K-selection, *a*-selection, effectiveness, and tolerance in competition: density-dependent selection revisited

A M I T A B H   J O S H I *, N. G. P R A S A D and M A L L I K A R J U N   S H A K A R A D [1]

Evolutionary Biology Laboratory, Evolutionary and Organismal Biology Unit, Jawaharlal Nehru Centre for Advanced Scientific Research, P.O. Box No. 6436, Jakkur, Bangalore 560 064, India

Abstract

In the *Drosophila* literature, selection for faster development and selection for adapting to high density are often confounded, leading, for example, to the expectation that selection for faster development should also lead to higher competitive ability. At the same time, results from experimental studies on evolution at high density do not agree with many of the predictions from classical density-dependent selection theory. We put together a number of theoretical and empirical results from the literature, and some new experimental results on *Drosophila* populations successfully subjected to selection for faster development, to argue for a broader interpretation of density-dependent selection. We show that incorporating notions of *a*-selection, and the division of competitive ability into effectiveness and tolerance components, into the concept of density-dependent selection yields a formulation that allows for a better understanding of the empirical results. We also use this broader formulation to predict that selection for faster development in *Drosophila* should, in fact, lead to the correlated evolution of decreased competitive ability, even though it does lead to the evolution of greater efficiency and higher population growth rates at high density when in monotypic culture.

Introduction

Our purpose in writing this paper is three-fold. Drawing upon a combination of previously published theoretical and experimental studies, and some new experimental data, we want to suggest that:

(i) The theory of density-dependent selection for single populations is better thought of in terms of selection in crowded environments favouring increase in competition coefficients, *a*, rather than in carrying capacity, *K*. It is important in this context to realize that intragenotypic and intergenotypic competition coefficients need not necessarily be correlated.

(ii) Specific considerations of 'aggression' and 'response' (*sensu* Eggleston 1985) or 'effectiveness' and 'tolerance' (*sensu* Joshi and Thompson 1995) are useful in thinking about evolution in crowded environments, and about the correlated effects of selection on development time on the evolution of competitive ability.

(iii) Contrary to a fairly widespread belief among *Drosophila* workers, evolution of faster development *per se* should not confer enhanced competitive ability; this prediction arises from a consideration of (i) and (ii) above, and is put forward as an empirically testable proposition.

Much of what we have to say is not new. However, most of the theoretical and experimental elements that we wish to weave together into an argument were originally presented in diverse contexts and, in some cases, seem to have escaped the attention of several subsequent workers

[1]Present address: Poornaprajna Institute of Scientific Research, 4 Sadashivanagar, Bangalore 560 080, India.
*For correspondence. E-mail: ajoshi@jncasr.ac.in.

in the field. What we would like to do is to put these various elements together to make a focused case for looking at density-dependent selection from the point of view of competition coefficients rather than carrying capacities, and to argue that this point of view leads to predictions about the relationship between development time and competitive ability in *Drosophila* that are at odds with a fairly widely accepted notion that faster development confers greater competitive ability. In the following sections, we review results from various theoretical and experimental studies of density-dependent selection, draw these elements together into what we think is a more useful way of looking at density-dependent selection, and then go on to present some new experimental results. The final argument, and some testable predictions, will be made in the last section.

Density-dependent selection theory

The theory of density-dependent selection was one of the first attempts to unite the fields of population ecology and population genetics, by explicitly considering population growth in genetic models of evolution, and suggesting that the fitness of different genotypes could be a function of the population density. Though it was first developed largely as a verbal theory by Dobzhansky (1950) and MacArthur and Wilson (1967), and extended in its verbal form to explain diverse life-history patterns (Pianka 1970), formal mathematical treatments of density-dependent selection were soon available (Gadgil and Bossert 1970; Roughgarden 1971; Clarke 1972; Matessi and Jayakar 1976; Anderson and Arnold 1983; Asmussen 1983). Density-dependent selection theory and its use and, occasionally, abuse in ecology have been extensively reviewed several times (Stearns 1977; Parry 1981; Boyce 1984; Mueller 1995, 1997) and we do not wish to rework that material. The verbal theory is, in our opinion, by now clearly discredited as being overambitious and muddled (Joshi and Mueller 1996; Mueller 1997), although for some inexplicable reason it still lives on in some fairly standard ecology textbooks (Pianka 1988; Begon *et al.* 1991), in student resource materials on the World Wide Web, and in talks given by some ecologists (A. Joshi, personal observation). While the latter state of affairs is somewhat deplorable, we prefer not to discuss it here, and would like to focus in this paper on some aspects of the formal theory that are pertinent to our argument.

Clearly, the basic premise of density-dependent selection theory is that genotypic fitnesses are a function of population density. The first formal models of density-dependent selection (Anderson 1971; Charlesworth 1971; Roughgarden 1971) were framed in the context of the logistic model of population growth with the fitness of a single-locus genotype $A_i A_j$ being represented by

$$w_{ij} = 1 + r_{ij} - \frac{r_{ij}}{K_{ij}} N \quad \text{or} \quad w_{ij} = 1 + r_{ij}\left[1 - \frac{N}{K_{ij}}\right]. \quad (1)$$

