

# Evolution of competitive ability in *Drosophila* by density-dependent natural selection

(*K* selection/*r* selection/life histories)

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**ABSTRACT** The theory of density-dependent natural selection predicts that populations kept at extreme densities should evolve different competitive abilities for limited resources. These predictions have been tested with laboratory populations of *Drosophila melanogaster*. Six independent populations were maintained in two environments, called *r* and *K*, for 128 generations. In the *r* environment, population sizes were small and resources for larvae and adults were abundant. In contrast the populations in the *K* environment were large and crowded, and resources, such as food and space, were in short supply. The relative competitive ability for food has been estimated for each population. Populations from the *K* environment consume food at a rate that is 58% greater than the average rate for the *r* population. The differentiation of competitive abilities in these populations is due to natural selection and is consistent with predictions from the theory of evolutionary ecology.

The ability to compete successfully for limited resources is an important trait for organisms that live in crowded environments. A major goal of evolutionary biology has been the development of a general theory that will allow the prediction of those life history traits most likely to evolve in different ecological settings. MacArthur and Wilson (1) initiated such a theory by concentrating on the various selection pressures acting at extreme population densities. They called the characteristic selection operating at low population densities *r* selection and the characteristic selection at high densities *K* selection. MacArthur and Wilson (1) and others (2, 3) have argued that *K* selection will favor efficient utilization of resources and increased competitive ability, whereas *r* selection will favor increased reproductive output even if this requires some sacrifice in competitive ability. These heuristic arguments concerning competitive ability have been formalized in a number of models (4-8). I report experimental evidence of competitive abilities that have evolved in response to selection at extreme population densities in a manner consistent with the theory of *r* and *K* selection.

## MATERIALS AND METHODS

This study utilized six independent populations of *Drosophila melanogaster* derived from the same source population: three were kept at low population density and three were kept at high saturation densities. In the low-density population, 50 adults, aged 3-6 days, were given 24 hr to lay eggs in half-pint cultures with standard *Drosophila* medium. At the end of the egg-laying period, the adults were discarded and the progeny were given 14 days to develop into a new adult population. A sample of 50 was chosen at random from the pool of 300-500 newly emerged adults and given 3 days to recover from

anesthetization to complete the cycle. The high-density population was maintained by the serial transfer system (9). This process results in an adult population size of 800-1200 in a half-pint culture. Resources were renewed at weekly intervals and adults were allowed to reproduce throughout their 2- to 3-week life span.

At the start of this study the populations had undergone 128 generations of selection. Previous work on these populations has documented large differences in density-dependent rates of population growth (10), density-dependent viabilities (T. J. Bierbaum, L.D.M., and F. J. Ayala, unpublished data), larval pupation site choice (11), and age-specific female fecundity (12). However, none of this work can be used to make inferences about competitive ability for limited food (13, 14).

The process of larval competition for food has been extensively studied in *Drosophila* (14-16). The process can be described as exploitative or scramble competition in that individuals do not monopolize food resources. Behavioral studies of *Drosophila* larvae have shown that larvae with the highest feeding rates (as measured by rates of retraction of the mouthparts) are also the best competitors (16). The populations studied here also showed a strong correlation between competitive ability and independently measured feeding rates (A. Joshi and L.D.M., unpublished data). There also appeared to be no consistent difference between male and female feeding rates. The best competitors appeared to be those that consumed food and grew the fastest, and this process was largely unaffected by the presence of other competitors (14). Quantitative models of competition by *Drosophila* larvae and its effects on viability have been developed and shown to be precise predictors of empirical results (15).

The three independent *r* and *K* populations were randomly assigned indices from 1 to 3. Each *r* and *K* population was matched by this index. All experiments reported here were conducted simultaneously on matched pairs of populations. Viability was determined by placing 100 newly hatched (within 2 hr) first-instar larvae in vials with measured amounts of live yeast and water (2.67 ml/gm of yeast). This solution was placed on nonnutritive Kalmus medium, which precluded growth of the yeast. The raw data consisted of the number of adults emerging from each vial. At any given time viability was determined at 10 yeast levels (25 mg-158 mg/100 larvae) in each matched population. These experiments were conducted on at least two occasions.

