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Quantitative genetics of zooplankton life histories

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Abstract. Quantitative genetic techniques are powerful tools for use in understanding the microevolutionary process. Because of their size, lifespan, and ease of culture, many zooplankton species are ideal for quantitative genetic approaches. As model systems, studies of zooplankton life histories are becoming increasingly used for examination of the central paradigms of evolutionary theory. Two of the fundamental empirical questions that zooplankton quantitative genetics studies can answer are: 1) How much genetic variance exists in natural populations for life history traits? 2) What is the empirical evidence for trade-offs that permeate life history theory based on optimality approaches?

A review of existing data on *Daphnia* indicates substantial genetic variance for body size, clutch size, and age at first reproduction. Average broad-sense heritabilities for these three characters across 19 populations of 6 species are 0.31, 0.31, and 0.34, respectively. Although there is some discrepancy between the two pertinent studies that were designed to decompose the total genetic variance into its additive and non-additive components, a crude average seems to suggest that approximately 60% of the total genetic variance has an additive basis.

The existing data are somewhat inconsistent with respect to presence/absence of trade-offs (negative genetic correlations) among life history traits. A composite of the existing data seems to argue against the existence of strong trade-offs between offspring size and offspring number, between present and future reproduction, and between developmental rate and fecundity. However, there is some evidence for a shift toward more negative (less positive) covariances in more stressful environments (e.g., low food).

Zooplankton will prove to be very useful in future study in several important areas of research, including the genetics and physiology of aging, the importance of genotype-environment interaction for life history traits, and the evolution of phenotypic plasticity.

Key words. Quantitative genetics; life history; evolution; cladocera; heritability; *Daphnia*; zooplankton.

Introduction

Although there have been several ambiguous references to the evolutionary process throughout history, we owe the foundation of modern evolutionary theory to Charles Darwin, and particularly to *The Origin of Species*[7]. For many of us, reading this book for the first time is a remarkable experience. I fully expected the book to contain a very rough approximation of the evolutionary process. Instead, it seems quite thorough and complete. What was missing from Darwin's theory was a mechanism of inheritance, i.e., the basis of genetics. This missing mechanism would have to wait for the 'rediscovery' of Mendel's work. One of my favorite observations to point out to students is that both the work of Darwin and that of Gregor Mendel were presented at very nearly the same time, but neither were generally accepted for several decades. Around the turn of the century, when Mendel's and Darwin's work were more widely known and accepted, there was still a substantial debate about the genetic basis of continuously distributed characters, such as height. While Mendel's mechanism was accepted to some degree, there was still disagreement about its universality. There was a school of thought at the time that held that although Mendel's Laws accurately described the inheritance of certain characters with discreet phenotypic classes, they were not sufficient to describe the patterns of inheritance in characteristics that are continuously distributed. Reconciliation of these opposing views had to await the legendary '1918 paper' of Sir Ronald A. Fisher.

Fisher's paper, entitled *The correlation among relatives under the supposition of Mendelian inheritance*[20] made two rather remarkable contributions. First, it unified mechanisms of inheritance for all characters. No longer was it necessary to invoke different mechanisms to describe the inheritance of different types of characters. Second, the statistical formulation therein served as the foundation of quantitative genetics. These contributions stand quite clearly, despite the decades of discussion about the details of Fisher's contributions.

Quantitative genetics was developed during the middle of this century by those interested in plant and animal breeding for the purpose of stock improvement. The explosion of quantitative genetics into the field of evolutionary biology was spear-headed by the initial papers of Russell Lande[35–37]. Particularly during the latter 1980s, the use of quantitative genetic techniques by evolutionary biologists increased exponentially. All the while, the book that served as the 'bible' was Falconer's

Introduction to Quantitative Genetics[17–19], which necessarily drew many of its examples from and placed its emphasis on plant and animal breeding. Very soon, however, a two-volume text entitled *Fundamentals of Quantitative Genetics* will serve as the first complete treatment of quantitative genetics from the perspective of evolutionary biologists studying natural populations[52,77].

The use of quantitative genetics in the study of natural populations of zooplankton began, to the best of my knowledge, with work by Ian McLaren, who used standard protocols from animal breeding designs to estimate the quantity of genetic variation for several demography characters in a marine copepod[54]. As with other taxa and ecological settings, the use of quantitative genetics in the study of both freshwater and marine zooplankton increased through the middle 1980s[44,45,81]. The utilization of quantitative genetics in studies of zooplankton has two primary motivations. The first is the interest that an investigator has in the particular organism. Investigators with interests in the evolutionary ecology of a zooplankton species quite often are drawn toward the use of quantitative genetics in order to answer organism-specific questions. The second motivation is that attributes of many zooplankton species make them ideal as model systems for testing conceptual hypotheses in evolutionary biology. Their small size, short generation time, and ease of laboratory culture has made *Daphnia*, for example, the organism of choice for several laboratories worldwide whose research is focused upon constructing and testing general evolutionary hypotheses. The utilization of quantitative genetic techniques for the analysis of standing levels of genetic variation and for estimation of potential avenues of evolutionary change continues today.

