

## The genetics of adaptation in *Drosophila sechellia*

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### Abstract

*Drosophila sechellia* is an island endemic of the Seychelles. After its geographic isolation on these islands, *D. sechellia* evolved into a host specialist on the fruit of *Morinda citrifolia* – a fruit often noxious and repulsive to *Drosophila*. Specialization on *M. citrifolia* required the evolution of a suite of adaptations, including resistance to and preference for some of the toxins found in this fruit. Several of these adaptive traits have been studied genetically. Here, I summarize what is known about the genetics of these traits and briefly describe the ecological and geographical context that shaped the evolution of these characters. The data from *D. sechellia* suggest that adaptations are not as genetically complex as historically thought, although almost all of the adaptations of *D. sechellia* involve several genes.

### Introduction

Renewed interest in the genetics of adaptation is improving our understanding of how individual genes affect adaptive phenotypic differences between closely related species. This work has focused on identifying the number and phenotypic effects of genes involved in adaptive differences between species (for simplicity, ‘adaptive’ refers to a derived condition that arose as a result of selection). In particular, many of these studies have tried to determine if adaptive evolution typically results from the action of many genes of small phenotypic effect or from a few genes of large phenotypic effect.

Historically, evolutionists and quantitative geneticists preferred a polygenic view of adaptive evolution that assumed that phenotypic change involved many factors of very small effect each. This view is being challenged by recent data from quantitative trait locus (QTL) analyses. QTL analysis allows genetic dissection of traits in species that can be crossed to form hybrids carrying random combinations of chromosomal regions

from the parental species. Once these hybrids are created, the species identity of chromosomal regions is inferred from genetic markers, and then the phenotype of each genotype is scored. From these data, one can map, count, and estimate the effects of genes underlying the trait studied. Such analyses have repeatedly shown that morphological differences often involve only a handful of chromosome regions of substantial effect each. Most QTL studies, however, have focused on agriculturally and economically important organisms. Unfortunately, the genetics of agricultural traits, with their long history of strong artificial selection by humans, may not be representative of the genetics of phenotypic differences that evolved in nature. Nevertheless, there is increasing evidence suggesting that ‘natural adaptations’ may also involve a modest number of genes. Moreover, it appears that the distribution of gene effects underlying morphological evolution may be roughly exponential – an idea supported by evolutionary theory (Kearsey & Farquhar, 1998; Orr, 1998, 2001). In many cases, genes of small effect are clearly involved, but a few factors of large

effect typically account for much of the phenotypic differences between species.

An ideal model species for studying the genetics of adaptive divergence would (1) have recently evolved adaptive traits, (2) be closely related to a genetic model system, and (3) allow the creation of transgenic animals. Remarkably, *D. sechellia* has all three of these attributes, and so provides a rare opportunity to address the genetics of adaptation. Here, I review what we have learned about the relationship of *D. sechellia* to its sister species, its natural history, and the genetic basis of its adaptations. These data highlight how useful *D. sechellia* is as a model system for studying the genetics of adaptation.

### Species relationships

*D. sechellia* is a member of the *D. melanogaster* subgroup and is most closely related to *D. simulans* and *D. mauritiana*. Which of these two species is the closer relative is not known, although recent evidence tentatively suggests that *D. sechellia* speciated before the split between *D. simulans* and *D. mauritiana* (Kliman et al., 2000). The genetics of reproductive isolation in this group has been recently reviewed by Coyne and Orr (1998; see related Macdonald & Goldstein, 1999). Thus, I will only discuss the basic biology of interspecific hybrids relevant to conducting genetic analyses of *D. sechellia*.

Both *D. simulans* and *D. mauritiana* produce fertile females and sterile males when crossed to *D. sechellia* regardless of the direction of the cross. (*Wolbachia* bacteria, while present in some strains of all three species do not appear to greatly affect the fertility or viability of hybrids (Giordano, O'Neill & Robertson, 1995). This means that backcross hybrids can be generated between these species. This allows us to take advantage of the genetic tools available in these species including a number of genetic markers, a few chromosomal aberrations, and some marker P-element insertion lines (True, Weir & Laurie, 1996; Flybase, 1999). It has also been shown that transgenic flies can be made in these species (Scavarda & Hartl, 1984; True, Weir & Laurie, 1996).

Typical for the *D. simulans* clade, *D. melanogaster* females when crossed to *D. sechellia* males produce only sterile F1 daughters, whereas

*D. melanogaster* males when crossed to *D. sechellia* females produce only sterile F1 sons. A number of hybrid rescue mutations have been discovered in *D. melanogaster* and *D. simulans* (Ashburner, 1989). These mutations typically lead to the production of both sterile males and females. Some combinations of these mutations can weakly restore the fertility of hybrids (Davis et al., 1996; Barbash, & Ashburner 2003). *D. sechellia* seems to be more recalcitrant to hybrid rescue than its sister species (Barbash, Roote & Ashburner, 2000; Barbash & Ashburner, 2003). This means that only those *D. melanogaster* genetic tools that are informative in F1 hybrids (e.g., deficiencies) are useful.

### Genetics in *D. sechellia*

Relative to *D. melanogaster* (or even *D. simulans*) the genetic tools available in *D. sechellia* are sparse. Several visible genetic markers are available and, recently, a number of molecular markers have been developed (Rux & Coyne, 1991; Colson, MacDonald & Goldstein 1999; Flybase, 1999). However, most mapping studies using visible markers have taken advantage of the far more plentiful tools available in *D. simulans* via interspecific hybrids. Unfortunately, these studies are still of limited resolution and power.

In principle, it is possible to use many of the chromosomal deficiencies and duplications available in *D. melanogaster* to map traits in F1 hybrids between it and *D. sechellia*. In practice, however, this mapping approach is frustrated by three facts. (1) The viability of F1 hybrids between *D. melanogaster* and *D. sechellia* is poor and gets worse in hybrids with a chromosomal aberration (Barbash, Roote & Ashburner 2000; Jones, unpublished). (2) F1 *melanogaster/sechellia* hybrids show a number of morphological abnormalities including degenerated reproductive organs, bristle loss, malformed cuticle, and other morphological defects (Takano, 1998). (3) *D. sechellia* is not completely chromosomally homosequential with *D. melanogaster*, which means a few regions cannot be adequately analyzed using deficiencies (Lemunier & Ashburner, 1984).

Recently, Colson, MacDonald and Goldstein (1999) expanded the number of genetic tools available in *D. sechellia* by developing a set of