



## Symbiotic bacteria affect mating choice in *Drosophila melanogaster*

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Mating preferences depending on *Wolbachia* infection were studied in two genotypically different strains of *Drosophila melanogaster*. Females from both strains carry two attached X chromosomes. Males from the red-eyed strain (R) have the wild-type X chromosome compared to males from the white-eyed strain (W), whose X chromosome contains two deleterious mutations (*white* and *singed*). Three types of competition tests showed that assortative mating depends on genotype, infection status and their combination in the mating partners. Males of strain R, genetically closer to the wild type, were more successful than males of strain W. *Wolbachia* infection increased the mating ability of W males but did not affect that of R males. Strain W showed positive assortative mating (preference for 'self') with regard to genotype and infection status. In strain R, negative assortative mating (preference for 'nonself') was observed. Moreover, the most affected flies (infected W) showed higher preference for 'self', while the least affected ones (uninfected R) showed higher preference for 'nonself'. These results support the idea that mating choice may involve testing the partner for degree of genetic or biochemical similarity with self, based on chemoreception with possible participation of immune system components.

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Selective mating and the principles of mate choice are important for maintaining the genetic stability and diversity of populations, as well as for microevolutionary changes. Changes in mating preference associated with ecological adaptation may be of key importance at early stages of speciation, particularly in sympatric populations (Korol et al. 2000; Schluter 2001).

Mating choice can be based on the principle of 'good genes', when a female chooses, for example, the largest and strongest male, or on the more general principle of 'genes that are a good fit' (Trivers 1972; Mays & Hill 2004). According to the theory of optimal outbreeding, mate choice may be directed at reducing inbreeding, on the one hand, and avoiding distant crosses, including interspecies hybridization, on the other (Bateson 1982, 1983). Such choices require mechanisms, for example chemoreception, for comparison of potential partners with 'self' to estimate the degree of genetic

similarity (relative versus nonrelative, similar versus different). In particular, olfactory signals, associated with gene alleles of the major histocompatibility complex (MHC), can be used in vertebrates for assessing kinship (Penn & Potts 1999; Milinski et al. 2005).

According to a recently formulated hypothesis (Markov & Kulikov 2006a, b), estimating the genetic relatedness of a potential partner via chemoreception, possibly using immunological signals and receptors, such as proteins and peptides of the MHC, may be important at the early stages of speciation. In general, this hypothesis states that individuals with an optimal (not too close and not too distant) degree of relatedness tend to be preferred as mating partners. The position of this optimum may vary depending on the environmental conditions. Under beneficial conditions, the optimum may shift towards more distant relatedness to avoid inbreeding and increase polymorphism and heterozygosity of the offspring, whereas under stress in a broad sense (Selye 1956), shifting towards closer relatives may be more advantageous, so that valuable traits and beneficial gene complexes, which have ensured the survival of the parents in a critical situation, are not disrupted by a distant cross.

The results of experiments on artificial speciation in insects suggest that in a stressful situation, for example, rearing on a poor medium or under strong directional selection for a morphological trait, the mating choice may indeed shift towards 'self', that is, to

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consanguineous mating. Consequently, strains that were subject to contrasting stressful treatment or disruptive selection may rapidly develop partial precopulatory reproductive isolation (Thoday & Gibson 1962; Kiliyas et al. 1980; Dodd 1989; Wilkinson & Reillo 1994). Similar phenomena have been observed in nature, for example, in *Drosophila* (Korol et al. 2000).

The rapid appearance of isolation in the above experiments cannot be explained by the reinforcement mechanism, that is, by selection of individuals that prefer genetically related mates occurring because of low competitive ability of hybrids (Dobzhansky 1951; Butlin 1989). Apparently, partial isolation (endogamy) may sometimes arise automatically, as a side effect of rapid genetic changes of the population subjected to strong selection. Individuals in such a changed population acquire genetic and biochemical differences; for instance, they may change their specific odour or, more generally, the antigen set presented to the partner for 'self/nonself' testing. It is conjectured that such changes may automatically lead to a situation in which members of a particular population perceive members of other populations of the same species as 'nonself' (Markov & Kulikov 2006a, b). A stress-induced shift in mating preference towards 'self' partners should promote isolation of the population and maintenance of its advantageous traits.

To test these views experimentally, we examined assortative mating in two genetically different strains of *Drosophila melanogaster*, depending on their infection with the intracellular bacterium *Wolbachia*. In this symbiotic system, *Wolbachia* does not induce cytoplasmic incompatibility (CI; nonviability of offspring from infected males X uninfected females) in *D. melanogaster* (Alexandrov et al. 2007). We expected the infection to change both the biochemical status of the animal and the antigen set tested during courtship. As a result, flies with different infection status should be more likely to perceive each other as 'nonself', compared to flies with the same infection status. On the other hand, infection may act as a stress or (see below), and may shift mate choice towards the preference for 'self'. Both proposed effects may be mediated by the genotype of the host fly and thus may vary among laboratory strains.

