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Summary

Sexual selection is, together with natural selection, the driving force for evolutionary change. Sexual conflict contributes to sexual selection because it has the power to generate potential for sexual selection. Hermaphrodites were long excluded from sexual selection research, but during the last decades it has become apparent that they, too, can experience strong selection on reproductive traits. In addition, hermaphrodites can experience sexual conflicts, even though they have both sexes joined within one body, and therefore deserve closer attention of the scientific community.

Just like separate-sexed species, hermaphrodites produce large, nutritious eggs and numerous tiny sperm. Consequently, they are theoretically predicted to experience stronger selection on characters that increase male fitness compared to characters that promote female fitness (i.e. Bateman's principle). Aside from this basic dichotomy between male and female function, the hermaphrodite condition can produce conflicts over mating roles and sex allocation that are absent from gonochorists. In addition, hermaphrodites appear especially prone to severe reproductive conflicts which have been explained by the fact that they can compensate fitness losses in one sexual function with fitness gains in the other function.

This thesis revolves around the quantification of sexual conflict experienced by the simultaneously hermaphroditic pond snail *Lymnaea stagnalis*. When two individuals of this species are willing to mate, it can occasionally be observed that a struggle commences over which individual will perform the male and the female role. However, this appears a mild conflict compared to the strong decrease in short term fitness after copulating as a female. I investigated whether reduced egg laying is caused by a seminal fluid component. By experimentally injecting animals with prostate gland extracts, I revealed that a component of the seminal fluid inhibits egg laying, thus providing the first direct evidence for involvement of such components in competition for fertilization in hermaphrodites. This result suggests that recipients of sperm and sem-

inal fluid lose fitness as a result of mating, and should be selected to withstand such manipulation.

In itself, reduced fecundity of female mating partners does not fit the expected enhancement in reproductive investment, as sperm donors would clearly benefit from higher egg production. However, recipient sex allocation may still be shifted in the theoretical direction –higher investment towards the female function– if the male function was disproportionately reduced compared to the female function in recipients. In order to test this idea, I introduced prostate gland extract into individual pond snails, which were subsequently assessed for male motivation and performance. I found that the propensity to mate as a male was not affected by injection of seminal fluid extract. However, sperm numbers transferred during a sperm donation of treated snails was reduced by 54%. Moreover, injecting single purified seminal compounds revealed that this effect is mediated by two distinct proteins, one of which was previously also found to be involved in the reduction of female investment (i.e. ovipostatin). These results suggest that these two proteins act in concert to target the relative sex allocation of recipients, because male reproductive investment may be even more reduced in the short term than female function.

However, not all changes in reproductive investment of both sex functions can now be attributed to a shift in sex allocation due to receipt of semen. Another factor, namely investment in copulation itself, is known to be costly in many sexually reproducing species, and should therefore be included in the quantification of the costs of mating. By experimentally limiting copulation of focal individuals in pairs of pond snails to either the male role or the female role, I was able to compare the fecundity of single sex individuals with paired hermaphrodites and non-copulants. Additionally, I examined the investment in sperm and seminal fluid of donors towards feminized snails and hermaphrodites, to obtain a measure of male investment. Compared to non-mating focal snails, reciprocating individuals as well as male and female copulants experienced a significant fecundity reduction (~40%) after mating in their allowed roles. In a single copulation, significantly more sperm was do-

nated to partners that were restricted to mating in the female role than to hermaphrodites, while seminal fluid transfer was unaffected by recipient type. These results indicated that the costs of mating in both sex functions are considerable. Therefore, the observed reduction in female fecundity of reciprocally mating individuals is not only caused by receipt of bioactive seminal compounds, but also by the transfer of costly ejaculates when copulating in the male role. Crucially, these findings reconciled two conflicting views on this topic expressed in earlier papers.

