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A search for trade-offs among life history traits in *Drosophila melanogaster*

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Summary

Are there underlying developmental and physiological properties of organisms that can be used to build a general theory of life history evolution? Much of the theoretical work on the evolution of life histories is based on the premise of negative developmental and genetic correlations among life history traits. If negative correlations do not exist as a general rule then no general theory taking them into account is possible. Negative genetic correlations among life history traits can come about by antagonistic pleiotropy. One cause of antagonistic pleiotropy is cost allocation trade-offs. Since cost allocation trade-offs are due to underlying physiological constraints they are expected to be common to closely related groups. A second form of antagonistic pleiotropy is specialization of genotypes to different niches. This type of antagonistic pleiotropy is expected to be specific to each population. We looked for trade-offs in life history traits of longevity and fecundity in *Drosophila melanogaster*. We used a half-sib mating design and raised the offspring at two temperatures, 19°C and 25°C. Correlations between longevity and fecundity showed some evidence of antagonistic pleiotropy at high temperature with no evidence of any trade-offs at low temperature. Correlations of early and late fecundity traits did show evidence of cost allocation trade-offs at both temperatures. Antagonistic pleiotropy was also found for cross-environmental correlations of fecundity traits. We conclude that, although life history trade-offs can not be generally assumed, they are frequently found among functionally related traits. Thus, we provide guidelines for the development of general theories of life history evolution.

Keywords: Antagonistic pleiotropy; cost allocation trade-offs; *Drosophila melanogaster*; fecundity; life history; longevity.

Introduction

Controversy has arisen about whether genetic and developmental correlations among life history traits of fecundity and longevity are primarily positive or negative (Wattiaux, 1968; Rose and Charlesworth, 1981a, 1981b; Rose, 1984a; Giesel *et al.*, 1982; Giesel, 1986; Bell, 1984a, 1984b, 1986; Reznick *et al.*, 1986). Resolving this issue is important with regards to two issues in evolutionary biology. First, negative genetic correlations between two traits can act to preserve genetic variation (Falconer, 1981). The discovery of significant amounts of genetic variation for traits closely related to fitness (see reviews in Rose, 1983; Mousseau and Roff, 1987; Roff and Mousseau, 1987) is contrary to Fisher's (1930) proposition that selection should eliminate such variation. Negative genetic correlations among life history traits are one resolution of this problem. Second, much of the theoretical work on the evolution of life histories is based on the premise of negative developmental (within-environment) and genetic correlations among life history traits (e.g. Charlesworth, 1980). If these traits are not negatively correlated then the

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theoretical work will need to be reconsidered. The strong disagreement about the existence of trade-offs underscores the need for more data.

Related to the question of the sign of the correlation is the question of whether those correlations are consistent across environments. General rules governing life history evolution are only useful if they are true in many species and a majority of environments. If negative correlations do not exist as a general rule then no general theory taking them into account is possible. Recently, Clark (1987) questioned the utility of laboratory measures of genetic correlations since 'the estimates depend on the environment(s) employed, the environmental covariance, and the genotype–environment interactions' echoing concerns of others about genotype–environment interactions and the use of novel laboratory environments (e.g. Gupta and Lewontin, 1982; Service and Rose, 1985; Sultan, 1987). If it is true that genotype–environment interactions have overwhelming effects on genetic correlations then no estimate is informative. Natural environments are constantly changing from minute to minute, day to day, and year to year. If genotype–environment interactions are so pervasive then measurements done this year will have no predictive value for next year.

Instead of worrying about whether genotype–environment interactions are pervasive the search should be for correlations that are stable across environments. Are there underlying developmental and physiological properties that predict the existence of negative correlations under most circumstances? Since the search is for stable correlations then the issue of novel environments is moot. We do not mean to imply that any set of experimental conditions is acceptable. An experimental environment must still be constrained within the natural limits of the organism under study. Presently, few investigators have measured genetic correlations in more than one environment (Giesel *et al.*, 1982; Via, 1984; Service and Rose, 1985; Giesel, 1986; Groeters and Dingle, 1987).

