Proc. Natl. Acad. Sci. USA
Vol. 78, No. 2, pp. 1303–1305, February 1981
Population Biology

Trade-off between *r*-selection and *K*-selection in *Drosophila* populations

(population dynamics/density-dependent selection/evolution/*Drosophila melanogaster*)

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Contributed by Francisco J. Ayala, October 17, 1980

ABSTRACT Density-dependent genetic evolution was tested in experimental populations of *Drosophila melanogaster* subject for eight generations to natural selection under high (*K*-selection) or low (*r*-selection) population density regimes. The test consisted of determining at high and at low densities the per capita rate of population growth of the selected populations. At high densities, the *K*-selected populations showed a higher per capita rate of population growth than did the *r*-selected populations, but the reverse was true at low densities. These results corroborate the predictions derived from formal models of density-dependent selection. However, no evidence of a trade-off in per capita rate of growth was observed in 25 populations of *D. melanogaster*, each homozygous for a different second chromosome sampled from a natural population.

Evolutionary ecology strives to understand—and, hence, to predict—the kinds of evolutionary change that different environmental conditions may bring about in populations. An important environmental variable is population density relative to essential resources. MacArthur and Wilson (1) examined this question by considering two alternative situations, called *r*-selection and *K*-selection. According to their predictions, natural populations commonly kept at low densities by density-independent mortality (and, hence, having abundant resources) should evolve high *intrinsic rate of growth* (*r*), but be unable to have superior performance at high population densities. In contrast, populations usually living at high density (and, hence, experiencing strong competition for limiting resources) should evolve high intraspecific competitive ability and enhance their *carrying capacity* (*K*).

Drawing from the theoretical work of ref. 2, Gadgil and Solbrig (3) have argued that *r*-selected species should devote a greater proportion of their resources to reproductive activities than *K*-selected species. According to ref. 4 the expected effects of *r*- and *K*-selection are indeed manifest over a broad range of taxa: *r*-selected species are characterized by small body size and a generation time shorter than one year, while *K*-selected species have larger body sizes and longer generations. A catalog of the phenotypes expected from *r*- and *K*-selection is given in ref. 5.

The consequences of density-dependent selection have been explored mathematically by several workers (6–10). Roughgarden (9, 11) assumes that fitness is equivalent to an individual's per capita contribution to population growth; fitness is further assumed to be a linear function of the total population size (N). The fitness of the *ij*th genotype (W_{ij}) can be expressed as

$$W_{ij} = 1 + r_{ij} - (r_{ij}N/K_{ij}),$$

in which the values of r and K vary among genotypes. If it is assumed that an initial population is polymorphic for genotypes that show a trade-off—i.e., genotypes with high *r*s have low *K*s and *vice versa*—the outcome of evolution in Roughgarden's model is dependent on the environment. In stable environments, the population reaches its carrying capacity and the genotype with the largest value of K ultimately becomes established and all others are eliminated. When the population is often below its carrying capacity owing to frequent episodes of density-independent mortality, the genotype with the highest r is favored. Thus, according to this model evolution favors the genotype that makes the highest per capita contribution to population growth, at either high or low densities depending on the environmental conditions.

It has been pointed out by Stearns (5) that empirical work on the evolution of life history traits has fallen into two categories. The comparative approach (3, 12–14) examines the life history traits of natural populations whose past evolutionary history must be inferred from the properties of the present population. The direct approach (15, 16) predicts the outcome of natural selection based on known differences in the environment. Although we agree with Stearns in preferring the direct approach, we have performed two experiments. The first experiment tests Roughgarden's (9, 11) crucial assumption that populations have genotypes showing a trade-off in their fitness at high and low densities. This experiment examines the extent to which such a trade-off exists among a large sample of unselected genotypes of *Drosophila melanogaster*. The second experiment follows the direct approach and tests whether selection under different density regimes (high and low density) modifies the per capita growth rates as predicted by models (9, 11) that postulate a trade-off between *r*- and *K*-selection.

