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DENSITY-DEPENDENT EVOLUTION OF LIFE-HISTORY TRAITS IN *DROSOPHILA MELANOGASTER*

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Abstract.—Populations of *Drosophila melanogaster* were maintained for 36 generations in *r*- and *K*-selected environments in order to test the life-history predictions of theories on density-dependent selection. In the *r*-selection environment, populations were reduced to low densities by density-independent adult mortality, whereas populations in the *K*-selection environment were maintained at their carrying capacity. Some of the experimental results support the predictions or *r*- and *K*-selection theory; relative to the *r*-selected populations, the *K*-selected populations evolved an increased larval-to-adult viability, larger body size, and longer development time at high larval densities. Mueller and Ayala (1981) found that *K*-selected populations also have a higher rate of population growth at high densities. Other predictions of the thoery are contradicted by the lack of differences between the *r* and *K* populations in adult longevity and fecundity and a slower rate of development for *r*-selected individuals at low densities.

The differences between selected populations in larval survivorship, larval-to-adult development time, and adult body size are strongly dependent on larval density, and there is a significant interaction between populations and larval density for each trait. This manifests an inadequacy of the theory on *r*- and *K*-selection, which does not take into account such interactions between genotypes and environments. We describe mechanisms that may explain the evolution of preadult life-history traits in our experiment and discuss the need for changes in theories of density-dependent selection.

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The modern theory of density-dependent selection has its origins in the works of MacArthur (1962) and MacArthur and Wilson (1967), who introduced the concept of density-dependent rates of population growth as measures of fitness and the notion that divergent environmental factors might lead to the evolution of different population characteristics. They argued that, in an environment with abundant resources, populations reduced to low densities by density-independent mortality should evolve a high intrinsic rate of growth (r) but would perform poorly at high densities. In contrast, populations experiencing high densities and strong competition for limiting resources should evolve high intraspecific competitive ability and enhance their carrying capacity (K).

The basic concepts formulated by MacArthur and Wilson (1967) have been expanded and made explicit through several mathematical theories (Charlesworth, 1971; King and Anderson, 1971; Roughgarden, 1971; Clarke, 1972). For example, Roughgarden (1971) assumes that the fitness (W_{ij}) of the ijth genotype is a linear function of total population size (N) as follows:

$$W_{ij} = 1 + r_{ij} - \frac{r_{ij}N}{K_{ij}}$$

where r_{ij} and K_{ij} refer to the intrinsic rate of growth and the carrying capacity, respectively, of the various genotypes. Assuming that an initial population is polymorphic for genotypes exhibiting a trade-off, so that genotypes with high r values have low K values and vice versa, the evolutionary outcome in Roughgarden's model would be dependent on the environment. In stable environments, the genotype with the largest K value is ultimately fixed, and all others are eliminated. Alternatively, when the population size is often reduced below its carrying capacity due to frequent episodes of density-independent mortality, the genotype with the highest r will be favored. According to this model, natural selection should favor the genotype making the highest per capita contribution to population growth at either high or low densities.

The theory of *r*- and *K*-selection has been expanded through verbal arguments developed and summarized by Pianka (1970, 1972), Gadgil and Solbrig (1972), Stearns (1976, 1977) and Taylor and Contra (1980); the extended theory hypothesizes that traits correlated with high *r* values or increased competitive ability will also respond to *r*- or *K*-selection. Thus, *r*-selection should favor rapid development, earlier reproduction, a larger number of offspring with smaller body size, and a shorter lifespan. Alternatively, *K*-selection should favor slower development, delayed reproduction, fewer offspring with larger body size, increased competitive ability, higher efficiency of resource utilization under crowded conditions, and increased investment of resources in progeny, resulting in higher viability and longer lifespan (Pianka, 1970; Stearns, 1977). This verbal theory, however, goes considerably beyond the mathematical theory. The verbal arguments use a qualitative interpretation of parameters, such as *r* and *K* in the logistic equation, in order to extend theoretical results from discrete-generation models to populations with overlapping generations. Detailed theoretical analyses of evolution in populations with age structure and density-dependent regulation have sometimes yielded results at odds with the verbal arguments; for example, natural selection can favor increased fecundity at earlier ages in density-regulated populations (Charlesworth, 1980). Density-dependent regulation of either fecundity or adult survival can also affect the evolution of high fecundity versus high juvenile survival (Iwasa and Teramoto, 1980). Therefore, the presence or absence of density-dependent regulation and the mechanism of its operation are important theoretical determinants of the evolution of life-history traits.

