

Tarmo Ketola

Genetics of Condition  
and Sexual Selection



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## ABSTRACT

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Yhteenveto: Kunnon ja seksuaalivalinnan genetiikka

Diss.

Sexual selection has been thought to be a potent evolutionary force in which females, by exerting a choice over potential mates, could provide benefits to their offspring or to themselves. A critical assumption is that the choice for a certain mate honestly brings the associated benefits to the one making the choice. A potent mechanism that could bring honesty to some parts of this system is condition. Individuals in good condition are supposed to be able to use more energy on fitness enhancing traits. Thus, mediators of this condition might be traits associated with energy metabolism. Experimental manipulation of genetic quality by inbreeding in crickets (*Gryllodes sigillatus*) revealed that the resting metabolic rate was inflated due to inbreeding. This furthermore reduced the amount of energy available for allocation. However, the size of the total energy budget was not affected by inbreeding. These metabolic traits, in addition to inbreeding, played a role in the determination of call activity. This suggests that females might receive correct information about males with good quality by choosing males with a high call activity. In addition to call activity, sexual signalling in crickets involves a courtship call that the male performs for a female in close proximity. I found that females were strongly attracted by this courtship call but the expected benefits of the choice were not visible in this study. To summarize, there might be some genetic benefits associated with sexual signalling by the avoidance of inbred individuals. The results of the role of resting metabolic rate in fitness were equivocal. Despite strong inflation due to inbreeding in *G. sigillatus*, I did not find any effects of gamma ray treatment or inbreeding on resting metabolic rate of flies (*Drosophila montana*). However, these studies of the effects of genetic quality on energy metabolism offer promising avenues to a more precise empirical measurement of condition, especially since previously used residual body mass indices were found non-responsive to inbreeding and not associated with energy metabolism.

Keywords: Condition; energy metabolism; inbreeding; mutations; quantitative genetics; sexual selection

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## LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following papers which are referred to in the text by Roman numerals. I have analyzed the data in manuscripts II to V and written them. Additionally, I have participated in writing and planning article I.

- I Puurtinen, M., Ketola, T. & Kotiaho, J. S. 2005. Genetic compatibility and sexual selection. *Trends in Ecology and Evolution*. 20, 157-158.
- II Ketola, T., Kortet, R. & Kotiaho, J. S. Testing sexual selection theories in Decorated crickets (*Grylloides sigillatus*). *Evolutionary Ecology Research*, in press.
- III Ketola, T. & Kotiaho, J. S. Can metabolic traits be used as surrogate of condition? Inbreeding increases resting metabolic rate and decreases energy that is available to allocation. Manuscript.
- IV Ketola, T. & Kotiaho, J. S. Inbreeding and energy metabolism in relation to sexual activity in decorated cricket (*Grylloides sigillatus*). Manuscript.
- V Ketola, T., Puurtinen, M., Kotiaho, J. S. & Mazzi, D. The response of resting metabolic rate on manipulation of genetic quality. Manuscript.

# 1 INTRODUCTION

Some individuals survive and reproduce better than others. These individuals leave suitable number of descendants which in turn survive and reproduce optimally. This progression of life provides the best available gene combinations to the next generations, hence leading to evolutionary change. Therefore, genes that contribute positively to survival and reproduction are favoured by evolution. In sexually reproducing species, such genes also include ones that influence mating. Thus, genes that exert an influence on the choice of individual(s) with whom the optimal output will be achieved are also under selection.

## 1.1 Components of fitness

Those who have high fitness leave their genes more efficiently to the next generations and thus, evolution is said to maximize the reproductive value of an individual (Fisher 1930, Roff 2002). The reproductive value of the individual is constituted by individual reproduction and survival over successive breeding attempts. Therefore, maximizing both would yield the best reproductive value. Since an individual's energy use is often limited, the scarce energy must be allotted between life-history traits. Therefore, if individuals are selected to produce more offspring, this could cause corresponding reductions in survival. This trade-off might be evident by negative correlation between these two traits at the population level. However, in contrast to this belief, the correlations between life-history traits are commonly found to be lacking or even positive (e.g. van Noordwijk & de Jong 1986, Roff 1996). Some individuals seem to have high survival chances and still possess high reproductive output. This can be explained by considering a third trait: one that is the amount of energy that could be allocated to these traits. This allows positive correlations between life history traits at the population level (e.g. van Noordwijk & de Jong 1986, de Jong & van Noordwijk 1992, Roff 2002). This "third" trait has been later

interpreted as a condition (Rowe & Houle 1996, Lorch et al. 2003, Hunt et al. 2004, Tomkins et al. 2004).

In addition to condition, how well the investments of energy on reproduction and survival match the selective pressure, is said to comprise an individual's quality. Thus, the condition sets up the maximal limit for usable energy whereas the optimality of energy allocation to reproduction and survival determines quality together with condition (Hunt et al. 2004). Fitness is a measure of how well this works over successive generations.

