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Sexual Selection and Adaptation to Novel Environments

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Abstract

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The work included in this thesis aims at exploring the environmental sensitivity of benefits and costs of sexual selection through a combined empirical and theoretical effort, to increase our understanding of the impact of environmental change on sexually reproducing populations. Can sexual selection promote adaptation to novel environments? Sexual selection for good genes should accelerate adaptation by granting higher reproductive success to individuals of high genetic quality. However, sexual conflict is a frequent outcome of sexual reproduction and may often be detrimental to population fitness. Experimental evolution has shown that the role of sexual selection in adaptation is variable, because of a complex balance between the detrimental and beneficial effects described above. The present thesis is investigating the role of sexual selection in adaptation by focusing on the sex-specific strength of selection and the intensity of intralocus sexual conflict (IaSC) in ancestral and novel environments. The sex-specific strength of selection is a valuable proxy for the benefits of sexual reproduction, since a male-bias in selection caused by sexual selection should allow efficient purging of deleterious alleles with little impact on female fecundity and cost to population fitness. This thesis investigates both sex-specific selection and IaSC across benign and novel environments in two species of seed beetles, *Callosobruchus maculatus* and *Acanthoscelides obtectus*, and includes a theoretical model of the effect of environmental change on of sexual selection. The empirical part of my results indicates that, generally, selection at the adult stage is male biased but that this male bias may be reduced under stress, pointing towards reduced benefits of sexual selection under rapid environmental change. Additional simulations suggest that the frequency dependent nature of sexual selection alone could explain this trend. No empirical support was found for the reduction of IaSC under stress. It is becoming crucial today to understand the impact of environmental change on natural populations. This thesis brings new material adding to our understanding of the role of sexual selection within that particular issue. The outcome of sexual selection is dependent on a variety of mechanisms, such as good genes processes and sexual conflict, which are very likely to be dependent on ecological factors and specificity of the system studied. For that reason, carefully controlled experiments on laboratory systems and mathematical modelling are necessary steps that should ultimately lead to the study of similar questions in natural systems.

Keywords: Sexual selection, Environmental change, Sexual conflict, Environmental stress, Adaptation, Adaptive landscape

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The world, unfortunately, rarely matches our hopes and consistently refuses to behave in a reasonable manner.

Stephen J. Gould

List of Papers

This thesis is based on the following papers, which are referred to in the text by their Roman numerals.

- I **Martinossi-Allibert, I.**, Arnqvist, G., Berger, D. (2017) Sex-Specific Selection under Environmental Stress in Seed Beetles. *Journal of Evolutionary Biology*, 30(1):161–173
- II Berger, D., **Martinossi-Allibert, I.**, Grieshop, K., Lind, M. I., Maklakov, A. A., & Arnqvist, G. (2016). Intralocus sexual conflict and the tragedy of the commons in seed beetles. *The American Naturalist*, 188(4), E98-E112.
- III **Martinossi-Allibert, I.** and Savković, U., Đorđević, M., Arnqvist, G., Stojković, B., Berger, D. The Consequences of Sexual Selection in Well-Adapted and Maladapted Populations of Bean Beetles. *Submitted manuscript*
- IV **Martinossi-Allibert, I.** and Rueffler, C., Arnqvist, G., Berger, D., The efficiency of purifying sexual selection under environmental change. *Manuscript*.

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The following papers were published during the course of the doctoral studies but are not included in the present dissertation:

Grieshop, K., Stångberg, J., **Martinossi-Allibert, I.**, Arnqvist, G., & Berger, D. (2016). Strong sexual selection in males against a mutation load that reduces offspring production in seed beetles. *Journal of Evolutionary Biology*, 29(6), 1201-1210.

Martinossi-Allibert, I., Clavel, J., Ducatez, S., Le Viol, I., & Teplitsky, C. (2017) Does habitat specialization shape the evolutionary potential of wild bird populations? *Journal of Avian Biology*, 48(8), 1158-1165.

Berger D, Stångberg J, Grieshop K, **Martinossi-Allibert I**, Arnqvist G. 2017. Temperature effects on life-history trade-offs, germline maintenance, and mutation rate under simulated climate warming. *Proceeding of the Royal Society of London, Series-B*. In Press.

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Introduction

Natural Selection and Sexual Selection

Natural selection is a major driver of evolutionary change. Because individuals in a population vary in the number of offspring they produce throughout their lifetime (Darwin 1871), and because this variation has a heritable component, the allele frequencies in the population changes generation after generation (Fisher 1930). Variation in fitness among individuals within a population is central to natural selection, and the genetic component of this variation represents potential for adaptive evolution.

In sexually reproducing populations, variation in fitness among individuals can also originate from their ability to secure a mating partner of the opposite sex and achieve successful fertilization (Darwin 1871). This is called sexual selection, and it can take several forms; two categories are generally defined, pre-copulatory and post-copulatory sexual selection (Andersson 1994). Pre-copulatory sexual selection includes mate choice and competition between individuals of the same sex for mating opportunities, which sometimes results in the evolution of elaborate morphological displays or complex courtship behaviors. Post-copulatory sexual selection encompasses sperm competition over fertilization of female gametes and cryptic female choice, female preference for male gametes expressed after mating (Thornhill 1983; Eberhard 1996).

Sexual Selection and Adaptation

Because processes of sexual selection do not originate from abiotic environmental factors, but from interactions among individuals within the same population, it is not always clear that sexual selection will increase adaptation to local environmental conditions (Lande 1980). According to the “good genes” hypothesis (Zahavi 1975; Hamilton and Zuk 1982), female preference is targeting a male trait that is a honest signal of genetic quality, and will therefore provide indirect fitness benefits to all offspring. Additionally, partners of high genetic quality may provide direct benefits such as increased fertility and parental care (Hoelzer 1989; Hamilton 1990; Møller and Jennions 2001).

Regardless of the underlying mechanism, theory predicts that competition among males is likely to drive the evolution of costly morphological or behavioral signals (Kodric-Brown and Brown 1984). For instance, female preference for a certain morphological display may favor males harboring the largest, most conspicuous display (famous examples are the peacock's tail and deer antlers); an enlarged sexually selected trait will help its bearer to secure mating partners and thereby increase its fitness, but is also predicted to be costly (Zahavi 1975, Andersson 1994) and may therefore also reduce chances of survival in the face of predation or food deprivation (Hunt et al. 2004). This form of sexual selection is therefore often thought of as acting "against" natural selection. However, if such traits are honest signals of genetic quality, then sexual selection may promote adaptation. Zahavi (1975) suggested that the cost to survival often associated with sexual signals was the very reason why such traits were useful signals: a costly signal can only be expressed by an individual of high genetic quality and cannot be faked, it is therefore automatically a honest signal. A crucial question regarding sexual selection is then whether the evolutionary changes resulting from it are generally adaptive or not. By definition, sexual selection is selecting for individuals with higher fertilization success. But are such individuals also well-adapted to their environment?

The Genic Capture Hypothesis

Individuals that can collect more energy from their environment and allocate it more efficiently are generally better at escaping predators and resisting stress; it seems logical that they would also be better at developing costly displays or producing competitive gametes. An individual's capacity to acquire and allocate resources (sometimes in the sexual selection literature referred to as the individual's "condition") is likely to be influenced by many loci (Rowe and Houle 1996), which implies that the ability to express costly sexually selected traits is also dependent on a large part of the genome. This means that whatever trait is the target of sexual selection, it should have the potential to reverberate this selection pressure over most of the genome. Following this argument, the genic capture hypothesis states that sexual selection should often benefit adaptation, because it favors individuals of overall good genetic quality (Zahavi 1975; Rowe and Houle 1996; Tomkins et al. 2004). Whether sexual selection is acting on males or females, it can benefit both sexes if it is targeting traits which phenotypic optima are similar across the sexes. If that is true, sexual selection should, in most cases, accelerate rates to adaptation to novel environments.