Few empirical studies have attempted to test the predictions of the verbal and mathematical theories of *r*- and *K*-selection using populations with known selection histories (for examples, see Gadgil and Solbrig [1972], Luckinbill [1978], Taylor and Condra [1980], and Mueller and Ayala [1981]). Due to the significant contribution of these concepts to the develoment of life-history theory, it seems important to test experimentally the fundamental predictions of *r*/*K*-selection theory. Therefore, we have used populations of *Drosophila melanogaster* maintained for several generations in either an *r*- or *K*-selection environment in order to test the following hypotheses: i) whether *r*-selected flies have shorter adult life spans and higher fecundity than *K*-selected flies; ii) whether *K*-selected offspring develop more slowly; iii) whether *K*-selected individuals have a larger body size; and iv) whether the higher rate of population growth observed for the *K*-selected flies under crowded conditions is due to a higher larval-to-adult viability. In addition, we have tested for differences in the larval competitive abilities of the *r*- and *K*-selection lines in other experiments that will be reported elsewhere.

MATERIALS AND METHODS

The flies used in this study were obtained from later generations of the populations described in Mueller and Ayala (1981). The following summarizes the method of selection used to maintain the *K*-selected and *r*-selected experimental populations; additional details are given in Mueller and Ayala (1981). The populations were kept at 23°C in half-pint culture bottles containing cornmeal and molasses medium treated with propionic acid to inhibit microbial growth. Three "*K*-selected" populations were maintained independently at their carrying capacity by the serial-transfer system. An initial sample of 100 adults laid eggs in culture medium for seven days, and the survivors and newly emerged progeny were transferred at weekly intervals to new bottles. Each bottle was kept for four weeks to provide sufficient time for the emergence of F_1 progeny. Thus, each population consisted of one bottle of egg-laying adults and three bottles containing eggs, larvae, pupae, and newly emerged adults. Under this regime, the carrying capacity of 700–1,000 adults was reached in 3–4 weeks and maintained during the course of the experiment. In the "*r*-selected" regime, 100 flies laid eggs for 24 hours in a culture bottle, and 100 progeny were collected 15 days later. They were given three days to recover from etherization and then placed in a culture bottle for 24 hours to repeat the cycle. After five generations, the size of the r-selected populations was lowered to 50 adults to reduce crowding; a major difference between the two selection regimes was the higher degree of larval crowding in the K-selected populations.

For the life-history experiments, two r-selected and two K-selected populations were taken at random from the set of six populations. There were two sets of experiments: the first dealt with adult lifetime fecundity and survivorship, and the other dealt with density-dependent adult body size, larval viability, and development rate. The adult survivorship and fecundity studies were started after 20 generations of selection; 36 generations had passed when the larval-survivorship experiments were initiated.

Adult Longevity and Fecundity

Fifty males and 50 females were sampled from the newly emerged adults of each r- and K-selected population. These flies were placed in half-pint culture bottles (25 pairs/culture) and allowed 24 hours to oviposit. After 15 days, the progeny from the bottles were aged two days, and 25 pairs per culture were again given 24 hours to oviposit. The emerging adults were then collected at daily intervals in order to start the fecundity and longevity experiments. Thus, the samples from the selected populations passed through two generations of common environmental conditions before the adults were used in experiments. The longevity of 100 males and 100 females from each selection line was measured at 23°C by placing ten pairs of adults per 6-dram vial and counting the survivors when they were transferred to fresh vials at two-day intervals.

Adult flies between one and 24 hours old were used to start the fecundity experiment. Three pairs of adults were placed in a 6-dram vial, and eggs were counted at daily intervals when the surviving flies were transferred to a new vial. Ten replicate vials were kept at 23°C for each of the two r- and K-selection lines.

Since we are interested in estimating fecundity at low densities and not the maximum fecundity, we did not follow the common procedure of placing a single pair of flies in each vial. As noted by Pearl (1932), however, even at low densities the fecundity per female may show significant density effects. Therefore, our per capita fecundity estimates may be low relative to other studies on *Drosophila melanogaster* (e.g., Giesel and Zettler, 1980; Rose and Charlesworth, 1981).