Quantitative genetics

The basis of quantitative genetics is the statistical representation of the phenotypic resemblance between relatives. In its simplest form, quantitative genetics analysis relies on the comparison of phenotypic characteristics of close relatives, such as parents and offspring, or groups of siblings. The resemblance between such relatives is used to partition the total phenotypic variance into components attributable to various genetic and non-genetic causes.

To begin, the phenotype (P_i) of an individual, in terms of its deviation from the population mean, is comprised of a genetic component (G_i) and an environmental component (E_i),

$$P_i = G_i + E_i.$$

The genetic component can be further decomposed into an additive effect A_i (a component due to the summation of the individual effects of all alleles across all contributing loci), a dominance effect D_i (a component due to non-additive effects of the two alleles at each locus, summed across all loci), and an epistatic effect I_i (a summation consisting of effects due to specific combinations of alleles across loci that cannot be attributed to additive or dominance effects),

$$G_i = A_i + D_i + I_i.$$

The factors that contribute to the environmental component are often misunderstood. In the most well-designed quantitative genetics assessments, the environmental component is not due to systematic differences in the environmental conditions experienced by different individuals, but rather due to random 'noise' that each individual experiences to some degree. Perhaps it can best be understood by thinking of it as the summation of a lifetime of Brownian motion at the molecular level. This results in slight variation in the environment experienced by different individuals, despite the fact that a particular setting (e.g., a small body of water) looks quite uniform, and despite the best efforts of experimenters. This results in individuals that have exactly the same genotype exhibiting phenotypes that vary, even in the 'same' environment.

At the population level, the variance at the phenotypic level can be partitioned into components associated with the above-mentioned causal factors:

$$\mathrm{Var}(P) = \mathrm{Var}(G) + \mathrm{Var}(E)$$

and

$$\mathrm{Var}(P) = \mathrm{Var}(A) + \mathrm{Var}(D) + \mathrm{Var}(I) + \mathrm{Var}(E).$$

It is important to note that this often-used equality is dependent on the assumption that higher-order interaction terms (e.g., genotype by environment) can be ignored. Often this is a perfectly reasonable assumption, because appropriate experimental design necessarily makes them disappear. However, in some field studies, or studies without proper control of environmental conditions, these higher-order terms need be considered, or may in fact be the focus of study.

Perhaps the most widely utilized parameter estimate in quantitative genetics is the heritability. The heritability has two common formulations. The first is derived from the causal components of variance mentioned above, from appropriate analysis of relatives, either from breeding designs, or from known relatives in nature:

$$h^2 = \mathrm{Var}(A)/\mathrm{Var}(P).$$

This is the narrow-sense heritability. The second common formulation involves regression analysis of parents and offspring. Narrow-sense heritability is equal to the slope of the regression of offspring values on the mid-parent values, or twice the slope of offspring on one parent. This narrow-sense heritability has the most utility for inference across generations in a sexually repro-

ducing species. This utility is best seen in the so-called 'breeder's equation'

$$R = h^2S$$

which relates the response to selection (R), or evolutionary change, to the heritability and selection differential (S). This latter term reflects the difference between the current population mean and the mean of the parents that contribute to the next generation. This is often abbreviated verbally as the difference between selected and unselected parents.

Another similar parameter estimate is the broad-sense heritability, commonly abbreviated H^2. This represents the portion of phenotypic variance comprised by the total genetic variance:

$$H^2 = Var(G)/Var(P).$$

Broad-sense heritability is often used to give an approximate value for heritability when narrow-sense heritability cannot be determined. However, broad-sense heritability is the appropriate measure of resemblance between parents and offspring in populations that are reproducing by ameiotic means at the time[67]. Therefore, in cyclical parthenogens, for example, the dynamics of evolutionary change are estimated by broad-sense heritabilities during the phase of asexual reproduction, and can be correctly inserted into the breeder's equation under these circumstances:

$$R = H^2S.$$

So far, we have seen two different ways to represent the quantity of genetic variation; the genetic variance (either Var(A) or Var(G) as appropriate), and the heritability (either narrow- or broad-sense as appropriate). Recently, Houle[29] has suggested that a more appropriate measure of genetic variation can be obtained by scaling genetic variance by the character mean. He suggests the genetic coefficient of variation is the most appropriate measure for comparing the quantity of genetic variation among species or among characters:

$$CV_A = 100(S_A/\bar{X})$$

where S_A is the square root of the additive genetic variance, and $\bar{X}$ is the character mean. His argument centers particularly on a perceived inappropriateness of using heritability in comparisons of the amount of genetic variation for different types of characters. Mousseau and Roff[57] present an extremely thorough compilation of heritability estimates for life history, morphological, behavioral, and physiological traits. Their conclusion was that although life-history traits are usually significantly heritable, they are less so than these other classes of characters. Houle re-analyzed a large portion of this data using CV_A as the measure of genetic variation and came to a conclusion opposite of that presented by Mousseau and Roff. Although other researchers might disagree with Houle's conclusion, he has rightfully called our attention to the fact that there are different ways to present 'quantity of genetic variation', and it is important to consider the alternatives before drawing conclusions.

