

Sexual size dimorphism in a *Drosophila* clade, the *D. obscura* group

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Abstract

The *Drosophila obscura* clade consists of about 41 species, of which 20 were used for analyses of wing and thorax length. Our primary goal was to investigate the magnitude of sexual size dimorphism (SSD) of these traits within this clade and to test Rensch's Rule [when females are larger than males, SSD (e.g., female/male ratio) should decrease with body size]. Our secondary goal was methodological and involved evaluating for these flies alternative measures of SSD (female/male ratio, female/male absolute difference, female/male relative difference), developing a bootstrap method to estimate the magnitude of intraspecific variation in SSD, and applying a new method of estimating allometric relationships that is phylogenetically based and incorporates error variance in both traits. All indices of SSD were strongly correlated for both size traits. Nevertheless, female/male ratio is the best index here: it is easily interpretable and essentially independent of size. For both traits, SSD (F/M) varied interspecifically, showed a strong phylogenetic signal, but did not differ for the main phylogenetic subgroups or correlate with latitude. Factors underlying variation in SSD in this clade are elusive and might include genetic drift. SSD (wing) tended to decrease with increasing size, as predicted by Rensch's Rule, though not consistently so. SSD (thorax) was unrelated to size. However, analysis of published data for thorax length of *Drosophila* spp. ($N = 42$) with a larger size range showed that SSD decreased significantly with increasing size (consistent with Rensch's Rule), suggesting our ability to detect SSD-size relations in the *D. obscura* data may be limited by low statistical power.

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Introduction

Patterns of sexual size dimorphism (SSD) have long intrigued ecologists as well as evolutionary and

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behavioral biologists. The causes of SSD are complex. They include such proximate factors as innate sex differences in energy intake, expenditure, and allocation, some of which are influenced by lower-level physiology and endocrinology (e.g., Cox et al., 2006). Many of these factors can in turn be influenced by ecological and behavioral differences between the sexes. Moreover, natural and sexual selection often will act differently on the sexes, which may lead to evolutionary divergence in male and female size within a species. Whatever their proximate and ultimate origins, differences in size between females and males can have important impacts on their life history, social behavior, physiology and energetics, and competitive relations (Schoener, 1967; Shine, 1978; Andersson, 1994; Fairbairn, 1997; Cox et al., 2003).

The primary purpose of this paper is to examine SSD in members of the *obscura* group of *Drosophila* as part of an ongoing series of investigations into their comparative biology. Previous studies have examined aspects of cold adaptation (Moreteau et al., 1997; Gibert and Huey, 2001; Gibert et al., 2001) and morphometrical evolution (Moreteau et al., 2003). This clade is attractive for comparative studies for several reasons. About 41 species are known (Ashburner et al., 2005), and most can be cultured in the laboratory, which is crucial for comparative studies that attempt to make evolutionary inferences (Garland and Adolph, 1991). They are largely holarctic in distribution, but some have colonized the afrotropical and neotropical regions. Thus they live in a variety of climates and ecological contexts. Their evolutionary relationships are increasingly well understood (O'Grady, 1999; Renard, 2000; see also references in Moreteau et al., 2003), which allows the application of modern phylogenetically based statistical methods (Garland et al., 2005). Moreover, the magnitude of SSD varies strikingly among species (see below) and thus offers opportunities to search for evolutionary patterns in the magnitude of SSD. Also, we use this opportunity to explore key methodological issues involving allometric scaling. Specifically, we evaluate the reliability of various indices of SSD (e.g., Fairbairn, 1997; Smith and Cheverud, 2002), test for phylogenetic signal in SSD (Blomberg et al., 2003), develop a new bootstrap method for estimating the magnitude of intraspecific variation in SSD, and apply a recently developed (phylogenetic) method to estimate scaling coefficients when both variables have error (Garland et al., 2004; Ives et al., in press).

The magnitude of SSD often varies in a predictable way with body size, and this phenomenon has been called Rensch's Rule (Rensch, 1960; Fairbairn, 1997). For species in which males are larger than females ("male-biased"), SSD typically increases with increasing body size; conversely, in species in which females are the larger sex ("female-biased"), SSD typically decreases

with increasing body size (Fairbairn, 1997). In *Drosophila* females are larger than males: thus SSD should decrease with increasing body size if Rensch's Rule holds. We test this expectation for the *D. obscura* group flies. In addition, we analyze published data on thorax length of males and females for 42 species of *Drosophila* from several species groups (Pitnick et al., 1995). Relative to our *D. obscura*-group data set, the Pitnick et al.'s (1995) data set offers a larger sample size, broader phylogenetic coverage, and has a larger range of thorax lengths (~2.6-fold greater on the log scale): the latter two factors should in principle enhance power to detect deviations from isometry of male vs. female body size. However, such increased power may come at a cost: the broader phylogenetic range may obscure patterns in the data (e.g., see discussion and references in Garland et al., 2005). Finally, we look for correlations with latitude because body size in *Drosophila* often varies with latitude (e.g., Karan et al., 2000; Moreteau et al., 2003) and thus SSD might co-vary as well. The causal explanation for any such allometric or geographic patterns – and any others involving SSD – will be obscure as little is known about the natural history and reproductive biology of these flies.

Material and methods

Drosophila strains and morphometrical measurements

Laboratory strains of 20 species (one strain per species) in the *D. obscura* clade were available for study. The size data analyzed here were originally published in Moreteau et al. (2003), which reports their geographic source and latitude, rearing conditions and population sizes, and time in captivity (if known). We assume here that SSD has not evolved significantly in laboratory culture, but of course it might have shifted by drift or by adaptation to the laboratory (Matos et al., 2002; David et al., 2006).

Groups of 10 adult pairs were used as parents. Oviposition took place on a high-nutrient, killed-yeast food (David and Clavel, 1965), which reduces crowding effects (Karan et al., 1999). Larval density was not precisely controlled but was approximately 100 per vial. [In *D. melanogaster*, larval densities up to 300 per vial do not affect adult size traits (Karan et al., 1999).] For each species, at least three different vials were used, originating from different parental groups. All experiments (oviposition and development) were done at 21 °C under a L:D 16:8 photoperiod.

Two size-related traits were measured on each species: total wing length (from the thoracic articulation to the wing tip) and total thorax length (from the neck to the

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