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COMMENTARY ON *J. GENET.* CLASSIC

Are bigger flies always better: the role of genes and environment

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Introduction

Body size, especially in invertebrates, is often positively correlated with major fitness components such as female fecundity and male mating success, and it is believed that the evolution of larval growth rate and adult body size in insects is largely shaped by a tradeoff between the fitness benefits of being large versus those of developing to adulthood fast (Santos *et al.* 1988; Partridge and Fowler 1993). Understanding the phenotypic inter-relationships between development time, body size and adult fitness components in insects, and how these relationships are affected by genotype and environment, is therefore directly relevant to two contentious and central issues in evolutionary genetics: (1) the nature of genetic constraints on the attainment of an optimal life-history, and (2) the relative role of genotypic and environmental variation and covariation in determining the magnitude and sign of phenotypic correlations between fitness related traits (Prasad and Joshi 2003). Almost half a century ago, in a characteristically rigorous and detailed study, Robertson (1957) examined the nature of genetic variation and covariation between body size (thorax length) and egg production (total fecundity between days 4–8 post-eclosion), under benign and uniform rearing conditions, in a large, genetically variable laboratory population of *Drosophila melanogaster*. The major findings of Robertson's (1957) study were that (a) there was a significant positive phenotypic correlation between body size and egg production, (b) about 50% of the phenotypic variance in body size was due to genetic variation, mostly additive, (c) about 60% of the phenotypic variance

in egg production was due to genetic variation, with a large non-additive component, (d) body size and egg production appeared to be independently genetically correlated with development time, the latter negatively and the former positively, and (e) the genetic correlation underlying the positive phenotypic correlation between body size and egg production was largely non-additive.

Quite apart from the significance of the results, there are several appreciable methodological features of Robertson's (1957) study, features that are important to experimental design and execution in evolutionary genetics but, unfortunately, often overlooked, although practitioners of experimental evolution have recently been repeatedly calling attention to them (e.g. Rose *et al.* 1996; Ackermann *et al.* 2001; Chippindale *et al.* 2003). For example, Robertson (1957) worked with a large, genetically variable, and reasonably well laboratory-adapted population that was close to genetic equilibrium for the traits being studied, explicitly controlled larval density during assays, recognized that trait relationships could be environment- and age-specific and tried to incorporate this knowledge in the choice of measures for size and egg production, and was sensitive to the fact that phenotypic measures of fitness related traits often vary from day to day, and assay to assay, and, consequently, tried to account for that variation in the experimental design and analysis. Except for the lack of population level replication, these precautions, and the caveats one finds throughout Robertson's (1957) discussion of the results, make for a very 'modern' paper in experimental evolutionary genetics, in stark and somewhat unfortunate contrast to many contemporary papers that often seem to be imbued with a combination of an abiding faith in selection as an inexorable optimizing force and an overly simplistic view of the evolutionary process.

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Consider, as just one example of ‘modernity’, the following extracts from the paper: “Where the phenotypic variation represents a complex interplay of effects, the familiar statistical partitioning into genetic, environmental and interaction effects can only be regarded as a first approximation. . . . There is tangible evidence of the influence of environmental conditions on the manifestation of genetic differences. . . . With less favourable but more natural conditions, the variation between individuals probably depends much more on gene-environment interaction than is the case under the favourable conditions which are usually chosen for experimental purposes”.