In this formulation, N represents the total population size, regardless of genotype, whereas the r and K terms are genotype specific; consequently, these models have often been referred to as pure density-dependent selection models because there are no frequency-dependent inter-genotypic interactions. At the time these models were developed, a major concern in population genetics was to understand forces that may maintain genetic polymorphism in populations, and one of the main results from these models was that the condition for maintenance of genetic polymorphism at a biallelic locus under density-dependent selection was overdominance of carrying capacity ($K_{ij} \geq K_{ii}, K_{jj}$; $i, j = 1, 2$). There is, however, an interesting problem in these models which becomes apparent if we formulate them in terms of coefficients of competition reflecting the sensitivity of realized per capita growth rate to the addition of one more individual to the population. In the logistic model, the sensitivity of per capita growth rate to density is given by $a = r/K$, the slope of the linear decline in realized growth rate with increasing population size (figure 1), such that $N_{t+1} = N_t[1 + (r - aN_t)]$. Thus, according to the formulation in equation 1, the impact of all individuals of all genotypes on the realized per capita growth rate of the target genotype $A_i A_j$ is mediated through the sensitivity of growth rate of this genotype to the addition of one more individual of its own genotype. Another way of
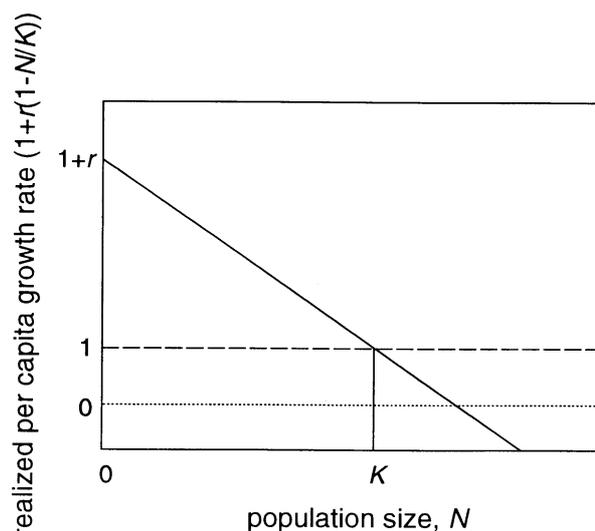
Figure 1. The linear density dependence of realized per capita population growth rate assumed in the logistic model. When $N = K$, the realized per capita growth rate is 1 and thus K is the equilibrium population size, as well as the saturation capacity of the environment. The slope of the line (r/K) is the coefficient of competition a in this formulation.

putting this is to say that in this formulation intragenotypic and intergenotypic competition coefficients are assumed to be the same. Several modified versions of the logistic model were subsequently proposed by workers uncomfortable for varying reasons with the assumptions of the logistic equation (e.g. Hairston *et al.* 1970; Gilpin *et al.* 1976; Hallam and Clark 1981), but all of these formulations make the assumption about intragenotypic and intergenotypic competition coefficients being the same.

Hairston *et al.* (1970) argue against the formulation of the *r–K* spectrum in terms of profligacy versus efficiency ascribed to MacArthur and Wilson (1967) and make a case for formulating density-dependent selection around birth and death rates, rather than realized growth rates, which are, after all, a function of the birth and death rates. Although some aspects of their argument are unclear (e.g. see Pianka 1972), they make the point that the logistic equation was derived in an ecological context and it should not, therefore, be forced into an evolutionary frame of reference because its parameters are not designed to capture the essence of evolutionary processes. We think that this is an important point but, in our opinion, Hairston *et al.* (1970) do not follow this argument up. Instead they eventually suggest that given a tradeoff between birth rate (*b*) and death rate (*d*), such that *b* cannot be increased while simultaneously reducing *d*, selection at low densities will favour higher *b* even at a cost of higher *d*, and at high densities lowered *d* will be favoured even though this implies lowered *b* as well. Intragenotypic and intergenotypic competition coefficients do not enter into their framework, which remains that of the logistic equation.

Another alteration to the logistic framework for density-dependent selection was proposed by Hallam and Clark (1981), and elaborated upon by Clark (1983) in the context of the expected *r–K* tradeoff in density-dependent selection. Their point of departure is their discomfiture with the observation that in the traditional form of the logistic model the parameter *K* incorporates in it the three distinct notions of environmental carrying capacity, equilibrium population size, and sensitivity of growth rate to density. In a way, their formulation may be viewed as an attempt to incorporate some of the realism introduced by models with an arbitrary matrix of competition coefficients (as in equation 4) into a heuristically useful 'logistic-equation-like' framework. Thus, they introduce two new parameters reflecting sensitivity to density (*c*) and saturation capacity of the environment (*B*), respectively, such that the recursion for population numbers becomes

$$N_{t+1} = N_t\left[1 + \left(r - \frac{c}{B}N_t\right)\right]. \tag{2}$$

In this formulation, the crucial slope parameter α is now given by c/B and both *c* and *B* can be manipulated independently. This is an interesting formulation, but the crucial point is that here, too, the linear framework of density-dependent effects posited by the logistic equation is preserved, and sensitivity to density is still affected by *K*, albeit now scaled by the ratio of *c* and *B* (figure 2).

Gilpin *et al.* (1976) suggest an alternative formulation which does away with the assumption of linear density dependence, a change that certainly makes more sense biologically than modifications retaining linearity of density dependence. They introduce an additional parameter **q** which governs the way in which realized per capita growth rate varies with density (figure 3) such that, in discrete time, one would get the following expression for the fitness of genotype A_iA_j :

$$w_{ij} = 1 + r_{ij}\left[1 - \left(\frac{N}{K_{ij}}\right)^{\mathbf{q}}\right]. \tag{3}$$

Their primary interest, however, is to show that under various situations traditionally considered to lie along the *r–K* spectrum, once one breaks out of the linearity assumption, selection can directly act upon the form of the density dependence of realized growth rate (in this case by inducing evolutionary changes in **q**). They, too, explicitly assume there are no interactions between genotypes, i.e. that intragenotypic and intergenotypic competition coefficients are the same.

This insistence on the equating of intragenotypic and intergenotypic competition coefficients is somewhat paradoxical, especially in light of the often used interpretation of carrying capacity *K* reflecting in some sense the
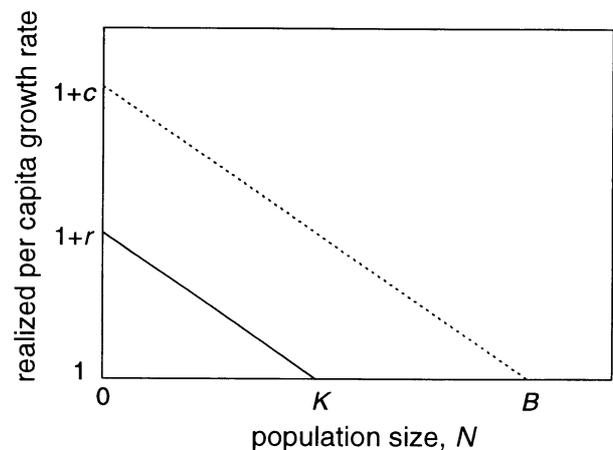
Figure 2. The linear density dependence of realized per capita population growth rate assumed in the model of Hallam and Clark (1981). Here the coefficient of competition **a** = *c/B*, and this slope determines the equilibrium population size *K*.