Density-Dependent Larval Survival, Development Rates, and Adult Body Size

Two hundred males and 200 females were sampled from the newly emerged adults of the four r- and K-selected populations. These adults were allowed to lay eggs for seven days at a density of 20 pairs per half-pint culture bottle. Fifteen days after the onset of egg-laying, adult progeny were collected to start the larval-survivorship experiment. Three hundred males and 300 females were obtained for each of the r- and K-selected populations. These were placed in separate culture bottles at a density of 30 pairs per bottle and allowed 12 hours for egg-laying. The adults were then removed, and the cultures were kept for an additional 24 hours while the eggs hatched into first-instar larvae. The larvae were picked from the surface of the culture medium with a camelhair brush and placed at fixed densities in 22 cm^3 vials containing 8 cm^3 of cornmeal and molasses medium. The larvae were kept at 21°C at the following densities: i) 30 (12 replicate vials/selection line), ii) 160 (eight replicate vials/selection line) and iii) 320 (six replicate vials/selection line). When the adult flies began to emerge, they were collected and counted at 12-hour intervals until no further emergence was observed over a 24-hour period. The flies emerging from each replicate were sexed and placed in empty vials at 3°C until the end of the experiment. At this time, the vials were placed in a drying oven at 100°C for 24 hours. After the vials had cooled, the dry weights of the males and females from each replicate were recorded.

RESULTS

Density-Dependent Larval Survival, Development Rates, and Adult Body Size

Experiments using first-instar larvae reared at three different densities show several life-history differences between the *r*- and *K*-selected populations. The magnitude of these differences and relative rankings of the *r*- and *K*-selected populations depend on the density of competing larvae. Figure 1 shows differences between the *r*- and *K*-selected populations in the number of first-instar larvae surviving to the adult stage. Compared to the *r*-selected populations, the larvae from the *K*-selected populations have a significantly higher rate of survival to adulthood at the 160 ($F_{[1, 28]} = 33.4$, $P < 0.01$) and 320 ($F_{[1, 20]} = 22.5$, $P < 0.01$) densities, but at the lowest density (30 larvae/vial) the mean viabilities of the *r*- and *K*-selected populations are not significantly different ($F_{[1, 44]} = 1.7$, $P > 0.05$). This pattern of larval viability results in a significant selection population × larval-density interaction in a two-way analysis of variance ($F_{[6, 92]} = 10.2$, $P < 0.01$).

Differences also exist between the *r*- and *K*-selected populations for mean rate of development from the larval to the adult stage (Fig. 2). Females from the *r*-selected populations take significantly longer to develop at the densities of 30 ($F_{[1, 637]} = 19.8$, $P < 0.01$) and 160 ($F_{[1, 2{,}082]} = 20.9$, $P < 0.01$) but have a shorter development time at a density of 320 ($F_{[1, 2{,}693]} = 5.0$, $P < 0.05$). Differences between males are in the same direction, but they are statistically significant at densities of 30 ($F_{[1, 650]} = 6.0$, $P < 0.02$) and 320 ($F_{[1, 2{,}667]} = 38.8$, $P < 0.01$) and not at 160 ($F_{[1, 1{,}940]} = 0.5$, $P > 0.05$). Two-way analyses of variance indicate that the population × larval-density interaction is significant for females ($F_{[6, 5{,}412]} = 2.6$, $P < 0.01$) but not at the $P = 0.05$ level for males ($F_{[1, 5{,}257]} = 1.7$, $P < 0.06$). In summary, whether the *r*- or the *K*-selected populations exhibit a faster rate of development depends on the larval density at which the test is performed.

The total weight of adult flies (Fig. 3) is higher for the *K*-selected populations than for the *r*-selected populations at larval densities of 160 ($F_{[1, 28]} = 54.6$, $P < 0.01$) and 320 ($F_{[1, 20]} = 20.1$, $P < 0.01$) but not at 30 ($F_{[1, 44]} = 0.02$, $P > 0.05$). Once again, there is a significant population × larval density interaction in a two-way analysis of variance ($F_{[6, 92]} = 9.7$, $P < 0.01$).

