

Evolutionary genetics: the *Drosophila* model

Preface

Evolutionary genetics straddles the two fundamental processes of life, development (the transition from egg to adult) and reproduction (the generation of eggs from adults), and scrutinizes, from an evolutionary perspective, the nature and consequences of the twin genomic attributes of expression and replication, respectively. Moreover, development and reproduction in the living world occur in, and are shaped by, the context of the ecology of organisms. Given this vast domain of evolutionary genetics, it is not surprising that its practitioners often work on very different issues, using varied approaches and methodologies. Historically, the early focus of evolutionary genetics was on heredity, more specifically on deducing the population-level consequences of Mendelian inheritance within families (Felsenstein 2000). The descendent lineages of these early studies in population and quantitative genetics can be categorized, for heuristic purposes, as efforts to understand the *consequences* of natural selection, and these lineages constitute a major 'tribe' within evolutionary genetics. These lines of investigation address the broad issue of how the distribution of genotypes in a population changes under the influence of a given fitness function acting on it. A contrast to this focus on the consequences of natural selection is provided by studies—sometimes characterized as evolutionary ecology—that attempt to understand how and why particular fitness functions are defined on the distribution of phenotypes in a population by its ecology. Studying how the interaction between phenotype and environment results in a fitness function is essentially an exercise in understanding the *causes* of natural selection (Wade and Kalisz 1990). Connecting the causes and consequences of natural selection, or, to put it another way, extrapolating a fitness function defined on a distribution of phenotypes to the corresponding underlying distribution of genotypes, is important to a fuller understanding of the evolutionary process. Basically, making this extrapolation requires not only a detailed understanding of the genome, but also an understanding of how genomes direct the development of phenomes through their expression in a given ecological context, also referred to as understanding the genotype-to-phenotype map (Lewontin 2000). Approaches addressing this issue constitute a relatively young 'tribe' within evolutionary genetics, and rudimentary empirical tools required to study genotype-to-phenotype mapping have only recently become available (White *et al.* 1999; Leips and Mackay 2000; Pletcher *et al.* 2002).

In the past, the domains of evolutionary genetics (in terms of understanding the consequences of selection) and evolutionary ecology (understanding the causes of selection) were separated by a conceptual and empirical gulf owing to the paucity of information about, and understanding of, the genotype-to-phenotype map (Lewontin 2000). Classical quantitative genetics was, in a sense, a clever and useful way of bypassing the expression aspect of the genome (genotype-to-phenotype map) by treating it as a black box, although with time the shortcomings of this approach have become clearer (Felsenstein 2000; Stepan *et al.* 2002). Classical developmental genetics tended to focus on the genotype-to-phenotype map for exclusively morphological traits, and has led to a greatly refined understanding of the ontogeny of form. What has been lacking is an understanding of the ontogeny of function, and through it the ontogeny of life histories in meaningful ecological contexts, an approach that has been termed developmental evolutionary biology, or devo-evo (Prasad and Joshi 2003). Today, with the increasing ability to empirically study the sequences and temporal patterns of expression of entire genomes, we are finally at the threshold of a 'complete' evolutionary genetics, encompassing both the expression and replication aspects of genomes (Houle 2001; Feder and Mitchell-Olds 2003).

Fruit flies of the genus *Drosophila* have been used extensively as model systems in experimental studies of genetics, development and evolution for almost a century. While *D. melanogaster* has reigned supreme as a laboratory system, especially for classical evolutionary and developmental genetics, other *Drosophila* species have been used extensively for more ecologically oriented evolutionary studies in the wild. Given the immense backdrop of relevant information we already possess about *Drosophila* genetics and development, together with more recently obtained information on ecology, physiology, genome sequence and gene expression patterns, it seems reasonable to assume that *Drosophila* species will continue to be major model systems for the 'new' evolutionary genetics that will

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mature in the years to come (Prasad and Joshi 2003). This special issue brings together a sampling of papers—all reporting studies on some species of *Drosophila*—that span several different areas of evolutionary genetics. Some papers deal with broad and classical issues like speciation (Ranganath and Aruna, p. 163), the evolution of genetic architecture (Chippindale *et al.*, p. 133), and the imprints of history, chance and adaptation on phenotypes and genotypes (Joshi *et al.*, p. 147, and Balakirev and Ayala, p. 115, respectively), that were not often addressed experimentally in the past. Other papers focus on more specific problems such as quantifying the extent of genetic variation for sexual size dimorphism (David *et al.*, p. 79), genotypic and environmental effects on bilateral asymmetry (Iriarte *et al.*, p. 95), and the role of a heat shock protein (Hsp70) in hormesis (Kristensen *et al.*, p. 89). The remaining papers attempt to integrate knowledge from the laboratory with studies of adaptation in the wild, by looking at geographical distribution and genetic variation for thermal adaptation (Magiafoglou and Hoffmann, p. 179), local abundance and life-history variation (Sharmila Bharathi *et al.*, p. 191), and patterns of allelic, cytogenetic and physiological variation underlying latitudinal clines in body size (de Jong and Bochdanovits, p. 207). I believe that this collection of papers serves to highlight several conceptually important issues in evolutionary genetics, as well as to underscore the continuing relevance of *Drosophila* species as model systems for evolutionary-genetics research in the post-genomics era. I hope this special issue will prove interesting, informative and thought-provoking for both established researchers and those just embarking upon a research career in evolutionary genetics. Finally, it is a pleasure to thank not only all the authors who responded positively to my request for contributing papers, but also the many evolutionary geneticists across five continents who did an admirably thorough job of reviewing the manuscripts, and whose efforts have helped make a good collection of manuscripts even better.

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