The Covariance Structure of Life-History Characters in Daphnia pulex

Ken Spitze; John Burnson; Michael Lynch

Evolution, Vol. 45, No. 5. (Aug., 1991), pp. 1081-1090.

Stable URL:
http://links.jstor.org/sici?sici=0014-3820%28199108%2945%3A5%3C1081%3ATCSOLC%3E2.0.CO%3B2-T

Evolution is currently published by Society for the Study of Evolution.

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at http://www.jstor.org/about/terms.html. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at http://www.jstor.org/journals/ssevol.html.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

The JSTOR Archive is a trusted digital repository providing for long-term preservation and access to leading academic journals and scholarly literature from around the world. The Archive is supported by libraries, scholarly societies, publishers, and foundations. It is an initiative of JSTOR, a not-for-profit organization with a mission to help the scholarly community take advantage of advances in technology. For more information regarding JSTOR, please contact support@jstor.org.

http://www.jstor.org
Thu Aug 30 13:01:50 2007

Evolution, 45(5), 1991, pp. 1081–1090

THE COVARIANCE STRUCTURE OF LIFE-HISTORY CHARACTERS IN *DAPHNIA PULEX*

KEN SPITZE,[1] JOHN BURNSON,[2] AND MICHAEL LYNCH[1]
[1]*Department of Biology, University of Oregon, Eugene, OR 97403 USA*
[2]*Department of Ecology, Ethology, and Evolution, University of Illinois at Urbana–Champaign, Urbana, IL 61820 USA*

Abstract.—The genetic covariance structure for life-history characters in two populations of cyclically parthenogenetic *Daphnia pulex* indicates considerable positive correlation among important fitness components, apparently at odds with the expectation if antagonistic pleiotropy is the dominant cause of the maintanence of genetic variation. Although there is no genetic correlation between offspring size and offspring number, present growth and present reproduction are both strongly positively correlated genetically with future reproduction, and early maturity is genetically correlated with larger clutch size. Although the ubiquity of antagonistic pleiotropy has been recently questioned, there are peculiarities of cyclical parthenogenesis that could lead to positive life-history covariance even when negative covariance would be expected in a similar sexual species. These include the influence of nonadditive gene action on evolution in clonally reproducing organisms, and the periodic release of hidden genetic variance within populations of cyclical parthenogens.

Examination of matrix similarity, using the bootstrap for distribution-free hypothesis testing, reveals no evidence to suggest that the genetic covariance matrices differ between the populations. However, there is considerable evidence that the phenotypic and environmental covariance matrices differ between populations. These results indicate approximate stability of the genetic covariance matrix within species, an important assumption of many phenotypic evolution models, but should caution against the use of phenotypic in place of genetic covariance matrices.

Key words.—Antagonistic pleiotropy, bootstrap, cyclical parthenogenesis, genetic covariance, life history, population differentiation, quantitative genetics.

Received August 15, 1990. Accepted January 24, 1991.

The close association between life-history characters and fitness should result in low levels of genetic variance for such characters due to the past action of natural selection (Fisher, 1930; Falconer, 1981). However, antagonistic pleiotropy (Williams, 1957; Rose, 1982, 1983), whereby mutations that cause positive covariance between characters that contribute positively to fitness become fixed rapidly in populations and only those mutations that lead to negative covariance between fitness components are left segregating, can allow the maintenance of greater genetic variance than possible by selection-mutation balance alone.

The past decade has seen considerable effort to test this idea through observation of the covariance structure of life-history characters. Although several studies have revealed negative genetic covariance among fitness components (Rose and Charlesworth, 1981*a*, 1981*b*; Rose, 1984; Service and Rose, 1985; Scheiner et al., 1989; Tucic et al., 1988), consistent with the preeminence of antagonistic pleiotropy, a number of studies have revealed positive genetic covariances (Giesel and Zettler, 1980; Giesel et al., 1982*a*, 1982*b*; Hegmann and Dingle, 1982; Murphy et al., 1983; Bell, 1984*a*, 1984*b*; Lynch, 1984*b*; Mitchell-Olds, 1986). Although there has been considerable debate on the validity of some of these results (Murphy et al., 1983; Service and Rose, 1985; Reznick, 1985; Reznick et al., 1986), recent theoretical work has suggested that positive covariance between key life-history characters is possible (van Noordwijk and de Jong, 1986) or expected in selection-mutation equilibrium (Houle, 1991).

Genetic covariance matrices have also been used recently in several studies of microevolutionary change. Phenotypic selection models (Lande, 1979, 1982*a*, 1982*b*; Lande and Arnold, 1983) have served as foci for studies of evolutionary patterns in behavioral (Arnold, 1981*a*, 1981*b*; Garland, 1988), morphological (Cheverud, 1984, 1988, 1989; Cheverud et al., 1983,

1989; Lofsvold, 1986, 1988; Kohn and Atchley, 1988), and life-history characters (Lynch, 1985; Conner, 1988). These models have been used for future evolutionary projection (Lynch, 1985; Cowley and Atchley, 1990), and for the estimation of selective pressures responsible for the divergence among extant taxonomic units (Lofsvold, 1988). An important assumption in the use of these models is approximate constancy of the genetic covariance structure during the interval across which microevolutionary change is measured or projected.