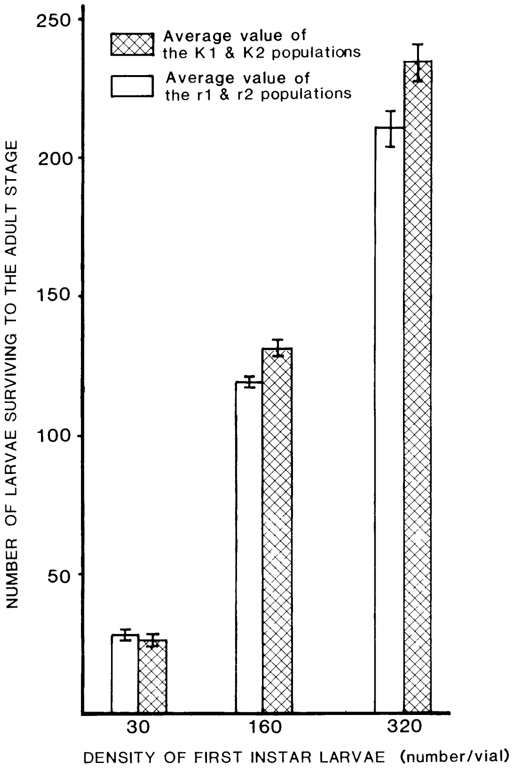

FIG. 1. Mean numbers of first-instar larvae surviving to the adult stage in the *r*- and *K*-selected populations. The lines at the top of each vertical bar show 95% confidence intervals on the mean.

Two factors contribute to the larger biomass produced by the *K*-selected populations: i) a higher rate of larval-to-adult survival at densities of 160 and 320 (Fig. 1), and ii) a higher weight per individual of males and females from the *K*-selected populations (Fig. 4). *K*-selected males are heavier than *r*-selected males at all densities, and differences are significant at densities of 160 and 320 ($F_{[1, 28]} = 8.8$, $P < 0.05$; $F_{[1, 20]} = 14.8$, $P < 0.01$) but not at the lowest larval density ($F_{[1, 44]} = 4.9$, $P < 0.05$). *K*-selected females also are larger than *r*-selected females when flies are reared at intermediate and high densities, but differences between populations are significant only for the intermediate density ($F_{[1, 28]} = 16.4$, $P < 0.01$).

Adult Survivorship and Fecundity

In contrast to results from the larval experiments, few statistically significant differences exist between the *r*- and *K*-selected

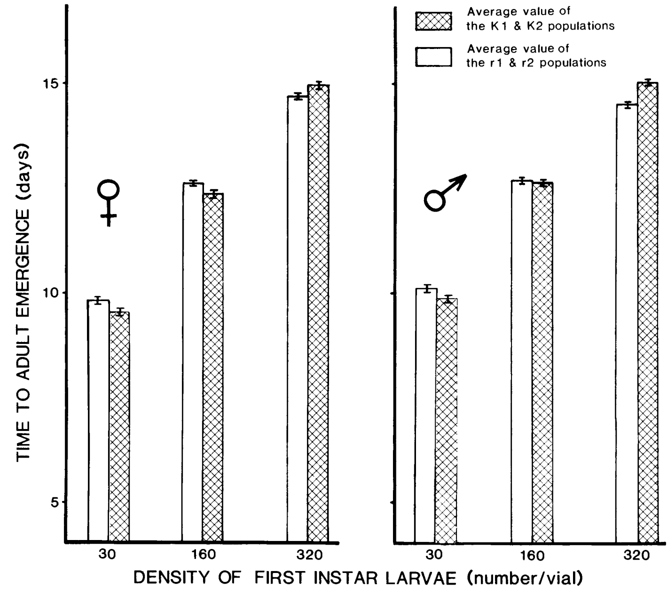

FIG. 2. Mean male and female development times from the first-instar larva to the adult stage. The lines at the top of each vertical bar show 95% confidence intervals.

populations for either adult survivorship or fecundity. The longevity curves for the adult males and females of each population are plotted in Figure 5. Pairwise comparisons between *r*- and *K*-selected populations are not significantly different for either female or male survivorship curves (Kolmogorov-Smirnov tests, all $P < 0.05$ [Sokal and Rohlf, 1981, p. 440]).

