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Mating strategies and conflicts in aquatic invertebrates:

consequences for evolutionary differentiation

Kristina Karlsson Green

Akademisk avhandling, som för avläggande av filosofie doktorsexamen vid naturvetenskapliga fakulteten vid Lunds Universitet, kommer att offentligen försvaras i Blå Hallen, Ekologihuset, Sölvegatan 37, Lund, fredagen den 26 november 2010 kl. 09.30

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Dissertation 2010

Till Malte och Tore

A doctoral thesis at a university in Sweden is produced either as a monograph or as a collection of papers. In the latter case, the introductory part constitutes the formal thesis, which summarizes the accompanying papers. These have either already been published or are manuscripts at various stages (in press, submitted or in ms).

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Mating strategies and conflicts in aquatic invertebrates: consequences for evolutionary differentiation

Introduction

To ask questions is my oldest son's favourite activity. Where is the sun now? Is dad really an adult? Why do I like this? Why, Mommy, WHY?

Most people pass this intense asking-question-phase at the age of five (Sjödén 1988), perhaps to the great relief of their parents' soar ears. Some people seem to never get out of this habit though. Those may well end up within science, perhaps within evolutionary research, given the opportunity to repeatedly ask: When? Where? How? Why? WHY?

This thesis is a compilation of the evolutionary questions, and hopefully some answers, that I have been working with the past four-five years. The main theme of the thesis is evolutionary ecology, particularly mating strategies, sexual selection and sexual conflict. Most of the studies in this thesis address questions about how mating behaviour and mating characteristics are affected by ecology, and how this in turn leads to differences between populations.

Diversity within a species

A fundamental requirement for evolution is heritable variation within populations (Darwin 1859). It is this variation that eventually may lead to population divergence and speciation, topics which have puzzled evolutionary biologists ever since Darwin's days (e.g. Coyne and Orr 2004). However, just as intricate as the process of speciation is, so are the cases when variation instead persists in the population and does not lead to divergence. Sometimes distinct genetic variation remains within and between populations, resulting in polymorphic species.

This thesis deals with two organisms and systems where the genetic variation is maintained and has not, at least not yet, caused speciation. The first is a case of distinct genetic polymorphism within populations. Such genetic polymorphisms could be a mere transient phase until any of the alternative alleles is fixed in the population and genetic uniformity is reached again (Ford 1945). In many cases, however, the alternative alleles persist as balanced polymorphisms, meaning that multiple alleles are maintained within the population at a more or less stable genetic equilibrium (Ford 1945). Polymorphic populations seem to be common in nature but the selective mechanisms for the maintenance of multiple alleles within populations are not fully understood (reviewed e.g. in Hedrick 2006). Balancing selection, especially in the form of negative frequency dependent selection, is generally thought to be the major factor behind maintenance of polymorphisms (Hedrick 2007). Under negative frequency dependent selection, the rare morph has a selective advantage. When the current rarest morph increases in frequency and becomes the more common, it loses this selective advantage and instead the other morph is favoured. This is illustrated with the classical example of scale eating cichlids (Hori 1993). This predator occurs in two different phenotypes: with a left-handed mouth or a right-handed mouth, and consequently they attack their prey from either the left or the right side. The frequency of these morphs fluctuates depending on the prey being more alert to attacks from the side which the most common morph preys upon. The least common morph thus has an advantage as the prey is not observant of predators from this particular side (Hori 1993).

The other case of distinct intraspecific variation that this thesis addresses is the occurrence of ecotypes living in different habitats, more or less separated from each other. An ecotype is a population that differs from other populations within the species dependent on its unique ecological factors (Turesson 1922). Ecotypes are excellent model systems to study parallel evolution (see e.g. Eroukhmanoff 2009), that is, when similar environmental selection pressures have favoured the evolution of similar phenotypes in populations that are not closely genetically related to each other and thus are evolutionary independent "units" (e.g. Langerhans and DeWitt 2004; Langerhans et al. 2006, for a discussion see Arendt and Reznick 2007). A familiar example where ecotypes have been studied with respect to parallel evolution

is the marine snail *Littorina saxatilis* where distinct ecotypes inhabit different microhabitats of the seashore (reviewed in Johannesson 2003; Johannesson et al. 2010).

Sexual selection and sexual conflict

One of the main factors responsible for the enormous diversity we see in nature is sexual selection. As so many other fundaments for evolutionary biology, sexual selection was suggested by Darwin (Darwin 1871) as an attempt to explain the many striking characters in plants and animals that are not important for survival. Cornerstones in this field are mate choice and intrasexual competition, which have been the focus for extensive research (Andersson 1994). Mating strategies are well-known to be affected by both ecological (Emlen and Oring 1977; Davies and Lundberg 1984) and demographic properties (Kokko and Rankin 2006; Kokko and Jennions 2008) of populations. Changes in mating strategies may happen rapidly on a short time scale, e.g. following environmental changes (Seehausen et al. 1997; Jarvenpaa and Lindstrom, 2004; Eroukhmanoff et al. 2009a). There is also increasing consensus that ecology may favour flexible mating strategies, e.g. with regards to sex roles (Forsgren et al. 2004) and mate choice (Forsgren 1992; Jennions and Petrie 1997; Chaine and Lyon 2008). In fact, even the sex itself could be considered as a plastic trait (Ah-King and Nylin 2010).

For a long time, the prevailing view was that sexual interactions were always mutually beneficial for both sexes. However, in 1979, Geoff A. Parker posed the question: "What happens when a characteristic of sexual selection advantage (benefit) to the male conveys a selective disadvantage (cost) to the genes in the female?" (Parker 1979). This radical question entails the fundamentals of the theory of sexual conflict. In his seminal paper Parker (1979) made the important point that the interest of males and females may often not coincide. A conflict between the sexes arises because individuals that mate are genetically different and are subject to opposing selection pressures regarding mating and reproduction. This means that a given trait or interaction could be selected for in one direction for males and in another direction in females. Either sex may thus increase their fitness at an expense of the other sex, through antagonistic traits and interactions (Parker 1979). Theoretically, the conflict may lead to coevolution between these male and female antagonistic traits (Parker 1979; Gavrilets and Waxman 2002). Populations are predicted to rapidly diverge when captured in a perpetual coevolution (Gavrilets 2000) and therefore sexual conflict has been suggested as an engine of speciation (Arnqvist et al. 2000). However, the often suggested coevolutionary "arms races" between the sexes may not be as common in nature as was previously thought (Härdling and Smith 2005; Fricke et al. 2009; Svensson and Råberg 2010) and polymorphic populations may be a likely alternative (Gavrilets and Waxman 2002; Svensson et al. 2005; Härdling and Bergsten 2006).

Today, sexual conflict is a well-established and fast growing research field (Arnqvist and Rowe 2005), and research on sexual interactions has even been discussed to experience a paradigm shift through the realisation of sexual conflicts (Tregenza et al. 2006). However, there are still major limitations of our understanding and there are many unresolved problems that remain. For example, there has been a call for deeper understanding of how ecology affects sexual conflict dynamics (Edward and Gilburn 2007; Bonduriansky and Chenoweth 2009) and also in the details of the conflict economics, i.e. the costs and benefits of the sexes (Fricke et al. 2009). Additionally, there are surprisingly few examples of female morphological antagonistic traits (cf. Fricke et al. 2009).