One way to examine the validity of this assumption is to determine whether the genetic covariance matrix is constant among contemporary populations, subspecies, and species (Lofsvold, 1986, 1988; Cheverud, 1988; Cheverud et al., 1989). Most such studies have relied on multivariate normality for estimation and/or hypothesis testing. To estimate the equivalence of covariance or correlation matrices, elementwise correlation (Lofsvold, 1986; Kohn and Atchley, 1988; Cheverud, 1988), Mantel's test (Lofsvold 1986, 1988, Cheverud 1988), eigenvector correlation (Lofsvold, 1986, 1988; Cheverud, 1988), an index of integration (Cheverud et al., 1983; Kohn and Atchley, 1988), and a log-likelihood ratio test (Shaw, 1991) have recently been used or suggested. Problems of unknown distribution of these test statistics and lack of independence among characters have precluded formal hypothesis testing in some cases (Lofsvold, 1986; Kohn and Atchley, 1988). To obtain distribution-free statistics, randomization tests (Mitchell-Olds, 1986), and jackknife (Mitchell-Olds and Bergelson, 1990), and the bootstrap (Cheverud et al., 1989; Riska et al., 1989) have been used.

The purpose of this paper is to estimate the covariance structure for life-history characters from two populations of *Daphnia pulex* to examine the issues discussed above. Specifically, we consider 1) are the observed patterns of genetic covariation among life-history characters consistent with the expectation of antagonistic pleiotropy, and 2) are estimates of the genetic covariance matrix equivalent among populations within the species? To avoid the necessity of assuming multivariate normality, we use the bootstrap for estimating the covariance matrix elements and their sampling errors, and for hypothesis testing of matrix similarity.

Materials and Methods

Study Species.—Daphnia pulex is a filter-feeding planktonic cladoceran. With adequate food at 20°C, individuals mature in the fifth instar, and thereafter usually produce a clutch of offspring each instar (every two to three days). As cyclical parthenogens in nature, they alternate multiple generations of ameiotic reproduction during environmentally favorable periods with bouts of sexual reproduction when conditions become less favorable. Low temperature, low food availability, and pond drying are possible cues that can induce the sexual phase, which results in the production of diapausing ephippial eggs. The alternation of asexual and sexual reproduction can cause populations of *D. pulex* inhabiting temporary ponds to exhibit seasonal cycles of expressed genetic variance (Lynch and Gabriel, 1983; Lynch, 1984*b*). Early each year populations contain considerable genetic variance, because each hatchling gives rise to a genetically unique clone (Lynch, 1984*b*; Lynch et al., 1989). During the subsequent period of asexual reproduction, clonal selection reduces broad-sense heritabilities for life-history characters from early season values of 0.4 to 0.6 to near zero at season's end (Lynch, 1984*b*). Throughout this period, a pool of hidden genetic variance accumulates via linkage disequilibrium. Sex, via recombination, converts 50–75% of the hidden genetic variance to expressed genetic variance (Lynch and Gabriel, 1983), which leads to the restoration of high heritabilities in the following year when ephippial eggs hatch.

Two populations of *D. pulex* inhabiting temporary ponds were investigated in this study. The populations (with two-letter codes as in Lynch et al., 1989 and Crease et al., 1990) were: Portland Arch pond (PA, near Portland Arch State Nature Preserve, Fountain Co., IN) and Kick-A-Pond (KA, in Kickapoo State Park, in Vermilion Co., IL). Extensive genetic study of these populations, using isozyme, mitochondrial DNA, and ribosomal DNA data (Lynch et

al., 1989; Crease et al., 1990; Crease and Lynch, *in press*), leaves no doubt that these populations consist entirely of cyclically parthenogenentic *D. pulex*. Early season collections of 79 clones from PA, and 119 clones from KA form the material for this study.

Laboratory Methods.—Standard life table procedures used to estimate *Daphnia* life-history characters are given in detail elsewhere (Lynch et al., 1989). The characters used in the following analyses were: L_i (body length in mm, exclusive of tail-spine, for instars $i = 1$–8), K_i (age at release of offspring, in days, from mature instars $i = 1$–4), C_i (number offspring released at end of mature instars $i = 1$–4), $L_{0,i}$ (mean length of five randomly chosen offspring from clutch i), and G_{ij} (growth increment between instars i and j ($G_{ij} = L_j - L_i$).

Analytical Methods.—The patterns of phenotypic, genetic, and environmental covariance were examined in three sets of characters commonly used in life-history theory: offspring number versus offspring size (characters: C_i and $L_{0,i}$, $i = 1$–4), investment in growth versus reproduction ($G_{1,4}$, $G_{4,5}$, $G_{5,6}$, $G_{6,7}$, $G_{7,8}$, and C_i, $i = 1$–4), and the amount of reproduction versus the age at reproduction (C_i and K_i, $i = 1$–4).

The relationship between offspring size and number was determined for each of the first four clutches. Pooled estimates of correlations across clutches within populations were estimated as means of the clutch-specific values. Significance levels for pooled evaluations were estimated by the means of z-scores of probability levels obtained from each clutch. This assumes that each clutch is nonindependent, and the approach is therefore quite conservative (Rice, 1990). Pooled correlation estimates across populations are means of the two population pooled values. The probability levels associated with these pooled estimates were obtained using a combined p-value test for independent trials (Rice, 1990).