Sex-specific Intensity of Selection

Despite the tremendous variety of mating systems observed in nature, it has been suggested that sexual selection should generally act stronger on males than on females. This view is supported by a recent meta-analysis gathering data from natural populations (Janicke et al. 2016). A male-bias in the strength of selection could result in faster adaptation and lower extinction risks for sexually reproducing populations (Manning 1984; Agrawal 2001; Siller 2001). This population-level benefit arises because stronger selection on males could accelerate adaptation while females, who limit population growth through their fecundity, would remain relatively unaffected by the cost of adaptation. This would be efficient only if sexual selection in males weeds out deleterious mutations that are affecting both sexes, i.e. sexual selection is foremost a “good genes” process. Measuring the relative intensity of selection in males and females is therefore of interest to assess the potential for sexual selection to promote adaptation (Whitlock and Agrawal 2009).

Sexual Conflict

In gonochoric species, males and females produce consistently different types of gametes. As a result, their reproductive strategies may differ and they may experience different, sometimes opposite, selection pressures on a variety of traits (Fisher 1958; Lande 1980; Andersson 1994)(Fisher 1958; Lande 1980; Andersson 1994)(Fisher 1958; Lande 1980; Andersson 1994). Such divergence in evolutionary interests can spur a conflict between the sexes (Parker 1979; Arnqvist and Rowe 2005).

Intra-locus Sexual Conflict (IaSC) occurs because males and females, while having different evolutionary interests and reproductive strategies, share a substantial part of their genome; when selection favors different alleles in the sexes at a single locus this will result in IaSC (Rice and Chippindale 2001; Bonduriansky and Chenoweth 2009). As a result, genetic variation at such loci may be maintained by balancing selection across the sexes. This type of conflict has great potential to impact the outcome of sexual selection, since if IaSC is intense, sexual selection on one sex is unlikely to benefit the other. Conflict can be resolved if the genetic correlation between the sexes is reduced for the trait under sexually antagonistic selection; this can happen through the evolution of sex-limited gene expression and results in sexual dimorphism (Lande 1980). Even if IaSC can be resolved, every new mutation arising in the genome is potentially a new site for IaSC to occur, which means that IaSC is expected to be common in natural populations (Connallon and Clark 2012).

Another form of sexual conflict, termed interlocus sexual conflict (IeSC, Parker and Partridge 1998; Arnqvist and Rowe 2005), can occur when selective forces act on different traits in the sexes, leading to a coevolutionary arms race between males and females. The conflict arises because of divergent interests of the sexes during a reproductive event, where each partner benefits from manipulating the other one in order to maximize their own reproductive success (Parker 1979; Rowe et al. 1994; Arnqvist and Rowe 2005). This type of conflict is likely to result in a chain reaction of counter-adaptations involving a variety of traits across the sexes. IeSC also has the potential to drive evolutionary changes that reduce average fitness of the population. A simple example is male harm to females which is well documented in a variety of species (Crudgington and Siva-Jothy 2000; Blanckenhorn et al. 2002; Rundle et al. 2006; Chenoweth et al. 2015; Berger et al. 2016); persistent males achieve higher reproductive success, but a high proportion of persistent males in a population causes harm to females and reduces their reproductive success.

Investigating the Role of Sexual Selection in Adaptation to New Environments

A powerful way to experimentally test the role of sexual selection in adaptation is provided by evolution in the laboratory. Many experiments have compared the rate of adaptation (fitness recovery) of populations exposed to various stressors (high temperature, parasites, food deprivation) with or without sexual selection (e.g. Rundle et al. 2006; Fricke and Arnqvist 2007; Holland 2008; Maklakov et al. 2010; Hollis and Houle 2011). Selection against deleterious mutations in males and females has also been studied widely (Radwan 2004; Jarzebowska and Radwan 2010; Hollis and Houle 2011; Mcguigan et al. 2011; Plesnar et al. 2011; Arbuthnott and Rundle 2012; Clark et al. 2012; Chenoweth et al. 2015; Lumley et al. 2015; Grieshop et al. 2016). However, such experiments have yielded quite variable results, and the question of whether or not sexual selection promotes adaptation remains open. This can be put in perspective with the various mechanisms discussed above that are linked with sexual selection: according to the genic capture hypothesis, sexual selection should enhance adaptation, but sexual conflict may just do the opposite. Depending on the balance of these various processes, sexual selection may or may not increase rates of adaptation.

One possibility is that sexual selection becomes inefficient under stressful conditions, for example if mate choice signals are affected (Kokko and Heubel 2007; Higginson and Reader 2009). Alternatively, IaSC may be reduced in novel environments if male and female phenotypic optima are similarly displaced in the new environmental conditions, a theoretical prediction

(Connallon and Clark 2014) that has found some empirical support (Long et al. 2012; Berger et al. 2014). Investigating the effects of environmental change on sexual selection and sexual conflict should bring some light on this complex issue.

Can sexual selection promote adaptation? In the present thesis, I have investigated several aspect of that question, through laboratory experiments and theoretical modelling. I have been particularly interested in the efficiency of sexual selection under various levels and types of stress (**papers I, III and IV**) and the prevalence and consequences of sexual conflict in the process of adaptation (**papers II and III**).

Methods

Study Species

I have conducted laboratory experiments with two different species of seed beetle, *Callosobruchus maculatus* and *Acanthoscelides obtectus*. They both represent useful laboratory systems, with relatively short life-cycles of approximately three weeks and are easy to maintain.

C. maculatus is a facultatively aphagous bruchid beetle that can infest leguminous crops; its preferred host plant is *Vigna unguiculata* (the black-eyed bean) on which it develops from egg to reproductively mature adult. Temperatures of 25-30°C represent a benign environment where juvenile survival is higher than 90% (Fox et al. 2003). I have used a population of *C. maculatus* originating from Lomé, Togo, in papers I and II, and an additional population from Ofuya (Nigeria) in paper II. From the Lomé population, 41 isofemale lines were created and 32 from the Ofuya population. All those lines were used in paper II, and 14 randomly selected lines from the Lomé population were used in paper I. All isofemale lines were kept in climate chambers at 29°C, 50% humidity and 12L:12D light cycle, since they were founded in 2010.

In paper III, I use replicate populations of *A. obtectus* that had undergone experimental evolution for more than 80 generations (ca. five years). These populations had been evolving on two alternative host plants which allowed me to test for a general effect of maladaptation on the efficacy of sexual selection by exposing each type of population to both its ancestral host and to the host on which the other population type had evolved. *A. obtectus* uses the common bean *Phaseoli vulgaris* as a preferred host, and similarly to *C. maculatus* larvae, develop inside the beans. The particular population I used was founded from individuals sampled from grain storages in the region of Belgrade, Serbia, in 1983 and have been maintained in laboratory conditions ever since (temperature 30°C and 30 - 40% humidity, Savković et al. 2016).



Figure 1. Photographs of a male and a female *C. maculatus* during copulation (left) and a female *C. maculatus* examining a *V. unguiculata* bean (right).