## 1.2 Genetics of fitness

Under constant selection pressure, the fitness should eventually be maximized. The most potent mediator of this evolutionary change is additive genetic variation which originates largely from additive effects of alleles over loci. Alternatively, dominance effects stem if alleles in loci do not function additively. Such a situation arises if, for example, certain (recessive) alleles affect phenotypes only when expressed in a homozygous state (e.g. directional dominance). Otherwise, dominance might be due to a heterozygote advantage or disadvantage over homozygotes (over dominance or under dominance, respectively). Epistasis refers to effects between loci. In addition, all traits are influenced by environmental effects, or effects of unknown origin.

Since additive genetic variation sets up the evolutionary potential, it is expected to be eroded under constant selection, leading to the situation where most of the remaining genetic variation is either dominance or epistatic variation. These genetic variances are not effectively culled by selection (Fisher 1930, DeRose & Roff 1999, Roff & Emerson 2006). However, the potential for evolutionary change is also limited by error variation. This is because the expected change between generations is predicted by heritability, which refers to the proportion of total variation that is explained by the additive genetic variation. Hence, a low heritability might not be solely due to low additive genetic variation since a similar effect on heritability can be found if there is a large proportion of unexplained variation in the corresponding trait (e.g. Lynch & Walsh 1998).

Within this framework, the maintenance of the genetic variation has been hotly debated (Merilä & Sheldon 1999): some studies have found heritability of the fitness related traits to be low (e.g. Gustafsson 1986, Kruuk et al. 2000), and others have found these fitness related traits to contain comparable or even higher amounts of additive variation than non fitness traits, but with a higher amount of environmental variation (Price & Schluter 1991, Houle 1992). However, for predicting the change of the mean trait between two generations, it does not matter whether low heritability is due to error variation or additive effects, since small changes between generations are expected with both (e.g. Lynch & Walsh 1998). It is also important to note that in theory, evolution is said to maximize fitness, not necessarily its components, and thus there might

be abundant additive genetic variation in individual traits contributing to fitness (see: e.g. Merilä & Sheldon 1999). These features concerning maintenance of genetic variation also play a predominant role in the realization of genetic benefits via mate choice.

### 1.3 Sexual selection for genetic benefits

In addition to just surviving and reproducing, individuals might gain additional fitness benefits via mating. In many species, females are attracted to the male's elaborate sexual signals, such as vocalizations, displays and ornaments. By pairing with males with strong signals, females are thought to obtain either genetic benefits or direct material benefits to themselves and/or their offspring (Andersson 1994). Either way, this could increase the female's fitness, proven that costs associated with choice do not overrun potential benefits (Pomiankowski 1987, Pomiankowski et al. 1991, Alatalo et al. 1998).

Genetic benefits associated with heritable attractiveness could be mediated if the male sexual ornament is heritable. Thus, by pairing with a male that possesses an elaborate signal, fitness benefits may result from the attractiveness of the female's offspring (Fisher 1930). In addition, if this sexual signal is genetically associated with higher male quality, then selection according to this signal could lead to higher quality offspring and therefore increased fitness (Zahavi 1975, 1977). Benefits from attractiveness or associated quality should vary with sexual selection intensity (Kokko et al. 2003). These benefits may follow only if the male sexual signal is heritable, and in the case of good genes, a genetic correlation between sexual signal and quality is also needed. Moreover, female choosiness should be heritable and genetically correlated with the male sexual signal (Kirkpatrick & Barton 1997, Qvarnström et al. 2006).

However, if quality is under both natural selection and also sexual selection, it should have a rather low heritability. Thus, it seems that the potential for the realization of this benefit is fairly low. Yet, the previously mentioned trait known as condition offers a potential explanation: if life history traits including sexual signals are condition dependent, then these traits could maintain their additive genetic variation and positive genetic correlations slightly more easily (Rowe & Houle 1996). Likewise, in "ordinary traits", alleles that contribute to this condition could also be driven to fixation. However, condition has been suggested to be affected by a large number of loci. This should make condition a large target of mutation. According to Rowe & Houle (1996), this condition dependence ultimately relied on mutation selection balance. Nonetheless, if influenced by large numbers of loci, this condition dependence could also enable other mechanisms that contribute to the maintenance of genetic variation to be more effective. Other mechanisms that contribute to the maintenance of genetic variation in fitness, and likewise in sexually selected traits, are genotype by environment interactions with variable selection pressures (e.g. Hamilton & Zuk 1982, Tomkins et al. 2004),

immigration (e.g. Barton & Keightley 2002) and antagonistic pleiotropy (e.g. Curtsinger et al. 1994).

Over the last 30 years, sexual selection literature has been dominated by speculation over the importance of additive genetic effects mediating sexual selection, either via sexy son effects or via heritable good genes. Initially, this was suggested to be doubtful by theoreticians, but then new theoretical work and some empirical results emerged that seemed to allow for the good genes view of sexual selection (Alatalo et al. 1997). However, additive genetic effects are again under suspicion. This shift is probably due to the realization that a vast amount of non additive genetic variation seem to determine fitness related traits (DeRose & Roff 1999, Roff & Emerson 2006).