In general, females often accept fitness costs from mating events beyond those necessary to fertilize their eggs. They may do so because additional copulations can provide indirect benefits such as enhanced genetic diversity and quality of offspring that may only become apparent after prolonged periods of mating activity. The costs and benefits of multiple mating have been investigated extensively in separate sex species. I described an experiment that also looked at the long term effects of mating on female fecundity of *L. stagnalis*. By using extensive experimental manipulation of mating opportunities, I tested for effects on female reproductive investment during a 10-week period. For mating rates up to once a week, fecundity remained at a level of around 75 eggs per week, while the dry weight of these eggs increased over this range. At higher mating rates, female fecundity decreased strongly, irrespective of the number of different mates an individual had encountered during the course of the experiment. Put together, these results indicate that mating rates of once a week may maximize female reproductive output.

These results were corroborated in another experiment that focussed on the relative strength of sexual selection in pond snails. Here, offspring quality was assessed by determining hatching rates of self-fertilized offspring, offspring produced by monogamous pairs, and offspring produced by polygamous individuals. Offspring developmental rates were strongly correlated with the number of partners of focal snails, while reproductive investment showed the opposite effect, providing an indication that intermediate mating rates can optimize female fitness in *L. stagnalis*. However, mating rates under laboratory conditions are generally much higher than the suggested optimum for female fecundity. This suggests

that mating rates are driven by the male function, which is therefore expected to experience to stronger sexual selection than the female function, as also predicted by theory. However, I found no evidence to support the prediction that the male function of pond snails is under stronger selection than the female function. On the contrary, under polygamy the variances in both mating success and reproductive success were higher for the female function than for the male function, and significant Bateman gradients were found for both sex functions at both young and medium age. This result indicated that the differential investment in gametes by male and female function in hermaphrodites may not always be the most important driver of sexual selection. Rather, I conclude that sexual conflict as a result of strong competition for fertilizations in *L. stagnalis* appears to drive strong counter-adaptation in the female function. To conclude, this work emphasizes that using hermaphrodites as model organisms in sexual selection research may generate new insights into the reproductive ecology of sexual species in general.

Samenvatting

Seksuele selectie is, samen met natuurlijke selectie, de drijvende kracht achter evolutionaire veranderingen. Seksueel conflict draagt hieraan bij omdat het als een brandstof is voor seksuele selectie. Hermafrodieten zijn lange tijd genegeerd in onderzoek naar seksuele selectie, echter, de laatste decennia is het duidelijk geworden dat ook zij sterke selectie ondervinden op eigenschappen die in dienst staan van de reproductie. Het feit dat hermafrodieten de mannelijke en de vrouwelijke seksen verenigen in één individu, belemmert het voorkomen van seksuele conflicten niet. Alleen daarom al verdienen ze een nadere inspectie van de wetenschappelijke gemeenschap.

Net als soorten met gescheiden seksen, produceren hermafrodieten grote, eiwitrijke eitjes en enorme hoeveelheden minuscule spermacellen. Hierdoor wordt vanuit een theoretisch oogpunt voorspeld dat seksuele selectie sterker is op eigenschappen die de mannelijke fitness verhogen dan op eigenschappen die de vrouwelijke fitness verhogen (het zogenoemde Principe van Bateman). Naast deze basale dichotomie tussen de mannelijke en de vrouwelijke functie, zijn hermafrodieten onderhevig aan diverse reproductieve conflicten die bij soorten met gescheiden seksen niet voorkomen. Bovendien lijken hermafrodieten gemakkelijk in extreme seksuele conflicten te belanden. Dit gegeven kan mede worden verklaard door de mogelijkheid dat verliezen van reproductief succes in de ene functie worden gecompenseert door een toename van reproductief succes in de andere functie.

Dit proefschrift is een verhandeling over de kwantificatie van het seksuele conflict in de hermaphrodiete poel­slak *Lymnaea stagnalis*. Als twee individuen van deze soort paringsbereid zijn, kan het gebeuren dat beiden de mannelijke rol op zich willen nemen, waarna tijdens een kortere of langere periode wordt uitgemaakt wie deze rol (het eerst) op zich mag nemen. Deze vorm van conflict lijkt mild in vergelijking met de sterke afname in eiproductie na een copulatie in de vrouwelijke rol. Ik onderzoek of deze reductie het gevolg is van stoffen die worden overgedragen in het ejaculaat. Door slakken op experimentele wijze te injecteren met het extract van prostaatklieren, werd duidelijk dat er inderdaad com-