Growth versus reproduction was analyzed to determine the relationship among: 1) present growth versus present reproductive investment, 2) present growth or reproduction versus future reproduction, and 3) present growth or reproduction versus future growth.

The correlation between present growth and present reproduction was examined for each of the first four clutches. The correlation between present and future investments in growth and reproduction was examined over several incremental separations in time. For example, growth or reproduction in instar i was determined separately for its effect on growth or reproduction in instars $i+1$, $i+2$, $i+3$, and $i+4$ as the data allowed. As stated in the preceding paragraph, the significance levels associated with pooled estimates within populations were assumed nonindependent, whereas pooled estimates across populations were assumed independent.

Correlations between amount of reproduction and the age at reproduction were examined analogously to those presented in the previous paragraph.

For each analysis, estimates of phenotypic, genotypic, and environmental covariance and correlation were obtained through MANOVA for unbalanced design (due to some missing data) following Sokal and Rohlf (1981 pp. 211–214), using "clone" as the model. Because measurement error inflates environmental (and therefore phenotypic) variance, we obtained estimates of measurement error variance and subtracted them from appropriate matrix elements (as in Lynch, 1988; Lynch et al., 1989). Such variance was estimated for instar-specific body size from multiple measurements within an individual, and for ages at reproduction, from a detailed study of the precision of an egg development stage protocol (Lynch et al., 1989). Clutch size was measured without error. Confidence intervals were obtained for the elements of each matrix in each population by a resampling procedure (the bootstrap, Efron, 1982). The clones from each population were resampled 1,000 times with replacement to form 1,000 "quasi-populations," from each of which the desired matrices were obtained. The reported values for correlations are the means of the 1,000 bootstraps, a procedure that reduces bias (Efron, 1982). The distribution of bootstrap element estimates was used to determine the desired confidence intervals for each element.

To examine the similarity of the covariance structure of the two populations, we

selected a subset of characters of the *Daphnia* life history. The characters were chosen to reflect growth and reproduction (quantity and timing) both early and late in life: $G_{1,3}$, and $G_{5,7}$ to reflect growth during immature and mature periods, $L_{0,2}$ and L_4 to reflect sizes at birth and maturity, C_1, and C_3 to reflect early and late fecundity, and K_1 to reflect age at reproduction.

For comparisons of matrices, we used six different measures of matrix similarity. Choice of the indices was motivated by their use in recent studies of matrix similarity and from normal-theory test statistics. Four of these were chosen to allow comparison of magnitude as well as of proportionality of like-elements, while two were chosen to reflect only a measure of matrix proportionality. The first of the measures allowing comparison of relative magnitude and proportionality is the sum of products of like-elements in the two matrices of interest:

$$I = \sum_i \sum_j (a_{ij} b_{ij})$$

for elements a_{ij} and b_{ij} of matrices A and B. This is the test statistic of Mantel's test (Lofsvold, 1986; Cheverud, 1988). The second magnitude-retaining measure is the sum of the squared differences between like-elements in the two matrices,

$$V = \sum_i \sum_j (a_{ij} - b_{ij})^2.$$

The third magnitude-retaining index is the absolute value of the difference between dominant eigenvalues of the matrices, D_e. The fourth index is the absolute value of the difference between determinants of the matrices, D_d. The fifth index, which examines proportionality without regard to magnitude, is the element-wise correlation coefficient:

$$r_{AB} = \frac{\text{Cov}(a_{ij}, b_{ij})}{[\text{Var}(a)\text{Var}(b)]^{1/2}}$$

where Var(a) and Var(b) represent the variance of elements (diagonal and one-half of off-diagonal) within matrices A and B, respectively (Lofsvold, 1986; Cheverud, 1988). The final index is the vector correlation of the first eigenvectors extracted from matrices A and B, and is denoted r_v (Lofsvold, 1986).

So that different measurement scales would not result in disproportionate contribution of particular characters to the similarity indices, we transformed the data before computing the elements of the matrix. The transformation was to render each scale of measurement to have mean within-character variance equal to unity. For example, we divided the values for characters measured in millimeters ($G_{1,2}$, $G_{5,7}$, $L_{0,2}$, L_4) by the mean of the four within-character standard deviations. This has the effect of standardizing millimeters, days, and offspring number with respect to each other, while retaining differences in magnitude of variance among characters measured on the same scale.

Because the distributions of similarity indices are unknown, we again used the bootstrap to estimate the empirical distribution of the measures, and thus allow hypothesis testing. To accomplish this, we pooled clones from both populations and then bootstrapped across clones to construct pairs of "quasi-populations." From these pairs, the desired matrices and similarity index values were obtained. This bootstrap procedure was iterated 1,000 times to construct an empirical null distribution for each index. The observed values were evaluated against this null distribution. Here, the null hypothesis is that the covariance matrices from the two populations reflect samples drawn from a common pool (the species).

Results

The phenotypic, genetic, and environmental correlations between offspirng number and offspring body size are presented in Table 1. None of the genetic correlations were significantly different from zero. The pooled estimate across clutches and populations was essentially zero. All of the environmental correlations were positive, with four of eight acheiving statistical significance. The pooled estimate was also significant. Seven of the eight phenotypic correlations were positive, although only one was statistically significant. The pooled estimate was not significant.

