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# Evolution of Signals: Genetic Architecture, Natural Selection and Adaptive Accuracy

Thesis for the degree of Philosophiae Doctor

Trondheim, February 2011

Norwegian University of Science and Technology  
Faculty of Natural Sciences and Technology  
Department of Biology



**NTNU – Trondheim**  
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Table 1. Potential sources of confusion in an experiment and means of reducing their effect.

Source of confusion	Features of an experimental design that reduce or eliminate confusion
1. Temporal change	Control treatments
2. Procedure effects	Control treatments
3. Experimenter bias	Randomized assignment of experimental units to treatments Randomization in conduct of other procedures “Blind” procedures*
4. Experimenter-generated variability (random error)	Replication of treatments
5. Initial or inherent variability among experimental units	Replication of treatments Interspersion of treatments Concomitant observations
6. Nondemonic intrusion†	Replication of treatments Interspersion of treatments
7. Demonic intrusion	Eternal vigilance, exorcism, human sacrifices, etc.

\* Usually employed only where measurement involves a large subjective element.

† Nondemonic intrusion is defined as the impingement of chance events on an experiment in progress.

Table from Hulbert S. H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* 52: 187–211.



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January 2011



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## LIST OF PAPERS

- I. **Bolstad GH**, Pélabon C, Larsen L-K, Viken Å, Fleming IA, Rosenqvist G. Contrasting responses of ornaments and life-history traits to inbreeding in guppies. Manuscript in review in *Journal of Evolutionary Biology*.
- II. **Bolstad GH**, Pélabon C, Rosenqvist G. A deleterious effect of purging. Manuscript.
- III. **Bolstad GH**, Armbruster WS, Pélabon C, Pérez-Barrales R, Hansen TF. 2010. Direct selection at the blossom level on floral reward by pollinators in a natural population of *Dalechampia schottii*: Full-disclosure honesty? *New Phytologist* 188: 370–384.
- IV. Pérez-Barrales R, **Bolstad GH**, Pélabon C, Hansen TF, Armbruster WS. Pollinators and seed predators generate stabilizing selection on *Dalechampia* blossoms. Manuscript submitted to *Ecology*.
- V. Pélabon C, Armbruster WS, Hansen TF, **Bolstad GH**, Pérez-Barrales R, Antonsen L. *Adaptive accuracy and the adaptive landscape*. Manuscript.

### **Declaration of contributions**

The long-term experiment used in papers **I** and **II** was initiated by Rosenqvist, Fleming, and Viken in 1998. This experiment has been maintained by Rosenqvist with the help of several co-workers. I have participated in this experiment since 2004 and Larsen since 2006. The idea of paper **I** was developed by me together with Rosenqvist and Pélabon. In this paper, I did the data collection, the data analysis, and wrote most of the manuscript. Pélabon gave helpful advice on the data analysis. All co-authors commented on the manuscript. The idea of paper **II** was developed by me and I planned part of the experiment (the part not already included in the long-term experiment). I collected and analysed the data, and wrote the manuscript. Pélabon and Rosenqvist commented on the manuscript. The project forming the basis of papers **III**, **IV**, and **V** was initiated by Armbruster, Hansen and Pélabon. In paper **III**, I did the data collection, developed the fitness model, estimated the parameters in the fitness model and wrote the manuscript. Hansen gave helpful advice on the construction of the fitness model. Pérez-Barrales taught me field procedures and assisted me in the field. The ideas of the paper was developed by me with help from all co-authors. In paper **IV**, Pérez-Barrales collected the data and wrote the manuscript. I taught Pérez-Barrales how to develop the fitness model and estimated the parameters, and we did this together. Hansen gave helpful advice on how to construct the fitness model. The ideas of this paper was developed by Pérez-Barrales with help from me and the other co-authors. All co-authors commented on the manuscript. Paper **V** was written by Pélabon. The data were collected by Pérez-Barrales, Antonsen, Armbruster and me. I analysed the data and produced the figures. I also assisted Pélabon in developing the ideas of the manuscript together with Armbruster and Hansen. All co-authors commented on the manuscript.

All authors included in the list above have given their consent for the use of their work in this thesis.

## INTRODUCTION

Signals are appealing traits to study as they fill the living world with colour, sound, and extraordinary shapes. There are many different types of signals, for example alarm calls, begging, warning colours, and attracting colours. By far the most studied group of signals is sexual signals, which are used for mate acquisition. From the very birth of evolutionary theory, sexual signals have been treated as a special class of traits. Darwin (1871) realized that he could not explain the evolution of elaborate male ornaments by the argument of better survival. On the contrary, many of these ornaments seemed to lower survival. He, therefore, developed his theory of sexual selection.

Theory on signals has mainly been developed in the animal literature, and the study of plant-animal interactions in the context of signalling theory has, until recently, been overlooked (Schaefer *et al.*, 2004). Plant signal systems are often less dynamic than animal signal systems, and are therefore a promising research area that can shed new light on signalling theory. For example, plant signals (e.g. colour of fruits and flowers) are often constant in space and time and are displayed against an unchanging background.

Our understanding of signal evolution is far from complete without knowledge of genetic architecture and selection. The distinction and importance of genetic architecture and selection is conceptually captured by the Lande equation (Lande, 1979):

$$\Delta \mathbf{z} = \mathbf{G}\boldsymbol{\beta}$$

where  $\Delta \mathbf{z}$  is a column vector of the expected changes in phenotype in the next generation (i.e. the evolutionary response to selection),  $\mathbf{G}$  is the additive genetic covariance matrix (i.e. the genetic architecture), and  $\boldsymbol{\beta}$  is a column vector of the directional selection gradients (i.e. selection). Hence, this equation separates selection from the ability of the population to respond and shows that their combined effect is important to predict evolution. Knowledge of genetic architecture is important to understand evolutionary response to selection on signals, and can help us to understand historical patterns of evolution. Studies of selection can be important in several ways. In addition to measure the strength and shape of the different selection pressures acting on the signals, studies of selection can identify which traits that are

used as signals, if there are multiple receivers (e.g. mutualists and antagonists), and may also help explaining differences in signals among species and populations. It is also interesting to know how well adapted the signaller is to the selective pressure caused by the receivers. This can be studied using a recently developed theory on adaptive accuracy.

Evolution is a complex mechanism. It can therefore be fruitful, and maybe even necessary, to study different parts of this mechanism separately to broaden our understanding of it. In this thesis I have studied three such parts: genetic architecture, natural selection, and adaptive accuracy. To accomplish this, I used two study systems. The first was captive populations of the guppy (*Poecilia reticulata*), a tropical fresh-water fish. Using this study system, I tried to disentangle some aspects of the genetic architecture of guppy ornamentation using inbreeding experiment. The second study system was wild populations of *Dalechampia*, a vine distributed throughout most of the lowland tropics. I used three phenotypic selection studies on three different species of *Dalechampia*: *D. ipomoeifolia* in Gabon, and *D. scandens* and *D. schottii* in Mexico. These studies were used to compare bee-mediated selection and the adaptive accuracy of floral signals across these three species. In the following, I first explain the three components of evolution (genetic architecture, natural selection, and adaptive accuracy) and their connection to signals. Although there are many kinds of signals, I restrict my discussion to sexual and floral signals. Then I turn to my own research, which deals with only a subset of these topics, but hopefully adds to the current knowledge in a constructive way.

### **Genetic architecture**

Genetic architecture refers to all underlying genetic effects that determine a phenotypic character and its variational properties. This includes number of genes and alleles, distribution of allelic effects, and patterns of pleiotropy, dominance, and epistasis (see Hansen, 2006 for a recent review).