The question arises: by choosing certain males, could females pick up benefits from abundant dominance and epistatic genetic effects? This could theoretically result from the avoidance of inbreeding. Alternatively, epistatic effects could be harvested by avoiding outbreeding depression. Individual fitness could be maximized, by optimal outbreeding (Bateson 1983, Mays & Hill 2004, Neff & Pitcher 2004). Cues that could be potent mediators of this kind of information are familial imprinting or kinship recognition (Penn & Potts 1998, Hurst et al. 2005). Mechanistically, this could be mediated via major histocompatibility complex alleles (in vertebrates), or via cuticular hydrocarbons (in insects). Despite being an appealing concept, this approach might still be too simplistic. Fitness may be maximized in certain cases even by mating with a close kin. This is because mating with a kin may help spread the shared genes and lead to better inclusive fitness (Kokko & Ots 2006).

#### **1.4 Reliability of the signal and male fitness**

The benefits mentioned above were discussed largely from the female perspective. However, it is the male that possesses the sexual signal. Thus, the value of the signal that indicates possible benefits is moulded by male "decisions". By advertising more, individual males could gain a better reproductive value and therefore higher fitness. What then happens to the benefits that females should receive? Honesty in signalling is suggested to be maintained by costly sexual signals that allow good quality males to advertise themselves better than lower quality males (Zahavi 1977, Kotiaho 2001). As before, the mediator of this is suggested to be condition dependence of the sexual signals because costly sexual signals consume the same energy that could be used on other traits that affect quality. Therefore, a good condition allows a simultaneous output of high energy to several traits. This should keep quality traits and sexual signals positively correlated (e.g. Rowe & Houle 1996).

Moreover, honesty of the sexual signal can be mediated by external factors such as predator avoidance or parasite resistance. Predators and parasites alike are attracted by sexual signals, thus only males that can withstand these threats can signal a lot. However, in the end, this might feed back to the energy budget

since keeping up parasite resistance and predator avoidance are very likely to be energetically costly (e.g. Andersson 1982). Hence again, condition dependence is evoked to explain the positive correlation between traits that compete for the same energy (van Noordwijk & de Jong 1986).

Signal reliability may deteriorate even more according to how males behave. The handicap hypothesis and condition dependence of the traits may be overly optimistic explanations since males also try to maximize their reproductive value. The ways to achieve this maximization are influenced by the prospects of mating. For example, if certain males have low survival probabilities, then to signal until exhaustion might be an optimal solution for them. Therefore, some males may signal against the assumptions of the handicap hypothesis and engage in costly sexual signalling without good survival probabilities (Candolin 1999, Gray & Eckhardt 2001, Sadd et al. 2006). In addition to signal honesty, the reward for females may be considered a sham. This might be the case if the nuptial gifts are not used as a paternal effort (Vahed 1998, Ivy et al. 1998) but as a mediator of male manipulation (Vahed 2007). However, it should be noted that signals need not be honest all the time, but only on average overall, for sexual selection to be maintained (Kokko 1997).

## **1.5 Sexual selection for other benefits**

Mating to yield maximal genetic benefits is full of uncertainties that are involved in sexual signal reliability and the underlying genetics. However, a simpler explanation for sexual signals could be that benefits are non genetic. In such a case, it does not matter if the sexual signal is genetically or environmentally determined. What matters is the positive correlation between the sexual signal and associated benefit. For example: females might benefit if the intensity of a male sexual signal is associated with the size of the nuptial gifts, which are a ration that confers energy or hydration to the female (Vahed 1998, Ivy et al. 1999 but see previous chapter). Similarly, a male trait might be associated with better territory or a safe place for mating (Andersson 1994). Moreover, just a signal and attraction towards it can confer fitness benefits. Responding to a species-specific sexual signal can assure an individual of a mating companion (Dobzhansky 1951, Sætre et al. 1997), or help individuals to locate mating companions more easily (Hack 1998). Naturally, benefits of this kind of attraction can be opposed by potential costs (Kokko & Mappes 2005, Kokko & Rankin 2006), such as non optimal mating rates or male induced harm (e.g. Pomiankowski 1987, Holland & Rice 1998).

## 1.6 Aims of the study

In previous paragraphs I have provided a brief overview of some life history theory with a particular emphasis on sexual selection. I have not tested all of the presented theories, but to put the following individual manuscripts in to the broader perspective, this was necessary. The aim of this thesis was to study factors that influence sexual selection and as a result, the individual papers presented here fall broadly within two topics: condition and sexual selection. The unifying theme of these papers is not necessarily evident from the individual papers alone, since these have all been written to be individual contributions to scientific literature. Moreover, the papers are presented in chronological order and not under themes because these articles partially build upon each previous work.

For the individual papers of this thesis, I first discuss the development of sexual selection theory for genetic benefits (I). The following empirical manuscript (II) approaches these hypotheses by testing multivariate sexual selection on male traits and relatedness. In addition, multivariate quantitative genetic methods were employed to reveal whether these male traits, some under sexual selection, possess heritable variation. A slightly different approach was adopted in paper III, where in addition to heritabilities, the effects of inbreeding and dominance variation on male traits were studied. In this article, the emphasis was strongly on quantifying condition in an empirical method by metabolic measurements. The fourth (IV) paper is based on the same dataset as the previous paper (III), but I additionally explore the metabolic determinants of condition and inbreeding that explain sexual activity. Finally, the effects of genetic quality on metabolic rate were experimentally studied by induced mutations (paper V).