Hypotheses explaining the cause of negative correlations among life history traits can be gathered under two headings. The first, antagonistic pleiotropy, is genetic (e.g. Williams, 1957; see review in Rose, 1983). The second, cost allocation trade-offs, is usually given only in phenotypic terms (see review in Bell, 1984a). We re-express the cost allocation hypothesis in genetic terms. In doing so we show that, while the two types of hypotheses may be referring to the same underlying phenomenon, antagonistic pleiotropy does not necessarily imply allocation trade-offs.

Antagonistic pleiotropy results when an allele enhances fitness through one trait while decreasing fitness through a second trait. It can be identified by negative genetic correlations among traits. For example, suppose that the fitness function was such that individuals with high early and late fecundities were favored. Then selection would fix any alleles that favored both traits and eliminate any alleles deleterious for both traits. Those alleles positive for one trait and negative for the other would continue to segregate. Genetic variation would be maintained for both traits and the genetic correlation of the traits would be negative (Falconer, 1981). Critical to the prediction of negative genetic correlations is the assumption that selection has been consistently in one direction for both traits long enough to eliminate variation in positively pleiotropic loci.

The cost allocation hypothesis supposes that either the environment or the developmental system imposes some sort of constraint on possible life history patterns. This hypothesis is usually expressed in phenotypic terms. For example, if there were a fixed total amount of resources available for egg-laying the laying of an egg early in the adult life span would necessarily mean that one egg less could be laid later. This trade-off creates a negative correlation between the traits if measured over an array of individuals with the same fixed amount of resources.

When placed in genetic terms cost allocation trade-offs are seen to be a form of antagonistic

pleiotropy. Consider a biosynthetic pathway with a bifurcation. At the ends of that bifurcation are two life history traits such as early and late fecundity. A single enzyme controls the relative amounts of substrate that pass down the two pathways, and forms exist which favor one pathway over the other. Assume that both traits are under positive selection and the substrate or its precursors are limited. Then the allelic variants will remain segregating in the population due to antagonistic pleiotropy. Other scenarios can be envisaged. For example, the pleiotropy may occur through indirect effects on resource use by multiple enzymes rather than by direct action of a single enzyme. Consider two enzymes that compete for the same substrate. If the substrate is limited, then the enzyme that is more efficient in garnering the substrate will dictate the physiological pathways which will have access to the substrate. Again, positive selection on both pathways will lead to the maintenance of genetic variation at both loci. Thus, we have recast the cost allocation hypothesis and shown it to be a form of antagonistic pleiotropy.

On the other hand, antagonistic pleiotropy does not have to result from allocation trade-offs. For example, a regulatory gene may be responsible for turning on genes that increase early fecundity while turning off genes that increase late fecundity. No resource limitation may be involved. Another form of antagonistic pleiotropy that does not include allocation trade-offs is the expression of genes in two different environments (Hedrick *et al.*, 1976; Hedrick, 1986; Bell, 1984a). If the same genes are responsible for the trait in both environments and different alleles are favored in the two environments, then we have a different form of antagonistic pleiotropy, niche specialization.

The allocation hypothesis and the pleiotropy hypothesis make several predictions that can be used to distinguish between them. The first prediction is that cost allocation trade-offs will be found among functionally related traits. The existence of allocation trade-offs can be identified by examining correlations among genetically identical or closely related individuals. We assume that genetically identical or closely related individuals raised in a uniform environment have approximately the same amount of resources. If that fixed total pool must be allocated among various life history components, survival vs reproduction or early vs late reproduction, then random differences in allocations will create negative correlations among the individuals.

We recognize that a very important assumption exists in the interpretation of the within-environment correlations as indicating allocation trade-offs. We assume that all individuals raised in the same environment have equal resources once genetic effects are removed by subtracting the genetic correlation from the residual correlation. If the assumption of equal total resources does not hold then we would expect positive correlations among traits (van Noordwijk and de Jong, 1986). Thus, the within-environment correlations represent upper bounds on the existence of allocation trade-offs. Our conclusions about negative correlations are likely to be robust, while conclusions about positive correlations are suspect.