Aims of the thesis

The overall theme of this thesis was to investigate how mating related strategies may differ among populations and how these strategies evolve in response to their local ecological environments. Among other topics, I have been interested in how genetic variation in mating traits is maintained within populations, and how

these traits diverge between populations due to environment-specific selection pressures. To address these questions, I have used two different study systems of aquatic invertebrates: diving beetles (Dytiscidae) and the fresh water isopod *Asellus aquaticus*. Together with my collaborators, I have used several different analytical and empirical approaches, including theoretical modelling, behavioural studies, biomechanical experiments, molecular biology and population genetic analyses. I have also addressed the problem of how sexual conflict theory is conceptualised with regard to sex roles. To address this last issue, I and a colleague performed a literature survey to examine the prevailing scientific terminology and to discuss how current terminology may affect the research programme of evolutionary biologists today.

This thesis consists of six papers and they address the following topics:

Paper I: How genetic polymorphism may be maintained in populations experiencing sexual conflict.

Paper II: The nature of the selection pressures acting on female genetic mating polymorphism.

Paper III: Biomechanical underpinnings and physical performance of a sexually antagonistic trait pair.

Paper IV: Parallel divergence and life-history consequences of precopulatory mate guarding in two ecotypes.

Paper V: Phenotypic plasticity in mating behaviour in response to demographic factors in two divergent ecotypes.

Paper VI: Research terminology and sex stereotypes in sexual conflict research.

Materials and Methods

Study species

I have worked with two different, and to me very interesting, study systems: a few species of diving beetles (family Dytiscidae) (Fig. 1) and the freshwater isopod *Asellus aquaticus* (Fig. 2). Both diving beetles and isopods are prime examples of species where sexual conflict is rife (Arnqvist and Rowe 2005). Both systems also have in common a remarkable genetic and phenotypic diversity below the species level: female mating polymorphisms among the diving beetles and two distinct ecotypes inhabiting different habitats in *A. aquaticus*.

Diving beetles (Dytiscidae)

Members of the family Dytiscidae, diving beetles, are found in freshwaters across the world, with some species also in brackish waters (Nilsson and Holmen 1995). All adults are aquatic but may leave the water for migration or overwintering (Nilsson and Holmen 1995). Mating is characterised by an intense struggle between the sexes (Aiken 1992; Wichard et al. 2002). Males of several diving beetle species have adhesive disks, formed as suction cups, on their forelegs (Fig. 3) (Nilsson and Holmen 1995). These suction cups are used to capture a female and withhold her during mating (Aiken 1992; Wichard et al. 2002) (Fig. 4). The beetles mate when the female is exhausted after an intense struggle and afterwards the male inserts a mating plug in the female genitalia that eliminates her chances of future remating (Aiken 1992; Wichard et al. 2002). These behaviours indicate both different interests between the sexes and costs at least for the female. Female beetles typically have structural modifications on their elytra; e.g. furrows or granulates (Nilsson and Holmen 1995). The rough structures on females are suggested to prevent adhesion of male suction cups and aid females in escaping mating (Bergsten and Miller 2007). Sexual conflict over mating and an ongoing arms-race between the male and female antagonistic traits has recently been proposed, based on the phylogenetic and morphological

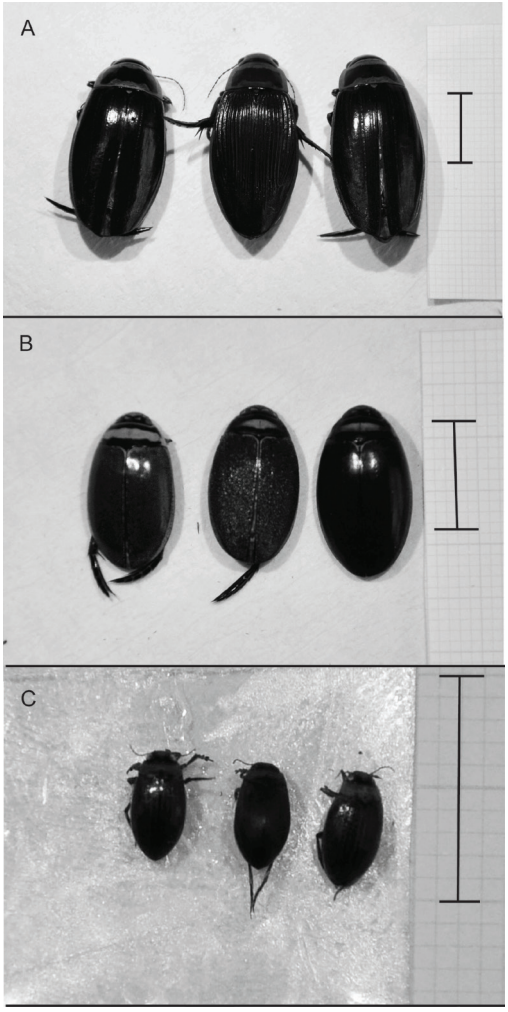

Figure 1. Diving beetle species used in this thesis. From left to right in each figure: male, rough female morph, smooth female morph. Scale bars indicate 10 mm. **A**. *Dytiscus lapponicus*. **B**. *Graphoderus zonatus* **C**. *Hygrotus impressopunctatus.*

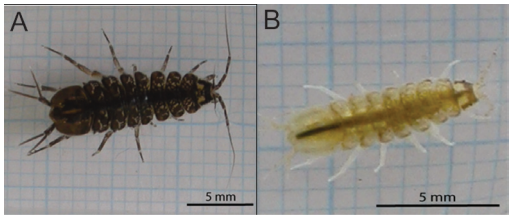

Figure 2. The two ecotypes of *Asellus aquaticus*. **A.** The reed ecotype **B.** The stonewort ecotype. Photo: Fabrice Eroukhmanoff.

properties of this system (Bergsten et al. 2001; Miller 2003; Bergsten and Miller 2007).

In some diving beetle species, two different female morphs co-exist within populations; one with smooth elytra (the "smooth" morph), and the other with rough elytra (the "rough" morph) (Nilsson and Holmen 1995). The morphology of suction cups has been shown to be significantly correlated with morph frequencies in populations (Bergsten et al. 2001). This suggests that some male suction cup phenotypes are better adapted to the different morphs. How the female polymorphism is being maintained is however not yet fully understood, although negative frequency dependent selection has been suggested to play a key role in sexual conflict dynamics (Härdling and Bergsten 2006).

For my thesis, I have worked with three different species of diving beetles: *Dytiscus lapponicus* (Fig. 1A), *Graphoderus zonatus* (Fig. 1B) and *Hygrotus impressopunctatus* (Fig. 1C). These species are of different sizes and belong to different genera, but all three species express the female polymorphism (Fig 1). The rough morph has in *D. lapponicus* 10 longitudinal furrows in the elytra, whereas in *G. zonatus* the rough females are granulated. Finally, in *H. impressopunctatus* the rough morph is matt with microreticulation. I used populations of *D. lapponicus* and *G. zonatus* from northern Sweden (the areas around Umeå) and populations of *H. impressopunctatus* from the Kalmar region and the Island of Öland, from Skåne and from eastern Denmark. The beetles were either captured with traps that were baited with fish and left over night, or by active netting along the shore line of ponds. Fieldwork was done in the beginning of the autumn, August-September, as the beetles are most active due to mating season during this time.