efficiency of conversion of biomass to offspring (MacArthur and Wilson 1967). In other words, in the models considered above (equations 1, 2, 3), even though the K_{ij} differ among genotypes suggesting that different genotypes can make different numbers of offspring from the same quantum of food, the impact of adding one A_iA_i individual on the growth rate of A_jA_j is the same as that of adding one A_jA_j individual. Intuitively, though, addition of an individual of genotype with larger K than others should, all else being equal, have a relatively smaller impact on growth rate because these individuals consume less food. It is, thus, intuitively clear that the reductions in the maximal growth rate for different genotypes in a polymorphic population should depend not on the total population size N (as it does in equations 1, 2, 3) but rather on the numbers of each genotype (N_{ij}). Indeed, if one ignores the issue of reproduction, then competition between genotypes is conceptually no different than competition among species, and typical competition models explicitly make the realized growth rate of each species a function of the numbers of the two species. In fact, the framework of the Lotka–Volterra equations for competition suggests itself as an appropriate analogue for intergenotypic competition, embodying as it does interspecific and intraspecific competition through separate competition coefficients, $\boldsymbol{a}_{ii}$ and $\boldsymbol{a}_{ij}$.

If we recast equation 1 in terms of the genotype-specific sensitivity of growth rate to density, we get

$$w_{ij} = 1 + r_{ij} - \sum_{k,l=1,2,\ldots,m} \boldsymbol{a}_{ijkl} N_{kl}, \qquad (4)$$

where $\boldsymbol{a}_{ijkl}$ refers to the reduction in realized per capita growth rate of genotype A_iA_j due to the addition of one individual of genotype A_kA_l, and N_{kl} is the number of individuals of genotype A_kA_l present in the population. This type of formulation, often referred to as density-frequency-dependent selection, is found in the models of Clarke (1972), Matessi and Jayakar (1976), Asmussen (1983) and Anderson and Arnold (1983). Once again, the focus of these analyses was on conditions permitting genetic polymorphism, and the general conclusion is that, in contrast to the pure density-dependent selection case, many interior equilibria are possible if one takes genotype-specific sensitivity to population density into account. Similarly, overdominance in carrying capacities is no longer the determining criterion for maintenance of genetic polymorphism; it is the interplay of the K_{ij} and the $\boldsymbol{a}_{ijkl}$ that determines whether or not a polymorphism will be maintained. In general, these models suggest that density-dependent fitnesses may be more likely to yield stable polymorphism than the analysis of the more restrictive formulations such as those in equations 1, 2 and 3. A further interesting result from numerical studies of this type of model with varying functional forms for the

density-dependent genotypic fitnesses is that the total population size at a stable interior equilibrium can be greater than any of the K_{ij} (Asmussen 1983).

An interesting and somewhat puzzling observation is that these more reasonable models of density-dependent selection do not seem to have achieved the representation we feel they warrant in the literature. The formulation of equation 1 is still what one typically encounters in textbooks (e.g. Hartl and Clark 1997), and models such as equation 4 are often mentioned almost as exotic extensions to equation 1, which is often referred to as a model of 'pure' density-dependent selection. Yet, being analogues to the Lotka–Volterra competition models, one would expect these models to be perfectly reasonable and acceptable abstractions of the process of intergenotypic competition, which is what density-dependent selection is all about (essentially, these models are discrete-time Lotka–Volterra models wherein the competing types are Mendelian genotypes at a single locus). We argue in a later section why we feel these models lend themselves to a more reasonable view of density-dependent selection, after we have first reviewed some empirical evidence on adaptations to crowding in *Drosophila*.

A far more complex and species-specific model for density-dependent selection was developed by Mueller (1988a) to explicitly abstract the relevant ecology of *Drosophila* cultures into a formulation that could then be used to make explicit predictions that could be tested using laboratory populations. The details of this model are not too pertinent to the issue at hand, but we would like to point out that analysis of this model suggested that it was
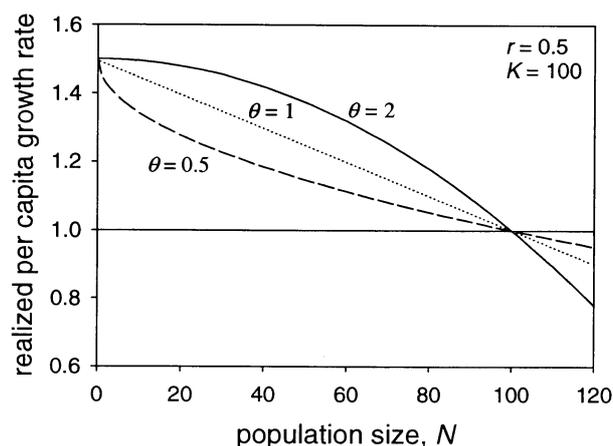
Figure 3. The density dependence of realized per capita population growth rate according to the formulation of Gilpin *et al.* (1976) shown here for some arbitrary values of r, K and $\boldsymbol{q}$. Here the density dependence can be nonlinear, depending on the value of the parameter $\boldsymbol{q}$ ($\boldsymbol{q} = 1$ reduces to the logistic case). Note that if there were three genotypes with identical r and K values as depicted here, the one with $\boldsymbol{q} = 2$ would be able to sustain higher realized growth rates than the others at all population densities from 0 to K.

possible for populations to evolve increased competitive ability without increasing K or decreasing body size (Mueller 1988a).

Tradeoffs in density-dependent selection

Much of the interest generated by the notion of density-dependent selection is due to the suggestion that there are tradeoffs between the ability to do well under uncrowded (*r*-selection) and crowded (*K*-selection) conditions (MacArthur and Wilson 1967; Gadgil and Bossert 1970; Luckinbill 1978, 1979; Mueller and Ayala 1981; Mueller *et al.* 1991). Clearly, if the same genotype could do well at different densities, then there would be no difference between populations that had evolved under different densities, and the notion of density-dependent selection would have little value in explaining observed patterns of diversity. There is, thus, an expectation that the fitness of genotypes varies with density in a manner such that no one genotype has the highest fitness at all densities. The first question that we are faced with here is how one is to measure fitness. It is reasonable to argue (e.g. Mueller 1997) that the trait that is ultimately under density-dependent selection is actually the density-specific realized growth rate and that, therefore, the appropriate fitness measure here is the realized growth rate at various densities.