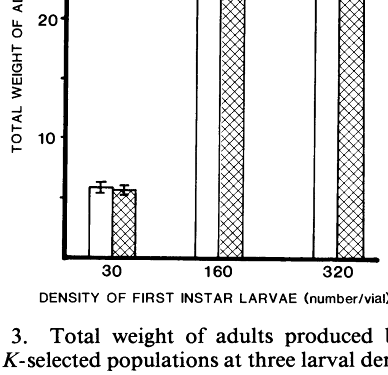

FIG. 3. Total weight of adults produced by the *r*- and *K*-selected populations at three larval densities. The histogram bars show the mean values, and the lines show 95% confidence intervals.

Longevity curves for the two *r*-selected populations are significantly different from each other, whereas those for the two *K*-selected populations do not differ. Compared to the r_2 line, the r_1 line has a higher percentage of male ($D = 0.19$, $P < 0.01$) and female ($D = 0.20$, $P < 0.05$) survivors in the middle region of the distributions (i.e., approximately days 40–72; Fig. 5), but there are no significant differences between the K_1 and K_2 lines for either male ($D = 0.05$, $P > 0.05$) or female ($D = 0.07$, $P > 0.05$) longevity.

Table 1 gives the mean number of eggs laid per female per day for each selection line. The mean fecundity of the *r*- and *K*-selected flies are not significantly different ($F_{[1,\ 3{,}001]} = 0.43$, $P > 0.50$), and there are no age-dependent differences in fecundity among different populations.

DISCUSSION

Two major results emerge from this study: i) there are significant differences between *r*- and *K*-selected populations in preadult life-history traits, and ii) these differences

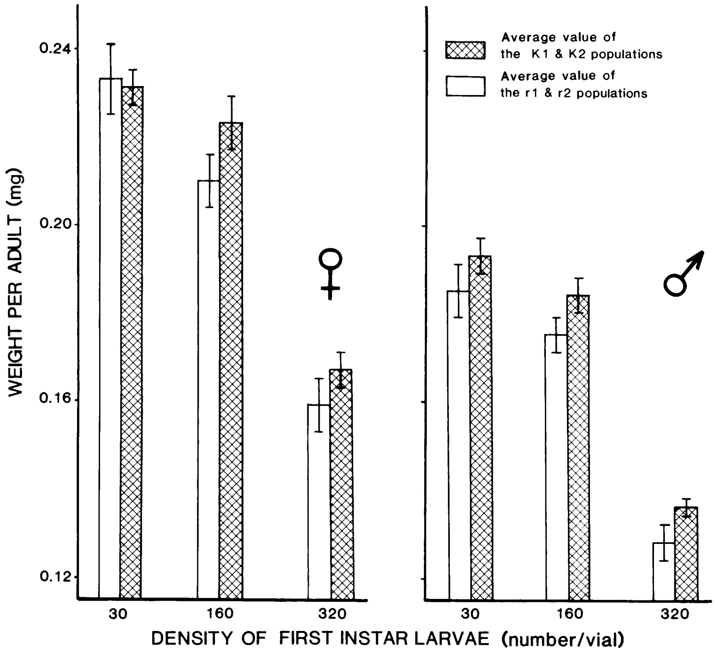

FIG. 4. Individual weights of male and female adults from the *r*- and *K*-selected populations. The histogram bars show mean values, and the lines show 95% confidence intervals for three larval-density treatments.

are strongly dependent on larval density. The most dramatic results are the increased first-instar–adult survivorship and adult size in the *K*-selected populations. The differences between populations for both traits are greatest at the highest densities and are not significant at the lowest densities (Figs. 1, 4), resulting in a significant interaction between selection populations and larval density. Genotype × density interactions were also found for larval-to-adult emergence times (Fig. 2) and larval competitive ability (Bakker, 1961, 1969); these results indicate that the theory of *r*- and *K*-selection is incomplete, since it does not account for genotype × density interactions, and there is a need to incorporate them in more realistic theoretical models.