The classic population genetics models, initiated by Fisher (1918) and further developed by Cockerham (1954) and Kempthorne (1954), explore the genetic architecture of segregating variation in a population. These models decompose the phenotype into contributions from different genes and their interactions (Lynch & Walsh, 1998), which are defined

as regression parameters on gene content, with epistatic parameters as interaction terms. From this, total genotypic variance can be decomposed into additive, dominance, and epistatic variance components. For multiple traits, the variance components are replaced by variance-covariance matrices, the G-matrix (Lande, 1979) replaces the additive variance component. Traditionally, using these models, the genetic architecture affecting evolution has been assumed to be very simple, depending only on the additive variances and covariances. Fisher's motivation for this simple model was not that genetic architecture is simple, but rather that in a large recombining population, all combinations of alleles will occur, and the evolutionary effect of an allele is found by averaging over all these genotype combinations. These models have proven to be very useful for predicting short-term evolutionary effects. However, aspects not captured by this simple model can have a strong effect on longer time perspectives of evolutionary dynamics and therefore deserve to be studied (Hansen, 2006).

Genetic architecture can also be examined in relation to the genotype-phenotype map. The genotype-phenotype map describes how individual genotypes translate into phenotypes. The distinction between studying genetic architecture at the level of segregating variation and the level of the genotype-phenotype map is captured by the distinction between variation and variability (Wagner, 1996; Wagner & Altenberg, 1996). Studying segregating variation involves direct measures of variation in characters, while studying the genotype-phenotype map concerns the propensity of characters to vary (their variability).

One important aspect of the genotype-phenotype map is pleiotropy (Fig. 1). Pleiotropy is the property of a gene to affect more than one character. It is a strong genetic constraint, as it hinders independent

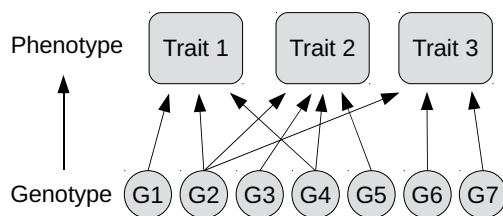


Fig. 1: Pleiotropy in the genotype-phenotype map. Seven genes (G1 – G7) affecting three traits. Two of these genes (G2 and G4) are pleiotropic as they affect more than one trait, indicated by more than one arrow.

evolution of characters, and a mutation beneficially affecting one character may have a deleterious effect on another (Kondrashov & Turelli, 1992). Together with linkage-disequilibrium, when the genes affecting two different characters are statistically or physically associated, pleiotropy is the underlying cause of genetic covariance between characters. However, the relationship between pleiotropy and genetic correlations is not necessarily simple, as different pleiotropic interactions may cancel each other out. For example, if the genetic variation in resource acquisition is high, this may hide strong pleiotropy between characters due to resource allocation (Houle, 1991).

Another important aspect that goes into the description of the genotype-phenotype map is functional epistasis (Fig. 2). Traditionally, epistasis has been defined as the deviance from additive effects between loci and measured as the interactions between genetic variance components of a phenotype (Cockerham, 1954; Kempthorne, 1954; Lynch & Walsh, 1998). Under this definition, epistasis is a population property that has been termed statistical epistasis (Cheverud & Routman, 1995; Wagner *et al.*, 1998; Hansen, 2006). Functional epistasis, on the other hand, is a property of the genotype-phenotype map, and is defined as the influence of the genetic background on the effect of an allelic substitution (Wagner *et al.*, 1998). This distinction was first made by Cheverud and Routman (1995). For epistasis to

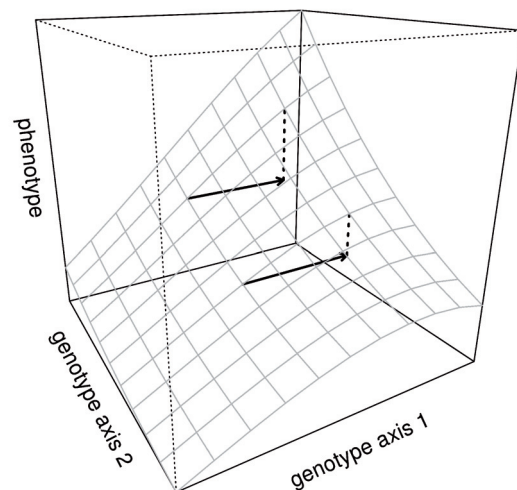


Fig. 2: Genotype-phenotype map (grey grid) with two genotype axes, indicating different phenotypic effect (dotted lines) for the same genotypic change (arrows) in two different genetic backgrounds.

## Synopsis

affect the response to selection it needs to be directional, so that it creates a systematic relationship between changes in phenotype and changes in gene effects, and thereby systematically changes the additive genetic variance of the population (Hansen & Wagner, 2001). Directional epistasis is the net effect of all epistasis, and can either reinforce (positive directional epistasis) or diminish (negative directional epistasis) the effect of other genes.

The main challenge in the study of the genotype-phenotype map is to obtain an accurate and meaningful description of genetic differences between individuals or groups of individuals. Inbreeding (mating among relatives) is a valuable tool in this respect because it increases the probability of two alleles at a specific locus being identical by descent, and therefore it increases the average homozygosity in the genome. Using individuals with different level of inbreeding enables regression of phenotypes on corresponding inbreeding coefficients (the probability of two alleles being identical by descent). The response to inbreeding will be due to a systematic change in phenotype with increased level of genome-wide homozygosity. This response is therefore the net effect of all dominance on the phenotype, termed directional dominance (analogous to directional

epistasis).

Directional dominance is a fundamental feature of the genotype-phenotype map and has several evolutionary consequences (Charlesworth & Charlesworth, 1987). Generally, increased homozygosity leads to decreased fitness (inbreeding depression). Whether this is due to heterozygous advantage (overdominance) or recessive deleterious alleles has been discussed for several decades and is fundamental for evolutionary dynamics (Falconer & Mackay, 1996). It is commonly believed that recessive alleles are the main source of inbreeding depression, and in a recent review, Charlesworth and Willis (2009) concluded that overdominance is rare. The underlying reason for directional dominance being important for evolutionary dynamics is that it systematically changes the additive effects of a trait, and thereby influences both the additive genetic variance and the optimal genotype frequencies. This is because the additive effects are defined as least square regression coefficients of genotypic values on gene content, and when the number of heterozygous individuals changes with changing allele frequency, this will change the additive effects (Fig. 3, Lynch & Walsh, 1998). In cases where there is a systematic relationship between the degree of dominance and the trait expression (i.e.

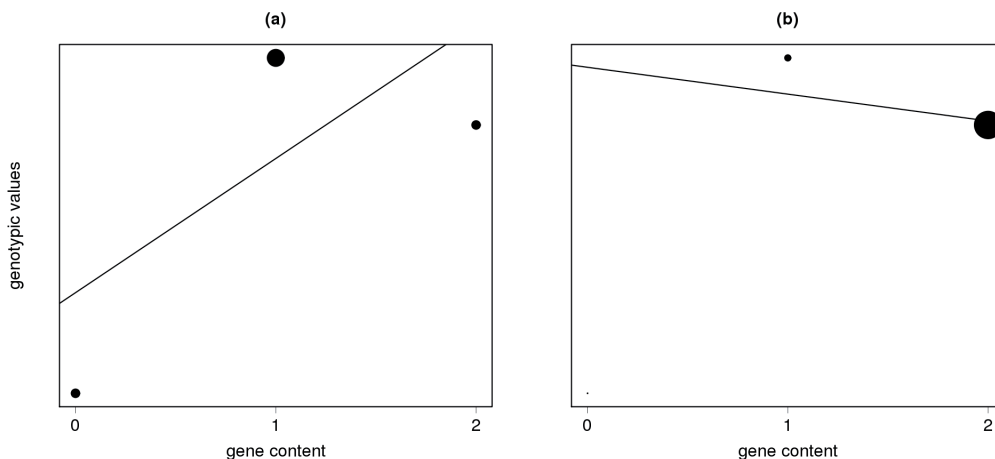


Fig. 3: Least square regression of genotypic values on gene content. Gene content is the number of a particular allele, say  $B_2$ , in the genotype. Hence, in a diallelic case, from left to right, the points represents the  $B_1B_1$ ,  $B_1B_2$ , and  $B_2B_2$  genotypes. A genotypic value is the expected phenotype of a genotype in a given environment. The additive effect of  $B_2$  is defined by the slope. Dominance is the same in (a) and (b) but the genotype frequencies differ as indicated by the size of the points. In (a) the allele frequency of  $B_2$  is 0.5. Assuming Hardy-Weinberg equilibrium, this gives genotype frequencies of 0.25, 0.5, and 0.25, for the  $B_1B_1$ ,  $B_1B_2$ , and  $B_2B_2$  genotypes, respectively. While in (b) the allele frequency of  $B_2$  is 0.9, giving genotype frequencies of 0.01, 0.18, and 0.81. This shows that the additive effects rely on allele frequencies when there is dominance. The stable equilibrium of genotype frequencies when selecting for larger genotypic values is reached when the additive effect of  $B_2$  (the slope) is zero.

directional dominance), selection on this trait will systematically change the additive effects and thereby the additive genetic variance.

