

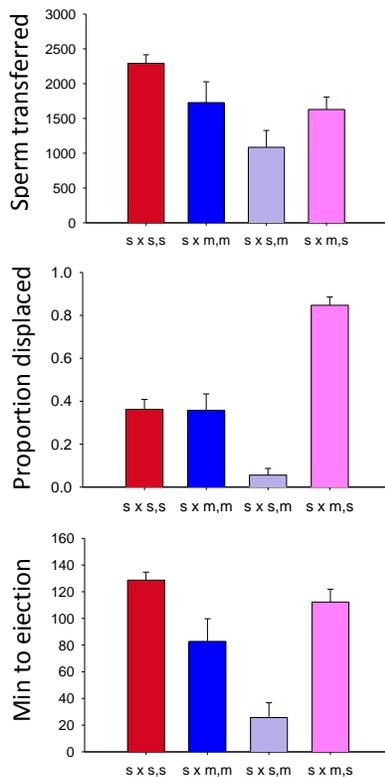
RESEARCH STATEMENT

My research explores the causes and consequences of adaptive variation in reproductive traits using species-level comparisons, population biology, animal behavior, quantitative genetics, genomics, and molecular and cell biology. I am particularly interested in sperm morphology and its interactions with other reproductive traits, taking advantage of the remarkable sperm length diversity in *Drosophila*, ranging from the modest *D. persimilis* (320 μm) to the record-holding *D. bifurca* (58,000 μm). Evolution of giant sperm is thought to be driven by post-copulatory sexual selection, but our understanding of sperm competition has been hampered by our inability to distinguish the sperm of different males inside the female. Our recent development of transgenic *Drosophila* with GFP- or RFP-labeled sperm heads has transformed our view of sperm biology and allows us to test previously untestable hypotheses about sperm competition, female sperm use and sperm behavior *in situ*. Fundamental questions that I am pursuing include (1) how does the extraordinary diversity in reproductive traits relate to male and female fitness and what role may they play in reproductive isolation (i.e., connecting phenotype and adaptive function), (2) what is the genetic basis for this diversity (i.e., connecting genotype to phenotype), and for my future directions, (3) what is the process of sperm morphogenesis, and how does it compare with somatic cellular morphogenesis (i.e., evolutionary development of sperm)?

The question of how species form has been a central problem of evolutionary biology since the *Origin of Species*, with a more recent revival beginning with Ernst Mayr. One recurring theme within this distinguished history began with Darwin and asks about the role of within-species variation in divergence between species. In other words, how does microevolutionary process influence speciation on a macroevolutionary scale? Another theme arose more recently with Mary Jane West-Eberhard and questions the role of sexual selection in generating and maintaining reproductive isolation. A third theme investigates the role of ecological differences in population divergence and ultimately speciation.

I am simultaneously addressing all of these overarching questions by examining mechanisms of post-mating pre-zygotic reproductive isolation both within species and in hybrid matings in *Drosophila simulans* and *D. mauritiana*. These species form a recently diverged complex that have become one of the best studied groups in speciation biology. One mechanism of reproductive isolation between *D. simulans* and *D. mauritiana* is conspecific sperm precedence (CSP), in which hybrid single matings are highly successful but double matings involving both a conspecific and heterospecific male result primarily in conspecific-sired progeny. The female reproductive tract is the natural selective environment of the male ejaculate, and species-specific adaptations that maximize sperm performance within their natural environment are expected to play a large role in maintaining species boundaries.

Using these lines, I have found that *D. simulans* males transfer fewer sperm if a conspecific female was previously mated to a *D. mauritiana* male. Despite a smaller ejaculate size, *D. simulans* males are much better at displacing heterospecific sperm than conspecific sperm from storage. This result can be explained by interspecific differences in sperm length and velocity, which we have also found to influence paternity success in *D. melanogaster*. Furthermore, *D. simulans* males transfer fewer sperm to virgin than to mated conspecific females, demonstrating that ejaculate tailoring occurs within species as well as in hybrid crosses. Female *D. simulans* eject heterospecific sperm faster if previously mated to a conspecific male, suggesting a role for



Sperm transfer, percent sperm displaced, and timing of ejection in *D. simulans* (red) and hybrid matings. ♀ × ♂₁♂₂,

sequential mate preference and cryptic female choice in CSP (see figure). I predict that female ejection should play a role in cryptic female choice against low quality males within species as well.