MATERIALS AND METHODS

Experiment 1. Twenty-five strains of *D. melanogaster*, each homozygous for a different second chromosome, were obtained by standard procedures (17) from a sample of wild flies collected at Strawberry Canyon (Berkeley, CA). Density-dependent rates of population growth were determined for each of the 25 strains (18), using the "type II" experiments of ref. 19. Briefly, a specified number of adults, N^*, (consisting of equal number of males and females) are allowed to lay eggs for 1 week in a half-pint (235-ml) culture with fresh medium. After 1 week, the survivors are counted and discarded; the adults emerging from the culture are then recorded at 1-week intervals over the following 3 weeks. The initial densities used for each of the 25 strains are $N^* = 10$, 20, 50, 100, 250, 500, 750, and 1000, with six replicates for each strain at each density, except for $N^* = 1000$, which had only three replicates. It deserves notice that the flies used to initiate each experiment had been raised at the same density as used in the experiment.

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Experiment 2. The 25 homozygous strains described for experiment 1 were thoroughly intercrossed and six experimental populations were established with random samples of the F_2 progenies from such crosses. Three populations (*r*-selected) were started, each with 100 adult flies that were allowed to lay eggs for 24 hr in a half-pint standard culture. After 14 days, 100 of the 400–800 emerged flies were again placed in a culture and allowed to lay eggs for 24 hr. The cycle was repeated for eight generations except that 50 rather than 100 flies were used in the last three generations. The other three populations (*K*-selected) were maintained by the "serial transfer" method ("type I" experiments of ref. 19) so that the populations reached their carrying capacity in 3–4 weeks and maintained it thereafter. These *K*-selected populations were kept for 5 months contemporaneously with the *r*-selected populations. Briefly, the serial transfer method is as follows. A number of adults are introduced into a culture, allowed to lay eggs there, and transferred at weekly intervals to new cultures. When flies start to emerge in cultures where the eggs were laid, the emerging flies are collected once a week and added to the culture into which the surviving adults were transferred, at the same time when the transfer is made. Each culture is discarded at the end of the fourth week after the time when the adult egg-laying flies were introduced into it. Thus, a population consists at any time of four cultures, one containing the egg-laying adults and the other three containing eggs, larvae, and newly emerged flies.

The evolutionary effects of the two different selection regimes described for experiment 2 were tested as follows. After completion of the experimental treatments described above, both the *r*-selected and the *K*-selected populations were maintained for two generations by mass culture, all in identical conditions; this should eliminate any nongenetic differences between the two types of populations that could be due to the selection regimes. Then, density-dependent rates of population growth were determined with type II experiments at $N^* = 10$, 500, and 750. All tests were started on the same day. The lowest density was chosen to approximate the degree of larval competition experienced by the *r*-selected lines. The two higher densities were chosen to be close to the carrying capacity of the two populations, although now, after the test has been performed, it appears that their carrying capacities were somewhat higher than 750. Six replicate tests were performed at the density of 10 with each of the six selected populations; and three replicate tests at each of the densities 500 and 750.

All experiments were performed at 23°C and ca. 70% relative humidity.

Statistical Methods. As described in ref. 18, a general model of the serial transfer system is

$$N_t = f_1(N_{t-1}) + f_2(N_{t-2}) + f_3(N_{t-3}) + f_4(N_{t-4}), \qquad [1]$$

in which N_t is the number of adults in the population at a given time, and $f_i(N_{t-i})$ is an unknown function that relates the number of adults emerging (or surviving, in the case of f_1) from an *i*-week-old culture with the number of individuals that laid eggs in that culture. The type II experiments described above yield repeated observations of the $f_i(N_{t-i})$ functions. The observations from one experiment may thus be represented as $f_1(N^*)^j$, $f_2(N^*)^j$, $f_3(N^*)^j$, $f_4(N^*)^j$, in which the superscript refers to the *j*th replicate of the experiment at N^*.

Density-dependent rates of population growth are determined by using a linear version of Eq. 1,

$$N_t = a_1 N_{t-1} + a_2 N_{t-2} + a_3 N_{t-3} + a_4 N_{t-4}, \qquad [2]$$

in which a_i is a constant per capita output of an *i*-week-old culture that is estimated from the observations at a particular N^*. The estimation of each a_i proceeds directly from the observations as

$$\hat{a}_i = \frac{1}{m}\sum_{j=1}^{m} f_i(N^*)^j/N^*,$$

in which *m* is the total number of replicates (which is three or six in these experiments). Eq. 2 is a fourth-order homogeneous and linear difference equation. The largest eigenvalue of Eq. 2, λ_{N^*}, is used as an estimate of the rate of population growth for each N^*. Thus, at each value of N^*, a different set of observations is made in order to estimate the a_is in Eq. 2, which yield a different per capita rate of increase, λ_{N^*}, for each N^*.