Within the constraints of the logistic formulation, it is clear that if such *r–K* tradeoffs exist then genotypes with higher K will sustain higher growth rates at relatively high densities (figure 4). In the model of Gilpin *et al.* (1976), it is possible for higher density-specific growth rates to evolve through changes in the parameter q, reflecting the way in which growth rate responds to increasing density. Similarly, in the class of models incorporating genotypic interactions (equation 4), or in the *Drosophila* model of Mueller (1988a), genotypes with high competitive ability (**a**) may be favoured by selection at high densities, rather than genotypes with high carrying capacity (K). Consequently, the primary tradeoff that needs to be sought is not between maximal growth rate (r or, as sometimes designated, r_{max}) and carrying capacity (K), but rather between realized growth rates at low and high densities. Evidence for such tradeoffs has been seen in experiments on laboratory populations of *Drosophila* (Mueller and Ayala 1981; Mueller *et al.* 1991), and *Paramecium* (tradeoff between competitive ability and maximal growth rate: Luckinbill 1979), but not in populations of *Escherichia coli* (Luckinbill 1978; but see also Vasi *et al.* 1994; Bell 1997, p. 459).

As is the case with any overall measure of fitness, density-specific realized population growth rates are likely to be the culmination of a multitude of specific traits at the physiological and/or behavioural level that could affect how well organisms are able to cope with a particular level of crowding. It is, therefore, only to be expected that the specific adaptations underlying the evolution of higher density-specific growth rates, and consequently the low versus high density growth rate tradeoff, will vary considerably among species with differing basic ecologies (Mueller 1997). In the next section, we briefly review what is known about the specific adaptations underlying the evolution of higher growth rates at high density in populations of *D. melanogaster* subjected to extremely high levels of crowding for many generations in the laboratory.
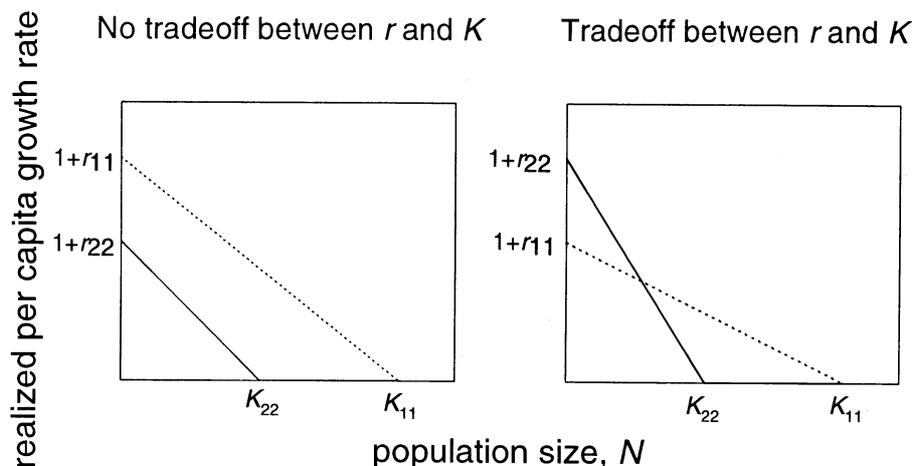
Figure 4. If one considers two genotypes with different r and K values within the confines of the logistic formulation, the only mechanism whereby one genotype can have superior realized per capita growth rates (fitness) at high densities is by having greater K. In both cases shown, selection in a crowded environment will favour genotype A_1A_1.

Adaptation to crowding in *Drosophila*

Two sets of selection studies on laboratory populations of *D. melanogaster* carried out over the last 20 years or so have yielded considerable insight into the mechanisms by which populations maintained at high density adapt so as to be able to sustain a higher rate of population growth at high density, relative to control ancestral populations. These studies have been reviewed several times (Mueller 1995, 1997; Joshi and Mueller 1996; Joshi 1997), and we shall, consequently, restrict ourselves to a brief summary of the traits seen to repeatedly evolve in *Drosophila* under density-dependent selection. In a *Drosophila* culture with very high larval density the environment deteriorates in two ways over time: food tends to run out, and toxic nitrogenous metabolic wastes tend to accumulate. There is, thus, selection favouring the ability to develop fast under crowded conditions, and also to be able to withstand fairly toxic levels of wastes such as ammonia and urea. Adaptive evolution in response to both these selection pressures seems to occur in *Drosophila* populations.

Compared to control populations reared at low larval densities, populations subjected to many generations of crowding evolve higher population growth rates at high densities, and higher *K* (Mueller and Ayala 1981; Mueller *et al.* 1991), as well as higher competitive abilities when competed against a common marked strain (Mueller 1988b). Other traits seen to evolve in the populations maintained at high density are larval feeding rate (Joshi and Mueller 1988, 1996), pupation height (Mueller and Sweet 1986; Joshi and Mueller 1993, 1996), larval tolerance to metabolic waste (Shiotsugu *et al.* 1997; Borash *et al.* 1998), foraging path length (Sokolowski *et al.* 1997), and minimum food required for pupation (Mueller 1990; Joshi and Mueller 1996). Although the crowding-adapted populations have shorter egg to eclosion development time and higher pre-adult survivorship than controls at high larval density (A. Joshi, personal observation), they do not differ from controls in development time, survivorship or size at eclosion when tested at low larval density (Santos *et al.* 1997).

Thus, it appears that *Drosophila* populations evolve enhanced competitive ability when evolving at high larval density primarily by becoming better at acquiring food fast, and by being better able to withstand relatively high levels of metabolic waste, even though this ability comes at the cost of decreased efficiency at converting food to biomass (Mueller 1990; Joshi and Mueller 1996; Borash and Shimada 2001), perhaps partly offset by greater efficiency at assimilating lipids (D. J. Borash, personal communication). It is interesting to note that although evolution in crowded conditions in these populations led to an increased carrying capacity, it was not through the predicted mechanisms of greater efficiency of conversion of food to biomass or reduced body size. It is also worth noting that the evolution of increased competitive ability through a mechanism such as faster feeding, which evolved twice in separate experiments with flies from different ancestries, cannot be accommodated within the framework of the 'pure' density-dependent selection models (equations 1, 2, 3).