Two additional experiments were conducted on each matched pair to evaluate competitive ability. Larvae from each experimental population were placed in competition with larvae homozygous for the white (*w*) allele. Adults homozygous for the *w* allele are phenotypically distinct from the experimental adults and allow a direct estimate of competitive ability of experimental larvae relative to the *w* stock (the competitive ability of the *w* stock was arbitrarily set to 1.00). In one set of experiments, 50 experimental larvae and 50 *w* larvae were placed in each vial; in the second set 67

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experimental and 33 *w* larvae were placed in each vial. These experiments with various mixtures of larvae were conducted at 10 yeast levels for each population at a single time and each matched pair experiment was conducted twice.

The experimental populations studied here differ in the population densities experienced and in the selection pressures inherent in the various environments, and these populations also differ in the level of random genetic drift they have experienced. The *r* populations will certainly be more affected by genetic drift due to their small adult population. This raises the possibility that deleterious recessive alleles present in the founding populations may become fixed in the *r* populations, due to drift, and cause a decline in competitive ability. To examine this hypothesis the competitive ability of the  $F_1$  hybrids of the *r* populations have been examined. The likelihood that all three *r* populations have become fixed for the same sets of deleterious alleles is quite small. The  $F_1$  population, therefore, should be heterozygous for the deleterious recessive alleles at the relevant loci and exhibit high competitive ability relative to the parental populations, sometimes called hybrid vigor. If such hybrid vigor is not observed, then it is more likely that differences between the *r* and *K* populations are due to natural selection.

The  $r$ - $F_1$  population was created by crossing ( $\sigma \times \varphi$ )  $r$ -1  $\times$   $r$ -2,  $r$ -1  $\times$   $r$ -3,  $r$ -2  $\times$   $r$ -3, and the reciprocal crosses, where  $r$ -1 is group 1 of the *r* population, etc. Equal numbers of larvae from these six crosses were used to begin experiments identical in scope and magnitude to those described above. The matched pair for the  $r$ - $F_1$  population was a  $K$ - $F_1$  population created in an analogous fashion. In total, these experiments utilized 60,000 larvae in the viability tests.

The estimation of competitive ability rests on the analysis of a mathematical model of larval competition (15). The data analysis was as follows. The raw data, number of surviving males or females, were first adjusted to take into account mortality due to factors other than food, and then the probability of survival was transformed to a standard normal deviate (15). When this was done on the survival data of males (say, from a pure population of experimental larvae), the regression of standard normal deviates vs. the reciprocal of the food level yielded an estimate of  $m_{s,\sigma}$ , which is the minimum amount of food ( $m_s$ ) an individual male larva needs to pupate successfully. This derivation assumed male and female larvae from the experimental population had approximately the same competitive ability ( $\alpha$ ). As mentioned previously this assumption was supported by observations of larval feeding behavior. Nunney (15) has shown that in a given population the ratio  $(m_{s,\sigma} \alpha_\sigma) / (m_{s,\varphi} \alpha_\varphi)$  may not be equal to one and is often less than one. This finding is consistent with my supposition that male and female competitive abilities are equal and  $m_\sigma < m_\varphi$ . This latter inequality is quite reasonable since at any given food level males are invariably smaller than females. When a similar analysis was conducted on the survival data of the same males in the mixed experiments with an equal number of *w* larvae, the regression yielded an estimate of  $m_{s,\sigma}(\alpha_\sigma + \alpha_w) / 2\alpha_s$ , where  $\alpha_s$  is the competitive ability of experimental larvae and  $\alpha_w$  is the competitive ability of the *w* larvae. These calculations assume that mortality due to factors other than food take place after larvae have consumed all the food. This assumption is supported by the observation that at very high food levels almost all larvae placed in the vial pupate and, therefore, almost all larvae that fail to develop into adults died as pupae. If I set  $\alpha_w = 1.0$  and use the previous estimate of  $m_{s,\sigma}$ , then I can derive an estimate of  $\alpha_s$ . The data from female survivorship in the same two experiments can be used to get another estimate of  $\alpha_s$ . Likewise the data from the experiments with other mixtures of experimental to *w* larvae (2:1) yield additional estimates of  $\alpha_s$ . All of these experiments were utilized to yield one least squares estimate of  $\alpha_s$ .