Pooled estimates across populations for the genetic and environmental correlations between instar-specific investments in growth and reproduction were positive, al-

TABLE 1. Phenotypic (P), genetic (G), and environmental (E) correlations between offspring number and offspring size pooled across the first four clutches for populations PA and KA. Total correlations are pooled across populations.

Population	P	G	E
PA	0.14	−0.05	0.26†
KA	0.09	−0.04	0.21
Total	0.12	−0.04	0.23*

† $P < 0.10$, * $P < 0.05$.

though only the genetic correlation achieved significance (Table 2). The phenotypic correlation was positive and highly significant.

Correlations between either present growth or present reproductive investment and future growth revealed little in the way of a consistent trend (Table 2). The only significant genetic correlation was between growth in adjacent instars. Although six of the seven environmental correlations were negative, only one acheived statistical significance. Phenotypically, growth in adjacent instars was positively correlated, but growth in instar i was negatively correlated with growth in instar $i+3$.

Present investment in growth or reproduction was positively correlated with future reproduction genetically and environmentally (Table 2). The positive correlations were more pronounced genetically (all six comparisons significant) than environmentally (three of six significant). All phenotypic correlations were positive and highly significant.

There were few significant correlations between clutch size and age at reproduction, although eight of the nine that acheived or approached significance were negative, indicating an association between early maturity and large clutch size (Table 3).

Of the six indices of matrix similarity, none revealed evidence of significant differences among genetic covariance matrices (Table 4). However, three of the indices revealed significant differences among environmental covariance matrices (Table 4). Neither index that reflected only proportionality differences between matrices acheived statistical significance. Differences between phenotypic matrices was indicated by two indices. Collectively, these results suggest that the genetic covariance matrices do not differ between the populations, whereas the phenotypic and environmental matrices are different in terms of overall magnitude, but not in terms of proportionality.

TABLE 2. Phenotypic (P), genetic (G), and environmental (E) correlations pooled across instars and populations for the relationship between present and future growth and reproduction.

	P	G	E
Growth in instar i versus reproduction in instar:			
i	0.36****	0.51**	0.25†
Growth in instar i versus growth in instar:			
$i+1$	0.28****	0.46*	0.22†
$i+2$	−0.09	0.04	−0.15
$i+3$	−0.15*	−0.08	−0.14
$i+4$	−0.08	0.43	−0.34***
Reproduction in instar i versus growth in instar:			
$i+1$	0.02	0.04	0.00
$i+2$	−0.06	−0.01	−0.12
$i+3$	−0.05	0.16	−0.20
Growth in instar i versus reproduction in instar:			
$i+1$	0.42****	0.64***	0.28**
$i+2$	0.26****	0.49*	0.09
$i+3$	0.21****	0.37*	0.09
Reproduction in instar i versus reproduction in instar:			
$i+1$	0.52****	0.76****	0.37**
$i+2$	0.39****	0.60****	0.31**
$i+3$	0.33****	0.67****	0.14

† $P < 0.10$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.005$, **** $P < 0.001$.

TABLE 3. Phenotypic (P), genetic (G), and environmental (E) correlations pooled across instars and populations for the relationship between present and future reproduction and age at reproduction. Note that negative correlations indicate association between large clutch size and early reproduction, and are therefore positive correlations with respect to fitness.

	P	G	E
Clutch size in clutch i versus age at reproduction for clutch:			
i	−0.12*	−0.69*	0.02
Clutch size in clutch i versus age at reproduction for clutch:			
$i+1$	−0.16**	−0.24*	−0.03
$i+2$	−0.11†	−0.19†	0.03
$i+3$	−0.03	−0.08	0.14
Age at reproduction for clutch i versus clutch size for clutch:			
$i+1$	−0.14*	−0.43†	−0.07
$i+2$	−0.04	−0.10	0.03
$i+3$	0.06	−0.22	0.20†

† $P < 0.10$, * $P < 0.05$, ** $P < 0.01$.

TABLE 4. Probability levels associated with the statistics for tests of between-population differences for phenotypic (P), genetic (G), and environmental (E) covariance matrices. See text for description of individual test statistics.

Statistic	P	G	E
I	NS	NS	NS
V	0.001	NS	0.001
D_e	0.03	NS	0.005
D_d	0.09	NS	0.001
r_{AB}	NS	NS	NS
r_v	NS	NS	NS

NS $P > 0.10$.

DISCUSSION

Life-History Covariance

On first examination, the general pattern of genetic correlations among life-history characters revealed in this study does not provide support for the prevalence of antagonistic pleiotropy. The strong, positive genetic correlation between present and future reproduction, and the trend toward genetic correlation between earlier reproduction and larger clutch size all indicate positive covariance among important fitness components. The near-zero genetic correlation between offspring size and offspring number indicates that genotypes with greater reproductive investment may produce larger clutches, larger offspring, or both. No evidence of a genetic tradeoff between offspring number and offspring size was revealed.