## 2 METHODS

### 2.1 Study species

As a study species, I have mainly used *Gryllodes sigillatus* (Orthoptera, Gryllidae) crickets, commonly known as decorated crickets or tropical house crickets. The pair formation of these crickets is based on acoustic signals, which are produced by a resonating harp. The harp is a thickened part of the wing that by resonating produces a characteristic sexual signal of this species. Male crickets produce two types of sexual signals: one that is used to allure females from a distance (a call song), and one that males perform when a female is in close proximity (a courtship song) (Loher & Dambach 1989). If females are willing to mate, they mount on top of the male, consequently preventing forced copulation. After female approval, the male secretes a large spermatophore consisting of sperm ampulla that attaches to the female's reproductive tract. Meanwhile, the female begins to eat the spermatophylax, which is a gelatinous cover of the spermatophore. This is expected to provide females with some extra energetic (Vahed 1998) or hydration benefits (Ivy et al. 1999), whereas males ensure better sperm transfer. Lately, it has been suggested that these nuptial gifts might work as deceptive gifts, helping only males with their sperm transfer but offering nothing concrete to females (for review see: Vahed 2007).

In addition to decorated crickets, I have also used flies (*Drosophila montana*, Diptera: Drosophilidae) in paper V to study the determinants of maintenance metabolism.

### 2.2 Metabolic measurements

I studied the metabolic determinants of condition through metabolic measurements. However, the term condition has been often used without considering what it really means. To clarify what I mean and what I think others should mean by condition, I shortly justify my thoughts on how

condition is determined by measurable metabolic traits. This is followed by a brief overview of associated hypotheses and then a summary of how I measured these.

Condition dependency in its present form was adapted to sexual selection theory from life history literature (Rowe & Houle 1996), where it was offered as an explanation for positive correlations between life history traits (van Noordwijk & de Jong 1986). In this theoretical treatment, the trait that allows a simultaneous high energy output on several life-history traits was initially called acquisition. Later, this acquisition of energy was quite directly linked to mean condition (Tomkins et al. 2004, Hunt et al. 2004). However, here is a conceptual problem that may cause confusion: if acquisition is understood solely as hunting or grazing ability then it cannot be equal to condition. This is because the amount of energy that is available to fitness enhancing traits (Rowe & Houle 1996, Lorch et al. 2003, Hunt et al. 2004, Tomkins et al. 2004) is also dependent on how well this energy is assimilated (Speakman & Król 2005) and how much of this energy is devoted to maintenance (e.g. Tomkins et al. 2004). A second potential point of confusion might arise from the role of maintenance metabolism. Should this be seen as a trait that is under allocation or a trait that belongs to the acquisition? I have followed the definition by Tomkins et al. (2004) for condition determination, where the condition is determined by the traits “that show how efficiently the individual converts the environment into somatic tissue or to activity... ..and such traits involve foraging, digestion and metabolic efficiency”. Thus, in energetic terms, the condition is energy that is available to allocation after the maintenance metabolism is subtracted from this total energy budget.

As noted above, the energy that individuals can use is first affected by the energy acquisition. Assimilation efficiency then determines how much energy could be used for maintenance and other activities. The proportion of energy that can be directed to activities is the condition. Empirically, this amount of energy is estimable by measuring energy consumption both at rest and at forced activity, thereby yielding the resting metabolic rate and size of the total energy budget. The difference between these is allocation ability or metabolic scope, which is the amount of energy that individuals can use for activities.

From these definitions, it can be argued that resting metabolic rate and the total energy budget set the upper limit for condition. Hypotheses from physiological literature emphasise the role of the resting metabolic rate in facilitating high energy output. The high resting metabolic rate is expected either to reflect an individual's ability for high energy output over a short time interval (aerobic capacity, Bennett & Ruben 1979) or longer time (sustained metabolic rate, Drent & Daan 1980). The latter is expected for individuals with larger intestines that are needed for more efficient energy assimilation (Konarzewski & Diamond 1995). When these ideas are converted to the determination of condition, one would expect that the higher the resting metabolic rate, the higher the condition. Therefore, a high resting metabolic rate is suggested to reflect good genetic quality. However, recent evidence from a whole genome expression study indicates up-regulation of maintenance genes

due to inbreeding (Kristensen 2005). This finding offers a counter hypothesis which predicts that a high resting metabolic rate is associated with low genetic quality and probably with lower condition.

However, in addition to the resting metabolic rate, condition is affected by the size of the total energy budget. This is a critical assumption, especially in physiological hypotheses which expect an unlimited availability of energy (Johnston et al. 2007). This assumption might be incorrect since individuals are frequently found not to use energy over a certain limit (Speakman & Król 2005). Moreover, the availability of energy is frequently limited in the wild (Parsons 2005). If genetic quality also reflects the total energy budget, then this might have an additional effect on condition. Defining condition in energetic terms allows empirical testing of these and sexual selection hypotheses involving condition.