Selection for faster development in *Drosophila*

One way of looking at selection at high larval density in *Drosophila* is to treat it as selection for faster development because individuals failing to eclose before a certain point in time die because food runs out, or because the medium becomes too toxic to permit survival. This view has been important in thinking about selection on wild *Drosophila* populations because larvae of many species occupy ephemeral habitats such as rotting fruits. It has, consequently, often been suggested that faster development has been under strong natural selection in *Drosophila* (Clarke *et al.* 1961; Robertson 1963; Partridge and Fowler 1992). Indeed, larval growth rates in wild *Drosophila* populations are thought to be an evolutionary compromise between the need to develop fast and the constraint that faster development typically reduces adult size (Santos *et al.* 1988; Partridge and Fowler 1993). Yet, larvae in rotting fruits often have to deal with not just the need to develop fast, but also to do so under fairly crowded conditions (Atkinson 1979; Nunney 1990). One consequence of this confounding of selection for faster development and for adapting to high density in ephemeral habitats has been the often implicit assumption by many workers that the two kinds of selection will have fairly similar outcomes (Tantawy and El-Helw 1970; Wilkinson 1987; Santos *et al.* 1988; Prout and Barker 1989; Partridge and Fowler 1993; Borash *et al.* 2000).

However, a comparison of results from density-dependent selection experiments and experiments where shorter development time was directly selected for at low larval density clearly shows that the suites of traits evolving under the two selection regimes are almost exactly opposite. *Drosophila* populations in which only the first 20% or so of pupating or eclosing individuals are allowed to breed each generation evolve rapid development at low density, relative to controls, and this reduction in development time is accompanied by large reductions in adult weight at eclosion (Zwaan *et al.* 1995; Nunney 1996; Chippindale *et al.* 1997; Prasad *et al.* 2000). Moreover, faster developing populations evolve reduced pre-adult survivorship, larval feeding rate, foraging path length, digging propensity, pupation height, larval growth rate, and minimum food requirement for successful pupation and eclosion, relative to ancestral control populations (Prasad *et al.* 2000, 2001).

Effectiveness and tolerance in competition

One of the notions that follows from formulations of density-dependent selection that include interactions among genotypes (equation 4) is that of selection under crowded conditions acting on competition coefficients **a**. The idea of **a**-selection was first put forward by Gill (1972, 1974) and Case and Gilpin (1974) in the context of interspecific competition and the possible coevolution of competitors. Yet, in 12 major papers on density-dependent selection between 1972 and 1984, including a major review in 1984 and another in 1997, Gill's (1972, 1974) work is cited only six times, and four of these are merely passing references. In his detailed review, Boyce (1984) does make the point that models like equation 4 clearly show that selection for competitive ability and *K*-selection are not synonymous, but even his treatment suggests that he views these situations as somehow being a 'complication' of the 'pure' density-dependent case due to the incorporation of frequency-dependent selection. Pianka (1972) suggests that the notion of **a**-selection should be subsumed into a broadened concept of *K*-selection.

We agree that the notion of density-dependent selection needs to be broadened to incorporate **a**-selection. In fact, we would like to suggest that **a**-selection is more than a 'complication'; it is one of the primary aspects of what happens when organisms are faced generation after generation with a high-density environment. We would argue that *K*-selection, in fact, is likely to be a somewhat subsidiary aspect of density-dependent selection, relative to **a**-selection, in most cases. We also suggest that viewing density-dependent selection from more of an **a**-selection perspective enables us to make use of a further distinction between two types of competitive ability that is of heuristic value, and it is to this aspect that we now turn.

Since competition is typically defined as a mutual inhibition of population growth rates by the two or more competing groups (whether genotypes or species) it is possible to think of two components of competitive ability: the ability to inhibit the other group (henceforth 'effectiveness') and the ability to withstand inhibition by the other group (henceforth 'tolerance') (Eggleston 1985; Joshi and Thompson 1995). To our knowledge, these concepts have not been explicitly discussed in the literature on density-dependent selection (but see Eggleston 1985), even though there is clear empirical evidence that these two components of competitive ability are at least partially independent in situations of both interspecific (Peart 1989; Goldberg and Landa 1991) and intraspecific (Mather and Caligari 1983; Eggleston 1985; Hemmat and Eggleston 1988, 1990) competition, and that they are under partly genetic control (Eggleston 1985) and can evolve separately (Joshi and Thompson 1995), at least in *Drosophila* species.

The main proposition we would like to advance in this paper is that a view of density-dependent selection that explicitly recognizes that competition coefficients will often be the primary targets of such selection (**a**-selection) allows us to focus on some hitherto neglected but potentially important tradeoffs that we believe will also clarify some of the confusion regarding evolution of developmental rates and of adaptations to crowding in *Drosophila*. To construct this view, we begin with noting that even within the confines of a logistic formulation, density-dependent selection with arbitrary intragenotypic and intergenotypic competition coefficients, $\mathbf{a}_{ijkl}$, can lead to a variety of outcomes not all of which imply an evolutionary increase of *K*. Moreover, we would argue that the $\mathbf{a}_{ijkl}$ in such situations are not always constrained to be simple functions of the carrying capacities K_{ij}, K_{kl} (contra Pianka 1972).