Inducing Stress in the Laboratory

Stress was induced through two different environmental parameters modified during larval development: temperature and host plant. Both stressors were used on *C. maculatus* populations in paper I and host stress was used on *A. obtectus* populations in paper III. Temperature was regulated in climate chambers that also maintained a constant level of humidity and light cycle. As ectotherms, seed beetles are particularly sensitive to temperature changes that affect their development drastically. Similarly, the type of host plant is crucial because most adult resources are acquired during larval development.

Estimating Fitness

Estimating fitness is challenging. The fitness of an individual is highly dependent on the biotic and abiotic environment, and therefore any measure of fitness is to be considered in context. Seed beetles occur naturally in grain storages and have most likely done so since the early days of agriculture; therefore a jar filled with dried beans in a climate chamber is really close to their natural environment. When it came to measuring reproductive success, competitive assays were set up, where a focal individual would compete against a sterile individual of the same sex, for mating with two individuals of the opposite sex. Competitors were sterilized by irradiation from a cesium-137 source, which has been shown to produce life-long sterility while still leaving irradiated individuals able to compete (Eady 1991; Maklakov and Arnqvist 2009): sterilized males are able to mate with females and fertilize eggs (that leads to the death of the zygote) and sterilized females can also mate and lay

sterile eggs. This design allowed sexual selection to act, with equal opportunity in the sexes.

Measuring Selection

Selection on a trait can be estimated by its covariance with relative fitness (Price 1972; Lande and Arnold 1983). The upper limit of the strength of selection on any trait, called the opportunity for selection is then the variance in relative fitness $I = \sigma_w^2 / \bar{w}^2$ (Crow 1958). I 's additive genetic component, I_A , predicts the response to selection of fitness (Fisher 1958; Houle 1992). Sex-specific estimates of I can be used to compare the strength of selection across the sexes (Shuster and Wade 2003; Krakauer and Webster 2011).

Isofemale Lines

In my experiments, it was crucial to disentangle sources of variation in fitness originating from environment and from genetic differences between individuals. To achieve this, I used so-called isofemale lines, each one created by allowing a male and female to mate and produce offspring that were used to propagate the line in future generations. Maintained at large population sizes (200-300 individuals), variance among lines equals approximately that among full-sib families. Creating isofemale lines from a natural populations allows to preserve a snapshot of the genetic variation present in the natural population. Because of the relatively low genetic variability within lines, isofemale lines cannot evolve to rapidly adapt to laboratory conditions, but the variation between lines represents an estimate of the genetic variation present in the population originally sampled. Variation among isofemale lines can then be used to estimate narrow-sense heritability and additive genetic variance (Hoffmann and Parsons 1988).

Results and Discussion

Paper I: Sex-Specific Selection under Environmental Stress in Seed Beetles.

In this study, I investigated the strength of selection in males and females across five different environments to determine whether sexual selection in males could act efficiently under stress imposed by environmental change (See *Sex-specific intensity of sexual selection* in the introduction). Selection was measured as the opportunity for selection I (See *measuring selection* in the methods section). Starting from a simple Gaussian fitness landscape model, I hypothesized that males should be more sensitive to environmental stress than females, and consequently, environmental maladaptation should have larger fitness consequences in males, which might increase sexual selection against maladapted alleles in changing environments.

Males were indeed generally more sensitive to stress, showing a more pronounced decrease in mean fitness than females when exposed to novel environments. I increased with both stressors as predicted, but the underlying mechanisms were different for host plant and temperature stress: both I_{LRS} (selection at the adult stage) and I_{JS} (selection at the larval stage) increased with temperature stress, while the increase in I for host stress was driven by I_{JS} (Figure 2). I_{LRS} was stronger in males in all environments, driving a general male-bias in I (Figure 2) that suggests that sexual selection may act to remove deleterious mutations in both benign and stressful conditions. I_G (the additive genetic component of I , also the response of fitness to selection) was hard to estimate, but at face value it increased with stress, and exhibited no sex differences. This trend then suggests that there should be no greater response to selection through males induced by environmental stress. Genotype by environment interactions (GEIs) dominated genetic variance in juvenile survival (change in genotype ranking rather than inflation of variance), indicating that balancing selection across environments may have maintained genetic variance expressed in the juvenile stage. Those GEIs were sex-specific, which means that although one may have expected males and females to have similar strategies during larval development, their sexual dimorphism at the adult stage may already be reflected during early development.

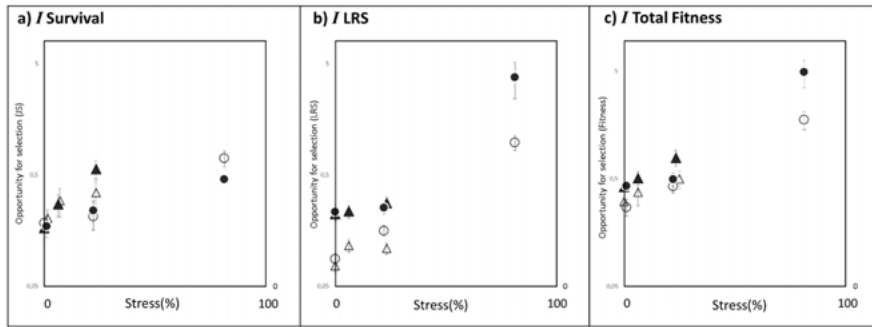


Figure 2. Sex-specific opportunities for selection in juvenile survival, adult LRS and total fitness as a function of stress level (expressed as a percentage of reduction in mean fitness as compared to ancestral conditions). The opportunity for selection is given by closed symbols in males and open symbols in females, under temperature stress (circles) and host stress (triangles) respectively. Error bars represent standard errors.

Paper II: Intralocus Sexual Conflict and the Tragedy of the Commons in Seed Beetles.

This study measured a large number of morphological and life history traits in males and females as well as individual reproductive success and population growth for the 41 and 32 isofemale lines from the two populations of *C. maculatus*. This empirical effort allowed the calculation of sex-specific selection gradients and inter-sex genetic correlations for a variety of traits and for reproductive success.

This study illustrates how IaSC and IeSC can reduce benefits of sexual selection. For example, female and male genotypes with the highest reproductive success were on opposite ends of a life-history “pace-of-life” continuum describing a live fast-die young strategy at one end of the continuum, and a live slow-die old strategy at the other. Females had higher LRS with slow metabolism and males with high metabolism (Figure 3). Because genes that encode male and female metabolic rate and activity are expressed in both sexes, there is IaSC over these traits. This means that sexual selection, by favoring males with high metabolic rate, could maintain, or even fix, alleles that lower female reproductive success.

High activity and metabolic rate of males can lower female reproductive success, which in turn may cause a reduction in the health and growth rate of the population as a whole. Indeed, paper II presents evidence for this effect (Figure X). Reduced population health may result from synergistic action of

the two types of sexual conflict: both through the maintenance of female detrimental alleles in the population (IaSC), and because direct male harm to females through harassment (IeSC) may be particularly pronounced in such populations.