It is perhaps ironic that part of the reason for the neglect of phenomena like genotype \times environment ($G \times E$) interactions in much contemporary evolutionary discourse is likely due to the stunning advances in genetics since the time of Robertson’s (1957) paper. One outcome of the methodology and approach of modern genetics is a disproportionate focus of attention on single genes of major effect. Thus, genetics is increasingly being viewed—especially in our own country—as being the study of genes, or DNA, rather than the study of ‘heredity and variation’, an older and much more useful definition that encompassed the important epigenetic and environmental influences acting between the genotype and phenotype. Coupled with this gene-centric view, perhaps a corollary to it, is a tendency to view selection as typically being directional, and leading to the attainment (fixation) of optimal phenotypes. Yet, at the same time, there is increasing empirical evidence of the subtleties of the process of adaptive evolution, highlighting the complex interplay between environmental conditions, past history, genetic variation and selection on various traits in different life-stages (reviewed in Prasad and Joshi 2003), as well as evidence for the ubiquity of genotype \times genotype ($G \times G$) and $G \times E$ interactions for the composite phenotypes that are usually of interest in evolutionary studies (Rose *et al.* 1996; Elena and Lenski 1997; Santos *et al.* 1999; Leips and Mackay 2000; Vieira *et al.* 2000; Remold and Lenski 2001).

Another repeated observation in experiments involving selection on life-history related traits is that of a reasonably rapid attainment of a plateau in selection response, at which point the populations typically harbour significant additive genetic variation for the trait(s) under selection, as evidenced by their rapid response to either increases in selection intensity or reverse selection (Teótonio *et al.* 2002; Joshi *et al.* 2003). This finding, in turn, suggests that selection on composite traits relevant to the life-history is often of a stabilizing type, inasmuch as the fitness function tends to be humped; in this view, directional selection is often no more than a transient discordance between the hump of a fitness function and the mode of the phenotypic distribution in a population (Joshi *et al.* 2003). In fact, $G \times G$ and $G \times E$ interactions, along with pleiotropy for fitness related traits, are likely to be major contribu-

tors to the humped shape of fitness functions (Joshi *et al.* 2003). If selection, indeed, is typically stabilizing, favouring intermediate rather than extreme phenotypes, then the implications for the gene-centric view of adaptive evolution are severe because, in such circumstances, the explanatory power of marginal allelic fitnesses diminishes to zero (Sober and Lewontin 1982). Once again, as in the case of $G \times E$ interactions, Robertson (1957) gives due attention to the issue of stabilizing selection on fitness related traits, and the maintenance of genetic variation for these traits at equilibrium. Indeed, his paper starts with the statement “The occurrence of extensive genetic variation, coupled with the stability of average phenotype, in populations adapted to prevailing conditions, raises many problems which call for a good deal more basic information than exists at present. In particular, we need comparisons of the behaviour of genetic variation in different sorts of ‘character’, and the extent and manner in which environmental variation affects the expression of such variation, together with tests of genetic correlation between different characters, especially those which directly affect fitness”. This is still broadly true, although our understanding of these issues has progressed quite a bit since 1957.

To return to the question of whether bigger flies are always better, the answer from Robertson’s (1957) study appears to be a “well . . . it depends on lots of other things, especially the environment”. This, too, is till true; notwithstanding the many studies showing fitness benefits of larger size in *Drosophila* males and females (e.g. Partridge and Fowler 1993; Bangham *et al.* 2002, and references therein), it is becoming clear that the relationship between fitness and body size in *Drosophila* is not all that straightforward. The available evidence indicates that the causes of the phenotypic size variation can greatly affect how size is correlated with male and female fitness components in *Drosophila*. When size variation is induced by substantial variation in nutritional quality or larval density, size is positively correlated with male mating success (Santos 1996) and female fecundity (Robertson 1957; Houle and Rowe 2003), whereas the lower degree of size variation seen in moderate density cultures does not appear to be correlated with male mating success (Joshi *et al.* 1999). Unlike in the case of larval density induced size variation, however, size variation induced by variation in rearing temperature does not appear to be correlated with male and female reproductive success (Partridge *et al.* 1995; Zamudio *et al.* 1995). Moreover, variation in body size, and the correlation between body size and male and female fitness components, are also known to be affected by $G \times E$ interactions, at least in the case of environmental variation in nutrition, larval density and temperature (Robertson, 1957; Wilkinson *et al.* 1987; Santos 1996; McCabe and Partridge 1997; Joshi *et al.* 1999). It is, therefore, important to recognize that orrelations between fitness related traits can vary across

environments, just as they can vary over time in a single population.

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