Inbreeding can also be used to study synergistic epistasis, a special type of directional epistasis. It occurs when deleterious alleles on average reinforce the effect of each other and therefore increase the mutational load. Synergistic epistasis is indicated by an increasingly negative response of log fitness to the inbreeding coefficient (Lynch & Walsh, 1998). This special type of epistasis has several important evolutionary implications as it influences the mutational load and may therefore be involved in the evolution and maintenance of recombination and sexual reproduction (Kondrashov, 1988), in the evolution of senescence (Rose, 1991), and in the evolution of mate choice (Hansen & Price, 1999). After appropriate scaling, inbreeding can also be used to study directional epistasis affecting other traits.

There is a challenge to studies of inbreeding, because, together with increasing homozygosity, selection may affect the phenotypic response to inbreeding. When homozygosity increases, more and more recessive alleles become exposed to natural selection, which increases the likelihood of a recessive allele being purged (Byers & Waller, 1999; Crnokrak & Barrett, 2002; Leberg & Firmin, 2008). The efficiency of purging depends on the genetic architecture of inbreeding depression (Charlesworth & Willis, 2009). Theoretical studies demonstrate that purging mainly acts on recessive alleles which are lethal or strongly deleterious (Fu *et al.*, 1998; J L Wang *et al.*, 1999), but with synergistic epistasis recessive deleterious alleles of smaller effect can also be purged (Fu, 1999). In addition, the extent of purging depends on the number of generations with inbreeding, because this influences the rate at which a recessive deleterious allele becomes exposed to natural selection in its homozygous state (Hedrick, 1994; Wang *et al.*, 1999; Boakes & Jinliang Wang, 2005). The effect of purging is rarely properly controlled for in inbreeding studies, and the conclusions from these studies must therefore be treated with caution. Although purging represents a problem in many inbreeding studies, we can exploit its effect to obtain more information about the genetic architecture by making a design that does not confound the effect of inbreeding and purging. One such design is to compare effect of inbreeding in purged and non-purged outbred populations (e.g. Willis, 1999). Because inbreeding depression caused by overdominance can not be purged, a strong effect of purging is evidence for recessive deleterious alleles

as the main cause of inbreeding depression (Lynch & Walsh, 1998).

### **Natural selection**

Understanding the dynamics of natural selection is one of the most important areas of evolutionary biology, as natural selection is important for shaping differences among species (Rieseberg *et al.*, 2002) and plays a major role in population divergence and speciation (Schluter, 2000; Funk *et al.*, 2006). It is important to realize that natural selection acts on phenotypic variation regardless of its genetic basis and can be measured within one generation. Lande and Arnold (1983) introduced a simple, but theoretically well founded, way of measuring selection by a multiple regression of phenotypic traits on relative fitness. This was an extension and generalization of the seminal work of Pearson (1903), and has led to a large literature on selection in various study systems.

The directional-selection gradient vector ( $\beta$ ) obtained by the approach of Lande and Arnold (1983) describes the selection acting on the means of phenotypic traits, and have proven to be very useful in predicting evolutionary response through the Lande equation. The quadratic-selection gradient matrix ( $\gamma$ ) describes the selection acting on the (co)variances of traits independent of the directional selection gradients (which also act on the (co)variances). For multivariate normally distributed traits, the directional and quadratic selection gradients give the best quadratic approximation to the fitness surface, and can be interpreted, respectively, as the average slope and average curvature of the fitness surface experienced by the individuals in the population (Lande & Arnold, 1983). The fitness surface, or individual adaptive landscape, is a multivariate function relating the fitness of individuals to their phenotypic values, originally outlined by Pearson (1903). This surface is interesting in itself as it gives a complete description of the selection on individuals, and, in the absence of frequency-dependent selection, it can be thought of as a feature of the environment that is independent of the distribution of the phenotypes (Schluter, 1988). The selection gradients are also connected to the adaptive landscape outlined by Simpson (1944, 1953). This adaptive landscape is a multivariate landscape in which the height (the level of adaptation) is determined by the population mean fitness, and the other dimensions are population averages of phenotypic characters. The directional selection gradients are the slopes of the adaptive landscape, in the direction of their respective trait, at the

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multivariate mean of the trait distribution (Lande, 1979), while a combination of the linear and the quadratic selection gradients ( $\boldsymbol{\gamma} - \boldsymbol{\beta}\boldsymbol{\beta}^T$ ) gives the curvature (Phillips & Arnold, 1989).

Path analysis (Wright, 1920, 1934) and structural equation modelling have been suggested as extensions to the Lande and Arnold approach (Kingsolver & Schemske, 1991; Mitchell, 1992; Scheiner *et al.*, 2000). The main advantages of these methods are that they can take causal relationships into account, and allow a variable to affect other variables through intermediate steps. This provides insight into the selection process, and helps in identifying agents of selection. Traditionally, path analyses are done by setting up a predefined causal structure including direct effects and correlations between variables. Direct effects are estimated by multiple regression. An additional advantage of the path-analysis approach is that it can filter away some of the noise obscuring the relationship between traits and fitness, and can help reduce environmental and inbreeding covariance between fitness and phenotypic measurements. Environmental covariance between traits and fitness, misinterpreted as evidence of selection, is a recognized problem in phenotypic selection studies (Rausher, 1992; Scheiner *et al.*, 2002; Winn, 2004). Inbreeding, although not so often discussed, can also lead to such covariance (Willis, 1996). However, other methods also exist for removing this unwanted correlation. For example, in pollinator selection experiments, hand pollinated controls can be used to separate out the effect of pollinators (Galen, 1996; Fishman & Willis, 2008; Sandring & Ågren, 2009; Sletvold *et al.*, 2010; Parachnowitsch & Kessler, 2010).

Standard path analysis and structural equation models are limited as they are based on ordinary linear models, and can not include link functions and other types of residual distributions than Gaussian. To extend this approach, a customized fitness function based on functional biological relationships can be built to the available data. The parameters in this model can be estimated using generalized linear and non-linear mixed effects models or Bayesian techniques, allowing for many complexities beyond the standard path-analysis approach. This approach has an additional benefit as it can include any mathematical relationship between variables in order to model biological or physical constraints (see paper **III**).

Traditionally, selection gradients have been variance standardized in order to be comparable across traits. This measures selection in units of standard

deviations, and is a useful standardization, but not without disadvantages (Hereford *et al.*, 2004). Because the variance-standardized slope is a function of the population variance, it can not be used to describe the fitness surface. For example, two populations with different phenotypic variance that experience the same fitness surface will get different variance-standardized selection gradients. In addition, its standardization factor (phenotypic standard deviations) is not independent of additive genetic variance. Therefore, variance standardized selection gradients conflate selection with the response to selection, which was nicely separated by the Lande equation. However, variance standardized selection gradients are still useful as they measure the difference in fitness experienced by the extreme individuals in the population. Hereford *et al.* (2004) suggested using mean standardized selection gradients. Like the variance standardization, the mean standardization makes the selection gradients comparable among traits as a unit-free measurement, but with additional advantages. First, they are interpreted as the fitness consequence of proportional changes in trait values, and therefore capture a property of the fitness surface without regard to the variation within the population. Second, they can be used to measure the strength of selection since the mean standardized selection on fitness is one. This serves as useful benchmark as selection on fitness evidently is strong. Third, they link selection and evolvability (the mean standardized additive genetic variance (Houle, 1992)) in the mean standardized version of the Lande equation. Last, they are elasticities, and thereby link selection gradients to demographic elasticities (de Kroon *et al.*, 1986; van Tienderen, 2000).

