



Genetic Covariation Among Life-History Components: The Effect of Novel Environments

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GENETIC COVARIATION AMONG LIFE-HISTORY COMPONENTS: THE EFFECT OF NOVEL ENVIRONMENTS

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The findings of Bell (1984a, 1984b), Stearns (1983), and Murphy et al. (1983) seem to challenge life-history evolution theories involving trade-offs or antagonistic pleiotropy (Williams, 1957, 1966; Gadgil and Bossert, 1970; Schaffer, 1974; Rose, 1982, 1983). In particular, they do not obtain negative genetic correlations among fitness components: their correlations, when significant, are generally positive with respect to fitness. In contrast, Rose and Charlesworth (1981b), Rose (1984c), and Luckinbill et al. (1984) observed antagonistic responses to selection on life-history characters in the laboratory, results which clearly indicate underlying negative genetic correlations. Rose and Charlesworth (1981a) obtained a negative genetic correlation between early-life fecundity and longevity in a sib analysis of an outbred population of *Drosophila melanogaster*. The expectation of negative genetic correlations among fitness components arises from elementary considerations: alleles which give rise to positive genetic covariance should be driven toward fixation. At or near selective equilibrium, any remaining genetic covariance among fitness components will be predominantly negative (Falconer, 1977, 1981 p. 300; Rose, 1982).

Rose (1984b) showed that inbreeding may produce artifactual positive correlations among fitness components. We argue here that another aspect of experimental design, namely novel environmental effects, can also produce artifactual correlations that will tend to be positive. The experiments reported by Bell (1984a, 1984b), Stearns (1983), and Murphy et al. (1983) all involve laboratory life-history assays of organisms that had been subjected to the laboratory environment for only a few generations. Individuals with genotypes that fortuitously pre-

adapted them to the laboratory environment would be expected to have generally enhanced fitness, and vice versa. The effect of novel environments, then, should be to produce positive genetic correlations among fitness components or to reduce the degree of negative associations. A test of this hypothesis requires estimation of genetic correlations in one population under two sets of conditions: 1) the environment which the population has been subjected to for many generations and 2) a novel environment. Here we report such a test.

MATERIALS AND METHODS

We studied a population of *Drosophila melanogaster* that has been cultured in the laboratory since 1975. This population was derived from the wild S. Amherst, MA population (Ives, 1970), and is the population that was studied by Rose and Charlesworth (1981a). The laboratory population has been maintained in discrete generations of 2-weeks' duration, under conditions designed to insure outbreeding: the population size has consistently been in the thousands since founding. Since 1981, the population has been maintained at Dalhousie University in 25 × 95 mm shell vials, on banana-agar-corn syrup medium, at 25°C, and with a 24L:0D light regime. At the time of the present experiment, there had been approximately 80 generations in this environment. We will call it the "standard" environment.

Flies were reared for two generations in the standard environment at a controlled density of 30 per shell vial. Second-generation adults were collected as virgins, and 64 sires were then each mated with 12 unrelated dams. Mated dams were allowed to oviposit for 24 hr on yeast charcoal medium, and

TABLE 1. Means, heritabilities (h^2), and genetic correlation (r_A) for early-life fecundity and starvation resistance in standard and novel environments. Table entries are ± 1 standard error.

	Standard environment	Novel environment
Mean fecundity (eggs/24 hr)	69.5 \pm 1.11	25.9 \pm 0.78
Mean starvation time (hr)	33.2 \pm 0.32	40.7 \pm 0.43
h^2 , fecundity	0.702 \pm 0.175	0.503 \pm 0.191
h^2 , starvation	1.141 \pm 0.285	0.880 \pm 0.232
Genetic correlation, r_A	-0.913 \pm 0.027	-0.453 \pm 0.178
(95% C.I. for r_A)	(-0.859, -0.967)	(-0.093, -0.813)

30 eggs were collected from each laying tube for rearing in the standard environment (cf. Rose, 1979). Dams were then rejoined with their sires for another 24 hr and again allowed to oviposit individually on yeasted charcoal medium, 30 eggs per dam being subsequently collected for rearing in a novel environment. The novel environment consisted of Instant Drosophila Medium-Blue (Carolina Biological Supply Co.), a temperature of 15.5°C, and a 0L:24D light regime.

Phenotypic assays were carried out on one daughter per dam, all assays being conducted in the laboratory at room temperature (25°C). The characters assayed were 24-hr fecundity at an early age and starvation resistance (time to death). For fecundity assays, females were paired with males and placed on yeasted charcoal medium. Greater starvation resistance is characteristic of flies with genetically increased life span (Service et al., 1985). Flies were starved under conditions described by Service et al. (1985), time to death being estimated to the nearest 3 hr.

Flies reared in the standard environment were 13–14 days old (from oviposition) at the beginning of the 24-hr fecundity assay. Development was much slower in the novel environment, and the fecundity assay for the novel environment was conducted when flies were 34–35 days old (from oviposition). This age was chosen to correspond as closely as possible to the physiological age of the flies assayed from the standard environment. It was determined by comparing the times to pupation in the two environments and multiplying the ratio obtained by 14.

We did not assay half-sib families in which more than five dams failed to produce adequate numbers of offspring. Thus, daughters of 52 sires and 457 dams were assayed from the standard environment, and daughters of 41 sires and 347 dams were assayed from the novel environment. Heritabilities and additive genetic correlations, and their standard errors were estimated according to the formulae of Falconer (1981) and Kempthorne (1969 pp. 264–267).

RESULTS AND DISCUSSION

There was significant additive genetic variance for early-life fecundity and starvation resistance in both environments (all $P < 0.001$). Mean fecundity decreased by 63% in the novel environment, while

resistance to starvation increased by 23% (Table 1). Heritabilities for both characters were generally high (Table 1). The additive genetic correlation, r_A , between early-life fecundity and starvation resistance was -0.913 in the standard environment, and -0.453 in the novel environment (Table 1). The 95% confidence intervals for these correlations do not overlap (Table 1).

We conclude that the strength of the negative additive genetic correlation between early-life fecundity and starvation resistance in our population of *D. melanogaster* was significantly reduced when measured in the novel environment. This result is in conformity with the hypothesized effects of novel environments. It suggests that genetic correlations determined under novel conditions may be systematically biased toward positive values.

The existence of appreciable additive genetic variance for early-life fecundity, despite many generations of presumably directional selection favoring increases in this character, confirms the earlier similar findings of Rose and Charlesworth (1981a) and Rose (1984a). The strong negative genetic correlation between early-life fecundity and starvation resistance in the standard environment is evidence for antagonistic pleiotropy between reproduction and survivorship, such pleiotropy possibly also explaining the maintenance of the additive genetic variance for fecundity (Rose, 1982, 1983, 1984a).

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