Understanding the genetic basis of phenotypic variation has been another important and related problem of evolutionary biology, with humble beginnings in the breeding of crop plants and domestic animals. The development of inexpensive genomics methods and sophisticated computational and bioinformatics tools has launched genotype-phenotype mapping into a new millenium with greater potential than ever to explore the genetics of fitness-related traits. At the same time, we can now quantify a multivariate fitness-related phenotype comprised of ejaculate traits, sperm displacement, female ejection, and sperm use characteristics. My studies of this trait complex are addressing fundamental questions in evolutionary biology regarding the relationship between structure and function, genotype and phenotype, the genetic architecture of complex traits, and specific hypotheses about the evolution of female multiple mating.

To address questions of the genetic architecture of complex traits and evolvability of ejaculate function, we have generated 100 inbred isofemale lines that have been phenotyped across

multiple generations for sperm length, velocity, ejaculate size, sperm storage patterns, displacement, female ejection, and paternity success. We found a strong genetic signal for each of these traits, and I will assess their male- and female-mediated genetic variation and covariation and determine the extent of male x female and male x male x female interactions, as well as condition-dependence.

I will specifically test alternative models for evolution of female multiple mating by looking for additive genetic variance in male traits that I identify as being important in sperm competition as well as genetic correlations between male sperm traits and female sperm handling traits (e.g., storage, ejection, sperm use). A related model additionally predicts the evolution of genetic correlations between sperm competition traits and male condition. Finally, I will fully sequence all isofemale lines and use whole genome association mapping on the suite of sperm competition traits to identify loci that are associated with both ejaculate traits and competitive success. I will also obtain the genetic basis of heritable patterns of sperm storage, displacement, and ejection.

As part of a related project, I am examining how sperm length and female sperm storage organ length interact to affect sperm motility and behavior both within and between species. I am concomitantly using a RAD (restriction-site associated DNA) Illumina QTL mapping approach to identify genes/genomic regions associated with sperm length. I will then estimate rates of divergence for candidate loci and determine the molecular basis of parallel evolution of giant sperm across the *Drosophila* lineage.

My research investigates the evolution of reproductive traits along three complimentary tracks. The first asks what are the patterns of sperm precedence mechanisms within species, and how can they inform the evolution of reproductive isolating mechanisms between species? The second examines the functional significance of sperm length variation in *Drosophila* and its genetic basis. The third track explores the genetic architecture and genomics of sperm and sperm-handling traits important in sperm competition. My future research will further investigate the role of candidate sperm length genes in sperm morphogenesis within an evolutionary developmental framework. Evolution of adult form is best understood within the context of its development during embryogenesis, a concept which forms a fundamental basis for evo-devo research. Sperm, with their highly specialized function and autonomous nature, represent an apt cellular analog to organismal form at the level of the individual. Yet, the process of sperm formation during spermiogenesis (late-stage spermatogenesis) remains a vast unknown, especially regarding how natural variation in molecular and cellular processes can generate the extraordinary diversity of form found in mature spermatozoa. I am specifically interested in using spermiogenesis as a point of comparison with somatic cell morphogenesis in embryos and adults.

My extensive research interests will mesh well with the diverse research programs within the Department of Biological Sciences at the George Washington University by investigating factors influencing sexual selection within comparative, behavioral, functional, genetic, cellular, and developmental frameworks. I anticipate fruitful collaborations with diverse research groups, including but not limited to those studying reproductive biology, evolutionary development, *Drosophila* immunity, functional morphology, genotype-phenotype mapping, genomics and systematics.