The second prediction of both hypotheses is the existence of negative genetic correlations among life history traits in natural populations. Unfortunately, a failure to meet this prediction does not invalidate the hypotheses. A positive genetic correlation could be due to either the absence of antagonistic pleiotropy or a lack of consistently strong positive directional selection on both traits. For example, selection processes may have left segregating alleles at loci which affect total resource acquisition. These alleles would cause a positive genetic correlation among resource-limited traits. Linkage disequilibrium also can confound estimates of additive genetic variances and covariances (Lande, 1976). But, if allocation trade-offs exist, a negative correlation among the traits for genetically identical or closely related individuals will still be observed. Other forms of antagonistic pleiotropy do not make this prediction.

Previous studies (e.g. Rose and Charlesworth, 1981a; Giesel *et al.*, 1982; Service and Rose, 1985; Giesel, 1986) have focused on additive genetic correlations. However, Rose (1982) has

shown that genetic variation can be maintained by anatagonistic pleiotropy for the case of two loci with multiplicative fitnesses. This suggests that the non-additive component of genetic variance may be important in cases of antagonistic pleiotropy. Such epistatic systems can be very effective in maintaining genetic variation (Wright, 1969; Goodnight, 1987). The competition of two enzymes for the same substrate is one example of such epistasis.

In looking for trade-offs among life history traits in *Drosophila melanogaster* we concentrated on correlations among three pairs that have been the focus of most of the discussions about trade-offs: longevity and peak fecundity, longevity and total fecundity, and peak fecundity and fecundity in the last third of life. Fecundity in the last third of life can be a difficult trait to interpret since under laboratory conditions individuals may live well beyond egg-laying age. We include it here primarily for comparison with previous studies. We also examined correlations among three-day fecundities during the period of maximal egg-laying. To test the cost allocation and antagonistic pleiotropy hypotheses we examined the following: (1) correlations among half- and full-sibs, as evidence of genetic correlations; (2) within-environment correlations among full-sibs with the genetic correlation removed, as evidence of allocation trade-offs; and (3) cross-environment correlations among half- and full-sibs, as evidence of differential adaptation to niches, negative correlations among individuals indicating the existence of niche specialization.

A point of disagreement in previous studies concerned the use of long-captive but mass-cultured stocks versus newly caught but inbred lines (Giesel *et al.*, 1982; Rose, 1984a). The individuals used in this study were derived from flies captured two to three months before the start of the experiment and kept under conditions of mass culture.

Methods

Our base population was a line established with 301 flies captured in several locations in the DeKalb area during September 1986. The flies were maintained in mass culture at 21°C for two to three months before the start of the experiment.

Sibships were established by collecting 46 males and 138 females as newly eclosed adults. These parents were a combination of second- and third-generation captive bred individuals. The flies were kept for one day then each male was allowed to mate for 24 h with three females. The females were separated and allowed to oviposit in vials for six days, being given new vials daily. The food was standard cornmeal–molasses–agar, supplemented with live yeast. The vials from alternate days were placed at either 19°C or 25°C such that each male–female combination produced three vials at each temperature.

Two female offspring from the first and third vials from each temperature, eight offspring per dam, were measured. Each female was placed with one male in an oviposition chamber maintained at the same temperature as larval development. Each set of chambers consisted of 18 plastic tubes glued together. One end of the chambers was covered with bridal veil mesh and the other end of each tube was closed with a foam plug. The gauge of the mesh was wide enough to allow oviposition through it on to media without allowing flies to enter or leave the tube. Each set of chambers was placed in a large petri dish filled with media and transferred to a new dish daily. The medium was as above, except that it was supplemented with dark molasses to provide for easier egg detection and no live yeast was added, as substantial quantities of yeast were carried over on the mesh. The tubes were checked daily for death of the female and eggs deposited on the media were counted.

Statistical analyses

The following life history traits were measured: age at death, total fecundity, peak fecundity, age

at peak fecundity, fecundity during the last third of adult life span, and three-day fecundity totals from days 5 to 28 of adult life. Peak fecundity was determined from a three-day running average. For the data analysis we tried to balance the data as much as possible. To do this we eliminated all dams that did not have at least two offspring, not necessarily from different vials, and all sires that did not have at least two dams. Sires and dams were eliminated because of failure to produce offspring or escapes by flies from the chambers. Our final data set consisted of 31 sires, 71 dams, and 229 and 240 offspring at 19°C and 25°C, respectively.