The viability of larvae in these competition experiments depends on both *m* and  $\alpha$ .  $\alpha$  has been chosen as the measure of competitive ability since it accurately reflects the biological consequences of scramble competition, whereas *m* does not. The viability of an individual does not depend on the minimum food requirements of its competitors, but it does depend on the  $\alpha$  value of its competitors. Simple theoretical considerations lead to the prediction that, at high population density, natural selection should favor decreasing values of *m*. The actual investigation of minimum food requirements in these populations has become quite complicated and interesting, but space limitations preclude a full discussion here.

The algorithm for estimating the competition coefficients included utilizing ratios of regression coefficients and subjecting the raw data to a nonlinear transformation. Consequently, standard statistical techniques could not be utilized for making inferences on these competition coefficients. To circumvent these problems, the statistical analysis utilized the bootstrap technique (17, 18). This method generates new data sets by recreating the sampling process inherent in the collection of these data and by using the original data as an empirical estimate of the distribution function of the relevant random variables. This technique has been used to construct bias-corrected confidence intervals (19) for each competition coefficient. Bootstrap confidence intervals may be accurate in a wide variety of problems (20). Statistics reported here are based on 1000 independently generated competition coefficients. In addition the statistical significance of the difference in the competitive ability was calculated for each matched pair and the average *r* and average *K* population.

## RESULTS

In these experiments the outcome of combining a poor competitor with a good competitor should be that the viability of the poor competitor is decreased, relative to its value in the absence of the competitor, and the viability of the good competitor is increased. In Fig. 1 the percent increase or decrease in viability of each selected and  $F_1$  population in the competition experiments is shown. The same relative change in viability for the *w* population is also shown. Only the data from the competition experiments utilizing equal numbers of larvae were used in Fig. 1 since they were sufficient to illustrate the differences quantified in Table 1. The *r* larvae are usually poor competitors (Fig. 1). The typical outcome of competition between *r* and *w* larvae was a decline in viability of the former and an increase of the latter at low food levels. The results of competition between *K* and *w* larvae were quite different. The *K* and *w* larvae were more likely to have their viability increased or decreased in the same direction and by the same magnitude, indicating competitive abilities of similar magnitude. These qualitative impressions from the raw data can be quantified.

In every case, the competitive ability of the *K* population is greater than its matched *r* population (Table 1). In all cases except *K*-1 vs. *r*-1, these differences were statistically significant at the 5% level. The mean competitive ability of the three experimental *K* populations was 1.14, whereas this value was 0.72 for the *r* populations. Thus, the average *K* population consumed food at a rate that was 58% greater than the average rate for the *r* population.

The competitive abilities of the  $F_1$  populations shown in Table 1 gave no evidence of hybrid vigor. The competitive abilities of both  $F_1$  populations were intermediate, relative to the parental populations, and were very close to the means of the parental populations. This is precisely the result expected if one assumes the differences between individual *r* or *K* populations are due to alleles that have additive effects on competitive ability.