The water louse (*Asellus aquaticus*)

The freshwater isopod *Asellus aquaticus* is a common crustacean in lakes and slow-flowing waters across Europe (Verovnik et al. 2005), where it feeds on detritus (Økland 1978). In two South-Swedish lakes; Lake Krankesjön (55°

42´N, 13° 28´E) and Lake Tåkern (58° 21´N, 14° 50´E), a major ecological shift occurred during the last 20 years, which changed these two lakes from turbidity and phytoplankton dominant states to a clear water state, dominated by submerged macrophytes (Hargeby et al. 2007). Following this ecological shift, a new limnetic habitat emerged in both lakes. This new habitat consists mainly of the macrophyte stonewort (*Chara tomentosa*) and it became rapidly colonised by *A. aquaticus*, which dispersed from dense reed stands (*Phragmites australis*) along the shoreline (Hargeby et al. 2004). After the colonisation of the novel stonewort habitat, rapid phenotypic divergence took place in the isopod populations of both lakes, and this system is now a well studied example of parallel evolution (Eroukhmanoff 2009; Harris 2010). The ancestral "reed" ecotype (Fig. 2A) is for example larger and darker than the novel "stonewort" ecotype (Fig. 2B) (Hargeby et al. 2004; Eroukhmanoff 2009a) and also behavioural differences exists (Eroukhmanoff 2009a; Harris 2010). Indirect inferences about selection based on comparisons between neutral markers and quantitative genetic variation have revealed that the phenotypic divergence between the ecotypes is higher than expected from genetic drift alone (Eroukhmanoff et al. 2009b). Predation is thought to be the major selective agent behind the parallel divergence in different lakes (Eroukhmanoff et al. 2009a). Predator regimes differs quantitatively and qualitatively between the reed habitat (more invertebrate predators) and the stonewort habitat (more fish predators) (Hargeby et al. 2004; Eroukhmanoff and Svensson 2009). Fish predators have been shown to select for smaller body size in many prey, including the classical case of the guppies (Reznick et al. 1997). Invertebrate predators, on the other hand, are often not able to handle large preys and may thus select for a larger body size (Wellborn 1994; Wellborn et al. 1996).

As in other isopods (Jormalainen 1998), the female is only ready to mate when she has moulted to maturity (parturial ecdysis) and developed a ventral oviduct pouch (Økland 1978; Hargeby et al. 2004). On average, females of this species are receptive for only 24 hours after sexual moult (Unwin 1920). To ensure mating, the male therefore captures and carries a female in a precopula (amplexus) (Fig. 5) until she moults into mating state (Unwin 1920; Hargeby et al. 2004). Such precopulatory mate guarding is a male time-investment strategy (Parker 1974) but the preferred time to initiate a precopula may differ between the sexes (Jormalainen et al. 1994b; Jormalainen 1998).

Figure 4. Precopulatory mating behaviour in diving beetles. Drawing by Tord Sjödén.

Figure 3. Protarsal palette with suction cups. **A**. *Dytiscus lapponicus*. **B**. *Graphoderus zonatus.* **C.** Detail of suction cups in *D. lapponicus* (Scanning electron microscope image, 300 times enlargement).

For a female, the time in precopula may interfere with her feeding activity during the crucial time when she has to accumulate resources into her eggs (Jormalainen 1998; Jormalainen et al. 2001). Today, precopulatory mate guarding is one of the most studied examples of sexual conflicts (e.g. Jormalainen and Merilaita 1993; Jormalainen and Merilaita 1995; Jormalainen et al. 2000; Jormalainen et al. 2001) but has also been studied with respect to male mate choice and intra-sexual competition (Manning 1975; Ridley and Thompson 1979; Jormalainen et al. 1992; Jormalainen et al. 1994a).

Figure 5. Male and female *Asellus aqaticus* in precopula.

For the studies of *A. aquaticus* I have used populations from both the ecotypes in Lake Krankesjön and in Lake Tåkern. The isopods were collected during their breeding period in the spring (March-May) (Fig. 6).

Results and Discussion

Paper I

Several studies suggest that sexual conflict may lead to genetic differentiation, reproductive isolation and even speciation (Holland and Rice 1999; Arnqvist et al. 2000; Martin and Hosken 2003; reviewed in Gavrilets and Hayashi 2005).

Figure 6. Fieldwork in Lake Krankesjön. The author of this thesis sampling in the reed habitat (left), Sanna Harris is sampling in the stonewort habitat (right). Photo: Sanna Harris.

Speciation is, however, not the only possible consequence of genetic diversification due to sexual conflict (Gavrilets and Waxman 2002; Haygood 2004; Härdling and Bergsten 2006). Alternatively, polymorphic populations may become established (Gavrilets et al. 2002) and maintained through frequency-dependent sexual conflict (Härdling et al. 2006).

In Paper I, we investigated the effect of sexual conflict and mating system on the maintenance of a genetic mating polymorphism. As our starting point, we used a population where both males and females occur in two distinct morphs. The two morph pairs were assumed to mate assortatively with respect to morph. Two alternative outcomes were observed in our model; either both sexes maintain a stable genetic polymorphism or polymorphism is lost in both sexes as one morph pair goes to fixation. We found that mating system characteristics and indirect effects are decisive for the outcome of the sexually antagonistic coevolutionary process.

In our model, polymorphism is maintained through negative frequency-dependent selection in combination with indirect selection. Females are exposed to negative frequency dependent selection because the female morph that is compatible with the most common male morph suffers more from conflict costs. Since assortative mating between morphs establishes a genetic correlation, the corresponding male morph will be affected by the female mating costs through indirect selection (Lande 1981). This indirect selection leads to fluctuations in the frequency of male morphs, which in turn is necessary for the continued fluctuation of female morphs.

Mating system may, however, alter this basic scenario and affect the evolutionary outcome. A stable evolutionary equilibrium, with a genetic polymorphism in both males and females, can be reached both with a promiscuous and a polygynous mating system (Fig. 7A). In both cases, increasing female mating cost increases the stability of the polymorphism (all else being equal). Costly mating can therefore help preserve genetic variation.

Unstable equilibria, where one morph pair sometimes goes to fixation, is only found for the promiscuous population. In this mating system, the stabilising effect from female conflict costs seems to be offset by assortative mating (Fig. 7B). When non-random mating exceeds mating costs, males ”matching” the most common female morph will always be favoured by selection. This is because strong direct selection on the male morph affects females through linkage disequilibrium. As a result, the direct selection effect on female morph frequencies through mating costs is outweighed and female morphs suffering from direct sexual conflict costs will still increase in frequency. The most common morph pair will therefore increase in frequency via indirect selection and eventually become genetically fixed. In a promiscuous mating system, the evolutionary outcome therefore depends on whether direct selection is stronger on males (because of assortative mating) or on females (because of conflict costs). In both cases the opposite sex is “dragged along” by indirect selection.