The data were analysed using the SAS statistical package (SAS Institute Inc., 1985). For the three-day fecundities individuals which had died were assigned a value of zero fecundity. Only 7% and 9% of the flies at 19°C and 25°C, respectively, had died by the 28th day. Analysis excluding these values produced no significant change in the conclusions. Not excluding these values would have seriously complicated the examination of the correlations because of unequal sample sizes. All traits were found to conform sufficiently to the assumptions of analysis of variance (Scheffe, 1959, p. 227), so no transformations were done. Analysis of variance was performed with procedure GLM. Results were taken as significant if $p < 0.1$, not the usual $p < 0.05$. Variance components were estimated with procedure NESTED using the model:

$$Y_{ijk} = u + s_i + d_{ij} + e_{ijk}$$

where u is the overall mean, s_i is the sire effect, d_{ij} is the dam nested within sire, and e_{ijk} is the within full-sib family error. Narrow-sense heritabilities were estimated as:

$$h^2 = 4\sigma_S^2/\sigma_P^2$$

where σ_S^2 and σ_P^2 are the sire (half-sib) and total phenotypic variance components respectively. Broad-sense heritabilities were estimated as:

$$h^2 = 4\sigma_D^2/\sigma_P^2$$

where σ_D^2 is the dam (full-sib) variance component. Standard errors of the heritabilities were calculated using the methods of Becker (1984).

We examined both the additive and total genetic correlations using the sire covariances and the total genetic correlations. Correlations were calculated as:

$$r = \mathrm{COV}_{1,2} / \mathrm{VAR}_1\ \mathrm{VAR}_2$$

where $\mathrm{COV}_{1,2}$, VAR_1, and VAR_2 represented either the additive (sire) or total (dam) genetic covariances and variances, respectively.

Within-environment, non-genetic, variance components were estimated using the model:

$$\sigma_W^2 = \sigma_R^2 - (3\sigma_D^2 - \sigma_S^2)$$

where σ_R^2 is the residual variance. Covariance components were similarly calculated.

Standard errors for both the genetic and within-environment correlations were calculated using the methods of Scheinberg (1966). Comparisons of correlation coefficients were done with z-transformed values (Zar, 1984, p. 313) but using the calculated standard errors. We note that all of the estimates of standard errors for variance components, ratios of variance components, and correlations of variance components are not well understood and notorious for their lack of power at the sample sizes available for typical genetic experiments.

Cross-environment genetic correlations were estimated by two methods. The first method uses the Pearson product-moment correlation of the full-sib family means and tends to underestimate the true genetic correlation. The underestimate decreases with increasing family size (Via, 1984). This method has the advantage that the correlations can be tested for statistical significance. The

second method estimates the correlation by dividing the family mean covariance by the genetic variances estimated within each environment. This method tends to overestimate the true genetic correlation, and no statistical tests are available (Via, 1984). Thus, together these methods indicate the potential range of the true cross-environment genetic correlation.

Results

Effects of temperature

The overall effects of temperature are shown in Table 1 and the results of the analyses of variance are shown in Table 2. At the lower temperature, flies were longer-lived and had lower fecundities, both at peak and total. Mean adult life span was 27% shorter and total fecundity was 31% greater at the higher temperature. Only fecundity in the last third of life showed no effect of temperature. Genotypes reacted differently at each temperature for the traits of age at death, peak fecundity and total fecundity, as indicated by the significant dam–temperature interaction (Table 2).

Table 1. Means and standard errors of life history traits for flies raised at 19°C and 25°C.

		Life history trait				
Temperature		Age at death	Peak fecundity	Age at peak fecundity	Last third fecundity	Total fecundity
19°C	$\bar{x}$	57.7	25.6	17.0	39.7	410
	SE	1.0	0.5	0.3	2.9	9
25°C	$\bar{x}$	42.3	45.4	10.2	35.8	538
	SE	0.8	0.9	0.2	2.7	12

Table 2. Analyses of variance of life history traits for flies raised at 19°C and 25°C (values are mean squares).