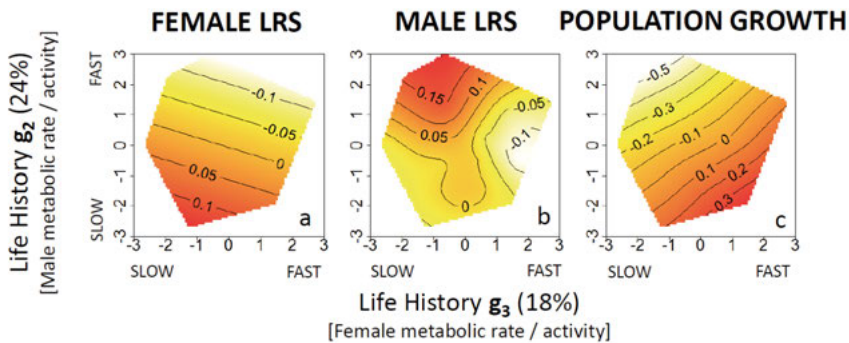


Figure 3. Sex-specific selection surfaces for adult life history in the Lomé population based on breeding values (a, b) showing evidence for sexually antagonistic selection and corresponding effects on line productivity (c). Red indicates high and yellow indicates low adult lifetime reproductive success (LRS) or line productivity. Male (female) fitness optima coincide with trait combinations associated with low (high) line productivities. Line productivity and LRS were mean standardized and log transformed, and principal components were mean centered and unit-variance standardized before plotting.

Paper III: The Consequences of Sexual Selection in Well-Adapted and Maladapted Populations of Bean Beetles.

In this study, I tested the prediction that IaSC should be reduced under stressful conditions, increasing the potential for sexual selection to aid adaptation. I used replicated experimental populations of the bean beetle *A. obtectus* that had been adapting to two different hosts for 80 generations. Populations from the two alternative host plant regimes were cross-reared on the two hosts before assessing sex-specific fitness in 15 genetic lines within each of the replicated populations. Males had higher genetic and phenotypic variance in LRS, consistent with findings of paper I.

IaSC was not intense (genetic correlations for fitness were generally positive between the sexes) and its magnitude did not change under stress (Figure 4), suggesting that sexual selection on males should also benefit females to some extent. Finally, I found that the effect of maladaptation on *I* was sex-specific:

The male-bias in the strength of selection was reduced in maladapted populations, and consistently so for the two replicated evolution treatments (Figure 5). This implies that sexual selection on males was reduced under novel conditions, which is supported by a previous study on the same populations that indicate that female mate choice can be reduced under stress. This shows that, even if sexual selection has potential benefits, sexual selection processes can be disrupted under stress and rendered less efficient when compared to fecundity selection. This can be linked to the model developed in paper IV that shows that under a wide range of conditions the efficiency of frequency dependent sexual selection will be reduced under environmental stress.

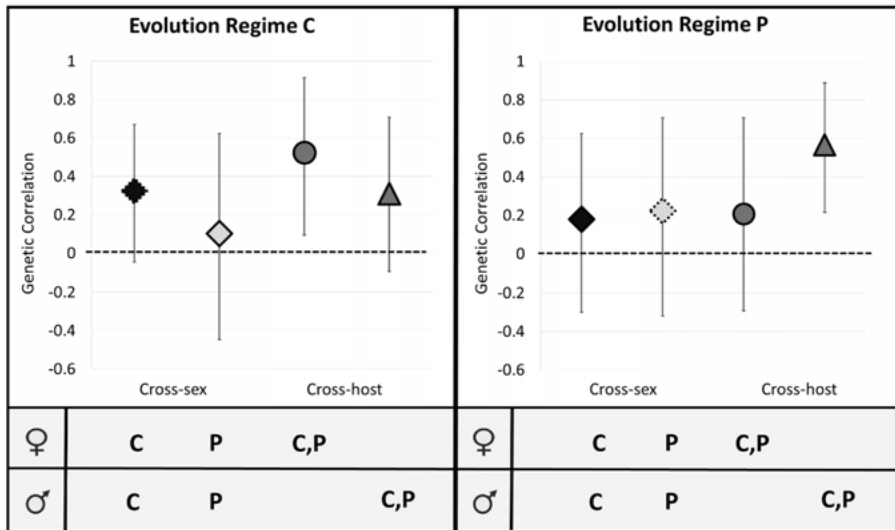


Figure 4. r_{MFS} and cross-environment genetic correlations for LRS. r_{MFS} are given for host C (filled diamonds) and host P (open diamonds). Diamonds depicting r_{MFS} of adapted populations (i.e. when the host treatment matches the evolution regime) are designated by a dashed outline. Cross-environment (i.e. across hosts) genetic correlations are depicted for males (triangles) and females (circles). Error bars represent a 95% credible intervals based on the Bayesian posterior distributions.

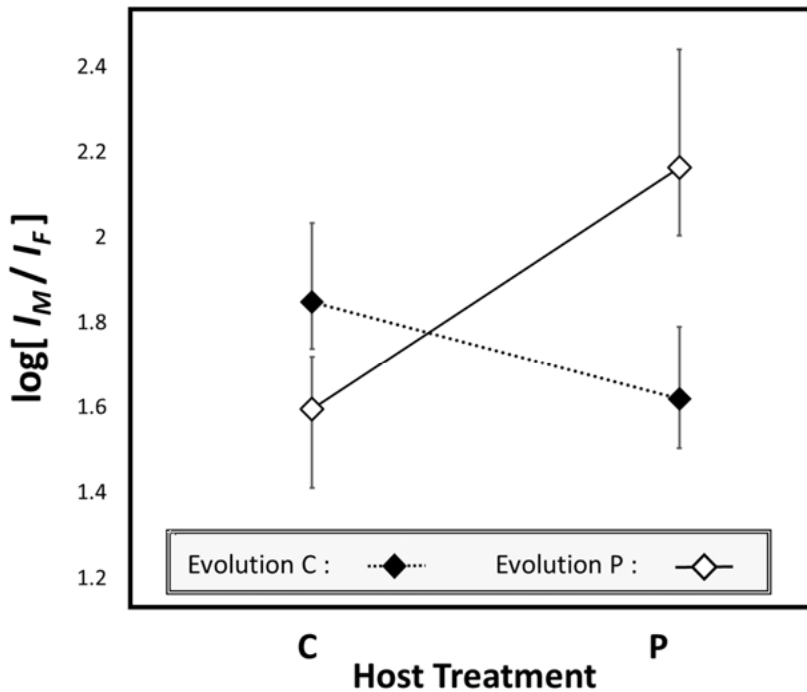


Figure 5. Comparison of the opportunity for selection in the sexes. The relative sex-difference in the opportunity for selection is quantified by a log-ratio of male over female variance in LRS ($\log[I_M / I_F]$). A log-ratio of zero indicates no difference in the opportunity for selection. Values above zero indicate greater opportunity for selection in males. The results imply that the male-bias in the strength of selection was reduced in maladapted populations.

Paper IV: The Efficiency of Purifying Sexual Selection under Environmental Stress.

In this study, I used mathematical modelling to make predictions of the effect of environmental change on sexual selection. In a population where males experience sexual selection by competing among each other, and females experience selection on fecundity, I compared the strength for selection in both sexes for various levels of environmental stress. A change in environment was allowed to displace the phenotypic optimum of a selection surface away from the mean phenotypic value of the population. This impacted the condition of individuals resulting in an increasing frequency of low condition individuals

in the population, which affected both male and female reproductive success. Because males compete with each other in groups (leks) of various size, they experience frequency-dependent selection (depending on the condition and frequency of other individuals in the population), but females do not. As a consequence, environmental stress affected selection in males and females differently, and I found that, for a biologically relevant set of parameter values, the relative strength of frequency dependent sexual selection was reduced compared to fecundity selection under stress (Figure 6). This result is concurring with empirical evidence from paper III, which shows that the opportunity for selection in males did not increase as much as in females in maladapted conditions. This model presents an extreme scenario with no sexual selection on females and no fecundity selection on males, but the results should remain qualitatively similar for a variety of mating systems as long as there is a sex-bias in the strength of (frequency dependent) sexual selection. While previous models studying the environmental sensitivity of sexual selection have been focusing on the resilience of mate choice or intra-sexual competition to environmental stress (Greenfield and Rodriguez 2004; Kokko and Heubel 2007; Higginson and Reader 2009), the present study shows that even if competition is not affected, the efficiency of sexual selection can nevertheless be reduced in a novel environment.