The variation we observed in viability and female body size can explain much of the differentiation found in the rates of population growth of the *r*- and *K*-selected flies (Mueller and Ayala, 1981). Since it is well known that larger *Drosophila* females lay more eggs (Chiang and Hodson, 1950; Robertson, 1957; Mueller, 1987), the increased rate of population growth of the *K*-selected flies under high-density conditions is probably due to both increased larval-to-adult viability and increased female fecundity. Mueller and Ayala (1981) used per capita rates of growth of the *r*- and *K*-selected populations as an estimate of relative fitness. When the average relative fitness of the *r*-selected populations was set equal to one, the relative fitness of the *K*-selected populations at low density (10 adults/bottle) was 0.91, whereas at high densities (500 and 750 adults/bottle) it was 1.25 and 1.56. In this experiment, differences between the *r*- and *K*-selected populations were largest at high densities, and fitness values ranked as expected from *r*- and *K*-selection theory (e.g., Roughgarden, 1971).

The lack of significant differences between populations for adult fecundity and survivorship may, in part, be due to testing adults reared from low larval densities. Fecundity differences would probably exist under more crowded experimental conditions, since studies on *Drosophila* have shown fecundity decreases with decreasing body size when the later is affected by larval crowding (Chiang and Hodson, 1950; Robertson, 1957; Prout and McChesney, 1985). For example, the thorough experiments of

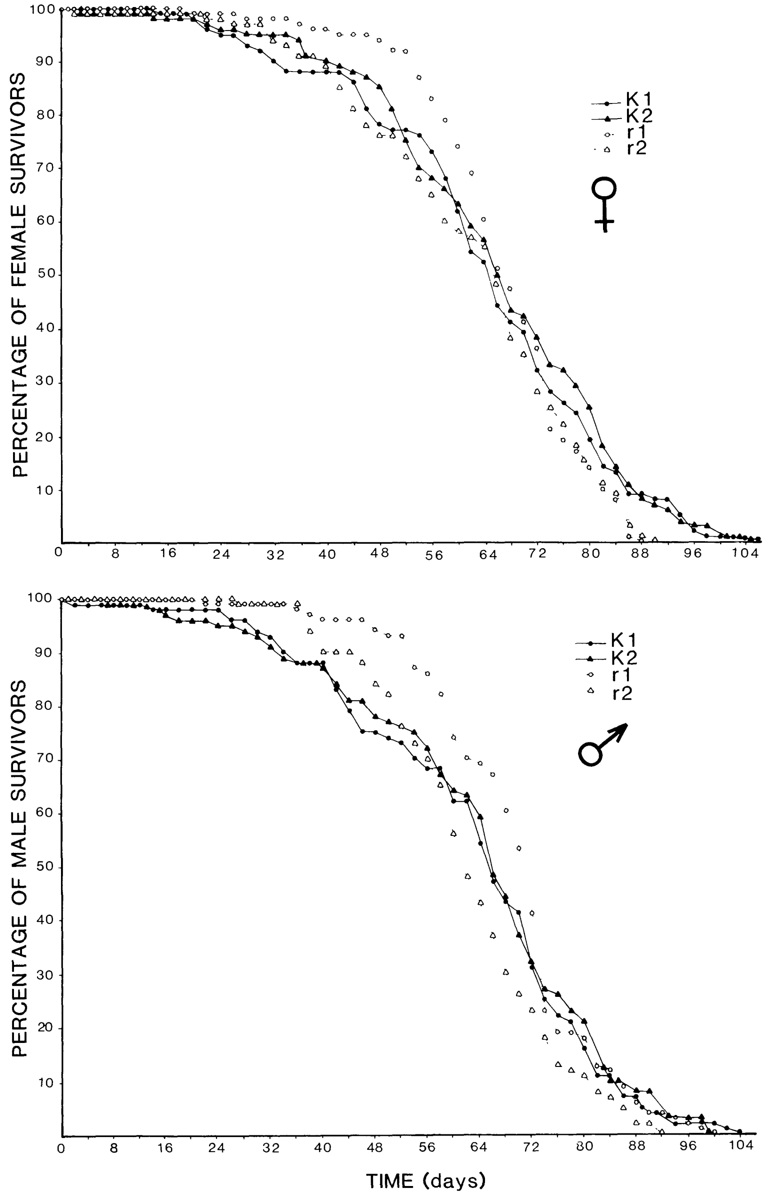

FIG. 5. Percentage of male and female adults surviving to a given age. The initial number in each cohort is 100.