		Life history trait				
Source	df	Age at death	Peak fecundity	Age at peak fecundity	Last third fecundity	Total fecundity[1]
Temp.	1	24361***	40624***	4912.5***	3252	14.51***
Sire	30	348†	137	21.5	3823†	0.32
Sire × Temp.	30	292	134	23.9	2279	0.21
Dam (sire)	40	219	168	17.0	2453†	3.68†
Dam (sire) × Temp.	40	243†	179†	20.0	2315	3.91*
Error	327	183	132	15.9	1855	0.26

[1]Values × 10^5.
†$p < 0.10$; *$p < 0.05$; ***$p < 0.0001$.

Genetic variation

Evidence for genetic variation, significant ($p < 0.1$) sire, dam, or dam–temperature interaction variance, was found for all traits except age at peak fecundity (Table 2). Within each temperature

Table 3. Variance components and narrow- and broad-sense heritabilities of life history traits for flies raised at 19°C and 25°C. Significance levels for heritabilities are based on ANOVA.

	Life history trait				
Source	Age at death	Peak fecundity	Age at peak fecundity	Last third fecundity	Total fecundity
Low temperature					
Sire	27.292	−2.636	0.503	−37.63	−662
Dam (sire)	24.296	6.197	1.642	109.27	1539
Error	231.348	55.356	21.664	1943.20	18892
Narrow-sense					
h^2	0.386	0.0	0.085	0.0	0
SE	(0.765)		(0.606)		
Broad-sense					
h^2	0.342	0.419	0.272	0.217	0.311
SE	(0.333)	(0.387)	(0.348)	(0.354)	(0.370)
High temperature					
Sire	−0.991	−6.167	0.766	189.94	−2427
Dam (sire)	7.114	19.933	0.629	188.10	6499
Error	138.412	203.260	10.440	1771.80	32688
Narrow-sense					
h^2	0.0	0.0	0.259	0.353†	0
SE			(0.662)	(0.749)	
Broad-sense					
h^2	0.197	0.366	0.212	0.349†	0.704*
SE	(0.330)	(0.359)	(0.310)	(0.321)	(0.415)

†$p < 0.10$; *$p < 0.05$; ***$p < 0.0001$.

the only statistically significant variance terms were for last third fecundity and total fecundity at high temperature (Table 3). Although age at death and peak fecundity showed evidence of genetic variance in the two-way ANOVA, the one-way ANOVAs failed to show statistical significance, underscoring the low power of these tests. The variance components showed most of the genetic variation to be non-additive, except for age at death at low temperature and total fecundity at high temperature (Table 3). Broad-sense heritabilities ranged from 0.20 to 0.66 and did not differ significantly across temperatures. But, the test for differences in heritabilities has very low power. Given the low power of analysis of variance to detect genetic variation (high Type II error rate (Bridges and Knapp, 1987; Shaw, 1987)), despite the lack of statistical significance for some of the variance components, we proceeded with the analysis of genetic correlations. We caution that we have accepted a high Type I error rate.

Correlations among traits

In general, little evidence of negative genetic correlations was found at low temperature, although negative correlations were found at high temperature (Table 4). At low temperature,

Table 4. Genetic (top) and within-environment (bottom) correlations of life history traits. Flies raised at 19°C above diagonal, flies raised at 25°C below diagonal. Cross-environment genetic correlations are on the diagonal, product-moment correlation (top) and genetic variance components (bottom).