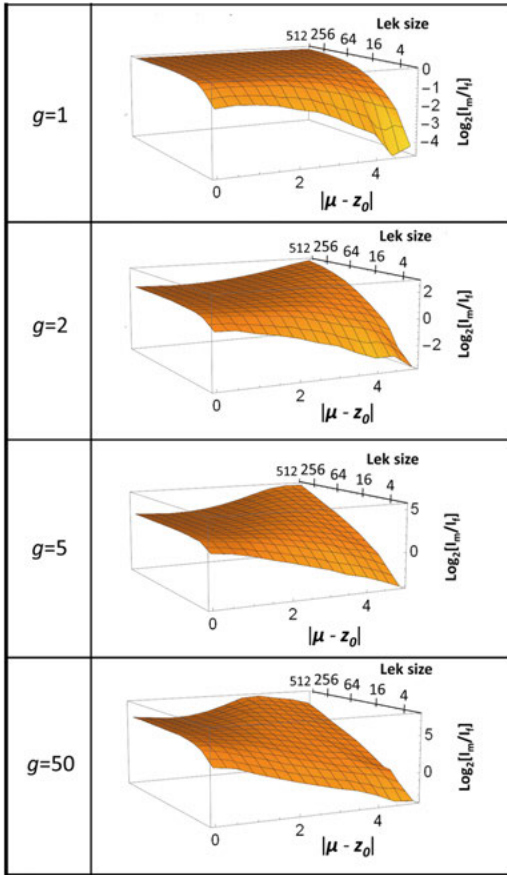


Figure 6. The effect of environmental change on the relative strength of sexual selection

Log₂-ratio of male over female strength of selection as a function of lek size and environmental change, presented for four different competition intensities g , and three different strengths of juvenile survival selection j .

Environmental change is plotted as the deviation of the population mean trait value from the optimum ($|\mu - z_0|$). Note that lek size is plotted on a log₂-scale.

Conclusion

This thesis is aimed at understanding the sensitivity of sexual selection to environmental change, in order to gain insight into the role that sexual selection plays in adaptation. This question was investigated by combining laboratory experiments on seed beetles (Papers I, II and III) and a theoretical approach (paper IV). I focused on sexual conflict, which is a consequence of sexual reproduction that may impede adaptation, and sex-bias in the strength of selection caused by sexual selection, which has the potential to speed up adaptive rates at low demographic cost.

The empirical data I gathered clearly shows stronger selection in males at the adult stage (Paper I and III), which agrees with compiled data on natural systems. If this male-bias holds also in novel environments, it may provide benefits to sexually reproducing populations, by efficient purging of deleterious alleles through selection in males. While paper I implies that selection acts strongly against males exposed to stressful environmental conditions, Paper III shows empirically that this male-bias in selection can be reduced if the whole population is exposed to generally stressful conditions, such as expected under rapid environmental change. The result of paper III depended only on the level of adaptation of the populations tested, and not on the specific nature of the environments (host plants), which suggests that the result could be general. If so, reductions in the benefits of sexual selection may occur in rapidly changing environments. It will be important to further investigate the effect of environment on sex-biases in selection by including more study systems and natural populations. Another important step in studying patterns of sex-specific selection is to understand of the ultimate causes for such patterns, as well as their sensitivity to ecological factors.

There are several mechanisms that can be invoked to explain a reduced efficiency of sexual selection under stress, such as the fact that sexual signals evolved in one environment could become misleading in a new one, or that female mate choice is costly and reduced under stress, in turn weakening sexual selection. Another possibility is developed in the theoretical model of Paper IV, which suggests that the frequency-dependent nature of sexual selection may also be responsible for a relative reduction in sexual selection under stressful conditions.

I observed a negative impact of sexual conflict on female fitness and population growth in paper II, and discovered that life-history traits played a prominent role in sexual conflict in these populations. Theoretical models predict that IaSC can be reduced in novel environments. However, looking for evidence of reduced intralocus sexual conflict (IaSC) in maladapted populations in paper III, I was not able to confirm that prediction. More refined experimental work could be conducted to answer this question. This work would certainly benefit from the use of a system in which specific traits subjected to IaSC are known. It would then be possible to directly measure sex-specific selection gradients across environments and estimate the displacement of phenotypic optima, to test theoretical predictions more directly.

Overall, this work has generated new data exploring the sensitivity of sexual selection to novel environments, and has also produced novel theoretical predictions that may inspire future empirical work.

Sammanfattning på svenska

Målet med den här avhandlingen är att utforska, både empiriskt och teoretiskt, för- och nackdelar med sexuell selektion, samt hur dessa för- och nackdelar påverkas av förändringar i miljön. Genom att studera detta kan vi öka vår förståelse för hur populationer som förökar sig sexuellt påverkas av t.ex. klimatförändringar. Kan sexuell selektion underlätta en populations anpassning till en ny miljö? Sexuell selektion för ”good genes” (Zahavi 1975; Rowe & Houle 1996; Tomkins et al. 2004) förväntas underlätta anpassningsförmågan genom att individer av god genetisk kvalitet gynnas och når högre reproduktiv framgång. Sexuella konflikter, som är en vanlig konsekvens av sexuell reproduktion, kan däremot påverka en population negativt (Arnqvist & Rowe 2005). Experimentell evolution har visat att effekten av sexuell selektion på populationens anpassningsförmåga är variabel just på grund av den komplexa interaktionen mellan för- och nackdelar som beskrivs ovan.

I den här avhandlingen undersöks betydelsen av sexuell selektion för anpassningsförmåga genom att fokusera på frågan om hur starkt selektionen verkar på honor och hanar, samt på hur stark intensiteten är av genetisk könskonflikt (hädanefter förkortat som ”IaSC” efter engelska termen ”Intralocus sexual conflict”) i olika typer av skonsamma och mer påfrestande miljöer. Mätningar av hur stark den köns specifika selektionen är kan fungera som ett verktyg för att utvärdera fördelarna av sexuell reproduktion. Detta eftersom en starkare sexuell selektion på hanar tillåter en mer effektiv utrensning av skadliga alleler med en marginell kostnad för honlig fekunditet och populationens bärkraft (Agrawal 2001, Siller 2001, Whitlock and Agrawal 2009). Majoriteten av tidigare studier visar en starkare selektion hos hannar vilket indikerar att sexuell selektion kan ha vissa fördelar, frågan är om dessa fördelar bibehålls i en ny miljö? Genom att studera denna fråga kan vi öka vår kunskap om hur sexuellt reproducerande populationer kommer påverkas om de utsätts för snabba miljöförändringar. IaSC som uppstår när selektionstrycket hos hannar är motsatt det hos honor har potential att minska honlig fitness genom att bibehålla alleler som är fördelaktiga för hannar men skadliga när de uttrycks i honor. Om IaSC spelar en betydande roll kan en stark hanlig sexuell selektion dra ner populationens bärkraft genom att många alleler som är skadliga för honor inte selekteras bort. Enligt både teoretiska (Connallon and Clark 2014) och empiriska bevis (Long et al. 2012, Berger et al. 2014, Plesnar-Bielak et al. 2014) föreslås att IaSC får en mindre betydelse i nya miljöer om hannar och honors

optimala fenotyp är lika illa anpassade till den nya miljön. Om detta är ett generellt fenomen kommer fördelarna av sexuell selektion öka om en population utsätts för nya påfrestande miljöer.