Until now, we have concerned ourselves with one character at a time. This is all that needs to be considered, perhaps, when one is using artificial selection. However, in evolutionary biology, we are almost always dealing with natural selection, which operates on many phenotypic characters simultaneously. For analyses of such situations, we must rely on multivariate methods which allow for phenotypic covariance among characters on which selection is acting, and genetic covariance among characters that are responding to natural selection. Note that in keeping with the definitions preferred by many evolutionary biologists and most quantitative geneticists, I use the term natural selection to refer to selection at the phenotypic level within a generation as distinct from the response to selection, that comprises Darwinian evolution. This is the usage in most recent literature in multivariate evolution[39]. Other authors[16] prefer to use the term natural selection to refer to the process of phenotypic selection and resultant evolutionary change. The terminology I chose is most consistent with quantitative genetic models.

For multivariate applications, the breeder's equation becomes:

$$\Delta\bar{\mathbf{z}} = \mathbf{GP}^{-1}\mathbf{s} \qquad (1)$$

where $\Delta\bar{\mathbf{z}}$ is a vector whose elements are the change in the mean across a generation for individual characters of interest, **G** and **P** are the genetic and phenotypic variance-covariance matrices among these characters, and s is a vector whose elements are the selection differentials associated with individual characters. The analogy with the univiariate breeder's equation can be seen if one recognizes that $\Delta\bar{\mathbf{z}}$ is the response to (natural) selection, and $\mathbf{GP}^{-1}$ can be viewed as multivariate heritability (recall that Var(A)/Var(P) is the narrow-sense heritability, which can be written as $Var(A)Var(P)^{-1}1$). Under the assumption of multivariate normality, Lande and Arnold[39] showed that $\mathbf{P}^{-1}\mathbf{s}$ is equivalent to the selection gradient $\boldsymbol{\beta}$ a vector whose elements are the average values of $\partial w/\partial z_i$ weighted by the phenotype distribution, and where w is relative fitness, and z_i is the value for the i^{th} character. Equation **1** then becomes:

$$\Delta\bar{\mathbf{z}} = \mathbf{G}\boldsymbol{\beta}. \qquad (2)$$

Equation **2** can be used to estimate evolutionary trajectory given a particular episode of natural selection, described by $\boldsymbol{\beta}$[6,45], or to estimate the forces of selection necessary to cause a certain past evolutionary change[42], by the following rearrangement:

$$\mathbf{G}^{-1}\Delta\bar{\mathbf{z}} = \boldsymbol{\beta}.$$

Use of the Lande-Arnold multivariate approach over time periods longer than one generation requires the assumption that the genetic covariance matrix remains constant over the time period of interest. Several different approaches for testing this assumption have been presented[41,66,70]. The general conclusion has been that although it is possible for the genetic covariance structure to change significantly over a measurable period in response to artificial selection[79], comparisons among natural populations and species seem to indicate that the genetic covariance structure remains similar in within-species comparisons, but not for any more distantly related taxa[34,41,70]. However, more data are needed before any such conclusion can be accepted as general.

An important fact to consider when exploring multivariate evolutionary dynamics is that it is the genetic variances and covariances and the selection gradient that determine evolutionary trajectory. Using selection differentials, phenotypic (co)variances, or genetic correlations inappropriately can cause misleading results. For example, it can be shown that even in populations that exhibit positive phenotypic and genetic covariances for a pair of characters, the direction of evolutionary change for one of the two characters may be opposite of the direction of selection, as represented by the selection differentials[11]. This is not true if one examines only the selection gradient and the genetic covariances: if genetic covariance is positive and the selection gradient reflects selection in the same direction for both characters, then both will evolve in the same direction, assuming that there are no other correlated characters that are not part of the analysis that are under selection. This underscores the importance of using elements of the selection gradient to represent the magnitude and direction of selection, rather than the selection differential. In addition, simply regressing an estimate of fitness on one character does not allow any useful approximation of the selection gradient[65]. Rather, this has the effect of scaling the selection differential by the phenotypic variance.