### **Adaptive accuracy**

Identifying how well organisms are adapted to their environments helps us to understand evolution by natural selection and its constraints (Crespi, 2000). The degree of adaptation, or maladaptation, of a population can be defined in relation to Simpson's adaptive landscape as the difference between a population's mean fitness, and the height of the local adaptive peak, termed "lag load" by Maynard Smith (1976). However, this does not separate different sources of maladaptation.

Analogous to statistical estimation theory, Armbruster *et al.* (2004) suggested understanding maladaptation as an adaptive inaccuracy (Fig. 4; paper **V**). A population's adaptive inaccuracy have several components which can be estimated from the individual adaptive landscape (*sensu* Pearson, 1903).

A population can have reduced fitness because the population average of a trait is far from the optimum (bias), but also because of variation among individuals (imprecision). Assuming a quadratic fitness surface with a known optimum, the load due to bias can be quantified as  $\text{bias}^2$ , while the load due to imprecision is equal to the variance of the trait. These components of adaptive inaccuracy can also be quantified from individual trait values on a estimated fitness surface.

Hansen *et al.* (2006) extended the accuracy theory by including developmental imprecision, and Armbruster *et al.* (2009a) further developed it to include variation in the optimum as sources of maladaptation. The concept of adaptive accuracy has been used to study developmental imprecision using published studies on fluctuating asymmetry (Hansen *et al.*, 2006), directional asymmetry in insects wings (Pélabon & Hansen, 2008), and in the stamen-stigma fit of blossoms, both within population (Armbruster *et*

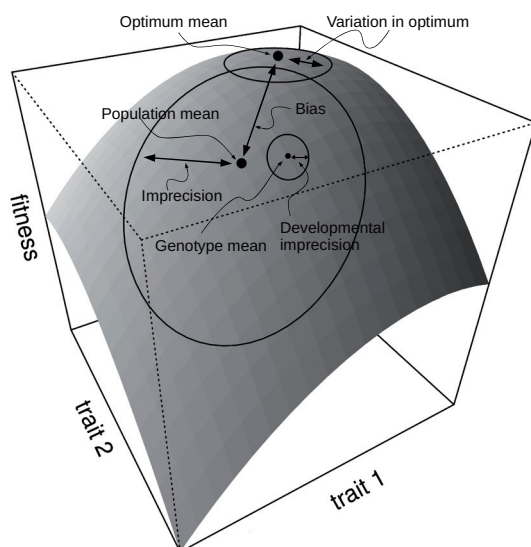


Fig. 4: The different components of a population's adaptive inaccuracy in two traits. Individuals in a population can have reduced fitness because the population mean is not at the optimum (bias) and because individuals on average have less fitness than the fitness at the mean of the population (imprecision). In addition, variation due to developmental imprecision can contribute if the average phenotype of a genotype have higher fitness than the mean fitness of all phenotypes of the same genotype. (Developmental imprecision is a component of imprecision if imprecision is defined by variation in phenotypes and not variation in genotype means.) Note that variation in the optimum will shift the whole fitness surface, and can also contribute to inaccuracy.

*et al.*, 2009a) and among populations and species (Armbruster *et al.*, 2009b).

#### **Genetic architecture, natural selection and adaptive accuracy of signals**

The abundant evidence for persistent female choice for highly ornamented males, when there is no apparent direct benefit, has been puzzling (Kirkpatrick & Ryan, 1991; Andersson, 1994). As a solution, “good genes” models of sexual selection (e.g. Zahavi, 1975, 1977; Hamilton & Zuk, 1982; Andersson, 1986; Whitlock & Agrawal, 2009) predict that sexually selected traits are honest indicators of genome quality. However, in the face of strong directional selection by females, genetic variance in sexually selected traits should erode, leaving little potential for genetic benefits of female choice. This forms the basis of the lek paradox (Kirkpatrick & Ryan, 1991; Andersson, 1994).

Rowe & Houle (1996) suggested a solution to the lek paradox, in which the functional genetic architecture underlying the sexual traits involves many genes pleiotropically linked to condition. This evolves by selection for high allocation of resources to build or maintain secondary sexual traits, which in turn leads to a strong dependence of secondary sexual traits on the resource pool (condition) of the individual. Sexually selected traits will therefore evolve condition dependence and capture genetic variation of traits affecting condition. Because many traits affect condition, sexually selected traits are expected to harbour much genetic variation. In this model, acquisition genes lead to positive genetic correlations between secondary sexual traits and other condition-dependent traits, and allocation genes lead to negative genetic correlations. The observed genetic correlation depends on the amount of genetic variation in the acquisition genes relative to the allocation genes (Houle, 1991). This theory is in line with the high additive genetic variance found in these traits when compared with morphological traits within similar taxa (Pomiankowski & Møller, 1995). Note that the study by Pomiankowski and Møller (1995) used mean standardization to compare additive genetic variance among traits, as variance standardization (such as heritability) is inappropriate (Houle, 1992).

Inbreeding can be used to study the model of Rowe and Houle (1996). The genetic variance captured by sexually selected traits includes the genetic load of condition, which is presumably high. Condition-dependent sexually selected traits should therefore be strongly influenced by inbreeding (Drayton *et al.*, 2007; Bolund *et al.*, 2010). Except for

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the effect of inbreeding on courtship behaviour, which in general is severe (e.g. Santibañez & Waddington, 1958; Sharp, 1984; Farr & Peters, 1984; Meffert & Bryant, 1991; Miller *et al.*, 1993; van Oosterhout *et al.*, 2003; Joron & Brakefield, 2003; Mariette *et al.*, 2006; Ala-Honkola *et al.*, 2009), other sexually selected traits are not very well studied. These include song characteristics (Aspi, 2000; Drayton *et al.*, 2007; Bolund *et al.*, 2010), ornamentation (Sheridan & Pomiankowski, 1997; van Oosterhout *et al.*, 2003; Mariette *et al.*, 2006; Bolund *et al.*, 2010; Zajitschek & Brooks, 2010), and sperm competition (Konior *et al.*, 2005). The effect of inbreeding on these traits varies within and between studies, and no consensus is reached on the effect of directional dominance on sexually selected traits.

In contrast to sexual signals in animals, it is in many cases easy to elucidate the purpose and honesty of floral signals. Floral signals often act as honest advertisements of amount of reward offered to the pollinators (e.g. Cresswell & Galen, 1991; Fenster *et al.*, 2006). Honesty of floral signals can easily be examined by the phenotypic correlation between the amount of reward and the size of the signal. Interestingly, there is a large variation in honesty among plants. They differ from being deceptive to providing very accurate information about the amount of reward (reviewed by Schaefer *et al.*, 2004). Different levels of honesty are probably selected for by differences in pollinator behaviour. For example, a nectar addition experiment on a deceptive orchid demonstrated that both pollinarium removal and geitogamy increased when nectar was added (Johnson *et al.*, 2004). Hence, in a pollinator-rich environment, the increased pollen export will favour deceptive individuals. On the other hand, high level of honesty may facilitate floral constancy of pollinators in environments where interspecific competition for pollinators occur (*sensu* Waser, 1983). The most honest advertisement is the direct and conspicuous display of the reward itself. I refer to this as “full-disclosure honesty” (paper III). This gives the reward a dual function of reward and signal (Hansen *et al.*, 2007; Raguso, 2008), and creates a potential for direct pollinator-mediated selection on the reward. Full-disclosure honesty has evolved in several species, for example in scent-rewarding plants (Dressler, 1968; Williams & Dodson, 1972; Ackerman, 1983), in plants where bees can detect the presence of nectar by visual

inspection (Goulson *et al.*, 2001), and in plants where pollinators can assess the amount of pollen by visual inspection (Cresswell & Robertson, 1994; Lunau, 2000; Goulson *et al.*, 2001). Despite the relative commonness of full-disclosure honesty, selection on reward has usually been assumed to be indirect, and few studies have focused on disentangling selection on signal from selection on reward (but see Cresswell & Galen, 1991; Schemske & Bradshaw, 1999; Golding *et al.*, 1999; Armbruster *et al.*, 2005; Fenster *et al.*, 2006; Makino & Sakai, 2007). Furthermore, I know of only four studies that have estimated selection gradients jointly for signal and reward (Mitchell *et al.*, 1998; Caruso, 2000, 2001; Castro *et al.*, 2009). Signals are not necessarily only costly through condition dependence and allocation of resources. Predators or parasites probably impose a major cost on sexual signals, as it is commonly observed that they exploit these traits in locating their prey (Kotiaho, 2001). For floral signals, evidence for selection by antagonists on these traits has recently started to accumulate (Strauss & Irwin, 2004; Adler, 2008; Carlson & Holsinger, 2010). To understand the total selection when several selective agents (e.g. both pollinators and seed predators) are involved, an integrative approach is necessary. Path analysis and structural equation models are excellent tools to disentangle the selective process, as they can identify effects of different selective agents. These tools have been used to demonstrate the relative effects of different pollinators and to disentangle the effect of pollinators and nectar robbers (Schemske & Horvitz, 1988; Stanton *et al.*, 1991; Irwin, 2006), and between pollinators and herbivores or seed predators (Schemske & Horvitz, 1988; Cariveau *et al.*, 2004; Ashman & Penet, 2007; Parachnowitsch & Caruso, 2008).

