

NEWS AND VIEWS

PERSPECTIVE

To be, or not to be, related: how female guppies bias sperm usage

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In the *Descent of Man*, Darwin wrote “the power to charm the female has sometimes been more important than the power to conquer other males in battle” (Darwin 1871). Since his pioneering work, the field of sexual selection has exploded as biologists strive to understand how females bias fertilization towards preferred males. In the context of genetic relatedness between potential mates, two main hypotheses exist to explain female mating preferences. First, a female may bias fertilization towards genetically dissimilar males if she gains evolutionary fitness through the production of genetically diverse offspring – a model known as dissortative mating or inbreeding avoidance. Second, a female may favour genetically similar males if her offspring are more likely to inherit coadapted gene complexes – a model known as assortative mating or outbreeding avoidance. In this issue of *Molecular Ecology*, Gasparini *et al.* (2015) demonstrate that female guppies bias fertilization towards males which are more related to them at major histocompatibility (MHC) class IIB genes. Amazingly, this bias occurs *after* insemination of sperm from two different males.

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All else equal, such assortative gamete usage should produce less diverse offspring, a counterintuitive result given the importance of MHC in pathogen resistance. After briefly describing their experiment, we return to this issue and suggest that spatially or temporally varying selection might swing the pendulum between these the two models (assortative vs. dissortative mating), which may reconcile the diversity of results reported in the literature.

Two facets of their experimental design made the inferences of Gasparini *et al.* (2015) particularly compelling. First, they mixed sperm from two different males in equal numbers prior to artificially inseminating female guppies

(fertilization takes place internally in this species, Fig. 1), focusing on postcopulatory interactions between the female reproductive tract and sperm. Second, because they fertilized two different females with the same sperm mixture, they could determine whether sperm competition outcomes correlated to inherent differences in male quality (in which case the same male would win paternity regardless of female) or due to specific male–female interactions (in which case the winning male could switch depending on female). In their experiment, the winning male shifted according to female. Furthermore, winning males tended to be more genetically similar to the female at the MHC class IIB loci, following the predictions of assortative mating. Although the precise mechanisms of nonrandom gamete usage remain unknown, MHC molecules are found on the surface of sperm, making some kind of biochemical interaction with the female reproductive tract possible (Tregenza & Wedell 2000).

How does the Gasparini *et al.* (2015) study fit in to the broader literature? Previous research on mate choice in guppies runs the gamut from random to nonrandom, and from assortative to dissortative (Evans *et al.* 2003; Pitcher *et al.* 2008; Gasparini & Pilastro 2011), patterns that are also seen in a diversity of other studies (Tregenza & Wedell 2000; Bernatchez & Landry 2003; Milinski 2006; Eizaguirre & Lenz 2010; Jiang *et al.* 2013; Kamiya *et al.* 2014). Further



Fig. 1 In this issue of *Molecular Ecology*, Gasparini *et al.* show that female guppies bias fertilization towards sperm from MHC-similar males, without ever seeing the male donors. Guppies are internal fertilizers – males (upper panel) use a modified anal fin called the gonopodium (under its body) to internally inseminate females (lower panel). Photographs are kindly provided by Dr. Gasparini.

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complicating the issue of mate choice, females have been shown to choose mates that yield offspring with intermediate, rather than strictly more or less, MHC diversity (Reusch *et al.* 2001; Milinski 2006; Kamiya *et al.* 2014). Population genetic studies demonstrated that MHC class IIB loci in guppies have been subject to balancing selection, making them less genetically differentiated between populations than neutral regions of the genome, (Oosterhout *et al.* 2006; Fraser *et al.* 2010a). This population genetic pattern is inconsistent with MHC-based assortative mating, which should increase interpopulational divergence. Taken together, these studies do not seem to form a consistent picture of long-term assortative mating. Besides the obvious fact that the guppy studies differed in populations sampled and genetic relatedness of individuals tested, consideration of spatially or temporally varying selection might help reconcile the results.

Spatially or temporally varying selection, which we will loosely refer to as local adaptation, offers a potential framework to interpret contrasting results. Local adaptation posits that what is adaptive at a particular locality or time point may be maladaptive at another (Kawecki & Ebert 2004; Eizaguirre *et al.* 2012). In a meta-analysis, Fraser *et al.* (2011) estimated that locally adapted salmonid populations had a fitness that was 1.2 higher in their own environment compared to a neighbouring population. With strong local adaptation, migration from foreign populations would be maladaptive, and assortative mating could evolve as a mechanism to preserve locally adapted genomes. However, local adaptation is unlikely to be static (i.e. Fraser *et al.* 2010b). As the fitness of locally adapted alleles shifts, for example due to co-evolutionary arms races between hosts and pathogens, perhaps populations pass through phases of assortative and disassortative mating.

In addition to the potential risk of migration, the genetic underpinnings of local adaptation could shape mating patterns. As the number of genomic regions that affect a locally adapted phenotype(s) increases, the risk that migration breaks them through subsequent recombination in their offspring is also expected to increase, especially if the genetic distance between interacting genes is reasonably high. Again, assortative mating may be a mechanism to preserve locally adapted genomes.

The guppy system might be considered a flagship for local adaptation, suggesting that the above hypotheses could be particularly relevant to explaining patterns of assortative mating. Perhaps most famously, Reznick *et al.* (1990) showed that guppies from parts of the river without cichlid predators reached sexual maturity at older ages compared to guppies facing the continuous threat of predation on adults, and this phenotypic divergence was genetically based. One could envisage how migration from other populations could introduce maladaptive alleles that disrupt the locally adaptive onset of sexual maturity. In a similar vein, the work of Gasparini *et al.* (2015) suggests that populations are locally adapted to parasites.

Testing whether shifts in spatial or temporal selection lead to assortative or mating requires an integrated set of

data that is probably still more hypothetical than reality. The data will have to extend far beyond mating assays in the laboratory, and integrate ecological parameters over time and space, genomic inference of the loci that underlie mate choice and fitness, elucidation of the mechanisms of selection and careful measurements of overall fitness effects. Well-designed experiments like Gasparini *et al.* (2015) represent an important piece of the puzzle, as we continue to marvel at the many ways that females can bias fertilization.

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