It is important to recognize that the correlation matrix may not be a particularly useful surrogate for the covariance matrix[4]. Often, it is convenient to present genetic covariance structure as genetic correlations, since they are bounded by -1 and 1. However, it is quite easy to find examples where two populations have identical genetic correlation matrices, but also have genetic covariances that are different enough such that the direction of evolutionary change of the characters will differ substantially when exposed to identical selection pressures, i.e., identical selection gradients. For example, consider two populations with the following genetic covariance matrices:

$$\begin{bmatrix} 1 & 1 \\ 1 & 4 \end{bmatrix} \quad \begin{bmatrix} 4 & 1 \\ 1 & 1 \end{bmatrix}.$$

Both will have identical correlation matrices. However, when both are subjected to selection represented by:

$$\boldsymbol{\beta} = \begin{bmatrix} -2 \\ 1 \end{bmatrix},$$

their respective evolutionary trajectories will differ qualitatively (i.e., have different directions of evolutionary change) as well as quantitatively.

The preceding two cautionary paragraphs strongly suggest that one should not attempt to substitute the phenotypic covariance matrix or the genetic correlation matrix for the genetic covariance matrix, or to use selection differentials to represent the action of selection, unless there is no alternative. Even then, caution should precede any conclusions based on such analyses.

Life histories

There is little general agreement on what constitutes a life-history trait. The most restrictive definition would include only age-specific fecundities and mortality rates, the components of life tables. The broadest definition I have seen is: '. . . the entire sequence of changes through which an organism passes in its development from conception to death'[38]. Most workers rely on a definition somewhat intermediate to these extremes. In his recent book entitled *The Evolution of Life Histories*, Stearns[73] listed as the 'principal life history traits': size at birth; growth pattern; age at maturity; size at maturity; number, size and sex ratio of offspring; age- and size-specific reproductive investment; age- and size-specific mortality schedules; and length of life.

One of the first important papers in the study of life histories posed the question about the relative consequences of two alternative reproductive patterns: semelparity and iteroparity[5]. For the next 25 years, the theory of life history evolution emerged, relying heavily on purely phenotypic models and on optimality approaches[22,53,64]. The late 1970s and early 1980s brought a growing awareness that since evolutionary change is a genetic process, genetic rather than purely phenotypic data were needed for examination of existing patterns of life history characters and for assessment of evolutionary potential[71,72]. The contributions of Lande[36,38] and Charlesworth[3] were instrumental in putting evolutionary changes for quantitative characters in a mathematical and genetic framework. A conference at the University of Iowa in 1980 resulted in an important volume entitled *Evolution and Genetics of Life Histories*[12] that helped emphasize this point.

Recently, genetical work on life history evolution has focused on two major questions. First, what is the level of genetic variation for life history characters in natural

Table 1. Heritability estimates for life history characters in copepods.

	Eurytemora herdmani		*Mesocyclops edax*		*Cyclops scutifer*
	10 °C	15 °C	Michigan	Florida	
Maturation time					0.32**
Males	0.10	0.00	1.12	0.00	
Females	0.20	0.71*	1.71**	0.00	
Body size					
Males	0.00	0.97*		0.39*	
Females	0.24	0.38	0.19	0.55*	
Sex ratio	0.11	0.27			
Clutch size			0.00	0.16	

*$p < 0.05$; **$p < 0.01$.
E. herdmani data from ref. 54; *M. edax* data from ref. 81; *C. scutifer* value represents an average for both sexes across 5 Norwegian populations, from ref. 75.

populations? Fisher's Fundamental Theorem of Natural Selection is often cited as the basis for expecting low genetic variation for life history characters[21]. The presumption is that constant selection on characters that are closely associated with fitness will lead to the erosion of standing levels of genetic variation for such characters. Second, what is the pattern of covariation among life history characters? This is a fundamental question because the current pattern of covariation dictates how current selection pressure will be translated into evolutionary change[36,39]. It has special significance, because one of the most widely held explanations for the significant heritabilities found for life history characters in natural populations is antagonistic pleiotropy. This hypothesis states that genetic variation is maintained for individual characters because the polymorphic loci that contribute to quantitative genetic variation and have pleiotropic effects on two life history traits are much more likely to remain polymorphic if the alternative alleles have opposite effects on the two traits[61–63,80].

While the commonly-cited expectations for a population at equilibrium with a particular environment are low levels of genetic variation with negative genetic covariation among life-history traits (but see ref. 59), several of the first studies designed to test these expectations revealed the opposite result[23–25]. Indeed many studies have indicated substantial genetic variance for life-history characters, with a mixture of evidence for and against negative covariation among them (see ref. 73 for review).

Quantitative genetic analyses of zooplankton

Although many different types of zooplankton are ideal for quantitative genetic analyses, relatively few have been studied in this way. By far, the majority of work has been done on *Daphnia*. Before I go into this body of work in detail, I want to call attention to the few studies that have been conducted on other species.

As mentioned above, the first zooplankton quantitative genetics work of which I am aware was published by Ian McLaren[54]. Using standard plant and animal breeding designs, he estimated the heritabilities of maturation time, body size, and sex ratio in the marine copepod *Eurytemora herdmani* at 10 °C and 15 °C. He found substantial and statistically significant heritabilities in one instance each for female developmental time, and male body size (table 1). Interestingly, heritability estimates were generally higher, and both significant estimates occurred at 15 °C.