The positive covariance, both genetic and environmental, between present growth and future reproduction may well be a simple consequence of the strong body size-clutch size relationship often found in cladocera, particularly in the first few clutches (reviewed in Lynch, 1980). This positive covariance may be viewed as positive or negative covariance with respect to fitness depending on how body size relates to survival. Different predation regimes lead to markedly different relationships between body size and mortality. Zooplankton experiencing predation from visually feeding fish or salamander larvae suffer increasing mortality with increasing body size (Werner and Hall, 1975; Zaret and Kerfoot, 1975). Invertebrate predators, such as *Chaoborus* larvae and copepods, selectively prey on smaller zooplankton, leading to a decrease in mortality with increasing size (Dodson, 1970, 1974; Kerfoot, 1977; Pastorok, 1981; Spitze, 1985). Therefore, if invertebrate predation is the most important source of mortality, the postive genetic correlation between growth and reproduction would be viewed as positive covariance among fitness components. When vertebrate predation is prominent, the converse would be true. If the two modes of predation alternated temporally, as is common in midwestern temporary ponds (pers. obs.), then the relationship between the fitness consequences of growth and reproduction would fluctuate in sign with time.

Recent theoretical work has suggested that positive genetic covariance between fitness components can occur when populations are in selection-mutation equilibrium (van Noordwijk and de Jong, 1986; Houle, 1991). Suppose that loci affecting life-history traits can be dichotomized between those having an effect on resource acquisition and those having an effect on resource allocation. Mutations at acquisition loci would lead to general positive covariance among life-history characters, whereas mutations at allocation loci would lead to negative genetic covariance (van Noordwijk and de Jong, 1986; Houle, 1991). Simulation studies indicate that if acquisition loci are 50 to 100 times as abundant (or mutable) as allocation loci, then positive genetic covariance among life-history characters is expected at selection-mutation equilibrium in a sexual organism (Houle, 1991). Houle argues that the ratio of acquisition to allocation loci may be several hundred, although Charlesworth (1990) disagrees. The relevant data needed to test such theory are genetic correlations among life-history characters resulting from mutations. Lynch (1985) provides such information on *D. pulex*. The only significant genetic correlations indicate positive association among instar-specific body sizes, among clutch sizes, and between body size at maturity and clutch size, which are consistent with Houle's contention. Clearly, more data from such studies are needed.

Alternate Covariance Expectations

There are several other potential reasons why cyclically parthenogenetic *D. pulex*

populations would have genetic covariance structures that do not appear to be consistent with the expectation of antagonistic pleiotropy. If the hidden genetic (co)variance released following a bout of sex (Lynch and Gabriel, 1983) is positive, then population samples taken directly following ephippial hatch may reveal positive life-history covariance.

To examine this possibility, consider a gene that can have an effect on two life-history characters, each of which contributes positively and additively to fitness. Qualitatively, three types of mutations can occur that affect one or both of the characters. A mutation may have the same effect on both characters, either positively (+,+) or negatively (−,−), it may have an effect on only one character, either positively [(+,0) or (0,+)] or negatively [(−,0) or (0,−)], or it may affect one character positively and the other negatively [(+,−) or (−,+)]. For hidden genetic covariance to occur, combinations of mutations must exist within a clone such that the net overall effect on each character and on fitness is zero. For example, cooccurrence of (+,+) and (−,−) mutations, or of (+,−) and (−,+) mutations would result in hidden genetic covariance.

If mutations at acquisition loci are more prevalent than those at allocation loci, then (+,+) and (−,−) mutations would be the most abundant type. Cooccurrence of (+,+) and (−,−) mutations within a clone would result in positive hidden genetic covariance. Release of a portion of this positive hidden genetic covariance, after a bout of sex, could result in positive expressed genetic covariance. The positive covariance among fitness components observed in early-season samples may progress toward negative covariance as the phase of clonal selection proceeds. This would be the expectation of antagonistic pleiotropy.

Unlike obligately sexual species, where evolutionary change is governed by the additive genetic component of variance and covariance, evolutionary change during clonal reproduction is mediated by the total genetic covariance structure. Each clone acts as a single linkage group, resulting in the contribution of both additive and nonadditive gene action to the response to selection. If the contribution of nonadditive gene action is positive genetic covariance, then the total genetic correlation among life-history characters may be positive, even if the additive components exhibit negative covariance (as expected under antagonisitc pleiotropy). Theoretical and empirical investigations of the consequences of nonadditive gene action and the release of hidden genetic variance, as well as the relative importance of selection during clonal and sexual phases of reproduction are currently underway and will help clarify the expected genetic correlation structure in cyclical parthenogens.

Even assuming that antagonistic pleiotropy among fitness components is the theoretical expectation for a population in selection-mutation equilibrium, temporally variable selection and significant genotype-environment interactions can prevent such an equilibrium from being attained. There is evidence for the existence of genotype-environment interactions for fitness components in the field (Via, 1984*a*, 1984*b*; Futuyma et al., 1984; reviewed in Hedrick et al., 1976) and laboratory (Giesel et al., 1982*a*, 1982*b*; Service and Rose, 1985; Spitze, 1991). Variation in phenology of population density (Lynch, 1983, 1984*a*, 1984*b*) and the presence of predators (pers. obs.) in midwestern ponds containing *D. pulex* suggest the possible importance of temporally variable selection. Year-to-year variation in selection regime has been documented for birds (Grant, 1985; Schluter and Smith, 1986) and plants (Kalisz, 1986).