Energy that individuals use could be measured indirectly by observing either consumption of oxygen or production of carbon dioxide. This relies on the fact that utilization of energy involves the oxidation of energy, which depletes oxygen and produces carbon dioxide as well as heat (Hill & Wyse 1989). In this thesis, I have used a CO<sub>2</sub> analyzer to gauge energy consumption of individuals. I mostly considered the resting metabolic rate (III, IV, V). This estimates the energy consumption of physiological maintenance of life (Hill & Wyse 1989). Forced exercise was used to measure the maximal amount of energy that individuals could use in total for both maintenance metabolism and exercise (III, IV). Thus, this should set up the limits for the energy budget. If individuals do not reduce their maintenance metabolism during exercise, then the difference between maintenance and the total energy budget should be indicative of how much energy individuals could use on fitness enhancing traits (Tomkins et al. 2004).

## 2.3 Statistical testing

The methods of statistical testing varied according to the problem, but papers II and III relied heavily on the animal model. This analysis is based on explaining the phenotypic similarity of the individuals by their relatedness (e.g. Lynch & Walsh 1998, Kruuk 2004). Relatedness between individuals was extracted to an  $A^{-1}$  -matrix from a pedigree, and this was used as a design matrix for statistical analysis employing the general linear model. This analysis was done with ASReml statistical software (version 1.10, VSN international Ltd, Hemel Hempstead, UK). During the analyses, I considered the additive effects as well as the common environmental effects. This was done, despite individual rearing, to control for possible maternal effects. In paper III, the effects of inbreeding were also considered. Inbreeding has often been considered problematic in the estimation of breeding values and variance components since directional dominance (i.e. inbreeding) increases resemblance between relatives and thus, confounds heritability estimation. However, this can be

addressed by including the inbreeding coefficient of individuals as a covariate in the model, thereby enabling a more unbiased estimation of additive genetic variation and inbreeding depression (deBoer & vanArendonk 1992). Since inbreeding was clearly present in the pedigree of paper III, this method was employed. In papers II and III, the log likelihoods of the alternative models, with and without common environmental effects, were compared to obtain a model that was parsimonious enough. Even though paper IV was based on the same dataset as paper III, I chose to explore the effects of inbreeding on sexual activity by regression analysis.

The variations of regression analysis were the most important analyses in this thesis. In paper II, I analysed the effects of various morphological and sexual traits on female preference by logistic regression. This method was also used in paper IV, however, the main results of that paper were obtained by the ordinary least squares regression which explored the linear effects of inbreeding and metabolic traits on sexual activity. To illuminate the potential causal effects of experimentally manipulated inbreeding, I used path analysis, which allows construction of “causal” paths for the exploration of phenotypic effects. For example: inclusion of inbreeding in the normal regression analysis with metabolic traits probably causes incorrect estimation of the effects of these traits. This is due to the fact that in the ordinary regression analysis, the expectation is that all traits have bidirectional effects on each other. However, in the case of inbreeding, this is not valid since inbreeding may affect metabolic traits but metabolic traits can hardly affect the level of inbreeding. Path analysis, however, allows some control over what might be possible.

Due to a (relatively) balanced design, paper V was analysed by an analysis of covariance. All analyses except animal models were analyzed by SPSS (v. 12.0.1, SPSS Inc., Chicago, IL, US).

## 3 RESULTS AND DISCUSSION

### 3.1 Condition

The concept of condition bears a significant role throughout life history theory (e.g. van Noordwijk & de Jong 1986, de Jong & van Noordwijk 1992, Roff 2002) as well as sexual selection theory (e.g. Andersson 1994, Tomkins et al. 2004). Moreover, it is a commonly assessed trait that is used in applied biology such as fisheries science (Bolger & Connolly 1989). Condition could be the mediator of several phenomena, including the maintenance of additive genetic variation in traits (a larger mutational target, Rowe & Houle 1996) and the maintenance of positive (genetic) correlations between life history traits (van Noordwijk & de Jong 1986, de Jong & van Noordwijk 1992). Additionally, the condition dependence of traits is especially important in sexual selection theory as a mechanistic basis of the handicap hypothesis (Kotiaho 2001, Tomkins et al. 2004).

Unfortunately, in several cases the condition is estimated by biologically (Jacob et al. 1996, Kotiaho 1999, Green 2001) and statistically (e.g. Darlington and Smulders 2001, García-Berthou 2001, Green 2001) unsound methods. Many researchers, like me in paper II, have relied on condition indices based on residual mass. Despite a clear theoretical definition that relates energy metabolism to condition (e.g. Tomkins et al. 2004, Hunt et al. 2004), energy metabolism studies have not been performed with this in mind. One of the aims of paper III was to bridge this gap between the theoretical expectation and empirical measurement of condition. The expectation was that energy from the total energy budget, measured by forced exercise, is first used for maintenance (resting metabolic rate), while surplus energy beyond this is the condition. However, to show that these metabolic measurements and this surrogate of condition are indeed fitness related traits, I manipulated the degree of inbreeding through the experimental mating of individuals. Particularly, I expected that due to the effects of inbreeding on total gene expression, low genetic quality is associated with high maintenance metabolism (Kristensen et