Prout and McChesney (1985) determined that higher egg densities (during rearing) decreased the fecundity of *D. melanogaster*. In our experiment, crowded females in the *r*-selected populations (from the 160 and 320 densities; Fig. 4) weigh 16% less than females from the *K*-selected populations. Using a regression of first-week fecundity on size for the K_1 population (Mueller, 1987), we estimate that the observed 16% weight reduction of the *r*-selected females represents a 14% reduction in fecundity for small (thorax length = 0.68 mm) flies. Therefore, under crowded rearing conditions, the *K*-selected females should have a higher fecundity than the *r*-selected females. This would be contradictory to the prediction that *r*-selected individuals evolve higher fecundity.

The evolved differences in viability and adult body size could be explained by changes in: i) efficiency of larval food utilization, ii) the digging behavior of larvae, iii) the height at which larvae pupate above the culture medium, and iv) larval tolerance to waste products. The verbal theory of *r*- and *K*-selection predicts that *K*-selected organisms should exploit food resources more efficiently (Cody, 1966; Pianka, 1970; Southwood, 1976). Competition for limiting food resources has been studied extensively in *Drosophila* (Bakker, 1961, 1969; Nunney, 1983). Crowded *Drosophila* cultures often have unused food on the bottom, and larvae able to gain access to this resource by digging more deeply might be at an advantage in crowded cultures. Godoy-Herrera (1977, 1978) found genetic variation in *D. melanogaster* for digging behavior, and evolutionary changes in this trait could explain the observed increase in the size and viability of our *K*-selected flies.

Another possible explanation for viability differences between the *r*- and *K*-selected populations is that larvae pupating close to or on the surface of the medium incur an increased risk of drowning in crowded cultures (Chiang and Hodson, 1950). Bauer and Sokolowski (1985) determined that pupation height in *D. melanogaster* is controlled by genetic variation on the second and third chromosomes; genetic differences in pupation height between the *r*- and *K*-selected populations (Mueller and Sweet, 1986) may explain some of the viability differences we have observed.

Differences in the development times of *r*- and *K*-selected males and females are also strongly affected by larval density (Fig. 2). Since the quality of food resources deteriorates rapidly for the *K*-selected populations, our experimental conditions should favor faster developing flies in these populations. Moreover, the semicontinuous nature of the serial-transfer system provides rapid developers with earlier opportunities for reproduction. At 23°C, most adults emerge 10–13 days after egg-laying; since the *r*-selected adults are collected after two weeks, our maintenance regime should only select against very slow developers (i.e., those taking longer than 14 days). The observation that *K*-selected flies develop more rapidly at low and intermediate densities is consistent with these ideas. At the highest density, however, males and females from the *K*-selected populations take longer to develop. In this case, we hypothesize that surviving larvae in the *r*-selected populations develop and pupate before waste concentrations get beyond a critical level (e.g., Botella et al., 1985), and the remaining slow-developing larvae linger in the third instar and ultimately die. In the *K*-selected populations, however, many very slow-developing larvae can survive. This additional class of surviving larvae could account for both the increased viability and the increased development time of the *K*-selected populations.

TABLE 1. Mean number of eggs per day (±standard error) laid by females from *r*- and *K*-selected populations. The two means for the *r*-selected populations are not significantly different from the two means for the *K*-selected populations (Scheffé's *F*-ratio method [Kirk, 1968, p. 81], $P > 0.05$). N = number of replicate egg counts.

Population	Number of eggs laid per female per day	N
r_1	5.9 ± 0.2	732
r_2	5.6 ± 0.2	820
K_1	5.2 ± 0.2	746
K_2	6.4 ± 0.2	707

Few experimental studies have tested for evolutionary changes in life-history traits in populations selected in *r* and *K* environments. Experiments on dandelions (Solbrig, 1971; Gadgil and Solbrig, 1972; Solbrig and Simpson, 1974) revealed the occurrence of different isozyme biotypes in sites with varying levels of density-independent disturbance due to mowing and trampling. In the least-disturbed site, the predominant biotype had higher competitive ability and lower seed set, and it allocated a higher proportion of resources to nonreproductive (leaf) biomass than the predominant biotype in disturbed sites. These results fit a subset of *r*- and *K*-selection theory and helped to further define its life-history predictions. Some predictions are also supported by the study of Taylor and Condra (1980) on laboratory populations of *Drosophila pseudoobscura.* They found that *r*-selected populations had a shorter egg-to-adult development time, lower preadult viability, and shorter adult life span than *K*-selected populations. The evolution of shorter development time in the *r*-selected populations is predictable, since their *r*-selection regime favored rapid development by using only the early-emerging flies for oviposition. Contrary to theory, several additional traits (i.e., body size, fecundity, time to first oviposition, intrinsic rate of increase, and carrying capacity) did not differ between the *r*- and *K*-selected populations. The lack of changes in carrying capacities in Taylor and Condra's (1980) study is surprising, since there are several previous observations of evolutionary changes in carrying capacities in laboratory populations of *Drosophila* (Buzzati-Traverso, 1955; Ayala, 1965, 1968).