In summary, whether a population

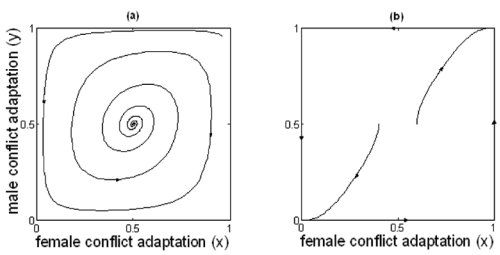

Figure 7. Evoutionary dynamics of male and female conflict adaptations in the promiscuous mating system. Panel (a) shows a case where the internal equilibrium is stable. When the population is initiated at a point with near fixation of a particular male-female trait pair, the effects of antagonistic direct selection leads the phenotype frequencies in a cyclic fashion towards a stable equilibrium. In (b) the equilibrium is unstable because of strong assortative mating. Disequilibrium leads to indirect selection on females. This overrides direct selection and pushes the population to either of the two points with matching male and female conflict adaptations.

remains polymorphic or loses genetic variation depends on the balance between female conflict costs and assortative mating, together with the details of the mating system. For all outcomes, however, indirect selection plays a crucial role. The model thus provides two important insights. First, indirect selection may be of importance in sexual conflict, with a potential to influence the dynamics just like direct fitness effects, the latter which are more recognised and generally accepted. The significance of indirect selection does not question the presence of a sexual conflict but it contributes with an additional dimension to the dynamics initiated by direct mating costs. Second, the results illustrate the crucial role of intersexual dynamics, showing how the impacts on one sex inevitably affect the other. Indeed it is not possible to assign winners and losers of sexual conflict since the sexes are mutually dependent on each other for their reproductive success (Arnqvist and Rowe 2005). Phenotypic and genetic polymorphisms are maintained over the major range of parameter space in our model. This suggests that sexual conflict, at least under these model assumptions, may restrain population differentiation and preserve genetic variation within local populations.

Paper II

Although polymorphic species seem to be common in nature, the selection regimes responsible for maintain the polymorphisms need more attention (Svensson et al. 2009). Inference of the selection regimes acting on polymorphic traits can be achieved by comparing population divergence in neutral genetic markers with population divergence in morph frequencies; discrepancies between these two measures of divergence indicate that selection operates on the polymorphisms (Abbott et al. 2008; Whitlock 2008).

In Paper II, we aimed to infer the selective regimes acting on the polymorphic trait of the female diving beetles: their elytral surface which could be either smooth or rough. We compared neutral genetic F_{ST} estimates obtained with an AFLP analysis with F_{ST} estimates of the presumably selected trait (F_{ST} (morph)). This comparison was performed in three different species and genera of diving beetles; *Dytiscus lapponicus*, *Graphoderus zonatus* and *Hygrotus impressopunctatus* (Fig. 1).

In two of the studied species (*D. lapponicus* and *G. zonatus*) we were not able to reject genetic drift as responsible for the population difference in morph frequencies. In contrast, in the third species (*H. impressopunctatus*), our results supported divergent selection as an explanation for the observed population divergence in morph frequencies (Fig. 8). Genetic drift may indeed affect genetic polymorphisms in nature but the failure to reject drift in our study could be due to a mix of stabilising and divergent selection regimes operating in this system.

Stabilising selection in form of negative frequency-dependent selection has been considered the most likely selection regime for maintaining polymorphic populations in nature, especially in populations where sexual conflict operates (Svensson et al. 2005; Härdling and Bergsten 2006; Paper I, this thesis). Sexual conflict in the diving beetle system is likely to be important and suggests a role for negative frequency-dependent selection. However, the elytral surfaces may also have a function which

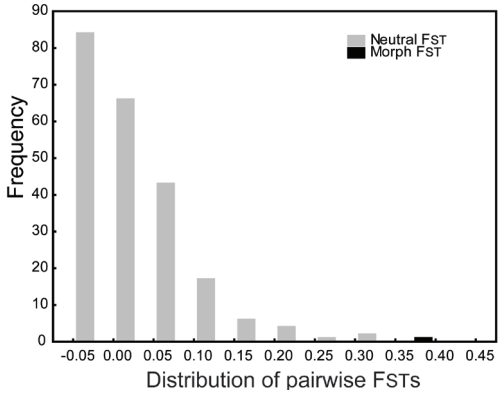

Figure 8. Distribution of mean pairwise F_{ST} values for all neutral loci (grey bars) and the mean pariwise F_{ST} values for the assumed morph locus (black bar) for *H. impressopunctatus*. Negative F_{ST}s were pooled to 0 in all statistical analyses.

is naturally selected. The frequency of the rough morph often show strong and variable geographic pattern, indicating that local ecological factors and not only sexual conflict may be important (Nilsson and Holmen 1995; Bilton et al. 2008) For instance, the elytral structures have been suggested to function as a protection to UV-radiation at higher altitudes (Drotz et al. 2010).

It should also be noted that the statistical power to reject genetic drift in favour of stabilising selection is usually considerably lower than the power to detect divergent selection using these indirect approaches to infer selection (Whitlock 2008). This is because the range and the 95 % confidence intervals of neutral F_{ST}s often have been found to approach zero (Beaumont and Nichols 1996; Excoffier et al. 2009).

In conclusion, we suggest that the failure to reject genetic drift is not because drift is the only force operating on these mating polymorphisms. Rather, it is more likely due to the fact that divergent and stabilising selection may outweigh each other. Clearly, more empirical research is needed on the diving beetle system for deeper knowledge of the multiple and opposing selection pressures that may operate on this fascinating mating polymorphism.

Paper III

One important factor in sexual conflict dynamics are the male and female antagonistic traits as they may increase the fitness of one sex at a cost for the opposite sex (Arnqvist and Rowe 2005). Male antagonistic traits and their function in sexual conflict is a relatively well-studied topic (Arnqvist and Rowe 2005). In contrast, there is relatively little knowledge of the corresponding female antagonistic traits. In particular, examples of female morphological traits are generally lacking, perhaps because behavioural responses evolve easier than morphology (Fricke et al. 2009). One of very few known morphological female adaptations to sexual conflict is the rough dorsal structures present in diving beetles (Fig. 1). In Paper III, we studied the biomechanical performance of male suction cups on the female elytra to better understand the function of the dorsal rough structures in females. We compared adhesion on surfaces of rough and smooth female morphs as well as on male elytra, and did this for two diving beetle species: *Dytiscus lapponicus* and *Graphoderus zonatus*.

We found that the adhesive strength of male suction cups was considerably lower on both the rough elytra and the rough pronotum compared to the other surfaces (Fig. 9). Our results thus showed that the dorsal modification of female diving beetles clearly obstruct adhesion of male suction cups. Although these results confirm that the female dorsal structure have important functions in sexual interactions,

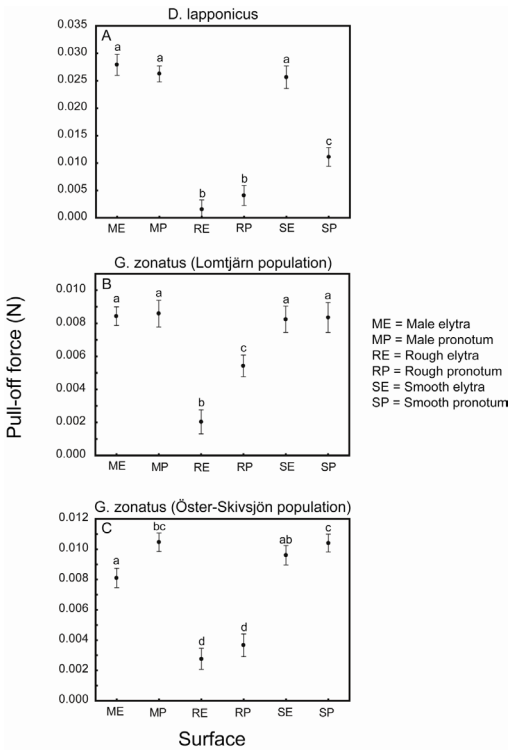

Figure 9. Adhesion (pull-off force in newtons, N) on the different surfaces for the three populations. Letters indicate results from Tukey's post hoc tests, where different letters indicate statistically significant differences in adhesion force between treatments. **A.** *D. lapponicus*. **B.** *G. zonatus* (Lomtjärn population). **C.** *G. zonatus* (Öster-Skivsjön population).

more empirical research on the actual mating behaviour and the antagonistic interactions would also be required to fully understand the mechanisms behind the male and female conflict traits in this system.