There are no previous studies focusing on the adaptive accuracy of signalling traits. However, in a meta-analysis, Hansen *et al.* (2006) quantified the contribution of developmental imprecision to adaptive accuracy. In sexually selected traits, developmental imprecision accounted for 9.1% (median) of the total variation in the traits, and seems therefore to contribute substantial to population maladaptation. For comparison, in naturally selected traits, developmental imprecision accounted for 4.5% (median) of the total variation.



## AIM

The aim of this thesis was to study three fundamental aspects of evolution: genetic architecture, natural selection, and adaptive accuracy. To accomplish this I used two study systems involving guppies, a tropical fresh-water fish, and *Dalechampia*, a genus of tropical vines. My specific research objectives were:

1. Genetic architecture of ornaments in guppies revealed by inbreeding experiment (papers I and II)
2. Natural selection on floral signals in *Dalechampia* (papers III, IV and V)
3. Adaptive accuracy of floral signals in *Dalechampia* (papers IV and V)

## GENERAL METHODS

### *The guppy study system*

*Poecilia reticulata* Peters (Poeciliidae), known as “the guppy”, is a popular aquarium fish as well as a commonly used model species in several scientific disciplines. The guppy is a livebearer (it gives birth to free-swimming offspring) and is native to streams of Trinidad and adjacent areas of South America. It has high sexual dimorphism with the drab female being larger than the male who displays multiple ornaments composed of diverse colour patterns and an enlarged caudal fin (Fig. 5). Substantial knowledge of the evolutionary ecology and the genetics of the guppy has accumulated through the work of many scientists (reviewed by Houde, 1997; Magurran, 2005). A large fraction of this work has focused on the diverse colour patterns of the male. Early work on guppies was mainly on the inheritance of these colour patterns. This work was initiated by Winge (1922a, b, 1927, 1937; Winge & Ditlevsen, 1947). He showed that most colour patterns are inherited as a unit, linked to the sex chromosomes (mostly Y linkage). The strong Y linkage has later been supported by quantitative-genetics studies in which the inheritance of male

colouration was high through the father relative to the mother (Houde, 1992; Brooks & Endler, 2001). This genetic architecture increases the probability of deleterious alleles to “hitch-hike” with preferential colour genes (Rice, 1987, 1994; Charlesworth & Charlesworth, 2000; Engelstädter, 2008). Haskins *et al.* (1970) found such deleterious alleles tightly linked with genes coding for the colour patterns on the Y chromosome, and a negative genetic correlation between ornamentation and survival has been reported in the guppy (Brooks, 2000).

Several studies have investigated the effect of inbreeding in guppies. The earliest (Farr & Peters, 1984) found no effect of inbreeding on several behavioural traits after one generation of full-sib mating. This was not the case in two recent studies which showed inbreeding depression in courtship behaviour (van Oosterhout *et al.*, 2003; Mariette *et al.*, 2006). Several studies have investigated the effect of inbreeding on the ornamental traits (Sheridan & Pomiankowski, 1997; van Oosterhout *et al.*, 2003; Mariette *et al.*, 2006; Zajitschek & Brooks, 2010). The results of these studies differed, probably due to difference in power (i.e. sample size and level of



Fig. 5: Male *Poecilia reticulata*. (Photos by Geir H. Bolstad)

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inbreeding) to detect an effect, but maybe also because of genetic differences among populations (e.g. Sheridan & Pomiankowski, 1997). Other traits studied include offspring survival (Fuijo & Nakajima, 1992), salinity tolerance (Shikano *et al.*, 2001), and sperm quality and quantity (Zajitschek *et al.*, 2009; Zajitschek & Brooks, 2010).

Sexual selection on male ornaments in the guppy has been extensively studied (e.g. Endler, 1983; Houde, 1987; Houde & Endler, 1990; Reynolds, 1993; Nicoletto, 1993; Endler & Houde, 1995; Brooks & Caithness, 1995; Brooks & Endler, 2001; Kodric-Brown & Nicoletto, 2001; Brooks, 2002; Blows *et al.*, 2003). These studies show that there is female preference for different aspects of the colour spots (area, number, and colour) and the enlarged caudal fin. However, preference differs among studies and populations. Mate choice has been shown to covary with patterns of divergence in male ornamentation, presence of predators, and light conditions under which male display takes place (Houde & Endler,

1990; Endler, 1991; Endler & Houde, 1995; Long & Rosenqvist, 1998). Other selection pressures have been less studied, but the classic study of Endler (1980) demonstrated that guppies evolved reduced ornamentations in artificial ponds with predators compared to ponds without predators. The selective pressure from predators on colour patterns was later confirmed by experiments in which predators consistently approached, attacked, and captured the most colourful in a pair of male guppies (Godin & McDonough, 2003).

The guppies used in this thesis stem from a founding population of approximately 500 guppies captured in lower Quare River in Trinidad in 1998. The guppies were collected by Gunilla Rosenqvist, Åslaug Viken, and Ian A. Fleming. This founding population was used to initiate several experimental treatments each with 10 replicates. In this thesis, I used three of these experimental treatments, giving 30 replicates in total. These three treatments were designed to expose the guppies to three different levels

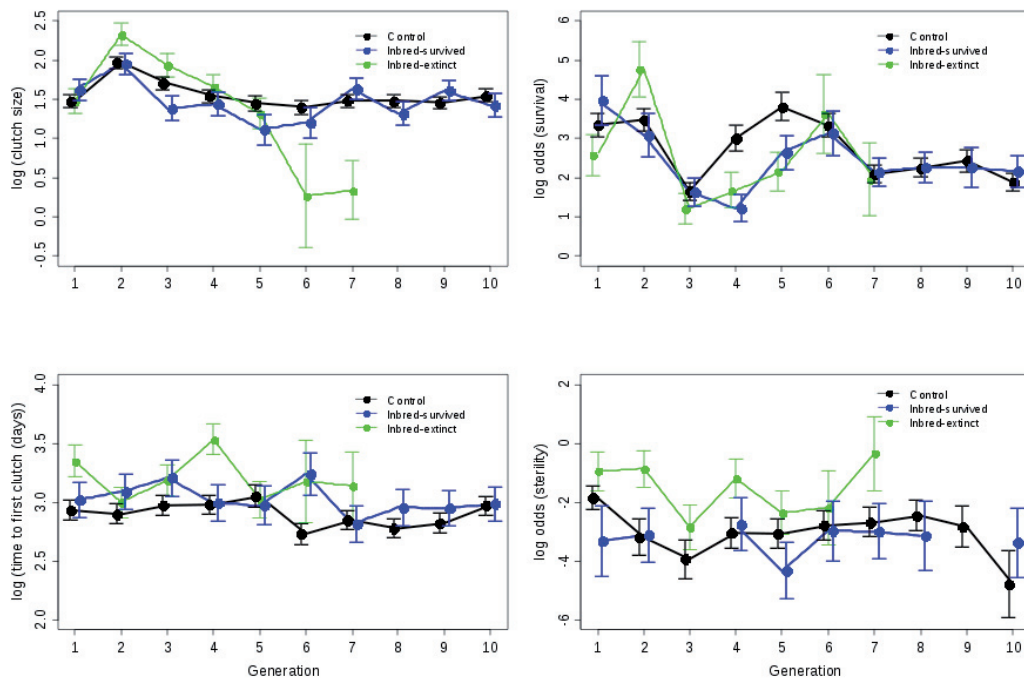


Fig. 6: Difference in the expression of life history traits between the control treatment (black line) and the inbred treatment across the ten generations. The inbred populations that went extinct (green line) are plotted separately from the populations that survived (blue line). Mean values for each treatment correspond to the parameter estimates (±SE) from a model controlling for variation in mother length (clutch size, time to first clutch and sterility) and rearing density (survival). The lack of parameter estimates for sterility at generation 3 and 9 is due to the absence of sterile females in the inbred treatment. The figure is taken from Larsen *et al.* (in review).