*Wolbachia* is a widespread endosymbiont of terrestrial arthropods and nematodes, which has strikingly diverse effects on its hosts (Stouthamer et al. 1999; Goryacheva 2004; Markov & Zakharov 2005). *Wolbachia* infection is transmitted almost exclusively vertically, transovarially and maternally. Most of its effects on host organisms are aimed at promoting the transmission of the infection. In different arthropod species, *Wolbachia* infection can lead to (1) CI; (2) parthenogenesis; (3) androcyde (nonviability of male offspring); (4) feminization (transformation of genetic males into females); (5) changes in fertility and viability of infected animals. Most of these effects promote the spreading of *Wolbachia* in the host population and are thus beneficial for the parasite but usually not for the host (Goryacheva 2004).

Many wild and laboratory *D. melanogaster* populations are infected with *Wolbachia*. The symbiont–host relationships vary depending on the bacterial strain and the host genotype. Sometimes these relationships are parasitic, as, for example, in the case of the strain 'popcorn', which leads to CI and reduces the life span of *D. melanogaster* (Reynolds et al. 2003). However, more often *Wolbachia* acts as a harmless commensalist for *D. melanogaster*. In some laboratory strains of *D. melanogaster*, the infected flies benefit from increases in life span, resistance to RNA viral infections and other fitness parameters, such as fecundity and egg-to-adult viability (Olsen et al. 2001; Fry & Rand 2002; Fry et al. 2003; Teixeira et al. 2008). This is also true for the bacterial strain and for at least one of the two infected *D. melanogaster* strains used in our experiments (IW, see below). In this symbiotic system, the bacteria

increase the life span of the insect, the competitive ability of the larvae and resistance to the pathogenic fungus *Bauveria bassiana* (Alexandrov et al. 2007; Pantelev et al. 2007). It seems plausible that the presence of intracellular bacteria may act as a stress factor (for instance, it may induce changes in gene expression and some kind of stress response at the biochemical level), despite the possible beneficial effects of *Wolbachia* on its hosts. This assumption is supported by numerous examples of the effects of *Wolbachia* infection on differential expression of host genes. For example, *Wolbachia* blocks the immune response of the host, controls some signal pathways, and regulates apoptosis in nurse cells within egg chambers (Siozios et al. 2008). It induces dramatic changes in expression of multiple genes in different *Drosophila* species, including *D. melanogaster* (Xi et al. 2008). Another possible link between stress and *Wolbachia* infection in *Drosophila* is that *Wolbachia* infection results in increased mRNA and protein expression of the nonmuscle myosin II gene *zipper*. This effect plays a crucial role in CI (Clark et al. 2006). Nonmuscle myosin II is responsible for maintaining the integrity of stress fibres, bundles of actin filaments that appear and disappear in response to mechanical stimuli and are thought to be one of the major components that sustain mechanical stresses in cells (Goeckeler et al. 2008). It is also known that *Wolbachia* strain wMel, which infects many strains of *D. melanogaster* including our experimental strains, is potentially harmful to its hosts. The transfer of seemingly harmless *Wolbachia* strains from *D. melanogaster* into *D. simulans* induces high levels of CI in the latter (Poinsot et al. 1998). CI in *D. simulans* is typically very strong, whereas it is weak or absent in *D. melanogaster* (Hoffmann et al. 1996). However, *Wolbachia* strains from *D. simulans* failed to induce strong CI when transferred into *D. melanogaster* (Boyle et al. 1993). These findings imply that the absence of deleterious effects in *D. melanogaster* most probably results from the active resistance of the host to attempted manipulations by the parasite. Therefore our assumption that *Wolbachia* acts as a stressor in the *Wolbachia*–*D. melanogaster* system appears plausible. Here we use it as a convenient framework for interpreting our results, although we recognize that the evidence is indirect and the question requires further clarification.

In a number of studies, the effect of *Wolbachia* on assortative mating of the host has been investigated. Most of these studies used *Drosophila* species as the host. Some of them failed to prove an association between assortative mating and *Wolbachia* infection (Jenkins et al. 1996; Sullivan & Jaenike 2006). Champion de Crespigny & Wedell (2007) showed male mating preference of females with the same infection status of *Wolbachia* in *D. simulans* at least in one series of experiments. Robinson (2006) examined mating choice in two partially isolated *Drosophila* species, one of which was totally infected (*D. recens*), and the other totally free of *Wolbachia* (*D. subquinaria*). Complete loss of the offspring induced by the endosymbiont was observed only in one crossing direction (infected *D. recens* male\*uninfected *D. subquinaria* female). In this direction, marked assortative mating was observed. In some spider mites, uninfected females preferentially mate with uninfected males. This selective mating avoids the negative consequences of CI (loss of offspring from crosses with infected males) and thus increases fitness (Vala et al. 2004). In both cases (in spider mites and *Drosophila recens*/*D. subquinaria*), mating of infected males with uninfected females occurs at a lower rate, which may be interpreted as host adaptation (defence against the CI effect).

According to Markov & Kulikov's (2006a, b) hypothesis, *Wolbachia* or other bacterial infection may automatically change mating preference, regardless of the parasite's effects on the host. Moreover, these changes in assortative mating will not necessarily be adaptive. Mating selectivity may change simply because animals with different infection status differ from one another

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