Wyngaard[81] reported on a similar study of the freshwater copepod *Mesocyclops edax*. She compared the levels of genetic variation between two populations, one in Michigan and one in Florida. She found that heritability for maturity time was high for both sexes in the Michigan population, but not for the Florida population. For body size, the opposite was true: both sexes exhibited significant heritability in the Florida population, but not in the population from Michigan (table 1). Finally, in a study on five natural populations of *Cyclops scutifer* in Norway, Twombly[75] reported data indicating that the average heritability for time to metamorphosis (averaged across the sexes) was approximately 0.32 (table 1). She also found substantial differences among neighboring populations for this trait.

Daphnia

Daphnia is a genus of freshwater crustaceans in the order cladocera. There are dozens of species, all of which are planktonic filter-feeders. Their primary food is suspended algae and detrital particles, although they are capable of scraping some periphyton from surfaces. Species range in size from *D. parvula*, which matures at well under 1 mm, and rarely exceeds 1.2 mm, to the helmeted species of Australia, such as *D. cephalata*, that reach sizes in excess of 6 mm. The primary mode of reproduction is cyclical parthenogenesis, whereby periods of ameiotic reproduction are interspersed with

bouts of sexual reproduction. Sex determination as well as the switch from ameiotic to meiotic reproduction occurs in response to environmental cues[33,40], although there is some evidence of a genetic basis to variation for sex ratio[82]. In cyclical parthenogens, the ameiotic eggs are all non-diapausing (subitaneous), whereas the sexually-produced eggs are in diapause and are enclosed in a protective, heavily melanized structure called an ephippium.

The normal phenology for populations inhabiting temperate zone temporary ponds is as follows. As winter and spring rains refill such ponds, the diapausing eggs rapidly hatch. Since all diapausing eggs are the consequence of sexual reproduction, all ex-ephippial hatchlings are genetically distinct. The numbers of such hatchlings often exceed 100,000 each year, even in relatively small ponds[44]. Each hatchling gives rise to a distinct clone which increases in number by ameiotic reproduction as long as environmental conditions remain favorable. Low food availability and high population density (two factors that nearly always co-occur in nature, but can be investigated separately in the laboratory) are two of the cues that elicit the switch from ameiotic to meiotic reproduction[33,40]. Males are diploid and genetically identical to parents.

Very little is known about the frequency of sexual reproduction in populations inhabiting permanent bodies of water. The substantial departure from Hardy-Weinberg expectations for genotypic frequencies suggests infrequent sex in some permanent populations[43,49,51]. However, stable frequencies in accordance with Hardy-Weinberg expectations have also been reported[55,56]. It is possible that extremely long periods of clonal reproduction without any recombination can occur in permanent lakes and ponds. The expectation under such conditions would be very low levels of clonal diversity and genetic variance, for which there is some empirical support[51].

It is becoming increasingly apparent that many clones of *Daphnia* in several species have been transformed from cyclical parthenogenesis to obligate parthenogenesis, whereby their diapausing eggs are also produced asexually[2,31]. At least for *D. pulex* in North America, there is substantial evidence that this transformation in mode of reproduction is due to a dominant, sex-limited meiosis suppresser, which arose in the species fairly recently[31]. Many of these obligate parthenogens retain the ability to produce males, who retain the ability to produce gametes through meiosis. These males are capable of mating with females from cyclically parthenogenetic lineages. The result is that half of the offspring are 'converted' to obligate parthenogenesis. In addition, some obligately asexual clones are apparently the result of interspecific hybridization: *D. pulex* × *D. pulicaria*[27].

Two different approaches have been used to analyze quantitative genetic variation of life-history characters in *Daphnia*. The first approach is at the level of the clone. One-way ANOVA with clone as the classification variable allows the variance to be partitioned into components due to total genetic causes (among clone) and environmental causes (within clone). The proportion of the total (phenotypic) variance that is genetic is the broad-sense heritability. Multivariate analysis of such data results in genetic correlations due to the total genetic values of the individual clones. These broad-sense heritabilities and total genetic covariances (and correlations) are pertinent when one desires to explore evolutionary dynamics across generations of asexual reproduction, such as occurs for 10–15 generations in temporary pond populations, or for potentially much longer periods in permanent lakes.

The second approach involves parent-offspring analysis, such that the additive component of the genetic variance can be estimated. Because *Daphnia* do not lend themselves easily to the breeding designs that work so effectively in other organisms, investigators have relied on the collection of ephippial females from natural populations during bouts of sexual reproduction. The ephippial female is isolated, allowed to release her ephippium and the sexually produced eggs that it contains, and is then well-fed, causing the switch back to asexual reproduction. When an ephippial egg can be hatched, the result is a pair of parent and offspring clones. Appropriate parent-offspring analysis can be used to obtain narrow-sense heritabilities as well as additive genetic variances and covariances (and correlations). In the discussion below, the use of broad-sense heritability and total genetic (co)variance (correlations) will indicate the use of the first approach, whereas narrow-sense heritability and additive genetic (co)variances will indicate the latter approach.