Service and Rose (1985) have argued that novel laboratory environments may be responsible for many examples of positive covariance reported for fitness components. They subjected a laboratory stock of *Drosophila melanogaster* (held under relatively constant conditions for 80 generations) to a different ("novel") set of culture conditions. When assayed in the "novel" environment, the previously documented pattern of antagonistic pleiotropy was found to change toward more positive covariation among fitness components. However, if the two environmental conditions are not viewed as "normal" versus "novel," but simply as two of many possible environmental conditions, then their results simply reveal the

presence of genotype-environment interaction. Clearly, if laboratory or greenhouse conditions are grossly distinct from natural conditions, the argument of Service and Rose is very pertinent, and may nullify many assays of population covariance. Without more definitive information on "natural" conditions and their spatial/temporal stability, such conclusions are hard to make. Murphy et al. (1983) have argued that laboratory stocks held for extended periods under specific environmental conditions may not effectively represent natural populations. There is at least some evidence that natural populations grown in completely natural conditions exhibit positive covariance among fitness components (Mitchell-Olds, 1986) and there are several examples of correlations changing in sign when assayed in different laboratory conditions (Giesel et al., 1982*a*, 1982*b*).

Covariance Matrix Similarity

Our tests of matrix similarity present no evidence to suggest that genetic covariance structure varies between the two populations of *Daphnia*. This offers support for the use of models that rely on the approximate constancy of the genetic covariance matrix for analyses within species (Lande, 1979, 1982; Lande and Arnold, 1983). Similar results have been found for analysis between subspecies of *Peromyscus* (Lofsvold, 1986). Comparison of laboratory rats and mice revealed that genetic correlation matrices were similar, but genetic covariance matrices were significantly different (Kohn and Atchley, 1988). It is important to note, as have Kohn and Atchley (1988) and Cheverud et al. (1989), that correlation matrix similarity is not the same as covariance matrix similarity. Since an infinite number of different covariance matrices can all have identical correlation matrices, it is important to make this distinction. Different covariance matrices with identical correlation structures under identical selection regimes can yield evolutionary trajectories that are qualitatively different.

The differences observed among phenotypic and environmental matrices among these *D. pulex* populations are consistent with previous work on aphids (Riska, 1985), but are at odds with previous work on rodents (Lofsvold, 1986; Kohn and Atchley, 1988). The fact that this study revealed significant differences in phenotypic but not genetic covariance matrices should caution against the use of phenotypic in place of genetic covariance matrices (Cheverud, 1988).

Food Availability

A potential criticism of the results of this study is our use of optimal environmental conditions (high food, constant temperature, low density). It may be argued that the sign of genetic correlations would change in more stressful conditions. This argument, again, points to the potential importance of genotype-environment interaction. It is unlikely that any *D. pulex* population would experience these optimal conditions for long in nature. However, these conditions were chosen to mimic conditions experienced by early-season populations. Effective food availability in nature can exceed those used here: clutch sizes in excess of 100 have been observed (Lynch, 1980; K. Spitze, pers. obs.). It is important to note that the covariance structure of a population with age-structure and overlapping generations is best represented as an instantaneous assessment (Lande, 1982*a*). Our intention is not to suggest that *D. pulex* always exhibit these patterns of covariation, but that these patterns represent that which occurs in early-season midwestern populations.

Acknowledgments

This manuscript was improved by comments from P. Jarrell, B. Sullender, and two anonymous reviewers. The analyses were made possible by use of the Cornell National Supercomputer Facility, a resource of the Cornell Theory Center, which is funded in part by the National Science Foundation, New York State, the IBM Corporation and members of the Center's Corporate Research Institute. Laboratory assistance was provided by Mary Berigan. Support was provided by a National Science Foundation graduate fellowship to K.S., and by NSF grants BSR 86-00487 and 89-11038 to M.L.

Literature Cited

Arnold, S. J. 1981*a*. Behavioral variation in natural populations. I. Phenotypic, genetic and environmental correlations between chemoreceptive re-

sponses to prey in the garter snake, *Thamnophis elegans*. Evolution 35:489–509.

———. 1981*b*. Behavioral variation in natural populations. II. Inheritance of a feeding response in crosses between geographic races of the garter snake, *Thamnophis elegans*. Evolution 35:510–515.

BELL, G. 1984*a*. Measuring the cost of reproduction. I. The correlation structure of the life table of a plankton rotifer. Evolution 38:300–313.

———. 1984*b*. Measuring the cost of reproduction. II. the correlation structure of the life tables of five freshwater invertebrates. Evolution 38:314–326.

CHARLESWORTH, B. 1990. Optimization models, quantitative genetics, and mutation. Evolution 44: 520–538.

CHEVERUD, J. M. 1984. Quantitative genetics and developmental constraints on evolution by selection. J. Theor. Biol. 110:155–171.

———. 1988. A comparison of genetic and phenotypic correlations. Evolution 42:958–968.

———. 1989. A comparative analysis of morphological variation patterns in the papionins. Evolution 43:1737–1747.