A remaining question is how the two female morphs are maintained within a population and how their coexistence affects the male antagonistic traits. Males may, for example experience conflicting selection pressures between adhering to the smooth and the rough structures of the different female morphs. The result of such biomechanical trade-offs may be that males end up as being relatively maladapted to both female types (cf. Gavrilets and Waxman 2002). Previous studies have found that the suction cup phenotype differs depending on the frequency of the rough morph in local populations (Bergsten et al. 2001). As a parallel from another insect system, males of the Colorado potato beetle (*Leptinotarsa decemlineata*) experience a trade-off between their capacity to adhere to smooth females during mating and capacity to adhere to rough surfaces of plants during locomotion (Voigt et al. 2008). Thus, a trade-off between the morph surfaces is clearly plausible. In our study we found that the rough and the smooth surfaces affect adhesion differently for different males, which could indicate the presence of such a trade-off between surfaces for males. An interesting possibility is the presence of two potential clusters of distinct suction cup composition among males, which may corresponds to one of the female morphs each. This would imply the existence of two male morphs, consistent with the scenario modelled in Paper I (see also Gavrilets et al. 2002; Härdling and Bergsten 2006).

Paper IV

Ecology has long been recognised to affect mating system and mating behaviour (Emlen and Oring 1977; Davies and Lundberg 1984; Forsgren 1992; Eroukhmanoff 2009). For example, rapid environmental changes may have profound effects on sexual selection and mating systems, such as in the sand goby (Jarvenpaa and Lindstrom 2004) and cichlids (Seehausen et al. 1997). Our study system of *A. aquaticus* provides us with a unique opportunity to compare mating characteristics between the different ecotypes and infer how ecology may affect the evolution of mating behaviour. As many other crustaceans, *A. aquaticus* exhibit precopulatory mate guarding. Males start guarding a female already before she becomes sexually receptive to reduce his time spent in mate search, which will be selected for if female receptivity is limited (Parker 1974). A sexual conflict over mate guarding duration may, however, arise if the optimal duration differs between the sexes (Jormalainen et al. 1994b).

We compared the length of mate guarding in the two ecotype populations in two different lakes. We found that mate guarding duration had differentiated in parallel between the ecotypes, in a similar fashion in both lakes. The novel "stonewort" ecotype has a significantly shorter mate guarding compared to the ancestral "reed" ecotype in both lakes. This is likely to reflect divergent selection from ecological differences between the habitats. Parallelism in phenotypic traits is a classical indication that natural selection, rather than non-adaptive processes, has caused differentiation between populations (Schluter 2000). Although this parallel divergence in mate guarding behaviour strongly suggests a role for selection, the mechanisms behind the parallel selection pressures are not clear. We suggest that in the stonewort habitats, the isopods may have a higher probability of finding a mate, or have a lower survival probability when being in precopula (Jormalainen et al. 1994b), compared to the situation in the ancestral reed habitat. This is supported by the fact that population densities are much higher in the stonewort habitat (Paper V), thus reducing time spent mate searching for both males and females.

Differences in predation regimes are likely to be the main cause of morphological divergence between the ecotypes (Eroukhmanoff 2009). The changed predation regimes could also directly or indirectly have affected the mate guarding duration and mating behaviours.

The state of precopula in the reed habitat may provide a size-refuge protection against the many small invertebrate predators that occur there, as a pair in precopula increases the overall size of the isopods (that is, the total size of the couple). In contrast, a large precopula or a large body size could be strongly disadvantageous in the stonewort habitat were fish predators predominate, and where invertebrate predators are few. A similar effect of predation has also been demonstrated in an amphipod species complex (Cothran 2004).

In addition to direct effects of predation, indirect effects caused by demographic differences between the different habitats (Paper V) may also affect mate guarding duration. Low isopod density in the reed habitat may select for longer optimal mate guarding duration. This low isopod density in the reed habitat means that the encounter rate between the sexes probably is low. In contrast, the much higher isopod densities in the stonewort may select for a shorter optimal mate guarding duration, as both sexes are likely to have higher prospects and options of finding other mates.

We also found ecotype differences in female survival during mate guarding and in their probability of producing offspring. The stonewort ecotype had both lower female survival and a lower probability of producing offspring than the reed ecotype, and this pattern was observed in both lakes. These intrinsic ecotype differences could reflect differences in overall female condition, physical

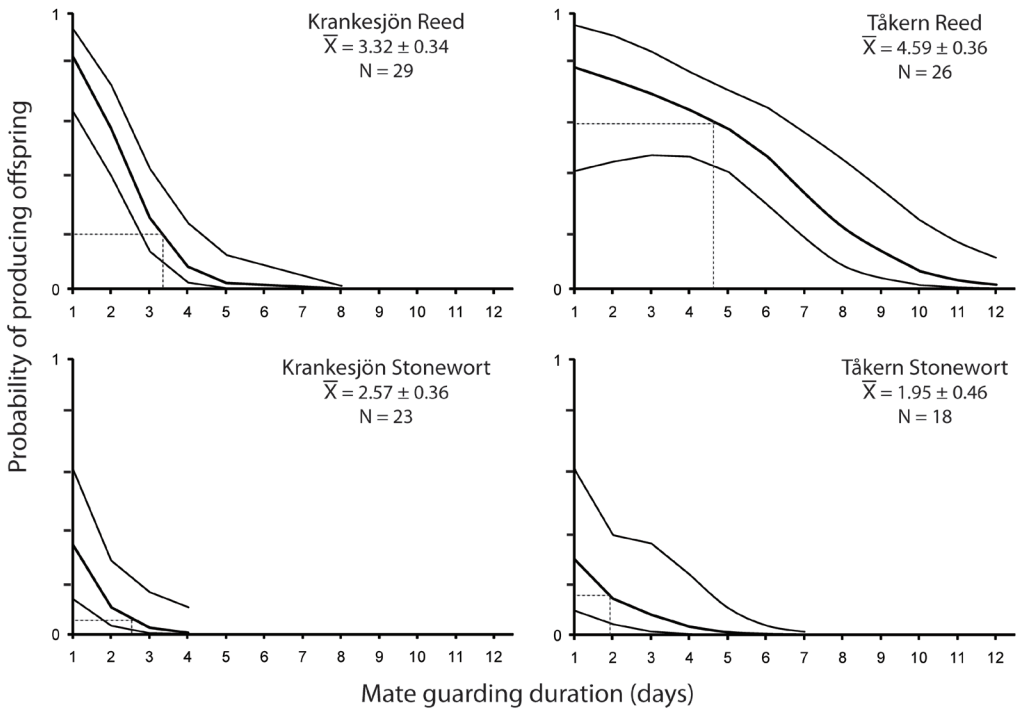

Figure 10. The probability of producing offspring in relation to mate guarding duration in *Asellus aquaticus*. Shown are females belonging to the reed ecotype (upper two figures) and the novel stonewort ecotype (lower two figures). The fitness functions are cubic spline regressions, and these are presented for the two different ecotypes in Lake Krankesjön (left panels) and in Lake Tåkern (right panels). The Y-axis shows our fitness measure: the probability for gravid females to produce offspring. The X-axis shows the duration of mate guarding (in days). Dashed lines indicate the population mean in mate guarding duration of each population. Included in the figures are population mean ± SE and sample size (N) for each population. In all four populations, mate guarding duration has a significant and negative effect on the probability of producing offspring.

vigour or capacity to withstand guarding. More interestingly, however, we found that mate guarding length *per se* seemed to negatively affect probability of producing offspring in all four populations (Fig. 10). This may indicate an invariant sexual conflict over mate guarding duration in this isopod species that has not been resolved in any one of the four populations. The failure to produce offspring may thus reflect the effects of male condition, female condition or a combined male and female effect. However, independent of which mechanism that is mainly affected by mate guarding, the failure to produce offspring will clearly affect both sexes and hence a too long mate guarding will be costly to both male and female fitness.