al. 2005). This clearly deviated from the long held tenet that a high resting metabolic rate enables higher energy use for activities, and thus, traits that enhance fitness (Konarzewski & Diamond 1995, Reinhold 1999). This assumption follows that the resting metabolic rate reflects the size of organs responsible for energy acquisition (Konarzewski & Diamond 1995). Paper III confirmed that the resting metabolic rate is indeed a fitness related trait. Inbreeding increased the resting metabolic rate, which indicated that energy conservation has been favoured by evolution (e.g. Parssons 2005). This result also supports the findings of Kristensen et al. (2005), who found an increased expression of genes involved in maintenance due to inbreeding. While this is an interesting finding on its own, it also has exciting implications for how condition is determined. Condition was expected to follow from the size of the total energy budget and in addition from proportion of energy that is allotted to maintenance. The total energy budget size was not affected by the inbreeding, suggesting some energy compensation as food was offered *ad libitum*. However, since individuals were not able to compensate for the increased needs of maintenance metabolism, the net effect of inbreeding on condition (allocation ability) was negative.

I additionally measured the effects of inbreeding on residual-based condition indices. Ideally, these indices should indicate inbreeding depression. If they resemble the theoretical definition of condition, then these should also co-vary with metabolic measurements. However, I found that these condition indices failed to indicate anything, as these traits were not affected negatively by inbreeding. The indices were also not correlated with mass-corrected metabolic measurements. This finding urges the reconsideration of these condition indices in previous evidence and encourages the validation of these indices prior to their application to condition in new studies (Weatherhead & Brown 1996, Green 2001).

As noted above, the resting metabolic rate has been considered an important trait that might confer fitness benefits. Unfortunately, studies that extensively concentrate on testing this view experimentally are scarce (paper III). To add to this short list of studies, I also performed an experimental manipulation of the genetic quality by gamma-ray induced mutations and manipulated the zygosity state of these mutations by inbreeding. Likewise, in study III, the expectation was that resting metabolic rate should have been inflated due to low quality. Contrary to expectations, the radiation with gamma rays did not cause any effect on phenotypes with mutations in homozygous or heterozygous forms. Therefore, it seems that mutation pressure was too weak or mutation events were too rare to be seen in this study.

High genetic quality is supposed to be reflected in sexually selected traits and one potent mediator of this is condition. The sexual signals are supposed to be condition dependent, and thus honestly indicative of the quality of the bearer.

### 3.2 Signalling genetic and non genetic benefits

After decades of research work, the concept of sexual selection is still undergoing tremendous research. Even though some of the sexual signals appear useless and even harmful to their bearers, they are supposed to enhance selection for improved fitness (Fisher 1930, Zahavi 1975, 1977). In addition to these signals, other cues might signal an even better fitness, at least in theory. Such extra benefits could follow from non random mating with respect to relatedness or to other genetic effects that could cause genetic incompatibilities (Zeh & Zeh 1996, Tregenza & Wedell 2000, Mays & Hill 2004, Neff & Pitcher 2004). To this topic of good and compatible genes, I contribute one correspondence article (I) and two empirical papers (II, IV).

Due to the review by Mays & Hill (2004) that concerned good and compatible genes, it was possible (and necessary) to comment on their work and contribute to the development of the theory. Particularly problematic in their paper was how they equated genetic dissimilarity as potential for compatibility benefits. Even though the avoidance of inbreeding might be useful, outbreeding might also possess costs. Outbreeding depression follows when co-adapted gene complexes that are important in local adaptation are broken. Although it has been claimed, the choice for good or compatible genes does not necessarily cause a dilemma for females, since it is possible for them to obtain both of these effects. A vast amount of non additive effects in fitness related traits suggests that if by choosing according to compatibility, large benefits could potentially be obtained. Scepticism towards this claim should follow from practical limitations that females face when “predicting” the outcome of the mating. The result is affected by complex genetics of fitness related traits, random segregation, and crossing over during meiosis in both the female and her mating companion.

The aim of the paper II was to study by which means and by which kind of benefits *G. sigillatus* females base their choice for a mate. In this study, I examined female attraction to several male traits that could be used to infer potential quality differences between males. Relatedness, which could possibly be used in a choice, was obtained from a pedigree of our laboratory strain of *G. sigillatus*. This pedigree was additionally used in the estimation of additive genetic variation of the traits, and thus I was able to study potential genetic benefits associated with female attraction. The spermatophylaxes were also weighed, which are potential nuptial gifts in this species.

I found that females were strongly attracted to males with high courtship call activity. Relatedness or other measured traits had no effect on attraction. The estimation of additive genetic variances revealed that there might not be high genetic benefits because heritabilities were generally low and a positive genetic correlation between fitness surrogates and courtship call was lacking. Moreover, nuptial gift mass was not correlated with the courtship call rate. Therefore, it seems that in this species the strong attraction towards high

courtship call activity prevails even in the absence of clear benefits. It should be noted that if costs associated with the choice are small, then there is no need to expect high benefits either (Alatalo et al. 1997). Moreover, in this species particularly, the benefits might come via multiple mating (Ivy & Sakaluk 2005). Thus, females may perform their best by mating with multiple males, the expected cost of mating is possibly even lower.