CHEVERUD, J. M., J. J. RUTLEDGE, AND W. R. ATCHLEY. 1983. Quantitative genetics of development: Genetic correlations among age-specific trait values and the evolution of ontogeny. Evolution 37:895–905.

CHEVERUD, J. M., G. P. WAGNER, AND M. M. DOW. 1989. Methods for the comparative analysis of variation patterns. Syst. Zool. 38:201–213.

CONNER, J. 1988. Field measurements of natural and sexual selection in the fungus beetle, *Bolitotherus cornutus*. Evolution 42:736–749.

COWLEY, D. E., AND W. R. ATCHLEY. 1990. Development and quantitative genetics of correlation structure among body parts of *Drosophila melanogaster*. Am. Nat. 135:242–268.

CREASE, T. J., AND M. LYNCH. 1991. Ribosomal DNA variation in *Daphnia pulex*. Mol. Biol. Evol. *In press*.

CREASE, T. J., M. LYNCH, AND K. SPITZE. 1990. Hierarchical analysis of population genetic variation in mitochondrial and nuclear genes of *Daphnia pulex*. Mol. Biol. Evol. 7:444–458.

DODSON, S. I. 1970. Complementary feeding niches sustained by size-selective predation. Limnol. Oceanogr. 15:131–137.

———. 1974. Zooplankton competition and predation: An experimental test of the size-efficiency hypothesis. Ecology 55:605–613.

EFRON, B. 1982. The Jackknife, the Bootstrap, and Other Resampling Procedures. S. I. A. M., Philadelphia, PA.

FALCONER, D. S. 1981. Introduction to Quantiative Genetics, 2nd ed. Longman, London, UK.

FISHER, R. A. 1930. The Genetical Theory of Natural Selection. Clarendon Press, Oxford, UK.

FUTUYMA, D. J., R. P. CORT, AND I. VAN NOORDWIJK. 1984. Adaptation to host plants in the fall cankerworm (*Alsophila pometaria*) and its bearing on the evolution of host affiliation in phytophagous insects. Am. Nat. 123:287–296.

GARLAND, T., JR. 1988. Genetic basis of activity metabolism. I. Inheritance of speed, stamina, and antipredator displays in the garter snake *Thamnophis sirtalis*. Evolution 42:335–350.

GIESEL, J. T., AND E. E. ZETTLER. 1980. Genetic correlations of life historical parameters and certain fitness indices in *Drosophila melanogaster*: r_m, r_s, diet breadth. Oecologia 47:299–302.

GIESEL, J. T., P. A. MURPHY, AND M. N. MANLOVE. 1982*a*. The influence of temperature on genetic interrelationships of life history traits in a population of *Drosophila melanogaster*: What tangled data sets we weave. Am. Nat. 119:464–479.

———. 1982*b*. An investigation of the effects of temperature on the genetic organizations of life history indices in three populations of *Drosophila melanogaster*, pp. 189–207. *In* H. Dingle and J. P. Hegmann (eds.), Evolution and Genetics of Life Histories. Springer-Verlag, N.Y.

GRANT, B. R. 1985. Selection on bill characters in a population of Darwin's finches: *Geospiza conirostris* on Isla Genovesa, Galapagos. Evolution 39: 523–532.

HEDRICK, P. W., M. E. GINEVAN, AND E. P. EWING. 1976. Genetic polymorphism in heterogeneous environments. Annu. Rev. Ecol. Syst. 7:1–32.

HEGMANN, J. P., AND H. DINGLE. 1982. Phenotypic and genetic covariance structure in Mulkweed Bug life history traits, pp. 177–185. *In* H. Dingle and J. P. Hegmann (eds.), Evolution and Genetics of Life Histories. Springer-Verlag, N.Y.

HOULE, D. 1991. Genetic covariance of fitness correlates: What genetic correlations are made of and why it matters. Evolution 45:630–648.

KALISZ, S. 1986. Variable selection on the timing of germination in *Collinsia verna* (Scrophulariaceae). Evolution 40:479–491.

KERFOOT, W. C. 1977. Competition in cladoceran communities: The cost of evolving defenses against copepod predation. Ecology 58:303–313.

KOHN, L. A. P., AND W. R. ATCHLEY. 1988. How similar are genetic correlation structures? Data from mice and rats. Evolution 42:467–481.

LANDE, R. 1979. Quantitative genetic analysis of multivariate evolution, applied to brain : body size allometry. Evolution 33:402–416.

———. 1982*a*. A quantitative genetic theory of life-history evolution. Ecology 63:607–615.

———. 1982*b*. Elements of a quantitative genetic model of life history evolution, pp. 21–29. *In* H. Dingle and J. P. Hegmann (eds.), Evolution and Genetics of Life Histories. Springer-Verlag, N.Y.

LANDE, R., AND S. J. ARNOLD. 1983. The measurement of selection on correlated characters. Evolution 37:1210–1226.

LOFSVOLD, D. 1986. Quantitative genetics of morphological differentiation in *Peromyscus*. I. Tests of the homogeneity of genetic covariance structure among species and subspecies. Evolution 40:559–573.

———. 1988. Quantitative genetics of morphological differentiation in *Peromyscus*. II. Analysis of selection and drift. Evolution 42:54–67.