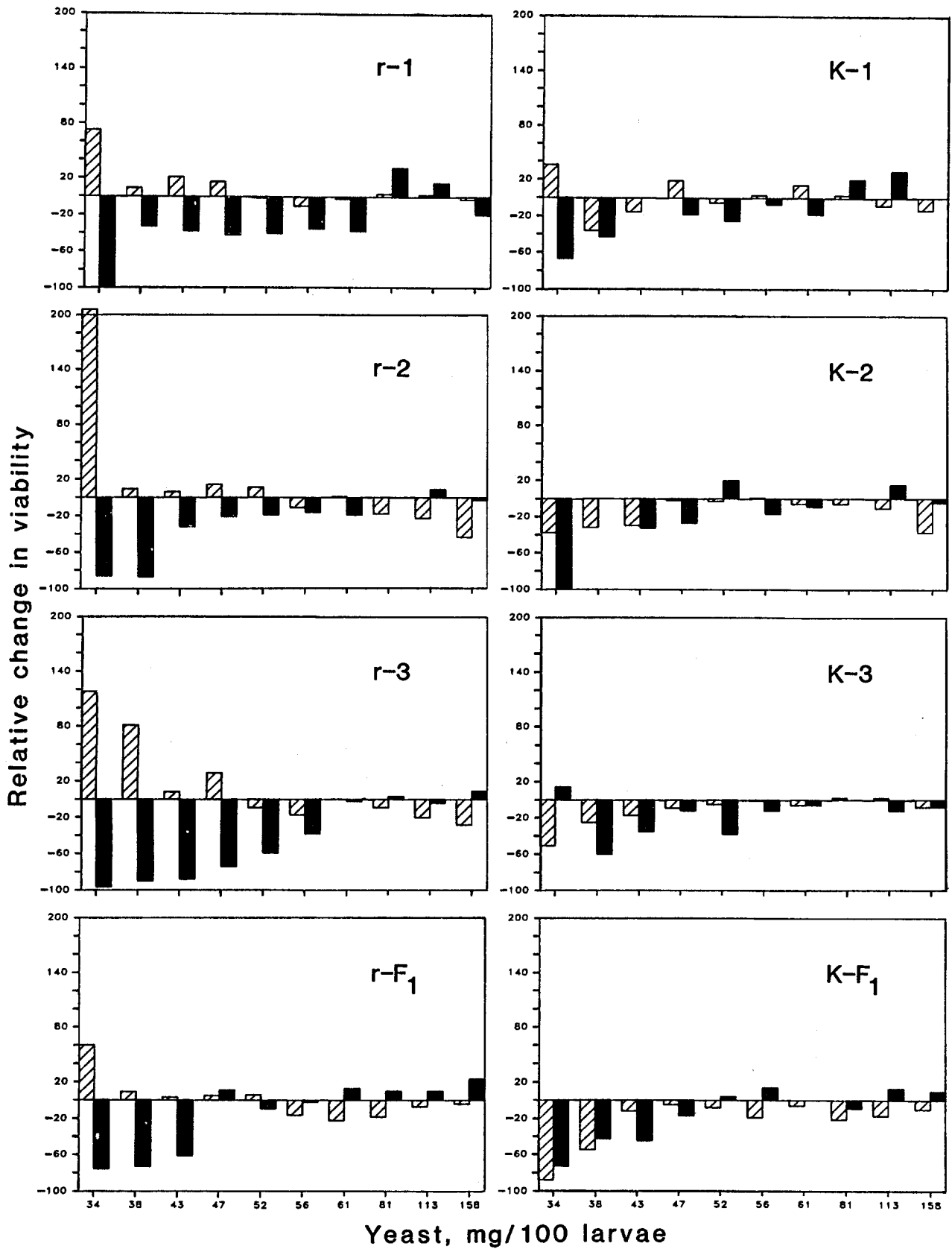


FIG. 1. The relative change in viability of each experimental population (solid bars) and the w (cross-hatched bars) population when they are placed in competition. This change is measured as the viability of the population in the competition experiment with equal numbers of competitors minus its viability in the absence of competitors all divided by the latter viability.

Table 1. Competition coefficients for each population relative to the  $w$  population

Population	Competitive ability*	Probability that $\alpha_K > \alpha_r^\dagger$	Probability that $\bar{\alpha}_K > \bar{\alpha}_r^\ddagger$
K-1	1.07 ( $\pm 0.24$ )	0.35	0.00066
r-1	0.95 ( $\pm 0.31$ )		
K-2	1.17 ( $\pm 0.33$ )	0.042	
r-2	0.74 ( $\pm 0.34$ )		
K-3	1.19 ( $\pm 0.26$ )	0.0015	
r-3	0.47 ( $\pm 0.28$ )		
K-F <sub>1</sub>	1.16 ( $\pm 0.20$ )	0.0088	
r-F <sub>1</sub>	0.77 ( $\pm 0.25$ )		

\*Competitive ability is reported, and the  $\pm 95\%$  confidence interval is in parentheses.

<sup>†</sup>Probability that the  $K$  population of a matched pair has greater competitive ability than the  $r$  population purely by chance.

<sup>‡</sup>Probability that the mean of the three experimental  $K$  populations has greater competitive ability than the mean  $r$  population purely by chance.

## DISCUSSION

The theory of  $r$  and  $K$  selection has developed along two lines. The verbal theory (2, 3, 21) attributed a large array of life-history phenomena to  $r$  and  $K$  selection whereas the mathematical theory (4–8) made more modest predictions. Initial tests of the theory relied on observations from field populations to which various regimes of density-dependent population regulation were attributed. Despite some early reports that generally confirmed predictions from the verbal models (22, 23), an almost equal number of studies with contradictory results have appeared (24, 25).