In the third study (IV) that falls into this category, I studied the metabolic and genetic determinations of condition (see previous chapter), and the effects of these traits on sexual selection. In other words, I studied whether the call rate is condition dependent (e.g. Kotiaho 2001). This study revealed that induced sexual activity was generally affected negatively by inbreeding. Therefore, inbreeding depression (genetic quality) contributed to the strength of the sexual signal. Sexual activity of these males was affected by the maintenance metabolism and total energy budget; both had a positive effect on induced sexual activity. To reveal how inbreeding affects these traits, I performed path analysis. From these analyses, it became clear that when inbreeding increases the resting metabolic rate, it also increases sexual activity. This is contrary to my expectations since in my previous study (III), higher resting metabolic rates were associated with higher inbreeding coefficients. However, a comparison of these results from induced calling to a smaller dataset of voluntary callers offers a potential solution for this finding. Voluntary calling that was initiated without a female was positively associated with high condition (allocation ability). In other words, the onset of the voluntary call was associated with a high total energy budget and low maintenance costs. These results together suggest that these males may adjust their behavior according to their prospects for mating.

## 4 CONCLUSIONS

This thesis is mostly about sexual selection. More specifically, it is about what kind of males females choose, and do they get some benefits from their choice. Condition, which is another topic of this thesis, plays an important role in various theories of sexual selection. However, it is additionally important in life-history theory and is used in several fields of biology.

I have suggested that condition is determined in part by the total energy that an individual could acquire. However, as food is assimilated, part of this energy is used on maintenance metabolism. By measuring maintenance metabolism (the energy consumption at rest) and the total energy budget by forced exercise, the metabolic determinants of condition can be measured. Thus, subtracting the amount of energy used on maintenance metabolism from the total energy budget results the empirical measurement of condition. By studying how inbreeding and these metabolic traits affect condition, I found that the total energy budget remained rather intact, despite inbreeding. This suggests some compensative acquisition since the food was provided ad libitum. However, the resting metabolic rate was strongly elevated due to inbreeding, which indicated that inbreeding increases the energetic costs of individuals. In a study with *Drosophila montana*, no such effects were found on resting metabolism. This was probably due to failure of experimental protocol.

The results from study of inbreeding effects on the resting metabolic rate of *Grylloides sigillatus* provide important implications. Firstly, to my knowledge, this was the first unequivocal experimental test that assessed the fitness role of the resting metabolic rate by genetic manipulation. Secondly, it provided results that dispute the common and largely untested tenet that a high resting metabolic rate is beneficial. Finally, I found that commonly used residual biomass-based indices were not affected by inbreeding. In addition, they were not correlated with metabolic traits. This is an unexpected result from indices that are suggested to indicate condition and fitness. Since these indices are commonly used in applied ecology, this result warrants attention.

In crickets (*G. sigillatus*), I found that females were very strongly attracted by the male courtship call rate. However, this attraction was not explained by

any of the assumed benefits. The heritability of the sexual signal was low and non significant. Additionally, high courtship call activity was not associated with larger nuptial gifts. According to this dataset, female benefits via these traits are not high in this species. In another study with this species, I studied the determination of energy allocation on sexual traits. This study also included the manipulation of quality through inbreeding. I found that males seem to adjust their behaviour according to their prospects of survival and mating. Despite some behavioural coupling with quality, inbreeding still negatively affected sexual activity. This suggests that females might get the correct information about male quality after all. Condition is suggested to be a mediator of many processes in sexual selection theory. However, I found condition to be sensitive to inbreeding and lacking additive genetic variation. Thus, it seems that condition might fail to be a mediator of the maintenance of additive genetic variation in life history traits. In addition, condition dependence via energetic traits seems to not mediate honesty of the sexual signal in this species.

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## YHTEENVETO (RÉSUMÉ IN FINNISH)

### Kunnon ja seksuaalivalinnan genetiikka

Tutkin väitöskirjassani seksuaalivalintateorioita, joissa yksilön kunnolla on keskeinen asema. Tämän lisäksi kunto on tärkeä myös soveltavissa tutkimuksissa arvioitaessa yksilöiden laatua. Koska tutkimukseni on tehty pääosin kvantitatiivisen genetiikan menetelmin, voi tulosten avulla arvioida geneettisiä mekanismeja, jotka johtavat esimerkiksi seksuaaliaktiivisuuden ja kunnan yksilölliseen vaihteluun.