Paper V

Phenotypic plasticity is the ability of organisms to react to environmental cues by changing their phenotypes (West-Eberhard 1989; West-Eberhard 2003). Genotypes with more plastic traits have been suggested to perform better when exposed to novel environmental conditions than less plastic genotypes (Price et al. 2003; Ghalambor et al. 2007). Phenotypic plasticity has also been suggested to facilitate population persistence in novel habitats, and plasticity may fuel further evolutionary divergence (Agrawal 2001).

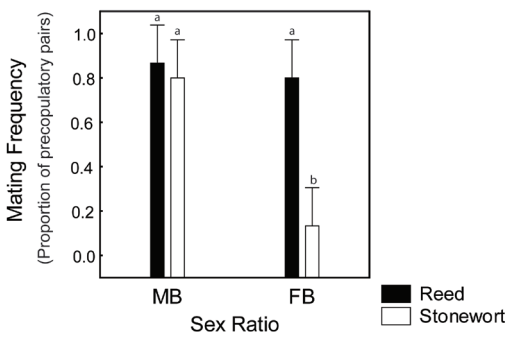

Figure 11. Mating propensity in the experimental sex ratio treatments, for the reed and the stonewort ecotypes, respectively. The stonewort ecotype, but not the reed ecotype, adjusts its mating propensity to the adult sex ratio (Ecotype * Sex Ratio treatment: $F_{1,8}$. = 16.20 p = 0.0038).

In Paper V, we used *A. aquaticus* to study plasticity in mating behaviour in response to differences in population density and adult sex ratio. First, we demonstrated, using field data, that the ecotype populations in Lake Krankesjön differed in adult sex ratio and population density. These differences between the habitats are important, as theory suggests that the initiation and length of mate guarding will be strongly affected by demographic factors, including density and sex ratio (Parker 1974; Jormalainen et al. 1994b). Density and sex ratio are also known to be important factors driving the selection pressures in both sexual conflict (Gavrilets 2000; Gosden and Svensson 2009) and mating dynamics in general (Emlen and Oring 1977; Kokko and Rankin 2006; Kokko and Jennions 2008). From our previous studies, we know that the novel "stonewort" ecotype has lower propensity to initiate pair bonding (precopula) than the ancestral "reed" ecotype. This lower mating propensity among stonewort isopods is reflected both in terms of time taken until a precopula is formed and in the probability of forming a precopula (Eroukhmanoff et al. 2009a).

We further showed that these two different ecotype populations have diverged in both mating behaviours and in their phenotypic plasticity for mating propensity. The ancestral reed ecotype does not respond to differences in either density or sex ratio. In contrast, the novel stonewort ecotype responds significantly to adult sex ratio, by increasing mating to a higher frequency in the male-biased experimental set-ups (Fig. 11). Thus, whereas the ancestral ecotype does not seem to exhibit any phenotypic plasticity with respect to the social and demographic environment, phenotypic plasticity in response to adult sex ratio seem to have emerged in the stonewort population. Interestingly, our recent work on evolution of behavioural syndromes in this system suggests that phenotypic plasticity in other behaviours is also more pronounced in the stonewort ecotype (Harris 2010).

Some of these results are clearly in line both with previous empirical studies

(Manning 1980; Jormalainen et al. 1994a) and theoretical models. Models predict that, in males, it will be more advantageous to initiate a precopula when male-male competition is intense (i.e. in a male biased sex ratio) whereas it pays off to wait for a preferred female when adult sex ratio is female-biased (Parker 1974; Jormalainen et al. 1994b). Always having a high mating propensity is likely to be costly if it decreases the opportunity for adaptive male mate choice. Thus, different mating phenotypes may be favoured under different demographic environments. We therefore suggest that environmental variation in adult sex ratios have selected for phenotypic plasticity in male mating behaviours (cf. Ghalambor et al. 2007). As phenotypic plasticity may play an important initial role in evolutionary divergence and speciation (Agrawal 2001; Price et al. 2003) it may fuel continued ecotype differentiation, perhaps by influencing both the direction and the intensity of sexual selection (Jennions and Petrie 1997; Cornwallis and Uller 2010).

Paper VI

The theory of sexual selection has been subjected to controversy and debate since Darwin (1871) presented the theory. Much controversy and criticism has concerned the sex roles: how the sexes are described (Hrdy 1986; Martin 1991; Fox Keller 2004), as well as the use of highly anthropomorphic terms with evocative connotations, e.g. rape (Gowaty 1982). It has also been proposed that research has been affected and hampered by a preconceived view of how males and females "should" behave (Birkhead and Pizzari 2002).

In paper VI, we performed a literature review to document how the sexes are described in sexual conflict research and what characteristics the two sexes are being assigned to in theoretical models. We found that the terminology is highly sex-specific and typically expressed as males being active and offensive, while females being reactive and defensive. That the terminology implies merely responsive acts from females may create a misleading image of the conflict dynamics since also female antagonistic traits and behaviours should be able to impose a reaction in males. This effect is reflected in the theoretical models, which we found mainly consider female conflict costs. Thus are only the male conflict adaptations granted the possibility of having any negative effect on fitness. The fitness effects on males of female conflict adaptations are seldom or never considered and, consequently, the research field is potentially narrowed. As a parallel from the related field of sexual selection research, that despite Darwin's broad definition of sexual selection in both sexes, intra-sexual competitive ability of individuals is thought to contribute to sexual selection if it occurs in males but not in females (e.g. through competition for food to offspring) (Clutton-Brock 2007). To approach the theory in a similar way for both sexes may give deeper insights. As an example, in sexual selection research male mate choice is now highlighted (Bonduriansky 2009).

The biased pattern we found may have several different causes, which we discuss in the paper. Our main focus is on the possibility that the distinct difference between males and females throughout the field stems from a preconceived and stereotyped view from researchers of how males and females are likely to behave. We believe that this view may hamper research and slow down scientific progress in the field. As an example, there are only a few empirical studies addressing male costs of female counter-adaptations, and little is known about female counter-adaptations in general. This may be due to the fact that male costs seldom are not given enough significance in theoretical models. As yet a parallel from sexual selection research, the importance of incorporating mutual choice in mate choice models and not using the traditional approach with only one sex that chooses, has been highlighted (Bergström and Real 2000), and approaches to construct broader and more neutral models are made (see Gowaty and Hubbell 2005; Gowaty and Hubbell 2009). The terminology may also affect the choice of study species, most research so far has focused on separate-sexed animals but the theory

could also be applied to plants (Madjidian and Lankinen 2009) and hermaphrodites (Abbott 2010). To counter the potential bias in sexual conflict research, whatever cause it may have, and to gain deeper insight in the field, we suggest that one look beyond the conventional sex roles (cf. Cunningham and Birkhead 1997; Kvarnemo et al. 2009), that more sex-neutral studies be made when possible and that the most captivating terminology be avoided.