Body size and reproduction: univariate data

Due to work over the last decade, there are now 19 populations including 6 species for which there are estimates of broad-sense heritability for body size, clutch size, and age at reproduction (table 2). For body size, 8 of the 19 estimates exceed 0.40. At least one population in five of the six species exhibits an H^2 of at least 0.39. In only two of the populations is the estimate less than zero, which, although theoretically impossible, can occur due to sampling error. Clearly, *Daphnia* populations harbor substantial genetic variation for body size: the average H^2 among these populations is 0.31.

Similar values can be found for clutch size. The estimates presented in table 2 represent the averages across four to six clutches and exhibit a range similar to that of body size: 6 of 19 populations have H^2 estimates in excess of 0.40, and the average across all populations is 0.31. Do populations with high heritabilities for body size also have similar values for clutch size? The rela-

Table 2. Broad-sense heritabilities for body size, clutch size, and age at maturity in *Daphnia* populations.

Species	Body size H^2	Clutch size H^2	Age at reproduction H^2	Reference[a] (Population name)
D. magna				
	0.50*	0.29*	0.23*	14[b]
	0.07	0.44*	0.45**	83
D. obtusa				
	0.42	0.22	0.58	44[c]
	0.51*	0.28	0.31	69: CT
	0.30*	0.21	−0.04	69: NH
	−0.14	−0.21	0.03	69: NP
	0.46*	0.42*	0.28	69: OJ
	0.45*	0.13	−0.02	69: BUF
	0.56**	0.37**	0.83**	69: HAP
	0.29*	0.55**	0.72*	69: MAY
	0.02	0.32	0.39	69: TRE
D. pulex				
	0.27	0.56	0.38	44[d]
	0.38**	0.37**	0.12	50: PA[e]
	0.45**	0.48**	0.37**	50: KA[e]
D. "amazon"[f]				
	0.24**	0.28**	0.38**	47
D. pulicaria				
	−0.03	0.06	0.48**	51: Hosmer
	0.52**	0.64**	0.55	51: Klamath
	0.31**	0.30**	0.23	51: Odell
D. galeata mendotae				
	0.39**	0.18*	0.19	74[g]

*$p < 0.05$; **$p < 0.01$.
[a]Population name is given only if more than one population is presented in the cited paper. See original citation for more details about populations.
[b]Values for body size and clutch size for the high food treatment were estimated from figure 1 in ref. 14, and represent an average of the presented age classes.
[c]This population was referred to as the *D. pulex* B-clone before its identification as *D. obtusa* was determined. No determination of statistical significance was reported.
[d]This population was referred to as *D. pulex* C-clone in ref. 44. No determination of statistical significance was reported.
[e]The estimates from populations PA and KA given here are from data sets presented in ref. 50, but were re-analyzed in ref. 49 or 51 to allow comparison of more similar characters.
[f]This population is related to *D. pulex*, but electrophoretic information indicates that it is a distinct species. It will be officially named soon (P. D. N. Hebert, pers. commun.).
[g]Values obtained from ANOVA tables for June sample.

tionship is a positive one, with a relatively high correlation: $r = 0.48$.

Finally, the H^2 estimates for age at maturity are, on average, quite similar to those for body size and clutch size: the average across all populations is 0.34. There does appear to be more variation among these populations with respect to their estimates: five are in excess of 0.55, while three do not exceed 0.03. Heritability for age at reproduction is not correlated with heritability for body size ($r = 0.14$). However, the correlation between heritability estimates for clutch size and age at maturity is highly positive: $r = 0.52$.

All of the heritability estimates listed in table 2 are broad-sense heritabilities. To determine the potential long-term consequences of these estimates, i.e., their significance across bouts of sexual reproduction, it is important to know what proportion of the genetic variance is additive genetic variance. Ebert et al.[14] and Lynch and Deng[47] used parent-offspring regression to estimate the narrow-sense heritability (h^2), and then compared it to the H^2 estimates from ANOVA (among-clone). Ebert et al.[14] found evidence for non-additive gene action for body size, but not clutch size (table 3). Lynch and Deng[47], on the other hand, found little non-additive variance for body size, but substantial amounts for clutch size and age at maturity (table 3). The common observation of inbreeding depression in *Daphnia*[9,30,47] certainly suggests significant non-additive genetic variance. The crude average across all values in table 3 suggests that roughly 60% of the total genetic variance is additive.

