NOTES AND COMMENTS

GENETIC COVARIATION IN *DROSOPHILA* LIFE HISTORY: UNTANGLING THE DATA

Giesel et al. (1982*a*) have presented a set of experiments using *Drosophila melanogaster* which are difficult to interpret in terms of the reproductive effort life history theory of Williams (1966) and Gadgil and Bossert (1970). Most importantly, no consistent pattern of negative genetic correlation between early and late life history characters was found by Giesel et al. This result was not fortuitous, as earlier studies from the Giesel laboratory have all indicated generally positive genetic correlation between life history characters, when there is any significant correlation at all (Giesel 1979; Giesel and Zettler 1980; Giesel et al. 1982*b*). Giesel and Zettler (1980, p. 302) offered the conclusion that "all components of fitness are positively correlated: within limits, a strain which is 'fit' in one respect is superior in other aspects as well," and there are now a number of published experiments of similar design from this laboratory, all of which ostensibly bear out this thesis.

If this conclusion is in fact well founded and of general significance, then a great deal of theoretical work on the evolution of life histories must be reconsidered, for the general assumption has been one of trade-offs between life history fitness components (Gadgil and Bossert 1970; Taylor et al. 1974; Stearns 1976; Charlesworth 1980; Schaffer 1983). If such trade-offs do not exist, then the central thrust of this theory is irrelevant; but there is a problem, in that other investigators have found results out of keeping with those of Giesel et al. Hiraizumi (1961) and Simmons et al. (1980) found that high-fitness *D. melanogaster* chromosomes generally exhibit pleiotropic gene action which is antagonistic over fitness components: enhancement of one fitness component depresses another. Chromosomes of low fitness, however, exhibited no such pattern of antagonism. Rose and Charlesworth (1981*a*, 1981*b*) used the methods of quantitative genetics on an outbred laboratory *D. melanogaster* population, finding two different lines of evidence for antagonistic pleiotropy: negative additive genetic correlations and antagonistic selection responses between life history characters. Thus there is an apparent contradiction between the results found from different laboratories, all working on the same problem of fitness-component covariation within the same species, *Drosophila melanogaster*.

In order to resolve this contradiction, Rose and Charlesworth (1981*a*) suggested that the crucial underlying factor was the degree of inbreeding in the experimental material. All of the Giesel laboratory's experiments have used some degree of

inbreeding to obtain genetically differentiated lines. But the fitness-component means of inbred strains derived from outbred populations depend on the number and severity of recessive deleterious alleles which have been made homozygous by inbreeding (Wright 1977, pp. 41–43). Varying degrees of realized inbreeding depression should give rise to a pattern of positive covariation among inbred line means, so that spurious patterns of genetic correlation may be inferred, patterns which were not present in the outbred population(s) from which the inbred lines were derived.

The crucial test of this interpretation requires derivation of inbred lines from an outbred population which is known to exhibit antagonistic pleiotropy between fitness components. If such lines exhibit positive covariation in mean fitness components, then the results from such experiments do not provide reliable evidence concerning genetic variability in the original outbred population(s). This communication gives the results from an experiment of this kind.

The base population used was that of Rose and Charlesworth (1981a, 1981b), itself in turn derived from the well-known Amherst population studied by Ives (1970). This population had been kept outbred in the laboratory under stable conditions (25° C, abundant food, etc.) for about 150 generations before the start of the experiment. Inbred lines were obtained by three generations of full-sib mating. Female progeny for these lines were sampled singly from separate mothers and reared apart, to avoid all common environment effects specific to individual inbred lines. Adult phenotypes were assayed using the methods of Rose and Charlesworth (1981a), giving data on daily fecundity and longevity. Thirty lines were assayed using five females each, for a total of 150 assayed females. Line averages were calculated and then used to examine patterns of between-line genetic correlation.

Table 1 gives the correlations between line means for fecundity over 5-day periods, longevity, and the duration of fecundity. Though some sort of formal genetic correlation parameter might be inferred from these data (cf. Giesel et al. 1982a), such parameters are somewhat difficult to interpret, because of the lack of additive-dominance genetic correlation partitioning with designs of this kind. Though individual significance levels are given for these correlation parameters, it is doubtful that they are of any reliable statistical significance, because of both Bonferroni's problem of significance levels with multiple hypotheses (Koopmans 1981, p. 331) and the lack of serial independence between the parameters. In this case, there is only one hypothesis under test: whether or not positive correlations predominate over negative correlations. As may be seen from the table, there is only one negative correlation, and it is not even nominally significant. All such nominally significant correlations are positive. The results thus parallel the results from the Giesel laboratory, and misrepresent the pattern of genetic covariation of the population from which the inbred lines were derived.

In addition to the work on inbred lines, the Giesel laboratory has published some results obtained from crosses of inbred lines (e.g., Giesel et al. 1982a, p. 474), in which the problem of inbreeding depression is mitigated. Not all of the significant genetic correlations are positive in such cases and fewer data of this kind have been published, so as yet there is no well reproduced, distinct, and

TABLE 1

Drosophila Life History Character Correlations among Line Means

	Five-Day Fecundities over the Indicated Days of Assay								Longevity	Duration of Fecundity
	1–5	6–10	11–15	16–20	21–25	26–30	31–35	36–40		
1–5		.623*	−.107	.264	.564**	.403*	.594**	.540**	.010	.447*
6–10			.337	.471**	.680***	.639***	.552**	.490**	.500**	.826***
11–15				.545**	.414*	.567**	.413*	.417*	.232	.406*
16–20					.856***	.864***	.743***	.794***	.451*	.705***
21–25						.921***	.821***	.804***	.536***	.778***
26–30							.856***	.794***	.537***	.822***
31–35								.874***	.303	.688***
36–40									.216	.613***

* $P < .05$.
** $P < .01$.
*** $P < .001$.

consistent pattern in the results from such crossed lines, as compared with the Giesel results using uncrossed inbred lines. In any case, depending on the likelihood of regained heterozygosity at loci with recessive deleterious alleles or true overdominance, a variety of genetic correlation patterns are a priori conceivable with such artificial genotypes.

These results do not show that the evolutionary conclusions adduced using the results of the Giesel studies are incorrect. The populations sampled in those studies could, in fact, have lacked antagonistic pleiotropy among high-fitness alleles. The present results only establish that there is no necessary relationship between the genetic covariation patterns of life history characters found from inbred lines and those of outbred populations. Thus the experiments of Giesel et al. do not refute the prevalent assumption of reproductive effort trade-offs, because there is no reliable evolutionary interpretation to be made of them.

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MICHAEL R. ROSE

DEPARTMENT OF BIOLOGY
DALHOUSIE UNIVERSITY
HALIFAX, NOVA SCOTIA B3H 4J1, CANADA