In practice, λ_{N^*} is estimated as the mean of *m* approximately independent and identically distributed (i.i.d.) random variables obtained from *m* separate experiments. These *m* approximately i.i.d. random variables are called pseudovalues and their method of estimation is called the "jackknife" (ref. 18; see ref. 20 for a review of the jackknife statistic).

In addition to determining the per capita rates of population growth, the same data can be used to estimate the "net productivity." Net productivity is defined as

$$f_1(N^*) + f_2(N^*) + f_3(N^*) + f_4(N^*) - N^*.$$

Unlike λ_{N^*}, the net productivity is not sensitive to the time at which flies emerge. Although we are primarily interested in per capita rates of population growth, the net productivity statistic reflects differences in survivorship and fecundity and can be more accurately estimated than λ_{N^*}. Thus it can provide some insights into differences between populations that λ_{N^*} may not yield.

RESULTS AND DISCUSSION

Experiment 1. We first explore the possibility that the homozygous lines exhibit a trade-off in their density-dependent rates of population growth. To accomplish this we have calculated the correlation between the growth rate at density 10 and at each one of the other densities for all homozygous lines as a whole. The results are given in Fig. 1. All correlations are positive, but there is in general a gradual decline of this positive correlation as density increases. It should be added that all correlations are

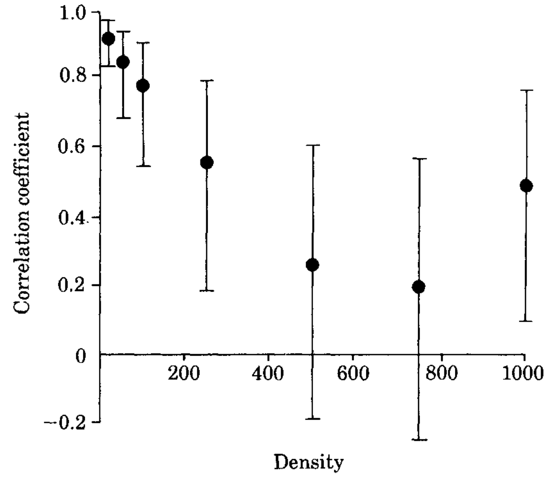

FIG. 1. Correlation between the growth rate at density 10 (λ_{10}), and the growth rate at each of seven other densities (λ_{N^*}); ($N^* = 20$, 50, 100, 250, 500, 750, and 1000). This correlation is for the 25 homozygous lines of experiment 1. Bars indicate the 95% confidence interval.

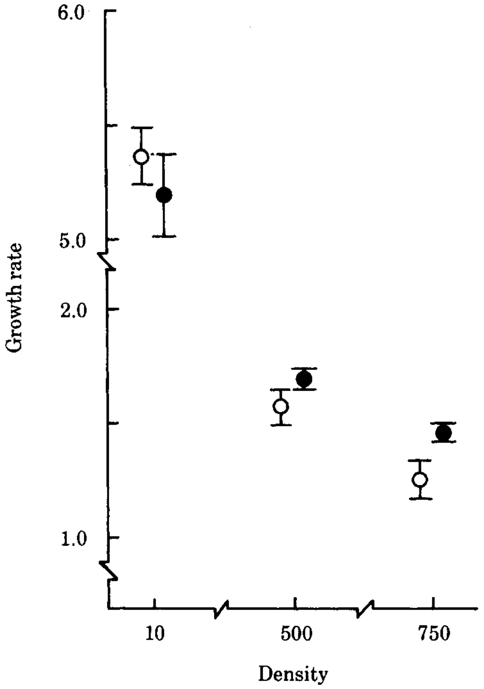

FIG. 2. Mean per capita growth rate (and 95% confidence intervals) at three densities in *r*-selected (○) and *K*-selected (●) populations (experiment 2).

also positive when the correlation is calculated between growth rate at 20 and all other densities, at 50 and all other densities, etc. Thus, the homozygous lines that have higher than average growth rates at one density in general do better at all densities. Therefore, the postulated trade-off assumed by Roughgarden is not seen within this collection of genotypes, although this does not preclude such a trade-off from appearing after the action of natural selection if the genotypes are intermixed and recombination becomes possible, as is in fact the case in experiment 2.

Experiment 2. The results of the selection experiment are summarized in Fig. 2 and Table 1. The figure shows the mean growth rate at each test density of the two types of selected populations. It can be seen that the *K*-selected populations have a greater mean growth rate than the *r*-selected populations at the high densities (500 or 750 flies) but smaller at the low density.