Mutational variance

Mutation is the ultimate source of all genetic variation. Measurement of the rate of new genetic variation per generation via spontaneous mutation is central to our understanding of the evolution of quantitative traits. This quantity has been termed V_m. Many zooplankton species are ideal organisms for the measurement of this quantity, although the necessary experiments are arduous. One such experiment was performed on an oblig-

Table 3. Comparison of broad- and narrow-sense heritabilities for *Daphnia*.

Character, food level	H^2	h^2	Reference
Body size, high food	0.50*	0.33	14
Body size, low food	0.19*	0.02	14
Clutch size, high food	0.29*	0.30	14
Clutch size, low food	0.16	0.27	14
Body size	0.24**	0.20	47
Clutch size	0.28**	0.06	47
Age at maturity	0.38**	0.04	47

*$p < 0.05$; **$p < 0.01$.
Note: the food level used in ref. 47 is higher than the high food in ref. 14. Ref. 14 studied *D. magna*, while ref. 47 studied a new species in the *D. pulex* group that will be officially named soon (P. D. N. Hebert, pers. commun.).

ately parthenogenetic clone of *D. pulex* by establishing 50 independent lines from the offspring of a single female from one clutch[45]. These lines were maintained for 75 generations under conditions that were designed to eliminate the action of natural selection as much as possible. After the two-year period, ANOVA was performed on replicate individuals for each of the surviving lines. Any genetic (among-line) variation must be due to spontaneous mutations that arose during the experimental period.

The values of V_m are best expressed as a fraction of the environmental variance, which is essentially equivalent to the 'mutational heritability', V_m/V_p. The estimated values were: offspring size: 0.00098; body size at maturity: 0.00325; age at maturity: 0.00133; clutch size: 0.00140, biotic potential: 0.00083. The average mutational heritability for these characters is 0.00156, a value in close agreement of those obtained for other organisms[46].

Body size and reproduction: multivariate data

I will summarize the available data for genetic correlations (all of which are total genetic correlations) that pertain to three major types of life history trade-offs that are often discussed: offspring size vs offspring number, present vs future reproduction, and fecundity vs age at maturity. Notice that in each of the tables that will be referred to, there is an estimate of 'mutational' correlation. This refers to the average pleiotropic effect of mutations in terms of correlations, which are derived from Lynch's[45] study of spontaneous mutations.

There is considerable variation in the estimated genetic correlations for offspring size and offspring number (table 4). While the mutational input indicates a positive (although not statistically significant) value, the estimates from natural populations reveal either no correlation, or a trade-off. In fact, all significant effects are negative. However, it should be noted that the majority of populations studied indicate no such trade-off. Ebert[13] points out that in all studies, there is a trend toward more negative genetic correlations in experiments conducted with lower food availability.

The genetic correlations between present and future reproduction are much more consistent: all values from natural populations are positive, with seven of the ten estimates achieving statistical significance (table 5). The only negative correlation, which would indicate a trade-off between present and future reproduction, is for mutational input. However, this value is not significant. There is a potentially interesting trend in these data: the correlations seem to decline slightly as the time between the clutches being compared increases. This might mean that comparison of clutch sizes from clutches early and very late in life might reveal a trade-off. However, since *Daphnia* seldom live that long in nature, it would probably have no significance with respect to life history evolution in natural populations. However, it could prove interesting for the study of aging.

Finally, there are a few estimates that examine the potential trade-off between quantity and timing of reproduction: the relationship between clutch size and age at first reproduction (table 6). Again, there is evidence for a difference between the mutational input and the values observed in natural populations: all values from natural populations show a negative value, which indicates that early reproduction is associated with large clutch sizes, while the mutational input, though non-significant, exhibits the opposite sign.

Table 4. Genetic correlations (r_G) among life history traits in *Daphnia*: offspring size vs offspring number.

Species	r_G	Populations	Clutches	Food	Reference
D. pulex	−0.33*	1	2	L[a]	44
	−0.05	2	4	H[b]	67
D. obtusa	0.20	8	6	H[b]	Spitze, unpubl.
D. magna	0.00	1	4	H[c]	13
	−0.37**	1	6	M[d]	13
	−0.42**	1	6	L[e]	13
D. pulex, mutational	0.23	1	2	H[f]	45

*$p < 0.05$; **$p < 0.01$.
Food levels in the experiments: L, low; M, medium; H, high level.
[a]Water was taken every two days from natural pond. Clutch sizes indicate that the level of food availability is most comparable to 'Low' food; [b]300,000 cells/ml *Scenedesmus*; [c]100,000 cells/ml *Ankistrodesmus*; [d]40,000 cells/ml *Ankistrodesmus*; [e]10,000 cells/ml *Ankistrodesmus*; [f]80,000 cells/ml *Scenedesmus* plus 16,000 cells/m *Chlamydomonas*.

Table 5. Genetic correlations (r_G) among life history traits in *Daphnia*: present vs future reproduction.