	Life history trait				
	Age at death	Peak fecundity	Age at peak fecundity	Last third fecundity	Total fecundity
Age at death	0.039	−0.050	0.826	−0.325	0.289
	0.241	0.117	−0.221	−0.678	0.248
Peak fecundity	−0.264	−0.002	−0.553	−0.518	0.871
	0.353	−0.009	−0.041	0.446	0.987
Age at peak fecundity	−2.374	−0.820	−0.088	1.986	0.289
	0.556	0.065	−0.577	−0.447	−0.153
Last third fecundity	−1.499	0.746	2.797	0.147	−0.369
	−0.460	−0.294	−0.541	0.916	0.373
Total fecundity	−0.296	1.043	−0.254	0.662	0.091
	0.524	0.536	0.179	−0.069	0.297

longevity and total fecundity were positively correlated, and no correlation was found between longevity and peak fecundity. A negative genetic correlation was found between peak fecundity and last third fecundity. Because of the low power of the test the correlation coefficient was not significantly different from zero. The only additive genetic correlation, age at death and age at peak fecundity ($r = 1.051$), was similar to the total genetic correlation in sign and magnitude. All other correlations are undefined since one or both traits had an estimated additive genetic variance of zero. For age at peak fecundity, since earlier reproduction is associated with greater fitness, negative correlations between this trait and others indicate positive pleiotropy.

At high temperature, negative values were found for the genetic correlations of longevity–peak fecundity and longevity–total fecundity. Peak fecundity and last third fecundity were positively correlated, in contrast to low temperature. However, the correlations are not significant. Again, the only additive genetic correlation, age at peak fecundity and last third fecundity ($r = 0.618$), was similar to the total genetic correlation.

The cross-environment genetic correlations were large ($r > 0.5$) for only two traits, age at peak fecundity and last third fecundity. The former correlation was negative, suggesting antagonistic pleiotropy, while the latter was positive, indicating positive pleiotropy. None of the family mean product-moment correlations was significantly different from zero. The small correlations for the traits of age at death, peak fecundity, and total fecundity suggest that their expression is independent in the two environments.

Cost allocation trade-offs will appear as negative within-environment correlations which represent non-genetic (residual minus genetic) correlations. At low temperature the longevity–fecundity and peak fecundity–last third fecundity correlations were all positive. At high temperature only the peak fecundity–last third fecundity correlation was negative. The negative correlations for age at death and last third fecundity are an artifact, since individuals that lived the longest were well beyond egg-laying age and thus had very low last third fecundities.

Fecundity schedule

Trade-offs in the fecundity schedule were examined in more detail by looking at correlations among three-day fecundity totals (Table 5). At low temperature, all but two of the genetic

Table 5. Genetic (top) and within-environment (bottom) correlations and broad-sense heritabilities of three-day fecundities. Significance levels are based on ANOVA. Flies raised at 19°C above diagonal, flies raised at 25°C below diagonal. Cross-environment genetic correlations are on the diagonal, product-moment correlation (top) and genetic variance components (bottom).

	Three-day fecundities								Broad-sense h^2 (SE)	
	5–7	8–10	11–13	14–16	17–19	20–22	23–25	26–28	19°C	25°C
5–7	−0.087	0.361	0.699	0.095	0.264	0.996	−0.482	0.068	0.208	0.791**
	−0.093	0.410	0.055	0.075	−0.330	−0.139	0.106	0.001	(0.269)	(0.410)
8–10	0.590	−0.120	0.428	−0.155	0.571	1.223	0.409	0.297	0.658*	0.453†
	0.301	−0.096	0.756	0.869	−0.442	−0.460	−0.563	0.057	(0.402)	(0.363)
11–13	0.754	0.891	−0.052	1.043	1.465	1.161	1.048	0.927	0.264	0.165
	0.059	0.824	−0.091	0.564	−0.013	0.172	−0.177	0.096	(0.354)	(0.343)
14–16	0.890	1.542	1.583	0.023	1.094	0.303	0.490	0.870	0.427†	0.225
	−0.443	−0.018	0.546	0.026	0.382	0.613	0.325	0.119	(0.375)	(0.332)
17–19	1.359	2.039	1.748	0.650	−0.012	0.628	1.146	1.153	0.472†	0.110
	−0.821	−0.174	0.385	0.736	−0.013	0.762	0.219	0.126	(0.381)	(0.314)
20–22	−0.184	0.305	1.380	0.239	0.906	−0.229	0.466	1.149	0.105	0.373
	0.067	−0.085	−0.160	0.490	0.537	−0.394	0.813	0.463	(0.294)	(0.352)
23–25	−0.345	−0.196	0.771	−0.471	0.309	1.079	−0.134	0.985	0.420†	0.400†
	0.213	0.184	−0.058	0.508	0.602	0.552	−0.121	0.608	(0.374)	(0.355)
26–28	−0.356	0.0003	0.439	−0.335	1.641	0.956	1.085	−0.030	0.157	0.415†
	0.462	−0.032	−0.093	0.411	0.080	0.209	0.393	−0.043	(0.341)	(0.357)