The strict dependence of $\mathbf{a}_{ijkl}$ on K_{ij}, K_{kl}, in fact, need not be assumed in order to apply models such as equation 4. Such dependence arises from a somewhat restricted view of competition involving only resource acquisition, with only the amount of resource required to survive and reproduce being considered and not the rates at which the resource is acquired. A phenomenon like the evolution of faster feeding rate in *Drosophila* populations adapting to crowding cannot be incorporated into the classical formulation of density-dependent selection (e.g. equation 1) at all. In such formulations, the only way to increase one's growth rate at high density, relative to other genotypes, is to have a higher *K* (or, as in Gilpin *et al.* 1976, to change **q**). These formulations do not permit a genotype to inhibit the growth rate of the other genotype while not altering its own basic parameters like *r*, *K* or **q**. Yet, this type of effect is exactly what is seen to happen in the *Drosophila* experiments: faster feeding, in itself, affects neither maximal growth rate nor carrying capacity (in fact it increases the minimum food necessary for pupation, implying reduced efficiency). When in competition with relatively slower feeders, however, faster feeders have a clear competitive edge: they can greatly inhibit the population growth rate of slower feeders, and this inhibition is independent of their own sensitivity to their own density and therefore of fundamental growth rate parameters such as *r*, *K* or **q**.

The notions of effectiveness and tolerance can be incorporated readily into this view of density-dependent selection. For a pair of genotypes $A_i A_j$, $A_k A_l$, the competition coefficient $\mathbf{a}_{ijkl}$ reflects the tolerance of $A_i A_j$ with regard to $A_k A_l$, whereas the competition coefficient $\mathbf{a}_{klij}$ reflects the effectiveness of $A_i A_j$ with regard to $A_k A_l$. This is an application of the argument made by Joshi and Thompson (1995) in the context of interspecific competition, and it should be noted that in this case the effectiveness of $A_i A_j$ with regard to $A_k A_l$ and the tolerance of $A_k A_l$ to $A_i A_j$ are the same quantity.

Clearly, intragenotypic competition coefficients cannot be split up in this manner: $\boldsymbol{a}_{ijij}$ reflects sensitivity of the population growth rate of genotype A_iA_j to the addition of more individuals of its own genotype, and this sensitivity subsumes both the effectiveness and tolerance of the genotype with regard to itself. There is also some empirical evidence for the evolution of these components of competitive ability; a study of interspecific competition between *D. simulans* and *D. melanogaster* revealed that populations could evolve higher competitive ability through changes in effectiveness or tolerance or both (Joshi and Thompson 1995).

If we now examine the observed evolutionary responses to selection under crowding in *Drosophila* in the context of effectiveness and tolerance, faster feeding will result in increased competitive ability through increased inter-genotypic but not intragenotypic effectiveness, whereas increased ability to withstand metabolic waste is likely to increase tolerance, both intergenotypic and intrageno-typic. Moreover, the expectation of increased efficiency of food utilization now appears far less unequivocal, because a genotype that can get by on less food will also thereby leave that much more for others. Thus, increased efficiency reduces effectiveness while increasing tolerance and can, therefore, have a net negative effect on com-petitive ability, especially in situations where the genotype with greater efficiency of food utilization is competing against a genotype with greater efficiency of food acquisition. Exactly this sort of tradeoff has been experimentally observed in *Drosophila* populations adapted to crowding (Mueller 1990; Joshi and Mueller 1996). If we looked at the traits that evolved in populations subjected to selection for faster development at low densities (Prasad *et al.* 2000, 2001), we would expect these populations to have reduced effectiveness due to slower feeding rates and lower adult weight and minimum food requirement for pupation and eclosion, perhaps partly offset by increased tolerance due to the latter. We might also expect them to have a higher *K* owing to the reduced adult size. We now discuss some experimental results on urea tolerance, early-life fecundity and population growth rates of the populations that have evolved faster development, and then return to this more general theme in the final section.

Materials and methods

Experimental populations: The experimental component of this study was done on eight populations of *D. melanogaster*, of which four served as controls and four were subjected to selection for faster development and early reproduction relative to the controls. These popu-lations have been previously described in detail (Prasad *et al.* 2000, 2001) and we consequently restrict ourselves here to the pertinent essentials. The four control popu-lations (JB_1, JB_2, JB_3, JB_4) are maintained on a 21-day discrete generation cycle at 25°C at a regulated larval density of about 60–80 larvae per 8-dram vial (9 cm height × 2.4 cm diameter) with 6 ml of food. The number of breeding adults is about 1800 per population and the adults are maintained in Plexiglas cages (25 cm × 20 cm × 15 cm) with abundant food. These four JB populations had been independent evolutionary entities for over 450 generations and had been on a three-week cycle for over 100 generations at the time the present study was initiated. The four populations selected for faster development and early reproduction were derived from the four JB populations and are designated as FEJ_1, FEJ_2, FEJ_3, FEJ_4 (F, faster development; E, early reproduction; J, JB derived). Each FEJ population was derived from one JB population; thus, selected and control populations with names bearing identical numerical subscripts are more closely related to each other than to other populations with which they share a selection regime (JB_i and FEJ_i are more closely related than JB_i and JB_j or FEJ_i and FEJ_j; i, $j = 1$–4). Consequently, control and selected populations bearing names with identical subscripts were treated as blocks in the statistical analysis. The selected populations are maintained on a regime similar to the JB populations except that only the 15 or so flies that eclose in each vial become part of the breeding population that typically numbers around 1000–1200 adults. Eggs are collected from these flies on the third day after eclosion by placing fresh food plates in these cages for one hour. The eggs are then dispensed into 80 vials at a density of 60–80 eggs per vial. Thus selection is essentially on (a) the total egg to eclosion development time and (b) on fecundity at an adult age of three days post-eclosion.

Collection of flies for assay: Imposition of different maintenance regimes can induce nongenetic parental effects. Consequently, all selected and control populations were maintained under common rearing conditions for one complete generation prior to assaying to eliminate all such nongenetic effects. Eggs were collected from the running cultures and dispensed into vials with about 6 ml of food at a density of 60–80 eggs per vial. On the 12th day after egg collection, by which time all normally developing individuals would have eclosed, the flies were collected into Plexiglas cages with abundant food. The adult numbers were usually around 1200–1800 per population. They were supplied with live yeast – acetic acid paste for two days prior to egg collection for assays. The progeny of these flies, hereafter referred to as standardized flies, were used for the assays.