LYNCH, M. 1980. The evolution of cladoceran life histories. Q. Rev. Biol. 55:23–42.

———. 1983. Ecological genetics of *Daphnia pulex*. Evolution 37:358–374.

———. 1984*a*. The genetic structure of a cyclical parthenogen. Evolution 38:186–203.

———. 1984*b*. The limits to life history evolution in *Daphnia*. Evolution 38:465–482.

———. 1985. Spontataneous mutations for life-history characters in an obligate parthenogen. Evolution 39:804–818.

———. 1988. Path analysis of ontogenetic data, pp. 29–46. *In* B. Ebenman and L. Persson (eds.), Size-Structured Populations. Springer-Verlag, N.Y.

LYNCH, M., AND W. GABRIEL. 1983. Phenotypic evolution and parthenogenesis. Am. Nat. 122:745–764.

LYNCH, M., K. SPITZE, AND T. J. CREASE. 1989. The distribution of life history variation in the *Daphnia pulex* complex. Evolution 43:1724–1736.

MITCHELL-OLDS, T. 1986. Quantitative genetics of survival and growth in *Impatiens capensis*. Evolution 40:107–116.

MITCHELL-OLDS, T., AND J. BERGELSON. 1990. Statistical genetics of an annual plant, *Impatiens capensis*. I. Genetic basis of quantitative variation. Genetics 124:407–415.

MURPHY, P. A., J. T. GIESEL, AND M. N. MANLOVE. 1983. Temperature effects on life history variation in *Drosophila simulans*. Evolution 37:1181–1192.

PASTOROK, R. A. 1981. Prey vulnerability and size selection by *Chaoborus* larvae. Ecology 62:1311–1324.

REZNICK, D. 1985. Costs of reproduction: An evaluation of the empirical evidence. Oikos 44:257–267.

REZNICK, D., E. PERRY, AND J. TRAVIS. 1986. Measuring the cost of reproduction: A comment on papers by Bell. Evolution 40:1338–1344.

RICE, W. R. 1990. A consensus combined p-value test and the family-wide significance of component tests. Biometrics 46:303–308.

RISKA, B. 1985. Group size factors and geographic variation of morphometric correlation. Evolution 39:792–803.

RISKA, B., T. PROUT, AND M. TURELLI. 1989. Laboratory estimates of heritabilities and genetic correlations in nature. Genetics 123:865–871.

ROSE, M. R. 1982. Antagonistic pleiotropy, dominance, and genetic variation. Heredity 48:63–78.

———. 1983. Theories of life-history evolution. Am. Zool. 23:15–23.

———. 1984. Genetic covariation in *Drosophila* life history: Untangling the data. Am. Nat. 123:565–569.

ROSE, M. R., AND B. CHARLESWORTH. 1981*a*. Genetics of life history in *Drosophila melanogaster*. I. Sib analysis of adult females. Genetics 97:173–186.

———. 1981*b*. Genetics of life history in *Drosophila melanogaster*. II. Exploratory selection experiments. Genetics 97:187–196.

SCHEINER, S. M., R. L. CAPLAN, AND R. F. LYMAN. 1989. A search for trade-offs among life history traits in *Drosophila melanogaster*. Evol. Ecol. 3:51–63.

SCHLUTER, D., AND J. N. M. SMITH. 1986. Natural selection on beak and body size in the Song Sparrow. Evolution 40:221–231.

SERVICE, P. M., AND M. R. ROSE. 1985. Genetic covariation among life-history components: The effect of novel environments. Evolution 39:943–945.

SHAW, R. G. 1991. The comparison of quantitative genetic parameters between populations. Evolution 45:143–151.

SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry. Freeman, San Francisco, CA.

SPITZE, K. 1985. Functional response of an ambush predator: *Chaoborus americanus* predation on *Daphnia pulex*. Ecology 66:938–949.

———. 1991. *Chaoborus* predation and life-history evolution in *Daphnia pulex*: Temporal pattern of population diversity, fitness, and mean life history. Evolution 45:82–92.

TUCIC, N., D. CVETKOVIC, AND D. MILANOVIC. 1988. The genetic variation and covariation among fitness components in *Drosophila melanogaster* females and males. Heredity 60:55–60.

VAN NOORDWIJK, A. J., AND G. DE JONG. 1986. Acquisition and allocation of resources: Their influence on variation in life-history tactics. Am. Nat. 128:137–142.

VIA, S. 1984*a*. The quantitative genetics of polyphay in an insect herbivore. I. Genotype-environment interaction in larval performance on different host plant species. Evolution 38:881–895.

———. 1984*b*. The quantitative genetics of polyphay in an insect herbivore. II. Genetic correlations in larval performance within and among host plants. Evolution 38:896–905.

WERNER, E. E., AND D. J. HALL. 1975. Optimal foraging and size selection of prey by the bluegill sunfish (*Lepomis macrochirus*). Ecology 55:1042–1052.

WILLIAMS, G. C. 1957. Pleiotropy, natural selection, and the evolution of senescence. Evolution 11:398–411.

ZARET, T. M., AND W. C. KERFOOT. 1975. Fish predation on *Bosmina longirostris*: Body-size selection versus visibility selection. Ecology 56:232–237.

Corresponding Editor: M. G. Bulmer