†$p < 0.10$; *$p < 0.05$; **$p < 0.01$.

correlations were positive. We found negative values for the within-environment correlations between fecundity from day 5 to day 13 and fecundity from day 17 to day 25. Peak fecundity was on day 17.

At high temperature there were negative genetic and within-environment correlations for day 5 to day 10 compared with fecundities from day 14 to day 28. Peak fecundity was on day 10. Of the cross-environmental correlations none of the product-moment correlations was significantly different from zero. But seven of the eight values were negative, which is significant (one-tailed binomial test, $p < 0.05$), suggesting antagonistic pleiotropy.

We tested for a significant relationship between sign of the correlation and separation of the time periods, whether they were on the same or different sides of peak fecundity, using log-linear models (Sokal and Rohlf, 1981, p. 747). The relationship was not significant for the genetic correlations ($G = 6.27$, df $= 4$, $p < 0.18$). The relationship was significant for the within-environment correlations ($G = 13.97$, df $= 2$, $p < 0.001$) and independent of temperature ($G = 2.89$, df $= 1$, $p < 0.09$). The above tests are weak in that we are combining all time periods into just two classes. However, as noted by Bell (1984a), there is no *a priori* expectation from theory as to how distant the time periods must be before negative correlations are expected. The use of age at peak fecundity as the division point is non-arbitrary and reasonable. Although on statistical grounds one would expect adjacent time periods to be positively correlated, the null expectation for more distant periods is no correlation, not negative correlations as was found here. Also, the pattern held at both temperatures with different ages of peak fecundity. Thus, we conclude that cost allocation trade-offs exist for components of the fecundity schedule at both temperatures.

Discussion

We have found some evidence for the existence of negative genetic correlations among life history traits. This conclusion is dependent on the environment within which the organisms were raised. Evidence for the existence of niche specialization was indicated by the presence of negative cross-environment genetic correlations for age at peak fecundity and components of the fecundity schedule. We note, however, that age at peak fecundity was the one trait for which there were no significant genetic variance terms.

The possibility exists that our population was unusually deficient in genetic variation. However, our collection and culture techniques were designed to foster genetic variation. Three of the traits showed additive variation in at least one environment, and the other two traits showed extensive amounts of total genetic variation. Similarly, the three-day fecundities also showed total, if not additive, genetic variation. Our measures of genetic variation were within the range of heritabilities reported by other workers (Roff and Mousseau, 1987). The lack of statistical significance may have been due in part to sample size. However, our sample sizes at all levels of the analysis were bigger than most comparable experiments (Giesel *et al.*, 1982; Giesel, 1986). Finally, measurements of genetic variation of thorax size on these same flies (Scheiner and Lyman, in press) found statistically significant heritabilities consistent with previous studies.

The only consistent evidence at both temperatures for cost allocation trade-offs was among components of the fecundity schedule. Not all correlations for time periods on opposite sides of peak fecundity were negative. However, the measures of the within-environment correlations were biased towards positive values (see later). We found little data supporting the notion that trade-offs are caused by costs of allocating resources among the more distantly related traits of fecundity and longevity.

Our findings in this study are, in general, consistent with the results of other workers. Rose and Charlesworth (1981a), raising flies at 24°C, reported finding negative genetic correlations for egg-laying over five-day intervals during the first two weeks of adult life. They also found a negative genetic correlation between peak fecundity and longevity. We found similar results for flies raised at 25°C, although different conclusions were reached for flies raised at low temperature. Genetic correlations of age at peak fecundity, peak fecundity, and last third fecundity of flies raised at 25°C reported by Giesel *et al.* (1982) were also consistent with present results. Also, like Giesel *et al.* (1982), we found changes in the direction of the correlations in different environments. The only reported genetic correlation which disagrees with our data is the finding of Giesel (1986) of a positive genetic correlation between longevity and peak fecundity. We disagree with Giesel's (1986) conclusion that negative genetic correlations are more prevalent under more extreme conditions. Rather, we found a greater number of negative genetic correlations at 25°C, which he classified as optimal.

