual steps, usually from very simple beginnings. Empirical experiments aid in the elimination of those components that fail to explain even those simple constructs. Thus, physics starts logically with laws of motion that ignore friction. This is not because the physicist believes there is no friction in the real world but rather because systems without friction are useful starting points from which to develop the more complicated theoretical machinery that includes friction and turbulence.

Because even laboratory experiments will often utilize a single species of plant or animal, models that include important aspects of the experimental organism's life history are useful (19). At least two important reasons exist for constructing models that account for specific qualities of an experimental organism. First, model predictions may be affected by life-history details. Second, the appropriate parameters to measure during experimental research may be suggested by the organism-specific modeling effort. Some examples follow.

As an aid for experimental research conducted with the species *Drosophila melanogaster*, I (61) elaborated upon a model developed by others (4, 26, 75) to describe the effects of density-dependent selection in food-limited environments. This model has yielded some important insights into experimental systems utilizing *Drosophila*. The theory demonstrated that competitive ability would not affect the equilibrium population size (61). The same theory provided the appropriate methods for estimating competitive ability in a way congruent with the theory (60, 61, 75).

Another interesting example is Vasi et al (107). In this study, populations of *E. coli* were subjected to a seasonal environment. Periods of exponential growth with adequate resources were followed by periods of growth at saturation densities. The results of these experiments, interpreted by estimating parameters from a model of bacterial population dynamics, showed that these populations had evolved traits that would be most important during the exponential growth phase of the environment, while parameters that would be most important during the periods of saturation density had not changed. An earlier study, by Luckinbill (51), of *r*- and *K*-selection in bacterial populations utilized a *K*-environment similar to the seasonal environment used by Vasi et al (107). Luckinbill observed that *K*-selected bacteria grew faster than *r*-selected bacteria at all test densities. The results of Vasi et al suggest Luckinbill's outcome could be due to selection in a seasonal environment favoring most strongly characters that affect growth at low densities. The important conclusion is that the interpretation and design of experimental research can be greatly facilitated by the development of specific models of the experimental organism's life history and population dynamics.

Field Studies and the Comparative Approach

Many early studies of *r*- and *K*-selection relied on comparisons of different species or different populations of the same species that occupied different environments. In principle, if the different environments differed only by the density experienced by members of the populations, any genetically based differences ought to be due to the results of density-dependent selection. In practice this almost never happens, and there are always multiple differences between populations, in addition to density, that confound simple interpretations. Many of the problems with these studies have been reviewed previously (11, 97). A short list of the most severe problems would include the following.

Often the exact density history of a particular population was not known with any certainty but was inferred from anecdotal or recent observations (31). In many cases no attempt was made to remove any lingering effects of environmentally induced differences (103). Thus, the genetic basis of any observed differences was uncertain. In essentially all cases of studies in natural populations, no control existed for other environmental factors that might affect life-history evolution, e.g. predation, density-independent sources of mortality, resource variation. Consequently, any result, whether positive or negative, may have been due to one of the uncontrolled factors rather than differences in density per se. Many studies of life-history evolution do not include real replication; the observation of any differences between compared populations is rendered almost completely uninterpretable (36). Thus a difference between a pair of populations could be due to initial sampling events, to genetic drift, or to natural selection. Without replication there is no simple means to distinguish among these alternatives.

These types of problems beset almost all studies of natural populations except the most carefully planned (86, 87). For the reasons outlined above, it had become obvious by the late 1970s (77) that the only powerful way to investigate the theory of density-dependent natural selection would be with the use of populations in controlled laboratory environments.

A recent study (56a) has looked at the relationship between survival and density of Soay sheep in Scotland. This study shows that survival declines with increasing density but is also dependent on the individuals' coat color phenotype, controlled by a single locus, and horn type, controlled by one or two loci. Thus, density-dependent natural selection appears to be an important force in the maintenance of these two genetic polymorphisms. It is remarkable that this is perhaps one of the only studies to document the action of density-dependent selection in a natural population.

Experimental Studies

Pitcher-plant mosquitoes are typically found in more crowded conditions in southern latitudes than in northern latitudes (12). Although estimates of population growth rates show no consistent differences between northern and southern populations, the southern populations are the better competitors, a result consistent with observations from *Drosophila*. Laboratory populations of mosquitoes selected for rapid development also showed no correlated changes in sensitivity to density although their generation time decreased (13).