Our results parallel those of Taylor and Condra (1980) in that several traits diverged in the direction predicted by theory, but additional key traits did not evolve differences. The increased larval-to-adult viability, longer development time at high larval density, and larger body size of the *K*-selected flies supports the predictions of *r*- and *K*-selection theory. The results of a recent experiment using a white-eyed mutant strain as a competitive standard are consistent with an additional prediction that *K*-selected larvae evolve greater competitive ability (Mueller, unpubl.). In contrast, the lack of differentiation in longevity and fecundity and the longer development time of the *r*-selected populations at the lowest density do not agree with theoretical predictions. There is also no evidence among our populations that *r*-selection produces type-III survivorship, whereas *K*-selection favors type-I or type-II-survivorship (Pianka, 1970).

A variety of factors can account for the absence of differentiation in major life-history traits. Several studies of life-history evolution in *Drosophila* (Taylor and Condra, 1980; Barclay and Gregory, 1981, 1982) have tested adults raised only at low densities. There is no reason to believe that adult fecundity and viability are insensitive to density or that observations at low densities can be used to predict differences at high densities. Although we have not examined age-specific fecundity and adult survival at high densities, our results on female body size indicate that fecundity differences would exist between the *r*- and *K*-selection lines if they were tested under more crowded conditions.

Differences between the *r*- and *K*-selected populations are very small at low densities (Figs. 1, 3; Mueller and Ayala, 1981) but are easily detected at high densities. This may be due to weaker selection pressure on the *r*-selected lines compared to the *K*-selected lines, and therefore, the *r* lines show less response to selection. Density-regulation can also strongly affect a specific life-history trait (e.g., adult longevity) without producing any selection pressure on the trait. This has been analyzed theoretically by Prout (1980) in a model incorporating density-dependent regulation in one life-history stage with density-independent selection acting on others.

The fit between the theory of *r*- and *K*-selection and experimental data on *Drosophila* and other organisms is inadequate. Since most models of density-dependent selection rely on general descriptions of the effects of density on population growth, there is a need for alternative models that incorporate more realistic and explicit biological assumptions. Generality in models is often achieved using assumptions that are imprecise and unrealistic for specific populations (Levins, 1966); this has led Stearns (1977) to point out that the parameter *K* of the logistic equation is unrelated to measurable life-history traits. We feel that current efforts towards understanding density-dependent natural selection in *Drosophila* and other organisms are limited by the paucity of models incorporating realistic biological assumptions.

Using recursion equations with life-history assumptions based on detailed laboratory experiments, Prout (1980, 1984) and Prout and McChesney (1985) substantially advanced the modeling of density-dependent population dynamics in *Drosophila.* Similar analyses could improve density-dependent selection models applicable to *Dro-*

sophila by incorporating key aspects of their biology (e.g., the effects of density on egg-to-adult survival and fertility [Prout and McChesney, 1985]; genotype × density interactions for larval viability, larval-to-adult development rate, and female body size [Figs. 1, 2, 4]; density-dependent effects on larval competitive ability [Bakker, 1961, 1969; Nunney, 1983; Mueller, unpubl.]). Recently, others have sought to improve theory by incorporating genetic variation for competitive ability in models of *r*- and *K*-selection (Christiansen and Loeschke, 1980; Anderson and Arnold, 1983; Asmussen, 1983) and by developing density-dependent selection models tailored to fit *Drosophila* biology (Mueller, unpubl.). We hope that continued integration of empirical and theoretical studies will lead to an increased understanding of the mechanisms of density-dependent selection and the evolution of life-history traits.

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