

## Genetics and adaptation in structured populations: sex ratio evolution in *Silene vulgaris*

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Received 21 May 2002 Accepted 9 December 2003

**Key words:** cytoplasmic male sterility, gynodioecy, mitochondrial DNA, subjective fitness

### Abstract

Theoretical models suggest that population structure can interact with frequency dependent selection to affect fitness in such a way that adaptation is dependent not only on the genotype of an individual and the genotypes with which it co-occurs within populations (demes), but also the distribution of genotypes among populations. A canonical example is the evolution of altruistic behavior, where the costs and benefits of cooperation depend on the local frequency of other altruists, and can vary from one population to another. Here we review research on sex ratio evolution that we have conducted over the past several years on the gynodioecious herb *Silene vulgaris* in which we combine studies of negative frequency dependent fitness on female phenotypes with studies of the population structure of cytoplasmic genes affecting sex expression. This is presented as a contrast to a hypothetical example of selection on similar genotypes and phenotypes, but in the absence of population structure. Sex ratio evolution in *Silene vulgaris* provides one of the clearest examples of how selection occurs at multiple levels and how population structure, *per se*, can influence adaptive evolution.

**Abbreviations:** CMS – cytoplasmic male sterility.

### Introduction

The role of population structuring (the degree of subdivision of individuals or genes in a metapopulation into discrete local breeding units) and its importance for adaptive evolution is a contentious issue (Wright, 1931; Fisher, 1958; Coyne, Barton & Turelli, 1997, 2000; Wade & Goodnight, 1998; Goodnight & Wade, 2000). However, there are some cases where, in the short term, the role of population structuring is likely to have emergent effects that cannot be determined through just understanding fitness at the level of the individual. For instance, the presence of population structure implies the restriction of gene flow and one

corollary of this restriction is that genotypes or phenotypes associated within demes are more similar to one another than they are to genotypes or phenotypes picked at random from all demes (Wilson, 1979). When these associations influence fitness, the fitness of individuals in demes cannot be predicted by averaging across populations. Such situations arise when fitness is frequency dependent and individual fitness is influenced by the presence of individuals with the same phenotype. In these cases, the population structure provides the context for an emergent property that affects fitness in such a manner that individual fitness cannot be predicted without incorporating the effects of structure.

The most well known theoretical example of how population structure can alter the outcome of evolution is in the evolution of cooperative or altruistic behavior (Goodnight, Schwartz & Stevens, 1992). Selection on cooperative versus selfish behavior is inherently frequency dependent, and cooperation is increasingly favored in structured populations because altruists are clustered into a subset of demes where they benefit from being the recipients of altruism. Although both frequency dependent selection and population structure are common in nature, there are few empirical examples of how population structure, *per se*, can influence evolution in this way.

Recently, the effects of population structuring on the relative fitnesses of the two sexes in gynodioecious species have drawn considerable interest in this context (McCauley & Taylor, 1997; Pannell, 1997; Couvet, Ronce & Gliddon, 1998; Hatcher, 2000; Frank & Barr, 2001). Gynodioecy is a breeding system characterized by the co-occurrence of females and hermaphrodites. Theoretical models suggest that population structure may contribute to at least two aspects of population sex ratio. First, it may create the conditions that allow cytoplasmic genes effecting male sterility (CMS or cytoplasmic male sterility genes) to evade nuclear male fertility restorer genes (Frank, 1989; Gouyon, Vichot & Van Damme, 1991). Second, population structure in the presence of pollen limitation may alter the fitness of CMS types relative to the case of no population structure (McCauley & Taylor, 1997).

### A complex web of selection at different levels

Sex ratio evolution in gynodioecious species is known to involve selection at different levels of organization (Cosmides & Tooby, 1981; Saumitou-LaPrade, Cuguen & Vernet, 1994; Hurst, Atlan & Bengtsson, 1996). In many gynodioecious species, gender is genetically determined by an interaction between CMS factors and nuclear male fertility restorers (Schnabel & Wise, 1998). The CMS factors block pollen production and are maternally inherited. Male fertility restorers, located in the nuclear genome, are biparentally inherited and reinstate viable pollen production. Individuals with CMS genes and lack nuclear restorers express a female phenotype, whereas

those with CMS and nuclear restorers express hermaphroditic phenotypes. Within a species, multiple CMS/restorer systems further complicate the association between genotype and phenotype (Schnabel & Wise, 1998). These CMS/restorer systems are generally thought to interact in a gene-for-gene manner whereby only one type of restorer will reinstate male fertility for a given CMS type (Frank, 1989; Schnabel & Wise, 1998), though this has not been studied extensively in natural systems.

A consideration of selection at the level of the gene is necessary to understand the spread of CMS genes. From the vantage of CMS genes, fitness is increased only via increasing seed production and the complete loss of male fertility does not directly affect fitness, or for that matter, the fitness of any maternally inherited element. In contrast, the nuclear male fertility restorer genes are biparentally inherited and their fitness is maximized through balancing allocation to both male and female reproductive modes (Fisher, 1958; Frank, 1989). What makes this system so compelling is that the CMS and restorer genes directly affect the genetic transmission system; thus, their expression affects the selective environment (Jacobs & Wade, 2003). Moreover, since gender is epistatically determined the fitness of each component of the genetic determination system is dependent on the frequencies of other components (Jacobs & Wade, 2003). The commonness of CMS/restorer systems in plants and their importance to agriculture (Levings, 1993; Frank & Barr, 2001) contribute to making this one of the most celebrated examples of the conflict of interest between cytoplasmic and nuclear genomes (Cosmides & Tooby, 1981; Hurst, Atlan & Bengtsson, 1996; Werren & Beukeboom, 1998).

Obviously, CMS genes will spread when they are over-represented relative to other cytoplasmic types in future generations. Such over-representation results from the production of more seeds or higher quality seeds by females than hermaphrodites and is a common attribute of gynodioecious plants (Gouyon & Couvet, 1987). This 'reproductive compensation' may result from reallocation of resources that would otherwise be used for pollen production (Ashman, 1999) and is affirmed by the observation that many gynodioecious species exhibit negative genetic tradeoffs between male and female reproductive allocation (Olson &