Den här avhandlingen undersöker könsspecifik selektion och IaSC i både gamla skonsamma, samt nya påfrestande, miljöer. Som modelsystem används två arter av fröbaggar, *Callosobruchus maculatus* och *Acanthoscelides obtectus*. Avhandlingen innehåller även en teoretisk modell som undersöker effekten av miljöförändring på utkomsten av sexuell selektion. Resultaten i avhandlingen visar att generellt är selektionen hos aduler starkare hos hannar men att detta ojämnlige selektionstryck mellan könen minskar under stress som uppstår i en ny påfrestande miljö. Detta indikerar en minskad fördel av sexuell selektion under påfrestande förhållanden. Den teoretiska modellen visar att det faktum att sexuell selektion innehåller en starkt frekvensberoende komponent kan förklara denna effekt. Inget empiriskt stöd kunde dock hittas för minskad IaSC under påfrestande förhållanden.

Att förstå hur naturliga populationer påverkas av miljöförändringar är något som idag är av yttersta vikt. Den här avhandlingen försöker förstå vilken roll sexuell selektion har för populationers förmåga att anpassa sig till nya miljöer och resultaten identifierar mekanismer som gör att fördelarna av sexuell selektion generellt sätt kan minska i nya miljöer. Resultatet av sexuell selektion är beroende av flera olika underliggande mekanismer så som selektion för ”good genes” och sexuell konflikt mellan könen, och båda dessa processer är beroende av artspecifik ekologi. Av den anledningen är det nödvändigt att använda noggrant utformade laboratorieexperiment samt matematiska modeller som ett första steg för att öka förståelsen om dessa processer, något som i slutändan kan leda till ytterligare utveckling och design av forskning tillämpad på liknande frågor i naturliga system.

Résumé en français

À l'attention des amis, membres de ma famille, et pourquoi pas d'autres francophiles s'étant égarés dans la salle de ma soutenance en ce Vendredi 15 Décembre 2017 (que je prédis sombre et glacial), j'ai préparé ce petit texte, qui je l'espère saura vous distraire autant que vous instruire pendant que je baragouine en anglais sur des sujets si spécialisés que même une tour d'ivoire particulièrement pointue ne suffirait pas à les atteindre.

Tout d'abord, merci ! J'apprécie énormément votre présence. Qui que vous soyez, si vous lisez ces lignes, vous avez probablement enduré un long voyage vers le Nord au cœur d'une saison qui se prête plutôt à la migration subtropicale, dans le but de m'apporter votre soutien. J'en suis touché. Pour vous remercier, je vais faire de mon mieux, dans le court texte qui va suivre, pour vous expliquer pourquoi. Pourquoi j'ai vécu quatre ans en Suède. Pourquoi vous êtes ici aujourd'hui. Et pourquoi la sexualité des coléoptères a beaucoup à nous apprendre. En plus, si vous avez l'air de lire ma thèse au lieu de regarder la neige tomber, ça fera plus sérieux !

Par où commencer ? Par quelques questions qui pourraient vous étonner par leur simplicité.

-Pourquoi le sexe (la reproduction sexuée) existe-t-il ?

-Pourquoi y-a-t-il des mâles et des femelles ?

Et bien je vous jure que nous (scientifiques), on n'en sait rien. Enfin... on a des pistes, mais rien de très solide. C'est mon envie de me plonger dans ces questions fondamentales qui m'a poussé à m'installer dans un nouveau pays pour élever des coléoptères par millions (littéralement) et autres activités occultes. Je vais essayer de vous éclairer sur ce que j'ai appris.

Posons les bases. Qu'est-ce que le sexe, pour un biologiste ? La reproduction sexuée est un type de reproduction parmi d'autres (beaucoup de plantes et d'animaux peuvent s'en passer). Voici pour ses caractéristiques : elle nécessite deux individus pour en produire un, ce qui la rend particulièrement inefficace en comparaison par exemple de la reproduction clonale. Elle permet de mélanger les deux génomes parentaux, de manière plus ou moins aléatoire pour donner de nouvelles combinaisons, contrairement à la reproduction clonale qui produit une copie identique du parent. C'est tout ! L'existence de deux sexes séparés, mâle et femelle, n'est pas une conséquence obligatoire de la reproduction sexuée. Une bonne quantité d'organismes se débrouillent avec

une reproduction sexuée (nécessitant deux individus) mais sans sexes séparés (tous les individus sont d'un seul et même type) ou alors avec chaque individu pouvant assumer les deux rôles alternativement (hermaphrodites). D'ailleurs qu'est-ce qui différencie un mâle d'une femelle ? La taille des gamètes tout simplement. Dans une espèce avec sexes séparés, le type qui produit des gamètes plus gros (ovocytes), en général immobiles et moins nombreux est femelle et celui qui produit des gamètes plus petits (spermatozoïdes), en général mobiles et nombreux est mâle. Il n'y a pas d'autre critère qui permette de distinguer mâles et femelles d'une manière parfaitement générale. Les mâles ne sont pas en général plus grands ou plus petits, ça dépend des espèces. Les femelles ne sont pas en général moins agressives. La seule différence, c'est les gamètes, et c'est tout !

On a vu que le sexe est un moyen particulièrement inefficace de se reproduire puisqu'il nécessite deux fois plus de parents que la reproduction clonale et permet donc un taux de croissance de la population deux fois moindre. On se demande alors pourquoi le sexe existe ! Ce problème est souvent appelé « le double coût du sexe » (*two-fold cost of sex*). Mais il faut se rendre à l'évidence, le sexe sert à quelque chose puisqu'il est bien là, et qu'un certain nombre d'espèces l'utilisent exclusivement (pour citer quelques exemples familiers, les humains, les pommiers, les ours blancs, les libellules et le maïs). C'est donc que le sexe doit procurer certains avantages... mais lesquels ? Et surtout, sont-ils suffisants pour compenser ce « double coût » en productivité ? Il y a quelques candidats. D'abord le mélange des gènes parentaux qui produit des individus complètement originaux à chaque génération. De cette manière, de nouveaux génomes apparaissent très rapidement, ce qui pourrait permettre de s'adapter plus vite à de nouveaux environnements, ou de mieux résister aux parasites (virus ou autres qui eux aussi évoluent, et très vite grâce à un temps de génération très court). Ensuite, dans un bon nombre d'espèces, les mâles entrent en compétition acharnée pour le droit de copuler. Les paons déploient l'éventail bariolé de leur queue pour séduire les femelles, les girafes se lancent dans des combats à cous (sic) redoublés, les cerfs entrechoquent leurs bois... les exemples abondent. Prenons-en un plus familier : vous marchez dans la forêt. Un chant d'oiseau se fait entendre. C'est à coup sûr un mâle qui défend son territoire et appelle les femelles à venir couvrir chez lui et profiter des ressources à disposition. Le résultat de ces parades et duels est que seuls les mâles les plus sains pourront avoir une descendance. Le sexe offre donc un moyen supplémentaire de sélectionner des gènes adaptés à l'environnement pour la génération suivante. À la « survie du plus fort », formule populaire qui désigne la sélection naturelle, vient s'ajouter la « copulation du plus fort ». Une des raisons majeures pour l'existence de la reproduction sexuée serait donc que le sexe permet de s'adapter plus vite, en ajoutant à la sélection naturelle la sélection sexuelle (le choix des partenaires pour la reproduction). Dans les articles I et III de ma thèse j'ai mesuré la sélection chez mâles et

femelles de deux espèces de coléoptères pour tenter de détecter ce bénéfice de la reproduction sexuée. J'ai aussi mesuré ces paramètres dans des environnements nouveaux (et donc stressants) pour déterminer l'effet que pourrait avoir un bouleversement de l'habitat (par exemple du au changement climatique) sur les espèces se reproduisant de manière sexuée. Appuyé par l'article IV, une simulation informatique du même problème, j'ai découvert que ce bénéfice de la reproduction sexuée pourrait bien être réduit dans les environnements nouveaux. Inquiétant, car cela signifie que le changement climatique pourrait provoquer encore plus de dommages que prévu.

