

THE GENOMICS OF SEXUAL SELECTION IN THE BULB MITE, RHIZOGLYPHUS ROBINI

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SUMMARY

Sexual selection promotes traits involved in reproductive competition and often leads to the evolution of elaborate secondary sexual traits, which function either as ornaments increasing the attractiveness of their bearers or as weapons used in competition between members of the same sex. Sexual selection shapes the genetic variance, which determines important evolutionary processes, such as adaptation, speciation or extinction. Sexual selection may improve population fitness if high reproductive competitiveness is associated with high organismal efficiency, which may allow for allocating resources to energetically demanding behaviours or developing more extreme sexually selected traits. In such a case, sexual selection can increase selection favoring beneficial alleles and purging detrimental ones. However, by imposing strong directional selection, limiting access to reproduction only to most competitive individuals may limit effective population size (N_e) and thus decrease the efficacy of selection. Also, the impact of sexual selection on the amount of genetic variance segregating in natural populations, and thus their evolutionary potential, is not easy to predict. On the one hand, by intensifying overall sexual selection, and by reducing N_e , sexual selection is expected to reduce genetic variance segregating in population. On the other hand, the latest genetic models predict that sexual selection, instead of decreasing, may contribute to the maintenance of genetic variation through a process called sexual antagonism, in which an allele beneficial to one sex decreases the fitness of the opposite sex, preserving polymorphism at a given locus. However, empirical evidence for the role of sexual selection on the amount and nature of genetic variance segregating in natural population is scarce. The research described in this thesis aims to fill this gap by applying genomic tools to understand how sexual selection shapes genetic variance in one of influential sexual selection models- the bulb mite, *Rhizoglyphus robini*. Populations of this species undergo strong sexual selection, consisting of struggles for the access to females as well as intense sperm competition for the access to female gametes. The former has led to the evolution alternative male reproductive phenotypes, with aggressive fighter males armed with a thickened third pair of legs and benign scrambler males.

In the first chapter, we constructed a genetic map of a bulb mite, which facilitated anchoring the reference genome of this species to a chromosome scale, allowing us to better understand the genetic architecture of the sexually selected weapon, as well as to scan a genome for regions responding to selection, as described in chapters 2 and 3. Additionally, holocentric chromosomes of bulb mites allowed us to study sex-specific recombination landscape without the influence of centromeres. Despite the increased risk of aneuploidy associated with crossovers near centromeres, across eukaryotes it is observed that females have higher recombination rates near centromeres, while in males crossover frequency increases toward chromosome ends. A major hypothesis suggests this paradox may be a result of a defense mechanism against selfish meiotic drivers, which manipulate centromeres to increase their chances of segregating into oocytes rather than inviable polar bodies. Consistent with this hypothesis, we found that in *R. robini* the crossover distribution is more similar between the sexes, and recombination rate increased toward chromosome ends in both males and females. Additionally, we found that female

recombination rate was twice as high as that in males and sex-averaged recombination frequency was positively associated with repeat content and negatively with gene density.

In the second chapter, we conducted an *evolve-and-resequence* experiment in which we manipulated sexual selection intensity by skewing the sex ratio, but keeping the ratio of fighters to scramblers at constant 50:50 ratio. Our experimental procedure did not result in a clear genomic response. We observed a decrease in genetic variance in both male biased and female biased sex-ratio procedures, but male-biased lines exhibited slower loss of genetic variance, particularly at synonymous sites. Although the sex ratio manipulation triggered a weak polygenic response, we identified large haploblocks which responded uniquely to selection in each treatment. Overall, however, we have not found evidence that elevating sexual selection by increasing the ratio of males to females affects the amount of non-neutral genetic variance segregating in populations.

The third chapter characterises the genetic architecture underlying male morph determination in *R. robini*. Firstly, we conducted a Pool-GWAS comparing whole genome sequences of scrambler and fighter DNA pools. The association of this genomic region with morph determination was further confirmed by analysis of inbred lines which were fixed for alternative male morphs. Both methods identified significant morph association with a 3.5 Mb region near the end of chromosome seven. To characterize this region, we additionally used individually sequenced mites that were previously used for the genetic map construction. We found that the region exhibited characteristics typical of supergenes- genomic regions, such as reduced recombination between alternative alleles, high nucleotide divergence between scrambler- and fighter-specific haplotypes and significant enrichment in transposons. These signatures are likely to be the result of suppressed recombination, which maintains a co-adapted set of alleles beneficial for discontinuous traits, like alternative reproductive tactics. The morph expression was also associated with hundreds of SNPs scattered across the whole genome, which were enriched with low frequency alleles in scrambler samples, presumably representing deleterious mutations. This last result is consistent with the notion that condition-dependence of sexually selected traits makes them reliable indicators of genetic quality.

Overall, this thesis provides significant insights into the genomic basis of sexual selection and male morph determination in *R. robini*. The findings highlight the importance of sexual selection in shaping the distribution of genetic diversity, which is an important factor in managing wild populations, especially endangered ones.

Keywords: sexual selection, alternative reproductive tactics, genetic mapping, genome anchoring, GWAS, supergene