The second sex

Laturney, Meghan Elizabeth

SUMMARY IN ENGLISH

From an evolutionary perspective the meaning of life is to reproduce; and thus, the objective of every living organism is to pass on its genes to future generations. For species that reproduce sexually, this involves the interaction between males and females in ways that result in offspring production. Although sex benefits both males and females as it potentially increases general reproductive success, reproductive related behaviours are also riddled with attempts of personal gain.

Initially, the interests of the sexes are aligned because mating benefits both males and females making sexual reproduction a cooperative task. Conflict arises, however, when either the male or the female attempts to maximize their own reproductive success at the expense of the other. For example, one way for both sexes to potentially increase the quantity and/or quality of offspring they produce is to mate with multiple partners. As female remating almost always results in a significant reduction in the siring capability of the initial mate, female remating behaviour is under conflict: beneficial for the female but costly for the male.

Sexual conflict theory suggests that males should develop tactics, over an evolutionary time-scale, which decreases the chances of their partners to commit future infidelities and thereby increasing the chances of siring offspring. There are various examples of how males restrict the reproductive behaviour of females ranging from intensive physical guarding, the installation of a mating plug within the female reproductive tract to block mating and/or sperm transfer, chemically depressing female sexual receptivity, and reducing female attractiveness with the application of anti-aphrodisiac pheromones. However, a major limitation of our understanding of sexual conflict is the inadequate understanding of the response of the female to such strategies and in general how the female exercises influence over her own reproduction. Furthermore, although it is widely accepted that females play an active role in pre-copulatory mate choice, their role in post-copulatory reproduction has been overlooked and dismissed.

The research contained in this thesis was motivated by the desire to understand not only the extent that females can control their reproduction but also the mechanisms in which they exercise such influence. In **Chapter 2**, I provide a comprehensive overview of the mechanisms supporting the female post-mating response in the fruit fly, the model organism *Drosophila melanogaster*. The post-mating response is a set of behaviours displayed exclusively by females after copulation. Previous investigations into post-copulatory female reproductive

behaviours in this species have identified various male-derived compounds transferred via the ejaculate to the female reproductive tract that increase ovulation and egg laying, for example, and the female cellular substrate that supports the general post-mating response. Importantly, within this review I highlight the gap in our understanding of the role of the female in reproduction. In sharp contrast to male oriented literature, few mechanisms supporting female reproductive behaviours have been identified and our understanding of the ability of females to modulate such behaviours is far from adequate. Although sex may have selfish aspects, it is fundamentally a social behaviour requiring interaction between the two sexes. Thus, any asymmetric understanding of reproduction is equivalent to none at all.

In **Chapter 3** I investigated the female influence over a well-documented male mate-guarding tactic. During copulation a male deposits chemicals both on and in the female, which results in a decrease in her attractiveness. By deterring courtship from potential mates, males increase the probability of siring offspring. However, this also simultaneously decreases the female's ability to remate and optimize her own reproductive success. As a response to this male chemical mate-guarding, females are predicted to develop counter-adaptations to remove these anti-aphrodisiac pheromones and regain control over reproduction. By performing chemical analysis on virgin females, recently mated females, and recently mated females who have removed unused portions of the ejaculate, I found that indeed females gain chemicals during mating and can remove some via "ejection". Interestingly, one such chemical that is gained and then almost entirely removed is a compound known to decrease female attractiveness. Moreover, I found that after removal, females receive significantly more courtship from males and are more likely to remate compared to females that have not yet "ejected". As I, and other researchers, have determined that the timing of ejection involves the female brain, the removal of the ejaculate is likely an active process by which the female can control her own attractiveness and remating behaviour. The removal of male-derived compounds and the resulting influence on attractiveness represents a fantastic example not only of female control over her own reproduction but also of counter-adaptation to male-derived restriction of female reproductive behaviour.

To continue this line of investigation, I followed up the previous results by examining the impact of remating. If females can control remating, what are the consequences of such power? When females of various species remate, they rarely produce equal number of offspring from each mate. Usually, offspring is biased towards the last male. Much of the literature investigating this phenomenon is centered around identifying male traits that influence the fraction of offspring sired

by each male. Not surprisingly, very little is known about the female influence on patterns of paternity. By varying both the number of mates and the timing between mating events, in **Chapter 4** I found that females that remated more often, and sooner, reduced the skew that favoured the last male. This result demonstrates that females can influence patterns of paternity via post-copulatory mechanisms and suggests an active role in post-copulatory sexual selection- faculties previously reserved for males.

The previous chapters all indicated an active female role potentially controlling various reproductive behaviours, and the results from Chapter 4 suggest that females may have control over the fate of sperm within the female reproductive tract. These findings, in turn, predict a strong contribution of the nervous system of the female. For example, an active modulation of sperm storage and/or use likely requires the integration of various social signals such as the number and quality of potential mates in the environment via sensory neurons. This information may be conveyed via a neural circuit terminating in motor neurons that innervate the reproductive tract capable of manipulating the location of sperm. To test this hypothesis and investigate active control, I screened various populations of neurons with thermogenetics, which allowed me to artificially manipulate neuronal activity and assess the influence on sperm storage (**Chapter 5**) and sperm ejection (**Chapter 6**). I identified neurons that could potentially influence sperm manipulation, demonstrating that the female central nervous system likely controls the fate of sperm after mating- a potential mechanism by which females may influence offspring production.

The experiments conducted here represent a response to the lack of understanding of the role that females play in reproduction in general and in sexual conflict specifically. This research is a small step to not just identify the influence that females have in remating, biasing patterns of paternity, or manipulating sperm within her reproductive tract, but ultimately to integrate that knowledge with previous findings on the male contribution and gain a full understanding of the complex interaction between the two sexes. As reproduction is the ultimate collaboration so too should be the research that investigates it and the literature that reports it.

Academic Curriculum Vitae

May 2012-December 2016

Doctorate degree candidate (PhD) in Biology

Thesis title: "The second sex: functions and mechanisms of sperm manipulation in female Drosophila melanogaster"

Evolutionary Genetics, Development, & Behaviour expertise group, Groningen Institute for Evolutionary Life Sciences, Rijksuniversiteit, Groningen, NLD

September 2009-December 2011

Master of Science (MSc) in Biology

Thesis title: "Genetics of interspecific female preference in Drosophila"

Department of Biology, University of Western Ontario, London, CAN

September 2006-May 2009

Bachelor of Science (BSc) specialization in Psychology, minor in Biology

University of Western Ontario, London, CAN