Mais voilà, le sexe apporte aussi son lot de complications. En tout cas lorsqu'il s'agit d'une reproduction avec deux sexes bien différenciés, mâle et femelle. Puisqu'ils produisent des gamètes différents, mâles et femelles ont des intérêts différents lors de la reproduction. Dans de nombreux cas, mâles et femelles ont aussi des stratégies de vie différentes. Revenons à l'exemple de l'oiseau qui chantait dans la forêt tout à l'heure. Dans cette espèce (disons une mésange), le mâle doit prendre le contrôle d'un territoire, une partie de la forêt qu'il aura à défendre contre d'autres mâles. La taille de son territoire dépendra donc de son agressivité à le défendre. Il doit aussi arborer un plumage coloré pour attirer une partenaire potentielle et chanter à longueur de jour pour revendiquer son territoire. Plus son territoire sera grand plus il aura de chance d'avoir une partenaire, et plus il aura de ressources pour nourrir ses enfants. Mais la vie d'une femelle est différente. Elle ne chante pas. Elle parcourt la forêt et examine les mâles et leurs territoires et fait un choix de partenaires. Elle doit aussi accumuler des ressources pour pouvoir pondre autant d'œufs que possible. On voit donc que mâles et femelles suivent différentes trajectoires. Les morphologies et comportements qui permettent de remplir ces deux types de tâches de manière optimale sont différents (on observe dans beaucoup d'espèces que mâles et femelles ne se ressemblent pas tout à fait). Or le problème le voici : comme chez les humains, mâles et femelles partagent dans toutes les espèces une grande partie de leur génome. Comment faire deux choses différentes avec un même génome ? Bien sûr il y a les chromosomes sexuels, qui ne sont pas complètement partagés entre les sexes (chez les humains, le Y se trouve uniquement chez les hommes accompagné d'un X, les femmes portent deux copies du X, chez les oiseaux les femelles portent un Z et un W, les mâles deux copies du Z), mais ils représentent une faible fraction du génome. Le reste est partagé. Or il ne peut pas être optimisé à la fois pour la vie d'un mâle et la vie d'une femelle ! Ce qui en résulte est un « conflit sexuel », dû au fait que les frères et sœurs d'une même famille partagent leur gènes et que ces gènes peuvent être soit bon pour un mâle, soit bon pour une femelle, mais pas les deux. Ce conflit a un coût car l'évolution de chaque sexe est limitée par l'évolution de l'autre, qui va dans une direction quelque peu différente. Tentons une analogie : imaginons que l'évolution est une route à parcourir pour atteindre une destination. Partant de Montpellier, un voyageur voulant rallier Rennes et un voyageur se rendant à Strasbourg

font un covoiturage... ils se retrouvent tous deux à Paris, plutôt mécontents ! Mâles et femelles évoluent vers des optimaux différents (Rennes ou Strasbourg) mais partage un génome unique (une même voiture), il leur faut donc se résoudre à un compromis (Paris). J'ai étudié ce conflit sexuel dans les articles II et III de ma thèse, et encore une fois l'impact d'un environnement stressant sur ce conflit. On pense en effet que le stress réduit ce conflit et je vais essayer d'expliquer pourquoi. Mon analogie va me resservir : Si mes covoiturés partent de Clermont-Ferrand, se rendant à Rennes et Strasbourg respectivement, quel enfer de partager une voiture ! Le conflit est intense car les deux voyageurs sont déjà très proches de leurs destinations, et ils ont très peu de route à faire ensemble. C'est le cas d'une population adaptée à son environnement, le conflit sexuel est intense car le chemin commun a déjà été parcouru. Mais si nos voyageurs partent de Cape Town (Afrique du Sud), leurs chemins paraissent bien plus parallèles et ils pourront voyager ensemble pour une bonne partie du trajet sans se disputer sur la direction à prendre. C'est le cas d'une population stressée. Mâles et femelles sont si loin de leur optimum qu'ils évoluent dans la même direction. Quand ils s'approchent de leur destination, bien sûr, le conflit s'intensifie !

J'espère que ce court texte aura éveillé votre curiosité sur ce sujet qui me passionne. Si vous avez suivi jusqu'au bout, malgré mes analogies bancales, vous avez jeté un coup d'œil sur un pan de la connaissance humaine dont peu de gens se doutent et vous ne pourrez plus revenir en arrière. La prochaine fois que vous entendrez un oiseau chanter...ce ne sera plus la même chose ! Si vous voulez en savoir plus, plongez-vous dans la partie anglophone de cette thèse, ou bien posez-moi des questions, je serais ravi d'y répondre.

Vous vous souvenez peut-être d'une autre question que j'ai soulevée au début. Pourquoi existe-t-il deux sexes, les mâles et les femelles ? Voilà une autre interrogation fondamentale, car sans mâles et femelles, pas de sélection sexuelle, pas de conflit non plus. Alors pourquoi ? Eh bien c'est la question qui me taraude maintenant, et si j'ai la chance de poursuivre ma carrière dans les milieux académiques, j'ai bien l'intention de m'y atteler.

Acknowledgements - Remerciements

We live alone and die alone, therefore there will be no acknowledgments.

Nah, just kidding!

As some of you may already know, I am not good at using words to express feelings. This is why the mere principle of writing down (for everyone to read!) inner feelings that one rarely dares to express in a private context completely escapes my understanding. However, I cannot resist a challenge and so I will do my best to complete that task as well, but please be aware that each line of the following text cost me more sweat and tears than, let's say, arguing over sample size with David.

Just a reminder, this is not an authorship list: *order is not important!*

To increase confusion, certain parts need to be in English while other would be meaningless if not in my mother tongue, and those parts will be completely mixed together. Starting now.

David Berger, my main supervisor. So many things to say! We haven't talked much over the years of anything outside science, but have we talked about science! As I write those lines, you are sitting in your office, strategically located just across the corridor from mine, which means that I can see you by just tilting my chair backward and ask you a question without raising my voice. This sums up your supervising style: ultimate availability. And needless to say that quantity (of supervising) did not undermine quality. For any type of question at any time, whether you are in the middle of a complicated analysis or trying to put your daughter to sleep, you will answer the call of your students. That's amazing! Your enthusiasm for science is inspiring and your mind is bubbling restlessly with new ideas. True, sometimes your imagination creates experiments that require sampling effort beyond the reach of normal human students, but as you told me one day "you have to aim for Mars if you want to land on the Moon" (can't help the feeling that you took this from someone). I may not have been as nerdy a student as you were dreaming of, I hope you were happy with my work. Thanks again for choosing me and making this PhD project possible.