Conclusions

When starting off as a PhD student five years ago, my ideal thesis would be a combination of different techniques and approaches. I wanted to disentangle a problem from several different angles and at different levels, working rather broad than being an expert on some minor details or on a single method. In hindsight, I can conclude that at least the broad combination of techniques and approaches is fulfilled – although the questions are a slightly more scattered!

In spite of the diversity of the studies in this thesis, I believe that some general conclusions can be made. I have addressed the influence of ecology on mating dynamics and how populations may differ in mating characteristics. Mating behaviour and mating traits are probably to a very large extent affected by ecological and demographic features (Papers I, II, IV and V). Mating traits may be affected by both divergent and stabilising selection, and even genetic drift could potentially operate in some populations (Paper II). Within a species, the mating dynamics could differ dramatically between different populations (Paper II, IV and V). Some basic characteristics of mating systems and mating phenotypes are, however, consistent across all populations; such as the obstruction of female dorsal modifications among diving beetles (III) and the negative effect of mate guarding duration on offspring production in *A. aquaticus* (Paper IV). The evolutionary change in mating characteristics may be rapid, as in the isopod system (Papers IV and V). Mating characteristics can clearly also change in parallel due to ecological similarities between populations (Paper IV).

The overall implications of my results are that to fully understand mating dynamics, deeper ecological knowledge is required. Mating system evolution and sexual conflict are complex phenomena, and they are clearly influenced by several different ecological factors and selective regimes. Environmental changes are likely to rapidly affect mating behaviour which in turn may affect direction of sexual selection and the organisation of mating systems. Mating system may further affect the conflict dynamics and population genetic structure. Changes in direction of sexual selection between populations may in turn later lead to divergence and even speciation. Counteracting and constraining factors against these divergence processes is genetic variation, and genetic polymorphisms may be maintained within a species due to the force of stabilising frequency-dependent selection.

In view of paper VI, several studies in this thesis could indeed have been made different. For example, incorporation of male costs and polyandry in Paper I, and evaluation of both male and female costs in Paper IV. Future research would likely benefit from taking into account similar approaches for both sexes and using more neutral terminology. To relieve ourselves from biases by contemplating how research is performed, particularly the connection between society and science, may be fruitful in several research programmes. After all, objective research is worth striving for.

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Parning och konflikter under ytan

Parning och konflikter under ytan

Hur sjutton har den enorma mångfald vi ser i naturen uppkommit? Det är kanske den mest centrala frågan för evolutionsbiologer genom tiderna. Många forskare inom detta ämne koncentrerar sig på artbildning, det vill säga hur variation inom en art uppstår och sedan leder till större och mer djupgående skillnader mellan populationer, till de slutligen är så olika att de klassificeras som olika arter. I mitt tycke är dock fallen då en distinkt variation bibehålls inom arten än mer fascinerande. Om det finns distinkta typer, varför fortsätter de inte att förändras i riktning från varandra, till skilda arter? Vilka är de sammanhållande krafterna och påverkar ekologiska skillnader variationen mellan populationer?

Något som har stor betydelse för den mångfald vi ser i naturen, är de selektionstryck som är relaterade till reproduktion. Som så mycket annat var det Darwin som var först med att presentera denna teori om sexuell selektion, i ett försök att förklara de karismatiska egenskaper som djur och växter har som inte är direkt kopplade till överlevnad. En, kanske något förenklad, grundsyn inom sexuell selektion är att det som gynnar det ena könet också gynnar det andra. Men, om det inte är så? Tänk om det finns fall där en företeelse som är fördelaktig för det ena könet inte är bra för det andra, kanske till och med skadlig? Vilket evolutionärt förlopp är då att vänta? Sådana frågor ligger till grund för teorin om könskonflikt. Detta forskningsfält har varit snabbt växande och blivit mycket inflytelserikt; en del menar till och med att det vi ser är ett paradigmskifte inom forskning om interaktioner mellan könen.

I denna avhandling har jag varit intresserad av hur just sådan variation i beteenden och egenskaper relaterade till sexuell selektion och könskonflikt förhåller sig mellan olika populationer. Jag har generellt varit intresserad av hur dessa egenskaper påverkas av både ekologi och inre populationsstrukturer. För att studera olika aspekter av detta har jag primärt använt två olika akvatiska system: några arter av dykarbaggar (Dytiscidae) och sötvattensgråsuggan *Asellus aquaticus*.

Dykarbaggar finns i sötvatten världen över och har föreslagits som ett av de främsta exempel där en konflikt mellan könen finns. Hos dessa arter är det vanligt att hannarna har en sammansättning av små och stora sugproppar på frambenen. Dessa använder de till att fånga en hona och hålla fast henne med under parningen. I många arter murar dessutom hannen igen honans könsöppning med en så kallad parningsplugg efter parningen, troligtvis för att hindra att hon efteråt parar sig med en annan hanne. Själva parningen föregås av en intensiv jakt innan hannen, bokstavligt talat, sugit sig fast vid honan. Detta i sig tyder på att könen inte är helt överens om parningen. Dessutom, i flertalet arter har honorna grova strukturer på sina täckvingar, till skillnad från hannarna som är helt släta. De grova strukturerna kan till exempel vara räfflor, gropar eller till och med små hår. Intuitivt kan man tänka sig att det är svårare för hannens sugproppar att fästa på dessa strukturer, och att de därmed skulle ha en antagonistisk funktion i konflikten. En studie som stärker denna teori visade hur dessa sexuella karaktärer (det vill säga sugproppar respektive grova täckvingar) följer varandra åt i arternas släktträd. Arter med mer modifierade strukturer har också mer avancerade sugproppar; de samevolverar i en ”kapprustning” mellan könen. Bilden kompliceras ytterligare av att det i vissa arter finns en honlig variant, en morf, med släta täckvingar. Om de grova strukturerna är fördelaktiga för honor med avseende på könskonflikt, varför finns då en slät hona? Vilka selektionstryck påverkar de honliga morferna?

I den första studien (Paper I) i denna avhandling har jag och min handledare tagit fram en matematisk modell för att undersöka det evolutionära förloppet i en population där två honliga morfer och två hanliga morfer, alltså två morfpar, finns. När vi analyserade modellen såg vi att alla morferna, och därmed den genetiska variationen, kan bevaras i populationen, under vissa omständigheter. En faktor som möjliggör att morferna bibehålls är könskonflikten. Om denna är kostsam för honorna, blir den negativa

effekten större för den honliga morf som är kompatibel med den vanligaste hanliga morfen. Denna honliga morf är då i högre grad utsatt för konfliktkostnader eftersom den oftare utsätts för parningsförsök. Dynamiken skapar en så kallad negativ frekvensberoende selektion där den mer ovanliga varianten i en population alltid har en evolutionär fördel. De två morfparen kommer därför att fluktuera i inbördes frekvens i populationen, men är alltid representerade i någon grad. Dock såg vi att förloppet till stor grad påverkas av vilket parningssystem som finns i populationen. Parningssystem kan ändra dynamiken och leda till att det ena morfparet dör ut och populationen blir monomorf; den genetiska variationen har därmed minskat.