Fig. 7: Three *Dalechampia* species, from left to right: *D. schottii*, *D. scandens*, and *D. ipomoeifolia*. (Photos left and center by Geir H. Bolstad, photo right by Scott Armbruster)

of inbreeding (low, intermediate, and high) by manipulating the effective population size in the replicates. The replicates are referred to as populations because they consist of interbreeding individuals, with no mating between replicates.

During the course of this experiment, ten out of the initial 30 replicates were lost, and in the later generations (from generation eight) nine low inbred, seven intermediate inbred, and four high inbred populations were remaining. During the first six generations, the four high inbred populations experienced purging affecting several life history traits (Larsen *et al.*, in review). This was suggested by an increase of inbreeding depression in survival and clutch size during the first four to six generations with a subsequent rebound to the level of the low inbred populations (used as control). Two other traits, sterility and number of days to first clutch, showed weaker, but similar changes across generations (Fig. 6). Selection acted probably most on survival as just a few offspring were needed to start a new generation, resulting in only a weak selection on clutch size. However, selection on pre-natal survival may have been strong and could be observed through differences in clutch size. The loss of six populations in the inbred treatment indicates that removal of deleterious alleles also occurred by extinction of populations that presumably harboured high genetic load.

At generation nine, I estimated differences between the low-inbred (control), the medium-inbred, and the high-inbred populations in several life-history and ornamental traits of male guppies. These included length at birth, juvenile growth rate, length at maturation, adult growth rate, adult body length, relative orange area, caudal-fin size, relative black area, and mean redness of orange spots (CIE  $a^*$ ). This

experiment was the basis of paper I. At generation 11, I mated fish between the four most inbred populations to make a completely outbred group of fish. Orange area and caudal-fin size in this group were compared to the four inbred populations and the control populations at generation twelve. This experiment formed the basis of paper II.

#### *The Dalechampia study system*

*Dalechampia* is a genus of about 120 species, mostly consisting of perennial vines, distributed throughout most of the lowland tropics (Armbruster & Mziray, 1987). Species of *Dalechampia* exhibit large variation in size and colour of blossom structures, as well as in pollination ecology (Armbruster, 1985, 1986, 1988, 1993; Armbruster & Baldwin, 1998). Blossoms have similar morphology, and usually comprise two large showy bracts, three pistillate flowers, 4-16 staminate flowers, and, in most species, a resin-secreting gland (Webster & Armbruster, 1991). The resin is collected and used in nest construction by female bees, including the euglossines *Euglossa*, *Eulaema*, and *Eufriesea*, the meliponine *Trigona*, and the megachilids *Hypanthidium* and *Heriades* (Armbruster, 1984; Armbruster & Herzig, 1984). A few species of *Dalechampia* (ca. 20) do not have a resin-secreting gland. In some, the gland has evolved to secrete fragrance (Armbruster, 1993), and in rest of the species not secreting resin, the gland is absent and fragrance or pollen is the main reward (Armbruster, 1993; Armbruster & Baldwin, 1998). The fragrance is collected by male euglossine bees which probably use fragrances to attract females (Webster & Armbruster, 1982; Armbruster, 1989, 1993).

Several aspects of the radiation of *Dalechampia* have been studied in detail. The genus

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originated in western Gondwana or South-America in the mid Cretaceous or early Tertiary, respectively, and spread through the tropics (Armbruster, 1994). A switch from specialist pollination by resin collecting bees to generalized pollination by a variety of pollen collecting insects occurred with dispersal to Madagascar, where the resin-collecting bees are largely absent (Armbruster & Baldwin, 1998). Pre-adaptations have played a major role in the evolution of novel attraction and defence systems of *Dalechampia* (Armbruster *et al.*, 2009c). For example, the resin gland is probably an exaptation of resin defence. This occurred sometime after the divergence between *Dalechampia* and its closest relative *Tragia*. The use of resin as a reward has been lost five or six times in *Dalechampia* followed by a redeployment of resin for defence of male flowers. Moreover, there has been correlated evolution of several defence systems of flowers, seeds and leaves (Armbruster *et al.*, 2009c). The gland size, the anther-stigma distance, and the gland-stigma distance seem to have evolved along an adaptive ridge or cordillera (chain of peaks) according to the size of the species pollinator (Armbruster, 1988, 1990). Competition over pollinators with congeners also seems to have played a role and can explain 10-20% of the among population differences in blossom morphology of *D. scandens* (Hansen *et al.*, 2000).

Quantitative-genetics analyses have revealed that there is additive genetic variation in several floral characters in *D. scandens*, but most traits are only expected to change by a fraction of a percent per generation in the face of selection (Hansen *et al.*, 2003a). Genetic correlations further reduce the capacity for *D. scandens* to evolve (Hansen *et al.*, 2003b). Consistent with the Berg's hypothesis (Berg, 1959, 1960), traits of *D. scandens* involved in pollination are canalized and decoupled from environmentally induced variation in vegetative traits. This is even true for the bract blade which is closely homologous to the leaf blade (Hansen *et al.*, 2007; Pélabon *et al.*, 2010).

In this thesis, I used data from three phenotypic selection experiments involving three species of *Dalechampia* (Fig. 7). The first was on *D. ipomoeifolia* Benth and carried out close to Lastoursville in Gabon from December 1996 to March 1997 by Liv Antonsen and Scott Armbruster (see Armbruster *et al.*, 2005). The blossoms of *D. ipomoeifolia* have 12 to 16 staminate flowers and three pistillate flowers; they have large involucre bracts and relatively small glands. The pollinator was female *Heriades* nr. *spiniscutis* (Megachilidae). This

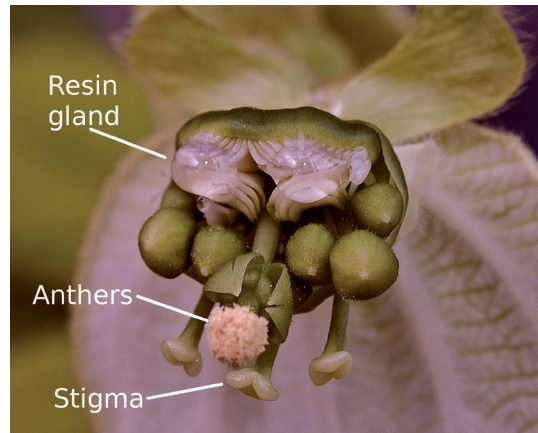


Fig. 8: Morphology of *D. scandens*. (Photo by Per Harald Olsen)

study is included in paper V. The second study was carried out in the state of Veracruz in Mexico from August to October 2006 by Rocío Pérez-Barrales on *D. scandens* L. The blossoms of *D. scandens* have 10 staminate flowers and three pistillate flowers. The relatively large bracts have a dual function of advertisement and protection. They close around the blossom at night, and later, around the maturing fruit. The pollinator was female *Hypanthidium* cf. *melanopterum* (Megachilidae). This study is included in papers IV and V. The last study was carried out by me close to Puerto Morelos in Quintana Roo, Mexico from September to October 2007 on *D. schottii* Greenman. Blossoms of *D. schottii* are relatively small and comprise only four staminate flowers and three pistillate flowers. While the other two study species have transparent or whitish resin, *D. schottii* has deep blue resin. The pollination in this period was mostly by female *Euglossa* cf. *viridissima* (Apidae), but also by female *Hypanthidium* cf. *melanopterum*. This study is included in papers III and V.