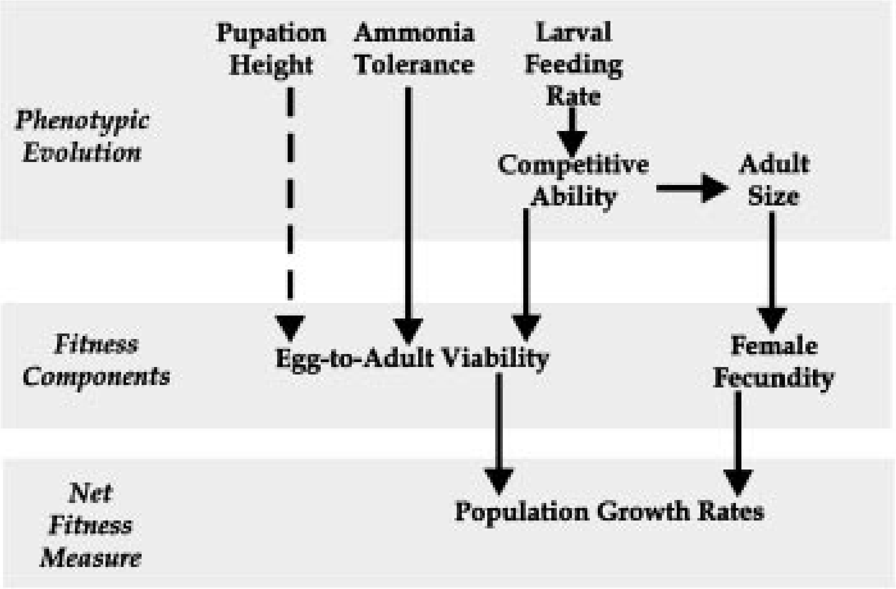

Figure 2 A summary of the effects of density-dependent natural selection in *Drosophila melanogaster*. The dashed line shows an effect that varies with the environment (in this case the type of food used).

Perhaps the most studied experimental organism in this field has been *Drosophila*. Taylor & Condra (101) found that *r*-selected *D. pseudoobscura* developed more rapidly than *K*-selected populations. However, no systematic measurements of population growth rates were made. Barclay & Gregory (5, 6) did selection experiments with *D. melanogaster*, but this study was flawed by a number of technical problems (57) that made the results difficult to interpret.

In Figure 2, I summarize the effects of density-dependent selection that have been inferred from the work of my laboratory over the last 17 years. These results have come from two experimental systems. My early work utilized three populations kept at low adult and larval densities, called *r*-populations, and three kept at high larval and adult densities, called *K*-populations (9, 63–65). These populations had two shortcomings: The adult *K*-population had overlapping generations, whereas *r*-populations were reproduced with young adults only; the *r*-populations were maintained for about 150 generations at a low effective population size (50 or less, compared to 1000 in the *K*-populations). Accordingly, any differences between the *r*- and *K*-populations, especially in the later generations, may have been due to inbreeding effects rather than natural selection. This latter problem was addressed in two ways. Hybrids of the *r*-populations were made to determine if overdominance occurred, and the phenotypic differences that arose due to inbreeding were eliminated (59, 60). For the phenotypes described in Figure 2, there was no evidence that the phenotypic difference between the *r*- and *K*-populations was due to inbreeding effects. After about 180 generations, the *r*-populations were placed in crowded environments, and then they differentiated from their parental populations in the same manner as *K*-populations originally had done (34, 70).

Nevertheless, in 1989 in my laboratory, three new types of populations were initiated to investigate the consequences of density-dependent selection. These populations all derived from large, outbred populations cultured in a laboratory for more than 10 years. Each population was replicated five times; the three population-types are called UU, CU, and UC, where the first letter of the name refers to the density at which larvae are raised (U, uncrowded; C, crowded) and the second letter, to the density at which the adults are raised.

A basic prediction from the general theories discussed previously is that rates of population growth should increase in a manner that depends on the environment the population experienced. Two tests of this prediction have yielded consistent results (65, 70): Populations of *D. melanogaster* raised at high densities experience an increase in population growth rates at high densities (and thus an increase in carrying capacity), but a decrease in population growth rates at low density. These results are supported by earlier studies (3a, 3b, 15a) which show that populations of *Drosophila* brought into the laboratory and allowed to reach their carrying capacity show an increase in equilibrium population size over many generations.

Three larval behavioral traits have become differentiated in the *r*- and *K*-populations. Feeding rates have increased in the *K*-populations relative to the *r*-populations (43, 70), and they have also increased in the CU populations relative to the UU populations (69, 93). This trait is highly correlated with larval competitive ability for food (15, 43). Competitive ability in *Drosophila* larvae is a frequency-dependent process (26, 61, 75). Thus, when food is limited and the superior competitors are rare, they will experience increased viability and adult size. Both of these changes will affect population growth rates (Figure 2). However, these changes will only be short-lived because as the fast feeding types become common, their fitness advantage vanishes.

There is also a demonstrable cost to high feeding-rates. CU populations that have been moved to environments with reduced larval densities show a decline in feeding rates over time relative to similar populations with high larval densities (A Joshi, LD Mueller, unpublished). Part of this cost may be due to reduced efficiency of the larvae, which have evolved high feeding rates. When individual larvae from high-density and low-density populations are given small amounts of food, the larvae from the crowded cultures require more food to complete development (45, 62). The fast-feeding CU larvae also gain more weight during the third instar than do the slow-feeding UU controls (93). However, this additional weight is lost either during the late third instar or during the pupal stage so that adult CU and UU flies are the same size. Together these results suggest that a trade-off between competitive ability (fast feeding rates) and energetic efficiency and that only under extreme larval crowding does the fitness gain due to increased competitive ability outweigh the fitness loss from this trait.