Göran Arnqvist, my second supervisor. You and David have completely opposite and complementary styles of supervision. You were more discrete but present, always keeping track at a distance and bringing invaluable input at

the right moment. Your experience in supervision and as a scientist was necessary to make my PhD the safe trip that it has been. As a group leader, you also have shown many qualities. Thank you!

Claus Rueffler, you were the element of strict logic and mathematical rigor that I needed to balance the kind of intuitive thinking that fester in the mind of an empiricist. Your door was also always open, (and you were also in an office next to mine!) and your unprejudiced attitude towards new ideas has been a great example.

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Johanna, I praise you, fair queen of the beetle lab! I will remember dearly the years that I have been serving under your benevolent reign. Your good spirits and care create that special atmosphere that is unique to the beetle lab and allows students to survive extreme experimental planning, and walk out with a smile. Not unlike a Swedish version of Shiva, you maintain beetle populations with one hand, fix a climate cabinet with another, fill-in on someone else's experiment with yet another hand and use the remaining one to select uplifting music and pour coffee in the tired lab-dweller's cup. Over the numerous hours I have spent in the lab, we have built a strong friendship that I treasure.

Elina, I am impressed by your ability to switch at lightning speed between casual conversation and hardcore science. This has made you both a friend and an inspiring example.

Julieta, you left animal ecology some time ago, but your exotic curse words are still echoing down the corridors and your cheerful spirits still linger in the air. You were a prominent figure of my early days as a PhD student and I will always be happy to meet you again.

Karl, the first thing I did when I moved to Sweden was sleeping on your couch. I reiterated a few months ago and, wow, have you changed during those four years! In any case those two versions of you (The Mr. Karl of the beginning and the Dr. Family of the end) were good companions during that adventure. Thanks!

Jesper the tall, aka mini-Göran, aka the joker from Göteborg, thank you for your incredibly positive, Spongebob-like attitude towards life in general, may you be happy in every possible way.

Kati and Laura, thank you for reminding me how it feels to enjoy simple, casual moments around a dinner with friends.

Josefine, you were a great friend first and then a great partner. You have spent much effort and time trying to understand me and make me happy. You have taught me much and I wish you the best. And to Strössel too.

Maman, merci pour ton soutien inconditionnel dans tous mes projets, celui-ci inclus. J'espère que tu ne t'inquiètes pas trop pour mon avenir ; je te rassure, je ne serais sûrement jamais riche, mais je ne risque pas de m'ennuyer. Merci de m'avoir poussé à toujours faire mieux, dans un souci constant de me voir heureux.

Papa, merci d'avoir gardé mon esprit toujours ouvert et curieux. J'ai sûrement appris de toi le goût de résoudre, comme par jeu, toutes sortes de problèmes. À pousser ce jeu un peu loin, me voilà docteur.

Michèle, merci de m'avoir porté tant d'attention au fil des années, faisant de moi la personne que je suis aujourd'hui.

La famille, Pierre, Camille, Michou, Dominique, Claude, Barbara, Antoine, merci pour votre tendresse sans faille, soyez sûrs que je vous le rends bien !

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Pierre, gros balourd, toujours en retard, je parie que tu vas rater ma soutenance après tout, mais je te pardonne ! Grâce à toi j'ai pris quelques pauses salutaires au long de ma thèse, par deux fois tu es venu me voir ici à Uppsala, et je t'ai aussi rendu visite à Montpellier pour absorber un peu de Soleil. C'est quand ta soutenance déjà ? Après ça, on se prendra quelques vacances bien méritées.

Adrien et les autres mokays, Cerrone, Shuback, This, Karl (pour ne citer que les plus célèbres), merci pour une amitié anti-rouille qui résiste à la morne routine de la vie d'adulte responsable. En particulier, merci à Cerrone d'être venu me voir, deux fois, dans mes contrées lointaines, et merci à Adrien et sa famille de m'avoir accueilli dans leur paradis caraïbe pour un repos salutaire.

Antoine, mon cher collègue Québécois, bientôt docteur toi aussi ! Bientôt 3 ans que je ne t'ai revu, mais le lien est toujours là et on se reverra de l'autre côté de la soutenance, docteur B.-S.

Martin, docteur Martin, mon pote du muséum, toujours là pour parler photo et partager des expériences. Tu verras, un jour on trouvera un post-doc...

Ludo, on a eu des trajectoires un peu parallèles, à juste un étage d'écart. J'ai mis du temps à t'apprécier à ta juste valeur. Mais voilà, j'ai fini par y arriver.

Venkat, thanks for the good party times! It may not seem like much, but in the dark of winter, a friend to discuss movies with over a beer is invaluable.

T-J, thanks man, for being yourself. I sense in you a truly kind and peaceful person, and I feel instinctive sympathy towards you.

Charlie, we haven't talked much over the years, but I feel some spontaneous sympathy for you. I wish you the best and maybe I'll see you again if I ever work with plants (Haha! No way!).

Mattias, you have proven the best discussion partner I have encountered in a while (but see just below). Street rules: no restrictions on topics or type of arguments used, that's the way I like it! You have also been a good friend in more difficult times. Thank you.

Paula, you are also a good contender for the discussion partner title. You are, just like me, a true lover of arguments. You know the beauty there is in arguing just for the sake of it, and I respect that. You are also, of course, a dear friend.

Rado, aka el Raderino, thanks for being such a laid-back, just plain nice person. Thanks for the good times, movies and game nights an all.

Brian, my friend and office mate for a while. Thanks for the fun times, the coffee breaks, the beers, the horrible gym classes we suffered through together. I miss you!

Uros, we pulled off some hard work in the beetle lab together. You were with us for a short time but you proved to be a great person to work with and a kind friend.

Steph et Steph, merci de m'avoir accueilli et guidé dans votre paradis sous-marin.

Sarina, we went through hard times together, but we never wanted it any other way. Your positive attitude was always a comfort to me, although I made fun of it at the time... You are a great diver, a natural!

Eryn, we've had a few talks over coffee over the years (I can't believe I'm saying that, "over the years", makes me sound so ancient). You have been a god life-choice advisor. Also a great scientific advisor. You even were my confident once in old times! Thank you.

Will Jones, you big British thing! You are some real old-school, all-animals knowing biologist! I respect that a lot. I'm telling you, one day you will be some old, super influential, trend-setting scientist. When that day comes, remember me, and CITE ME!

Warren...yeah I know it's starting to look like alphabetical order now, all the W's together... Warren, after a rough start between us, you have taught me much about accepting others and I am grateful for that. Thank you.

Animal ecology, thank you for a great working atmosphere, relaxed but productive, after four years it will be hard to say good-bye, and hard to find a better place to go to. Oh, and thanks for the (roughly calculated) 100 liters of free coffee I drew from that machine in the fika room.

Sweden, despite my typically French critical attitude towards you, I have appreciated your standards of living, strive for tolerance, and cult of social awkwardness. You have taught me much (except for Swedish, damn you Sweden!), and made me a different person than I was four years ago, in what I think is a good way.

And of course all of the others, how many pages would I need to cite all of you! Producing a thesis is like laying a big egg, and after four years of incubation my memory is probably biased towards those that have been there all along or appeared at the end and I may have been unfair to earlier ones. Forgive me.

We may now pause for a moment and have a thought for the animal lives that were taken for the purpose of this thesis. I calculated that (and this is only for directly creating data, I'm not including the long culturing periods) close to one million beetles have died by my hand. I'm not really sure what to think of that!

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