Four blossom traits were measured in each of these three studies (see Fig. 8): size of the bracts, area of the resin bearing surface (gland area), the minimum distance separating the gland from the middle stigma (gland-stigma distance), and the minimum distance separating the anthers from the middle stigma (anther-stigma distance). In addition, several components of blossom female fitness were recorded. These included pollen arrival in the last day in the female phase and the first day in the male phase (in all three studies), probability of being visited during one day (*D. schottii*), seed set (*D. scandens*), and number of predated seeds (*D. scandens*).

From these data I constructed a fitness

function for each of the three selection experiments. The relationship between pollen load and seed set estimated for *D. scandens* was used in the fitness functions of all three species. The parameters in these fitness functions were estimated by generalized linear

mixed models. From the fitness functions I obtained selection gradients by applying the methodology of Lande and Arnold (1983) and calculated difference components of adaptive inaccuracy.

## MAIN RESULTS AND DISCUSSION

### *Genetic architecture of ornaments in guppies revealed by inbreeding experiment (papers I and II)*

In paper I we estimated the effect of inbreeding on ornaments and life history traits in four small populations of guppies by comparing them to nine control populations. The effect of inbreeding was estimated at the ninth generation of laboratory breeding at which the average inbreeding coefficient had reached 0.33 (range: 0.20-0.53). The small populations had a history of purging (Larsen *et al.*, in review), and accordingly we did not find any inbreeding depression in the life history traits. In contrast, the relative orange area responded severely with 33% smaller relative area in the inbred populations compared to the control populations. The other ornaments, the caudal-fin size, the relative black area, and the redness of orange spots (CIEa\*), had a much weaker response. However, the reduction of 3% in caudal-fin size was marginally significant.

The lack of effect of inbreeding on some of the ornaments in these populations was probably due to lack of directional dominance. Either because these traits do not have this form of dominance, or because alleles causing this dominance had been purged. The relative orange area, on the other hand, seems to harbour much directional dominance. In addition, the response to inbreeding by the relative orange area was non-linear, with seven populations with intermediate level of inbreeding having a much larger orange area than expected. This non-linear response is strikingly similar with the one observed by van Oosterhout *et al.* (2003), and suggests that synergistic epistasis is present. However, we suggest an alternative hypothesis that also can explain this pattern. A negative genetic correlation between ornamentation and survival has been observed in male guppies (Brooks, 2000), suggesting that purging on survival could indirectly select for smaller orange area, and thereby causing the orange area to diminish with increasing inbreeding.

In paper II we tested the purging hypothesis by estimating how much of the decline in the orange area that was due to increased homozygosity, and how

much that was due to selection. We mated individuals between the four inbred populations at generation 11 to make a completely outbred group of individuals. This group had larger orange area than the inbred populations, but still far smaller than the control populations. The difference between the inbred populations and the control populations in orange area was 2.02 mm<sup>2</sup> (a decrease of 32.7%), of this 0.37 mm<sup>2</sup> (18.3%) was due to increased homozygosity (i.e. the difference between the inbred and the outbred treatment), while 1.65 mm<sup>2</sup> (81.7%) was due to selection (i.e. the difference between the outbred and the control treatment). This suggests that partly recessive alleles positively affecting orange have a negative effect on survival.

This result has several important implications. First, it shows that there may be strong genetic constraints on evolution towards larger orange area, and that sexual selection can have some deleterious effects. This is in line with Fisher's prediction, where sexually selected traits will evolve to the point where their positive effect due to sexual selection is counterbalanced by their negative effect on viability (Fisher, 1930). Second, it shows that purging can have a negative effect on an important fitness character. This is somewhat counter-intuitive, as purging is normally thought of as a fitness enhancing process. Last, it underscores the necessity of controlling for purging in inbreeding experiments, which has not previously been done in studies of inbreeding on sexually selected traits.

In the simple model for functional genetic architecture of genetic correlations put forward by Houle (1991), positive genetic correlations between traits stem from genetic variation in acquisition while negative genetic correlations stem from genetic variation in allocation. If we interpret our results according to this model there seems to be partly recessive alleles that allocates much resources to orange when they are in homozygous state.

A prediction of the "genetic capture" hypothesis (Rowe & Houle, 1996) is that condition-dependent sexually selected traits should be strongly affected by inbreeding (i.e. increased homozygosity) due to the



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high mutational load of condition (Drayton *et al.*, 2007; Bolund *et al.*, 2010). Our results suggest that the expected response to inbreeding by these traits is not so clear. This is because recessive alleles allocating resources to sexually selected traits can have an opposite effect than recessive alleles affecting condition. This can deflate the relationship between the mutational load of condition and sexually selected traits, leading to a weak response of these traits to inbreeding. In addition, when purging is not controlled for, it hampers our ability to interpret the effect of inbreeding.

The effect we observed on the orange area can also be explained by several confounded hypotheses including maternal effects and selection in addition to selection against deleterious alleles. However, there are good arguments against all of these hypotheses, and we think that the purging hypothesis is by far the most likely (paper II).

### **Natural selection on floral signals in *Dalechampia* (papers III, IV and V)**

Most species of *Dalechampia* have openly presented resin, which attracts pollinators, and two conspicuous petaloid bracts, which may play the role of advertisement. This genus is therefore excellent for exploring pollinator-mediated selection on advertisement versus reward. In two of the species we have studied, *D. ipomoeifolia* (Armbruster *et al.*, 2005, paper V) and *D. scandens* (paper IV), pollinators selected directly for larger bracts and only indirectly for larger reward. The bees pollinating these two species seem to rely on the “honest” correlation between the size of the bracts (the signal) and the size of the gland (the amount of reward) in order to maximize their foraging. In the third species, *D. schottii*, the bees directly selected for larger glands (paper III). In this way, the gland has a dual function of both signal and reward. We term this full-disclosure honesty (paper III). Interestingly, the resin of *D. schottii* is deep blue, while the two other species have transparent to white resins. The blue colour may be an adaptation to promote full-disclosure honesty. However, *D. schottii* may not be completely honest, as floral resins of *Dalechampia* are very sticky, and not all of the resin can be removed by bees (Armbruster, 1984). Consequently, the deep-blue resin may have the appearance of being abundant even when the gland is scraped almost clean by previous visitors.

There is also additional evidence for differences in the selection pressures acting on these three species. *Dalechampia schottii* has relatively large glands and small bracts when compared to the

other two species. This could be interpreted as an evolutionary response to the observed differences in selection pressures.

Although the estimated linear selection for larger glands in *D. schottii* was 14.6% of the strength of selection on fitness, there may not be an evolutionary response even in the presence of additive genetic variance in the trait. First, there may be other selective forces acting on the trait creating net stabilizing selection. Second, fluctuating selection, which is commonly observed in natural populations (Siepielski *et al.*, 2009), can create stabilizing selection on average. In our study, the main pollinator was a large female *Euglossa*, but this may be atypical, as *D. schottii* has previously been classified as a “small-bee-pollinated” *Dalechampia* (Armbruster, 1993; Hansen *et al.*, 2000). Last, multivariate genetic constraints may prevent the trait evolving through indirect selection (Hansen & Houle, 2008; Walsh & Blows, 2009). In all three studies we observed selection for reduced gland-stigma distance and anther-stigma distance, and both of these are positively genetically correlated with gland area and bract size in *D. scandens* (Hansen *et al.*, 2003b), which may constrain the evolutionary response to directional selection for larger gland area or bract size (Armbruster *et al.*, 2005).

For *D. scandens*, we estimated selection by pre-dispersal seed predators in addition to selection by pollinators (paper IV). The predators were weevil larvae which feed on the seeds where their mothers have oviposited. The net selection on bract size by pollinators and seed predators was stabilizing. Pollinators imposed a positive selection on bract size, as they visited blossoms with large bracts more frequently than blossoms with small bracts, and thereby increased seed set of large-bracted blossoms. However, these blossoms were also more frequently attacked by seed predators who imposed a negative selection pressure on bract size. Moreover, in addition to the direct effect of bract size on predation, seed predators also based their oviposition choice on pollen load in the bisexual stage and seed production, and since bract size positively influenced both pollen arrival and seed production, the negative selection on bract size from seed predators was strengthened.