Table 1. Differences between *K*-selected and *r*-selected populations at three densities, with respect to two parameters

		Difference: *K*-selected minus *r*-selected	
Density	Parameter	Mean	95% confidence interval
10	Net productivity	−80	−160 to 0
	Growth rate	−0.17	−0.41 to 0.07
500	Net productivity	160	40 to 280
	Growth rate	0.12	0.03 to 0.21
750	Net productivity	300	130 to 470
	Growth rate	0.19	0.11 to 0.27

Table 1 gives for each test density the mean difference between the *K*-selected and the *r*-selected populations, and the 95% confidence intervals on the difference. At high density (500 or 750) the *K*-selected populations have greater growth rate and net productivity than the *r*-selected populations, and the differences are significantly greater than zero. At the low density (10 flies), the *r*-selected populations perform better: both the net productivity and the mean growth rate of the *r*-selected populations are greater than those of the *K*-selected populations, but only the difference in net productivity is statistically significant.

The results of experiment 2 demonstrate that the outcome of natural selection with respect to the rate of population growth depends on the environmental conditions: the two populations (*r*-selected and *K*-selected) have evolved differently. Moreover, there is evidence of a trade-off, or at least of a failure to maximize the capacity to grow at all densities: the *r*-selected population performs better than the *K*-selected population at low densities but worse at high densities. Other attempts to ascertain the evolutionary changes under regimes of *r*- or *K*-selection have failed to give evidence of such a trade-off (15, 16). For example, Luckinbill (15) found that populations of *Escherichia coli* maintained at high density performed better at all densities tested than populations that had been maintained at low density. He also observed that populations of *Paramecium* subject to *r*-selection performed better with respect to both parameters, *r* and *K*, than did unselected stocks.

Thus, the results of experiment 2 corroborate the theoretical prediction that the evolution of the parameters *r* and *K* depends on the density regime to which a population is exposed so that both parameters are not simultaneously maximized. Experiment 1 failed to manifest a trade-off between *r* and *K* in the 25 second-chromosome genotypes sampled from nature but made homozygous in the laboratory. Nevertheless, the 25 genotypes collectively had the genetic variability that made the evolution of such a trade-off possible, after being subject to alternative selection regimes.

This work was supported by National Institutes of Health Training Grant PHS 1 T32 GM07467-1 and by a contract with the U.S. Department of Energy.

1. MacArthur, R. H. & Wilson, E. O. (1967) *The Theory of Island Biogeography* (Princeton Univ., Princeton, NJ).
2. Gadgil, M. & Bossert, W. H. (1970) *Am. Nat.* **104,** 1–24.
3. Gadgil, M. & Solbrig, O. T. (1972) *Am. Nat.* **106,** 14–31.
4. Pianka, E. R. (1970) *Am. Nat.* **104,** 592–596.
5. Stearns, S. C. (1977) *Annu. Rev. Ecol. Syst.* **8,** 145–171.
6. King, C. E. & Anderson, W. W. (1971) *Am. Nat.* **105,** 137–156.
7. Charlesworth, B. (1971) *Ecology* **52,** 469–474.
8. Clarke, B. (1972) *Am. Nat.* **106,** 1–13.
9. Roughgarden, J. (1971) *Ecology* **52,** 453–468.
10. Smouse, P. E. (1976) *Am. Nat.* **110,** 849–860.
11. Roughgarden, J. (1979) *Theory of Population Genetics and Evolutionary Ecology: An Introduction* (Macmillan, New York).
12. Abrahamson, W. G. & Gadgil, M. (1973) *Am. Nat.* **107,** 651–661.
13. Menge, B. A. (1974) *Ecology* **55,** 84–102.
14. McNaughton, S. J. (1975) *Am. Nat.* **109,** 251–261.
15. Luckinbill, L. S. (1978) *Science* **202,** 1201–1203.
16. Luckinbill, L. S. (1979) *Am. Nat.* **113,** 427–437.
17. Tracey, M. L. & Ayala, F. J. (1974) *Genetics* **77,** 569–589.
18. Mueller, L. D. (1979) Dissertation (Univ. California, Davis, CA).
19. Ayala, F. J., Gilpin, M. E. & Ehrenfeld, J. G. (1973) *Theor. Popul. Biol.* **4,** 331–356.
20. Miller, R. (1974) *Biometrika* **61,** 1–15.