Urea tolerance assay: Urea tolerance was assayed by recording egg-to-adult survivorship at three levels of urea—0 g/L, 7 g/L and 14 g/L. Following Shiotsugu *et al.* (1997), these levels of urea were added to regular

banana–jaggery food separately just before pouring it into vials. Ten such vials, with 5 ml of food each, were set up for each combination of population and urea level. Eggs from standardized flies were collected within a one-hour egg collection window, and 30 eggs were put into each of the vials. After the pupae had darkened, these vials were observed for eclosions at two-hourly intervals. After four days, most of the flies eclosed. Later, the checks were relaxed to once in six hours and finally terminated after finding no eclosions in any vial over a continuous period of one week.

Fecundity assay: Freshly eclosed progeny of standardized flies were set up in single male–female pairs in vials with ~ 3 mL of food. Forty such pairs were set up per population. Flies were transferred without anaesthesia to fresh vials every day for the first 10 days of adult life, and the number of eggs laid during the previous 24 hours was recorded. Any males dying were replaced with back-up males of the same age. Dying females were not replaced, but there were negligible deaths during the 10 days of the assay. Total fecundity per female over the 10 days was obtained by simply summing up the daily egg count data.

Population growth assay: From each FEJ and JB standardized population, two small populations were derived by seeding two vials with 8 males and 8 females each and allowing them to lay eggs for 24 hours, after which the adults were discarded. The larvae developed and pupated in these vials, and from day 8 through day 18 after egg-laying, any eclosing flies in these vials were collected daily into fresh vials with ~ 5 mL food in them. Eclosing flies were added daily into these adult collection vials and every other day all adults collected from a specific population till that time were shifted to a fresh vial containing ~ 5 mL food. On the 18th day after egg-laying, the egg vials were discarded and all eclosed adults of each population transferred to fresh vials. Each generation, the numbers of adult males and females present in each population (vial) were counted on the 21st day after egg-laying. The flies were then placed in a fresh vial with the appropriate amount of food and allowed to lay eggs for exactly 24 hours, after which the adults were discarded. This maintenance regime was continued for five generations to yield four pairs of N_t and N_{t+1} values for each population, which were used to construct a return map for the JB and FEJ derived populations.

Statistical analyses: All statistical analyses were implemented using Statistica^{TM} for Windows release 5.0 B (Statistica^{TM} 1995). Data on survivorship of each FEJ and JB population at the three levels of urea were subjected to an arcsine square root transformation (Freeman and Tukey 1950) and then subjected to a mixed-model analysis of variance (ANOVA) treating block (population

index, FEJ$_i$, JB$_i$, $i = 1, . . . , 4$) as a random factor crossed with selection regime and urea level. Ten-day fecundity data for FEJ and JB populations were analysed by comparing selection regime means by a paired *t*-test. For the data from the population growth assay, individual pairs of N_t and N_{t+1} values for each population were classified according to block, selection regime and density ($N_t < 50$, low; $50 < N_t < 100$, medium; $N_t > 100$, high). Values of N_{t+1} were treated as the dependent variable, and the data were subjected to a mixed-model ANOVA with block treated as a random factor crossed with selection regime and density. Assessment of FEJ and JB population growth rates at different densities was done by comparing mean N_{t+1} between the two selection regimes at each density through Fisher's least significant difference (LSD), fixing the comparisonwise error rate at 0.01 to allow for three comparisons being made.

Results

Urea tolerance: In general pre-adult survivorship declined with urea level for both FEJ and JB populations, and as previously noted (Prasad *et al.* 2000) the survivorship of FEJ populations was significantly less than that of JB populations even in the absence of urea (figure 5). The ANOVA revealed significant effects of selection regime, urea level and the selection regime × urea level inter-action (table 1). The difference in survivorship between the JB and FEJ flies was not significantly altered (paired *t*-test on difference) between treatments at 0 g/L and 7 g/L urea, and then increased significantly from about 0.28 to 0.48 at 14 g/L urea (figure 5).

Fecundity: Mean fecundity over the first 10 days of adult life in the JB populations (169.3 eggs per female) was
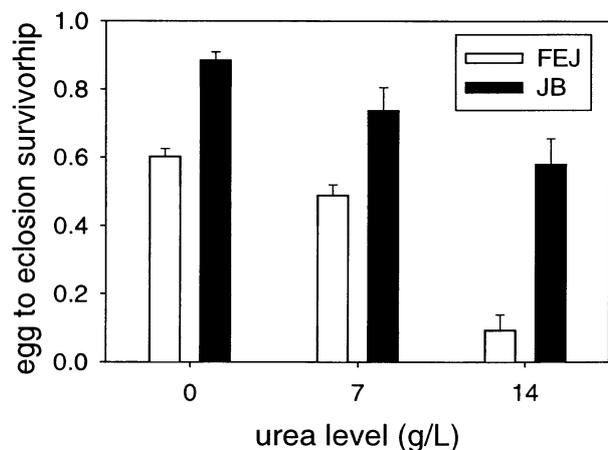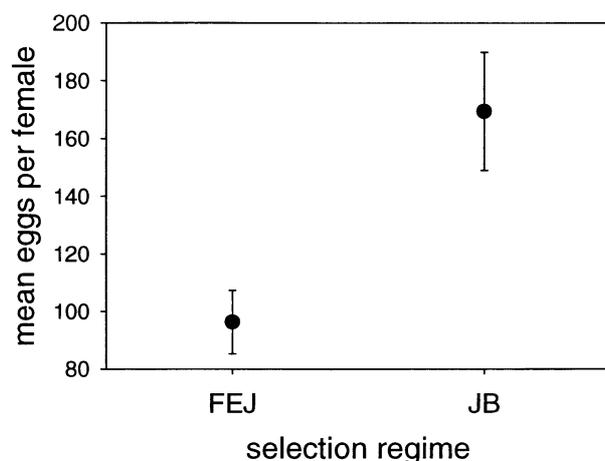

Figure 5. Urea tolerance of FEJ and JB populations. The bars depict mean survivorship, averaged across the four replicate populations within each selection regime. Error bars depict 95% confidence intervals about the mean.

significantly greater ($P < 0.01$) than that in the FEJ populations (96.3 eggs per female) (figure 6).