One recent study of density-dependent selection in *D. melanogaster* (88) reports no change in competitive ability after 45 to 50 generations of selection. In this experiment the uncrowded treatment consisted of 50 larvae per vial, whereas the crowded treatment had 150. A concern exists that the strength of selection at the higher density was insufficient to cause changes in feeding rates in this period of time or to overcome the effects of drift (total population sizes were kept at 500 or greater). Support for this view comes from the work of Mueller et al (69). In another experiment (69), no changes in feeding rates were observed for the first 12 generations when larval densities were kept at about 500 per vial. However, within a short time of increasing the larval densities to greater than 1000 per vial, feeding rates in the high-density populations increased.

The position or height above the food at which larvae pupate also differed in the *r*- and *K*-populations (34, 72). Larvae in the crowded cultures tend to pupate higher on the side of the vial and less frequently on the surface than do larvae from the uncrowded populations. This behavior has a dramatic impact on pupal survival; selection for pupation height in crowded environments is either directional or stabilizing, depending on the genotype tested (44). The CU and UU populations have shown inconsistent changes in pupation height; this most likely occurs because the CU and UU populations are raised on softer food than that used by the *r*- and *K*-populations. The soft food probably results in selection for increased pupation height even at low larval densities.

Foraging path length is a larval behavior perhaps largely determined by alleles at a single locus, *for* (24, 25). Two phenotypes have been described, rover and sitter, which differ in the distance traveled on a two-dimensional surface by a larva in a specified period of time (76, 94). Recently, Sokolowski and her colleagues (95) tested the UU and CU populations, the *r*- and *K*-populations and a new set of *D. melanogaster* populations that were handled like the *r*- and *K*-populations. In each of these three independent test systems, the populations kept at high larval densities evolved the more active rover phenotype, whereas the low-density population became predominantly the sitter phenotype. The fitness consequences of the rover phenotype in crowded culture have not been studied explicitly although they may be related to general competitive ability for food.

Adaptation to adult crowding has also been examined in the UU, CU, and UC populations (46, 47). Adults subjected to a 3–5-day episode of adult crowding showed elevated mortality rates; the CU population had the highest mortality rate, and the UC population the lowest (47). This suggests that the UC population adapted to periods of adult crowding and that the CU population was sensitive to such crowding perhaps as a by-product of their adaptation to larval crowding. Adults subjected to these short episodes of crowding suffered a reduction in later rates of survival and fecundity (46). However, the reduction was much greater in the UU and CU populations than it is in the UC population.

Limited food is just one way in which crowded and uncrowded environments are expected to differ; it is also likely that crowded cultures will suffer from increased levels of waste products. One of the few studies of *Drosophila* nitrogenous waste had suggested that urea is a major waste product (10). However, more recent work has shown that ammonia is the primary nitrogen waste product that appears in crowded *Drosophila* cultures and that urea, if present, is at undetectable levels (DJ Borash, AG Gibbs, LD Mueller, unpublished). Concentrations of ammonia in crowded *Drosophila* cultures steadily increase during the entire period of larval foraging and development (about 20 days in the CU cultures, for instance). During this period, other aspects of the environment are also changing; food is being consumed by voracious larvae; sugars and carbohydrates are also being consumed by the growing yeast populations, which produce increasing levels of fermentation products like acetic acid (35). Since development time in crowded cultures increases and becomes more variable (18), the larvae that develop most rapidly and emerge first from crowded cultures are likely to have experienced a very different environment than the larvae that emerge 10 days later. The more slowly developing adults will have experienced the toxic effects of food laced with ammonia for a greater length of time, and the concentrations that they ultimately experience will be much greater than those experienced by the earliest emerging flies.

This description of the environment suggests that our theoretical description of density-dependent selection, even in simple laboratory environments, may be oversimplified. In reality, a crowded environment cannot be characterized by a single number N, which describes the number of larvae or adults that are placed together. A crowded environment is actually one undergoing a profound temporal sequence of degradation that is not equally experienced by all members of the population. This type of environmental heterogeneity may complicate the dynamics of natural selection as much as do other types of environmental heterogeneity (33).

My laboratory has recently documented a polymorphism with the CU populations that is demarcated along an axis of larval development time (DJ Borash, AG Gibbs, LD Mueller, unpublished). Flies that emerge early in the CU populations have very high feeding rates (and thus should be good competitors for limited food), but their absolute viability, especially in food laced with ammonia, is significantly less than that of flies that emerge much later in the CU cultures. These observations suggest that there may be genotypes that specialize on the early part of the crowded environment by developing rapidly and emerging before food levels become very low and waste concentrations very high. However, these early specialists "pay" for this by sacrificing their ability to survive well and take advantage of the resources (albeit less than ideal) that remain in the old crowded cultures. The late specialists develop more slowly but can survive and successfully emerge as viable adults in the low-nutrition and high-waste environment that remains toward the end of the developmental profile.

These observations should be music to the ears of the field ecologist for they suggest one way in which environments become complex. This type of complexity is amenable to study under laboratory conditions and should pave the way to an understanding and appreciation of natural selection in complex environments.

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