Species (no. of pops)	i, i + 1	i, i + 2	i, i + 3	i, i + 4	Reference
D. pulex (1)	0.63				44
D. pulex (2)	0.76**	0.60**	0.67**		67
D. obtusa (8)	0.77*	0.42*	0.22	0.02	Spitze, unpubl.
D. pulicaria (1)		0.75**		0.64**	51
D. pulex, mutational (1)	0.48	−0.34			45

*$p < 0.05$; **$p < 0.01$.
Note: i, i + 1 refers to the genetic correlation between clutch size in successive clutches, i, i + 2 refers to comparisons of alternate clutches, etc.

Table 6. Genetic correlations (r_G) among life history traits in *Daphnia*: fecundity vs age at maturity.

Species	r_G	Reference
D. pulex	−0.22	44
D. pulex	−0.69*	67
D. pulicaria	−0.40**	51
D. pulex, mutational	0.59	45

*$p < 0.05$; **$p < 0.01$.
Note: the above figures are averages across irregular numbers of clutches, but represent the best available estimates from each study.

Discussion

Already, there exist sufficient data to begin to answer some fundamental questions in evolutionary biology. The substantial and statistically significant heritabilities for body size, clutch size, and age at reproduction that are found repeatedly indicate the potential for future evolutionary change due to natural selection in all of these traits. The similarity in the average heritability estimates for all of these types of characters does not provide support for the idea that life-history traits (clutch size, age at reproduction) are less heritable than morphological traits (body size), as suggested by[57]. However, before the results presented thus far can be accepted as general, data must be collected from environmental conditions that span those to which natural populations are exposed. There is some evidence that heritability estimates at high food availability may be larger than those measured at low food. To assess the pertinent measures of heritability, we must gather further information on the relative amounts of time that natural populations experience different environmental conditions, as well as the heritability estimates from these different environments. Further, we must expand our efforts to estimate the degree to which genetic variance has an important additive component.

Several other studies designed to investigate life history variation in zooplankton populations have shed some light on the existence of genetic variation for such traits[1,10,58,78]. However, it is important to note that inference at the population level is dependent upon random and substantial sampling. Non-randomly sampled genotypes from natural populations can provide little insight into the degree of genetic variation in such populations, or into the pattern of genetic covariation. The latter is particularly difficult to ascertain when sample sizes are small.

Taken together, these data do not provide much evidence for the existence of trade-offs among life history traits in natural populations of *Daphnia*. There are several possible reasons for this, of which I will mention two. The first follows from theory developed by van Noordwijk and de Jong[8,76]. The basic idea is that if the average pleiotropic effect of mutational input is highly positive, due either to different mutation rates or different relative abundances of loci with positive vs negative pleiotropic effects, then the expectation for genetic correlation between life history traits (where a trade-off is expected) may in fact be a positive genetic correlation at selection-mutation equilibrium[28]. Lynch[45] has provided some information on the average pleiotropic effect of spontaneous mutations. The positive correlations between mutational input for offspring size and offspring number (table 4) and between some measures of present and future reproduction (table 5) seem to provide support for these ideas. However, as seen in tables 5 and 6, not all data provide such support. The second is that populations may seldom be at evolutionary equilibrium. Price and Schluter[59] showed that it is quite possible for life history traits to exhibit substantial positive correlations (even when trade-offs are expected) if the population is not very close to the optimum phenotype set by the current fitness function.

Future zooplankton quantitative genetic research

There are three other areas in which we need substantial additional information to further our understanding of the microevolutionary process. Zooplankton species may prove ideal model systems for investigations in both. The first is the direction, magnitude, and temporal pattern of selection on quantitative traits. Much evolutionary theory (and essentially all life-history theory) is based on the attainment of equilibrium conditions. This means that the pattern of selection (i.e., the selection gradient) is essentially invariant. There are few published estimates of the degree to which elements of the selection gradient vary spatially and temporally[26], and

most of these are univariate[32,65], which actually reflect selection differentials scaled by the phenotypic variance. All of these studies found variation in selection, whether the investigation focused on temporal or spatial variation. Clearly, there is a need for more information of this type. Zooplankton species provide very fertile ground for such work, such as my recent assessment of the relative importance of selection in promoting interpopulational variation in body size[69].

Another important area of evolutionary research for which zooplankton will prove to be invaluable is the study of the prevalence and relative importance of genotype × environment interaction, and the evolution of phenotypic plasticity. The temporal variation in the pattern of selection and the evidence that genetic parameters can vary with environmental conditions both strongly suggest that genotype × environment interaction may be important in life-history evolution. Cyclical parthenogens, in particular, are ideal study organisms for such research, because genetically identical individuals can be reared in different environments. Already, some information on the genetic basis of phenotypic plasticity has emerged from studies of *Daphnia*[15,68].

Finally, as interest in aging research grows at nearly an exponential rate, zooplankton species may gain more prominence as study organisms, because of their ease of laboratory culture and short generation time[48]. The patterns of life-history covariation are already being examined in light of the existing theories on aging[60].

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