Naaraat voivat saada hyötyjä joko itselleen tai poikasilleen valitsemalla uroksia seksuaalipiirteiden perusteella sattumanvaraisen pariutumisen sijaan. Tätä käsittelevissä teorioissa oletetaan, että naaras pystyy arvioimaan luotettavasti koiraan laatua seksuaalisignaalien avulla. Seksuaalisignaalien luotettavuutta voi lisätä niiden riippuvuus yksilön kunnosta. Yksilöt, jotka ovat hyvässä kunnossa, voivat käyttää enemmän energiaa seksuaalisignaaliin kuin huonokuntoiset yksilöt. Manipuloimalla yksilöiden geneettistä laatua *Gryllobes sigillatus* -sirkoilla havaitsin, että peruselinkustannukset nousivat lisääntyneen sisäsiitoksen myötä. Vaikka kokonaisenergiankulutus pysyi kutakuinkin muuttumattomana, eri toimintoihin käytettävissä oleva energia väheni. Nämä energiametaboliaominaisuudet vaikuttivat myös seksuaalisignaaliin. Havaitsin lisäksi, että urokset saattavat manipuloida seksuaalisignaaliinsa voimakkuutta riippuen naaraan läsnäolosta. Signaali ei selittänyt uroksen kunnolla, kun naaras oli läsnä. Sen sijaan spontaanisti, ilman naarasta, alkanut siritys riippui kunnosta. Vaikka kunto ei täysin selittänyt seksuaalisignaaliin, saattavat naaraat silti saada tietoa urosten laadusta, koska sisäsiitos vähensi seksuaalisignaalin määrää myös suoraan. Tutkin sisäsiitosvaikutuksia urosten siritykseen, jota ne esittävät houkutellessaan naaraita kaukaa (call). Tämän sirityksen lisäksi koirilla on myös siritys, jolla ne houkuttelevat lähietäisyydellä olevaa naarasta (courtship call, "kosiosiritys").

Yhdessä tutkimuksistani selvitin, ovatko naaraat kiinnostuneita tästä "kosiosirityksestä" vai perustavatko ne valintansa muihin uroksen piirteisiin kuten uroksen kokoon tai uroksen symmetriaan. Tämän lisäksi on mahdollista, että naaras voisi käyttää sukulaisuusastetta valintaperusteenaan välttäänsä sisä- tai ulkosiitosta. Tässä tutkimuksessa havaitsin, että edellä mainituista ominaisuuksista ainoastaan sirityksen määrä kiinnosti naaraita. Seksuaalivalintateoriat olettavat, että naaraan valintaan liittyisi myös hyötyjä, joilla se paikkaa mahdollisesti valinnasta aiheutuneita kuluja. Tässä tutkimuksessa ei kuitenkaan löytynyt selviä hyötyjä, jotka voisivat selittää voimakasta valintaa koiraan seksuaalisignaaliin kohtaan. Koiraan parittelun aikana erittämän spermatophylaxin koko ei riippunut koiraan seksuaaliaktiivisuudesta. Tämän naaraan syötäväksi tarkoitetun "lahjan" on ajateltu antavan naaraille joko energiaa tai vettä. Tämän lisäksi seksuaaliaktiivisuus ei ollut selvästi periytyvää, eikä seksuaaliaktiivisuudella ja pitkäikäisyydellä ollut yhtenäistä geneettistä taustaa. Jos nämä ominaisuudet ovat periytyviä, voi naaraan tekemä

valinta johtaa poikasten parempaan pariutumismenestykseen tai parempaan selviytymiseen. Vaikka tutkimukseni ei paljastanut näitä hyötyjä, on kuitenkin muistettava teorioiden olettavan, että hyötyjen on oltava kustannuksia suurempia. *G. sigillatus* naaraat parittelevat normaalisti useiden urosten kanssa. Tällöin yksittäisen parittelun haitat ovat todennäköisesti pieniä ja hyötyjen osoittaminen vaatisi tarkempia tutkimuksia.

Sirkoilla tehtyjen tutkimusten lisäksi tutkin geneettisen laadun vaikutusta peruselinkustannusten määrään myös mahlakärpäsillä (*Drosophila montana*). Vaikka sirkoilla sisäsiitos selkeästi vaikutti peruselinkustannusten määrään, mahlakärpäsillä näin ei kuitenkaan tapahtunut. Tämä johtui todennäköisesti osin aineiston koosta ja osin gammasäteilyn pienistä mutaatiovaikutuksista. Sirkkatutkimuksissani sisäsiitoksen vaikutukset perusmetaboliaan olivat mielenkiintoisia. Yleinen ja harvoin kokeellisesti testattu hypoteesi nimittäin olettaa yksilöiden hyvän laadun heijastuvan korkeana perusmetaboliatasona. Tämä perustuu ajatukseen, että korkea metaboliataso mahdollistaa suuremman eri toimintoihin käytettävissä olevan energiamäärän. Tulokseni olivat kuitenkin täysin päinvastaiset, joten näyttääkin siltä, että evoluutio on suosinut pientä perusenergiankulutusta.

Metabolioominaisuuksien sijaan kuntoa on perinteisesti mitattu kunto-indekseillä, jotka perustuvat painoon, joka ei ole selitettävissä koolla. Yllättävä havainto oli, että näillä indekseillä ei ollut yhteyttä energiametaboliaan, eikä sisäsiitos vaikuttanut niihin.

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