I avhandlingens andra studie (Paper II), undersöker jag de möjliga selektionstryck som kan påverka morffrekvensen i naturliga populationer. Jag gör detta indirekt genom att jämföra den genetiska variation som finns mellan populationer i neutralt DNA (gener som inte selekteras för något) med den variation som finns mellan populationer i morfgenen. Genom en sådan jämförelse kan man få en indikation på om selektionen är divergerande (att populationerna blir mer olika) eller stabiliserande (att morferna bibehålls i ungefär samma frekvens mellan populationer). Resultatet kan också tyda på att genetisk drift, det vill säga att slumpmässiga förändringar i genomet förklarar de frekvenser som morferna förekommer i. I vår jämförelse såg vi att divergerande selektion verkar på morffrekvenserna i en av arterna, *Hygrotus impressopunctatus*. Detta beror troligen på någon ekologisk faktor som skiljer sig mellan populationerna. För de två andra arterna, *Dytiscus lapponicus* och *Graphoderus zonatus*, kunde vi inte förkasta påverkan av genetisk drift. Drift är ett omdebatterat ämne men kan ha betydelse i naturliga populationer, framför allt om dessa är små. Det är dock troligt att både divergerande selektion (genom populationernas olika ekologi) och stabiliserande selektion (till exempel genom könskonflikt) påverkar morffrekvenserna i dessa två arter.

Avhandlingens tredje artikel (Paper III) är en biomekanisk studie av skillnaden i fästförmåga hos hannarnas sugproppar på de två honliga morferna. Resultatet - att hannarnas sugproppar har svårare att fästa på den grova honliga morfen - kan tyckas trivialt, men bidrar till att stärka hypotesen om könskonflikt hos dykarbaggar och en antagonistisk funktion hos de honliga strukturerna. Uppföljande studier av hur sugpropparna fäster på de skrovliga ytorna (för otvivelaktigt gör de det och även den grova honan blir parad i naturen) kan även vara av ett kommersiellt och industriellt intresse.

Mitt andra studiesystem, gråsuggan *Asellus aquaticus*, berörs i avhandlingens fjärde och femte artikel (Paper IV och V). Denna art är intressant därför att den förekommer i två olika ekotyper, alltså varianter, som lever i två olika miljöer. Den ursprungliga ekotypen bor i vassen. Därifrån har individer spridit sig till kransalger i mitten av sjön. Den ursprungliga vass-ekotypen är större och mörkare än den nyare kransalger-ekotypen; man tror att det till viss del är olikheter i rovdjursfaunan som främjat dessa olika egenskaper. Det finns även en del beteendemässiga skillnader mellan ekotyperna; den ursprungliga ekotypen är exempelvis mer benägen att para sig. Anmärkningsvärt med detta system är att ekotyperna återfinns i flertalet svenska sjöar. Detta utgör ett exempel på parallell evolution där likheter i det nya habitatet har gynnat samma egenskaper på flera ställen. Jag har undersökt likheter och skillnader i parningsstrategier mellan de två ekotyperna i Krankesjön och Tåkern. Liksom andra gråsuggor har honorna endast möjlighet att para sig under en begränsad tid medan deras könsöppning är tillgänglig mellan två skinnömsningar. För att inte missa möjligheten till parning har hannarna som strategi att fånga en hona innan hon är receptiv och bära henne under sig till hon ömsar skinn och parning kan ske. Parformationen när hannen bär honan kallas precopula. Detta vaktbeteende gynnar hannarnas parningsframgång, men själva tidpunkten för när det är fördelaktigt att ingå en precopula kan skilja sig åt mellan könen. Honornas rörelseutrymme begränsas och möjligen kan de inte söka föda som de behöver.

Detta kan framför allt vara ett problem med tanke på att honorna just under perioden före parning måste lagra energi till sina ägg. Därför är könskonflikt om parning hos gråsuggor och andra kräftdjur ett välstuderat ämne.

I den fjärde artikeln (Paper IV) undersöker jag hur länge precopula hos båda ekotyperna varar, närmare bestämt hur många dagar de sitter ihop som ett par före egentlig parning. Jag gör denna undersökning hos ekotyper från två sjöar för att indirekt kunna dra slutsatser om ekologins betydelse för vaktbeteendet. Den ursprungliga vass-ekotypen har en längre precopula än den nyare ekotypen och detta mönster fanns i båda sjöarna. Det verkar alltså ha funnits en liknande selektion i de båda habitaten för en längre respektive kortare precopula. Dessutom har honor av den nyare ekotypen sämre överlevnad och de får också färre avkomma än den ursprungliga ekotypen. Den nya ekotypens honor verkar alltså sämre rustade att klara tiden i precopula. Ett annat intressant resultat är att sannolikheten att alls få någon avkomma minskar med tiden paret varit i precopula. Detta mönster fanns i båda ekotyperna från båda sjöarna och kan tyda på att en kostsam könskonflikt finns inom hela arten.

I den femte artikeln (Paper V) fortsätter jag att undersöka ekotypernas parningsbenägenhet. Jag gjorde försök där jag studerade frekvensen av parbildning i olika sammansättning med avseende på könskvot och populationsstorlek. Den nyare ekotypen hade generellt lägre parningsbenägenhet, men benägenheten ändrades beroende på könskvot, till skillnad från vass-ekotypen, som hade en oföränderlig benägenhet under alla förhållanden. Dessa resultat tyder dels på att vassen verkar vara selekterad för att para sig under alla omständigheter men att gråsuggorna i kransalgerna gynnats av ett mer flexibelt beteende.

Slutligen, i den sjätte artikeln (Paper VI), tar jag ett steg tillbaka och betraktar från ett utanförperspektiv hur könskonfliktsforskning bedrivs. Även om man som forskare strävar efter objektivitet i sin verksamhet, kan man vara färgad av det samhälle man lever i, vilket i sin tur påverkar forskningen. Tillsammans med en kollega undersöker jag vilka termer som används för att beskriva kön samt vilka egenskaper könen tillskrivs i teoretiska modeller. Vi fann att olika termer genomgående används för de två könen. Generellt används termer för hanliga egenskaper som implicerar en aktiv handling medan termer för honliga egenskaper implicerar passivitet eller en handling som enbart sker som en respons på hannens beteende. Detta mönster kan möjligen avspegla traditionella mänskliga könsstereotyper. Vi föreslår att man ska eftersträva en mer könsneutral terminologi och även försöka bedriva studier som undersöker liknande egenskaper hos båda könen.

Sammanfattningsvis tyder min avhandling på att parningsstrategier kan skilja sig mellan populationer både beroende på ekologiska och demografiska faktorer. Parningsstrategier kan också ändras mellan populationer i ett relativt snabbt evolutionärt förlopp. Dock finns även sammanhållande evolutionära krafter som bibehåller likheter mellan populationer och som kan bevara variation inom arter, istället för att leda till större olikhet mellan populationer och i förlängningen ny artbildning.

Så är det dags att sätta punkt, och att skriva den del i avhandlingen som faktiskt kommer att läsas av fler än opponenten. Denna lilla bok hade givetvis inte kommit till utan det stora stöd och den hjälp jag fått, både på ekologen och utanför. Det är många som förtjänar ett tack men jag vill börja med att skicka en tanke till hela **zooekologiska avdelningen** – jag har alltid uppskattat vänligheten, diskussionerna och humorn. Man kanske borde masa sig ner till kaffet lite oftare… ;-)

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Tina

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