Stearns (26) has discussed the difficulties with many field studies and, it has become clear that carefully controlled laboratory studies will be most useful for testing these theories. There are presently a small number of such studies that have utilized *Escherichia coli* (27, 33) and *Drosophila* (10, 28–30). Only the studies by Luckinbill (27) and Mueller and Ayala (10) have dealt with phenotypes that are components of the mathematical theories. The other studies have largely dealt with the predictions of the verbal theory, and the results have been mixed (for a review, see ref. 31). The current study adds competitive ability to a growing list of phenotypes (10, 11) that have been shown to respond to density-dependent natural selection.

The results from this study are consistent with the idea that natural selection favors high competitive ability for resources that are limited. The theory of density-dependent natural selection provides a general framework for predicting the

evolution of life-history phenomena, such as competitive ability and density-dependent rates of population growth in environments with various density-regulating mechanisms. The present results and other studies with *Drosophila* (10) have verified key predictions of this theory and thereby justify the central role this theory has assumed in the field of evolutionary ecology (32).

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- MacArthur, R. H. & Wilson, E. O. (1967) *The Theory of Island Biogeography* (Princeton Univ. Press, Princeton, NJ).
- Pianka, E. R. (1970) *Am. Nat.* **104**, 592–596.
- Southwood, T. R. E. (1976) in *Theoretical Ecology*, ed. May, R. M. (Saunders, Philadelphia), pp. 26–48.
- Anderson, W. W. (1971) *Am. Nat.* **105**, 489–498.
- Charlesworth, B. (1971) *Ecology* **52**, 469–474.
- Roughgarden, J. (1971) *Ecology* **52**, 453–468.
- Anderson, W. W. & Arnold, J. (1983) *Am. Nat.* **121**, 649–655.
- Asmussen, M. A. (1983) *Genetics* **103**, 335–350.
- Mueller, L. D. & Ayala, F. J. (1981) *Theor. Popul. Biol.* **20**, 101–117.
- Mueller, L. D. & Ayala, F. J. (1981) *Proc. Natl. Acad. Sci. USA* **78**, 1303–1305.
- Mueller, L. D. & Sweet, V. F. (1986) *Evolution* **40**, 1354–1356.
- Mueller, L. D. (1987) *Proc. Natl. Acad. Sci. USA* **84**, 1974–1977.
- Lewontin, R. C. (1955) *Evolution* **9**, 27–41.
- Bakker, K. (1961) *Arch. Neerl. Zool.* **14**, 200–281.
- Nunney, L. (1983) *Am. Nat.* **121**, 67–93.
- Burnet, B., Sewell, D. & Bos, M. (1977) *Genet. Res.* **30**, 149–161.
- Efron, B. (1979) *Ann. Stat.* **7**, 1–26.
- Efron, B. (1979) *SIAM Rev.* **21**, 460–480.
- Efron, B. (1981) *Can. J. Stat.* **9**, 139–172.
- Efron, B. (1985) *Biometrika* **72**, 45–58.
- Stearns, S. C. (1976) *Q. Rev. Biol.* **51**, 3–47.
- Gadgil, M. & Solbrig, O. T. (1972) *Am. Nat.* **106**, 14–31.
- McNaughton, S. J. (1975) *Am. Nat.* **109**, 251–261.
- Tinkel, D. W. & Hadley, N. F. (1975) *Ecology* **56**, 427–434.
- Wilbur, H. M. (1976) *J. Ecol.* **64**, 223–240.
- Stearns, S. C. (1977) *Annu. Rev. Ecol. Syst.* **8**, 145–171.
- Luckinbill, L. S. (1978) *Science* **202**, 1201–1203.
- Taylor, C. E. & Condra, C. (1980) *Evolution* **34**, 1183–1193.
- Barclay, H. J. & Gregory, P. T. (1981) *Am. Nat.* **117**, 944–961.
- Barclay, H. J. & Gregory, P. T. (1982) *Am. Nat.* **120**, 26–40.
- Mueller, L. D. (1985) *Evol. Biol.* **19**, 37–98.
- Roughgarden, J. (1979) *Theory of Population Genetics and Evolutionary Ecology: An Introduction* (MacMillan, New York).
- Luckinbill, L. S. (1984) *Ecology* **65**, 1170–1184.