Studies such as ours, which use newly caught flies, have been criticized for measuring the genetic correlations in a novel environment. An experiment by Service and Rose (1985) found that the genetic correlation between fecundity and starvation time became less negative for a population of *D. melanogaster* when subject to new husbandry conditions. They concluded that novel environments will bias results towards positive genetic correlations. First, this criticism does not explain changes in the sign of the correlation among our treatments, since both environments are novel by their criteria. Second, our genetic correlations measured at 25°C are in general agreement with previous studies done with long-cultured populations (Rose and Charlesworth, 1981a, b; Luckinbill *et al.*, 1984). *Ad hoc* explanations would be needed to explain away the positive correlations measured at 19°C as artifacts of novel environments, while accepting the negative correlations measured at 25°C.

Generality of conclusions

Can any conclusions be reached, generally, about the existence of trade-offs and, specifically, about whether the trade-offs are due to cost allocation mechanisms or other types of antagonistic pleiotropy? Bell (1984a, 1984b), in a review of studies of *Drosophila*, birds, and freshwater invertebrates, found no general evidence for the existence of any trade-offs, although specific instances had been shown in some organisms under some conditions. Those studies which have demonstrated trade-offs typically measured only total phenotypic or additive genetic trade-offs.

A critical test of the cost allocation hypothesis comes from the results of long-term selection. We predict that cost allocation trade-offs will be found to be consistent across populations. Also, long-term responses to selection experiments should be in agreement with our observation of allocation trade-offs in the fecundity schedule. Our measures of genetic correlations, and, therefore, antagonistic pleiotropy in general, have less predictive value as they depend on the previous selection histories of the populations. Experiments selecting on early and late reproduction have been performed by Wattiaux (1968) using *D. subobscura*, and by Rose (1984b), Luckinbill *et al.* (1984; 1987) and Mueller (1987) using *D. melanogaster*. In the present context that is equivalent to selecting on age at peak fecundity and late fecundity. In all experiments (except that of Wattiaux) total fecundity was not affected by selection; just the shape of the fecundity schedule changed. This result is consistent with our finding of allocation trade-offs primarily among parts of the fecundity schedule. With regard to the relationship between longevity and fecundity, the selection experiments are in disagreement. Wattiaux found a decrease in longevity of both lines. Luckinbill found selection to decrease age at peak fecundity had no correlated response on longevity. Conversely, selection to increase late fecundity increased longevity. A similar result of selection on late fecundity was found by Rose (1984b). Thus, the results of the selection experiments are in general agreement with our main conclusions: (1) there is a pervasive trade-off among the closely related traits of the fecundity schedule; and (2) no general pattern can be claimed for the more distantly related traits of fecundity and longevity.

Predictions and future models

Allocation trade-offs represent fundamental constraints on developmental and physiological systems. These constraints will likely be common to all populations of a species and possibly any group of closely related species. In contrast, niche specialization is expected to be dependent on the particular selection history of each population, and general predictions based on it cannot be made. Furthermore, we can make no predictions about the universality of other sources of antagonistic pleiotropy. Presently, the only other studies reporting within-environment correlations of life history traits are those of Bell (1984a, 1984b) on unrelated organisms. More data are needed.

Rose (1983) contrasts two views of life history traits, the unitary hypothesis and the particulate hypothesis. The former sees all traits as tightly and positively correlated. The latter sees all traits as independent. He advocates a third viewpoint, the variable pleiotropy hypothesis, in which traits are partially correlated with negative correlations predominating. We suggest that an expansion of life history theory is needed. A general presumption about the existence of trade-offs among life history traits is unwarranted. However, among traits that might be expected to be functionally linked, such as different parts of the fecundity schedule or the same traits in different environments, trade-offs do exist. Models need to take into account this continuum of interactions.

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