Population growth: In both FEJ and JB derived populations, population numbers tended to rise over the five generations of the assay (data not shown). However, mean N_{t+1} attained when N_t fell into one of the different density categories showed a clear pattern (figure 7), with the only significant ANOVA effects being due to density and the selection regime × density interaction (table 2). Multiple comparisons revealed that at low and medium values of N_t, the mean N_{t+1} attained by FEJ and JB derived populations did not significantly differ from one another, whereas at high values of N_t, the mean N_{t+1} attained by FEJ derived populations was significantly greater than that of the JB derived populations (figure 7).

Table 1. Results of ANOVA on population mean survivorship data from the urea tolerance assay subjected to arcsine square root transformation. In the analysis, block was treated as a random factor and, consequently, block effects and interactions involving blocks cannot be tested for significance.

Effect	d.f.	MS	F	P
Selection	1	0.8574	339.35	0.0003
Block	3	0.0097		
Urea level	2	0.4756	20.06	0.0022
Selection × block	3	0.0025		
Selection × urea level	2	0.0748	6.73	0.0293
Block × urea level	6	0.0237		
Selection × block × urea level	6	0.0111		

Figure 6. Mean total number of eggs laid per female over the first 10 days of adult life, averaged across the four replicate populations within each selection regime. Error bars depict 95% confidence intervals about the mean.

Discussion and conclusions

The experimental results clearly suggest that in monotypic cultures FEJ populations are likely to sustain higher rates of population growth at high densities than the JB controls (figure 7). In the context of the logistic model, this would have to be interpreted as an indication that the FEJ populations have higher K than the JB controls, and this interpretation would be consistent with the reduced minimum food requirement (Prasad *et al.* 2001) and adult size (Prasad *et al.* 2000) of the FEJ populations. However, it could also be that the functional forms of density dependence in the FEJ and JB populations are different, with or without an accompanying difference in carrying capacity. The population growth assay suggests that r in the FEJ and JB populations may not be significantly different, whereas the reduced fecundity over the important early part of adult life of FEJ females at a density of two flies per vial (figure 6) suggests that r in the FEJ populations should be substantially smaller that in the JB controls. One reason for this apparent discrepancy may be the difference in density in the two assays. In the fecundity assay the density was two flies per vial, whereas in the low density classification of the population growth assay data densities ranged from 16 to 50 flies per vial, and fecundity in *Drosophila* populations closely related to the JBs and FEJs is known to decline rapidly as the density increases from two to 16 flies per vial (Mueller *et al.* 2000). Especially if there are any differences in the functional form of the density dependence of growth rate between FEJ and JB populations, differences in r
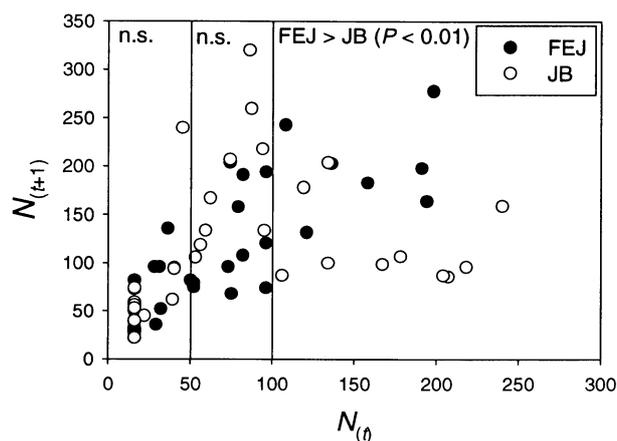
Figure 7. Return map based on five generations of census of adult numbers in 16 small populations (two populations derived from each FEJ and each JB population). Vertical lines divide the data into three groups based on population size N_t ($N_t < 50$, low; $50 < N_t < 100$, medium; $N_t > 100$, high). Mean N_{t+1} of FEJ and JB derived populations was not significantly different ($P > 0.01$) for low or medium N_t, whereas mean N_{t+1} for FEJ derived populations was significantly greater ($P < 0.01$) than for JB derived populations for high N_t.

Table 2. Results of ANOVA on one-step population sizes (N_{t+1}) attained by populations for whom N_t fell into one of the arbitrarily designated categories of low, medium or high (see Materials and methods: statistical analysis for details). Block was treated as a random factor, and variation among replicate small populations within selection × block is subsumed in the error term.

Effect	d.f.	MS	F	P
Selection	1	411.67	0.182	0.6984
Block	3	3860.48	1.263	0.2999
Density	2	60839.76	73.794	0.0001
Selection × block	3	2260.76	0.740	0.5346
Selection × density	2	19031.57	21.554	0.0018
Block × density	6	824.46	0.270	0.9478
Selection × block × density	6	882.99	0.289	0.9387
Error	40	3055.80		

may not be seen when looking at mean growth rates over a range of densities that are already in excess of 16 flies per vial.

We have noted earlier that the FEJ populations may be expected to have evolved reduced effectiveness in competition owing to slower feeding rates and lower adult weight and minimum food requirement for pupation, perhaps partly offset by increased tolerance due to the latter. To this we must now add a further decrease in tolerance due to heightened sensitivity to high levels of urea (figure 5). It thus becomes apparent that, contrary to many earlier expectations, selection for faster development at low density is unlikely to lead to the evolution of greater competitive ability. Ironically, though, the traits classically expected to evolve in *K*-selected populations—smaller size, increased *K* or population growth rates at high density, greater efficiency of conversion of food to biomass—actually seem to evolve in populations selected for faster development, rather than in populations selected for adaptations to high density. Yet, given the lower feeding rates, urea tolerance and minimum food requirements of the FEJ populations, we would predict that these populations should be poorer competitors than the JB controls, their greater efficiency and higher *K* notwithstanding.

Indeed, we suggest that part of the confounding of selection for adaptations to crowding and selection for fast development in the *Drosophila* literature has been due to expected outcomes of density-dependent selection being based on the restrictive formulation within the constraints of the logistic equation. Although formulations incorporating genotypic interactions (arbitrary a_{ijkl}) were available in the literature, as were the notions of splitting competitive ability into components due to effectiveness and tolerance, these ideas were not put together when viewing the issue of selection for faster development versus adaptations to crowding. We hope the present arguments will help convince readers that the broader view of density-dependent selection we have outlined

is of value in trying to understand these important evolutionary phenomena, and in reconciling empirical results with theoretical formulations.

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