All three selection experiments were done at the blossom level, which is not necessarily the same as selection at the individual (plant) level. The main reason for this is that the plants grow in entangled clumps, making it difficult to identify single individuals, but also the fact that bees and pre-dispersal seed predators probably choose among

blossoms and not among individual plants within a patch. This makes it reasonable to work on the blossom level. However, the selection for the average blossom trait of the plant may not be fully explained by selection at the blossom level if these selective agents can distinguish between plants and use this information to choose differently among the blossoms within a plant than among all the blossoms within a patch. Although this effect may be present, we think that most of the selection caused by pollinators and seed predators was captured by their effect at the blossom level.

#### ***Adaptive accuracy of floral signals in Dalechampia (papers IV and V)***

A population's maladaptation can be estimated as an adaptive accuracy which can be decomposed into several components (Fig. 4). In papers **IV** and **V**, we developed a multivariate theory of adaptive accuracy, which enabled us to estimate a population's adaptive inaccuracy due to several traits, and to compare the contribution of the different traits to inaccuracy. We employed this theory on the three *Dalechampia* species using the estimated fitness functions from the three phenotypic selection experiments. The results are essentially heuristic as we probably did not capture all selection pressures acting on these traits, and the experiments were carried out in a limited time frame not capturing the temporal dynamics. Nevertheless, the results give us information about the adaptive accuracy regarding the estimated fitness surface, and because we know the selective agents of these surfaces, we can interpret the results accordingly.

The traits on which the pollinators based their foraging decisions (gland area in *D. schottii*, and bract size in *D. scandens* and *D. ipomoeifolia*) had an inaccuracy of only a few percent of maximum fitness. Therefore, these traits seemed to be relatively well adapted to the estimated selection pressures. This was true even for the two species (*D. schottii* and *D. ipomoeifolia*) where we estimated only pollinator selection that was directional. In these two species, bias was the main contribution to inaccuracy of the traits attracting pollinators. In *D. scandens*, where the selection for bract size was stabilizing due to

conflicting selection from pollinators and pre-dispersal seed predators, imprecision was the main contributor.

The fitness penalty for inbred seeds was not included in our models, which may explain the large bias in anther-stigma distance (ability to self pollinate). For *D. scandens*, we therefore fixed anther-stigma distance at its mean in order to investigate the imprecision of the other measured traits assuming that the anther-stigma distance was perfectly adapted (i.e. does not contribute to population inaccuracy) and that the population mean was the adaptive optimum. Under this scenario, the inaccuracy of the population was reduced substantially (from 9% to 3%) and the signal (bract size) had virtually no bias. This means that the population mean almost perfectly matched the optimum, and all the contribution from the signal to inaccuracy was due to imprecision.

For *D. scandens*, we also investigated within individual imprecision, that is, imprecision due to morphological differences between blossoms within a plant. Such imprecision is due to developmental noise, but also spatial or temporal micro-environmental variation may contribute. Within- and among-individual imprecision in bract area contributed almost exactly the same to inaccuracy (0.06 seeds and 0.08 seeds respectively), showing that within-individual maladaptation was surprisingly high when compared to the among-individual maladaptation. This may be due to the stabilizing selection on the signal, because stabilizing selection can lead to low among-individual variation, but does not necessarily affect the within-individual variation. This analysis was done on phenotypic data collected in the greenhouse and the adaptive surface of *D. scandens* estimated from the natural population.

Variation in the fitness landscape may also contribute to imprecision. This was investigated in *D. scandens* by estimating differences in the adaptive landscapes between patches of blossoms. We estimated contribution of patch variation to both bias and imprecision. Bract size contributed substantially to an increase in environment-specific bias, but also to a decrease in environment-specific imprecision. The negative environment-specific imprecision suggests that the individuals are locally adapted for this trait.

## CONCLUSION AND PERSPECTIVES

This thesis demonstrates several important aspects regarding signal evolution. Investigation of the genetic architecture of ornaments in male guppies revealed that some sexual signals can be genetically

constrained to evolve further elaboration, and may therefore have deleterious evolutionary consequences for the receiver. However, such signals may still be honest indicators of good genes as long they are

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positively correlated with lifetime fitness (Kokko, 2001). Investigation of the selection pressure on floral signals in *Dalechampia* revealed that in some species the pollinators rely on an honest correlation between the reward (amount of resin) and the advertisement (size of the bracts) to maximize their foraging, causing a direct selection on the advertisement but only an indirect selection on the reward. In another species this relationship was the opposite. In one phenotypic selection study we included the selection pressure from an antagonist and showed that this can be important for understanding the evolution of signals, by imposing a cost on the signaller. By developing a multivariate theory of adaptive accuracy and using this in combination with the phenotypic selection studies, we demonstrated how to estimate meaningful parameters for maladaptation. These estimates suggest that the floral signals included in this thesis were fairly well adapted to the selective pressure caused by the receivers.

Several future challenges emerge from the work of this thesis. The involvement of antagonistic pleiotropy in the genetic basis of sexual signals needs further investigation. This can be studied by inbreeding. In studies of inbreeding, the effect of purging through pleiotropy, and in particular through antagonistic pleiotropy, have largely been neglected. This effect deserves to be studied, first of all because it provides valuable information about the genetic basis of the traits, but also because it needs to be controlled for in cases where directional dominance is the primary focus. Thus, there seems to be a need for a quantitative genetics model for estimating the various parameters affecting phenotypic response to inbreeding (i.e. directional dominance, synergistic epistasis, and purging) in the same experiment. Making such a model should be possible by

implementing the inbreeding coefficient into line-cross theory, which could be used to analyse inbreeding experiments with various crosses between control and inbred lines. A further extension would be to combine such a model with the quantitative genetics model for estimating family variance parameters of inbreeding depression (e.g. Moorad & Wade, 2005).

Much is known about the evolution and ecology of various floral traits in *Dalechampia*. However, the colour of the resin remains little studied (but see Armbruster, 2002). The studies included in my thesis predict that the colour of the resin may be involved in the degree of honesty among *Dalechampia* species, and call for a phylogenetic analysis of this. The effect of selection on advertisements versus rewards also needs further investigation.

The fitness model approach used for analysing the fitness surface of the three species of *Dalechampia* can be extended in several ways. First, implementing the cubic-spline method introduced to estimate fitness surfaces by Schluter (Schluter, 1988; Schluter & Nychka, 1994) would give the benefit of a non-parametric estimate of the fitness surface. Second, including environmental variables would allow us to study and explain environmental variation of the fitness surface. Last, to develop it into a stochastic model would allow us to obtain fitness surface distributions rather than deterministic estimates.

Adaptive accuracy theory can also be extended. In particular it would be interesting to include constraints in the model, first of all because some constraints are universal and can not be circumvented by adaptive evolution, but also in order to study the maladaptation due to some constraints while others are controlled for.

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# Paper I

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# Paper II

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# Paper III

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# Paper IV

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# Paper V

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**Doctoral theses in Biology**  
**Norwegian University of Science and Technology**  
**Department of Biology**

<b>Year</b>	<b>Name</b>	<b>Degree</b>	<b>Title</b>
1974	Tor-Henning Iversen	Dr. philos Botany	The roles of statholiths, auxin transport, and auxin metabolism in root gravitropism
1978	Tore Slagsvold	Dr. philos Zoology	Breeding events of birds in relation to spring temperature and environmental phenology
1978	Egil Sakshaug	Dr.philos Botany	"The influence of environmental factors on the chemical composition of cultivated and natural populations of marine phytoplankton"
1980	Arnfinn Langeland	Dr. philos Zoology	Interaction between fish and zooplankton populations and their effects on the material utilization in a freshwater lake
1980	Helge Reinertsen	Dr. philos Botany	The effect of lake fertilization on the dynamics and stability of a limnetic ecosystem with special reference to the phytoplankton
1982	Gunn Mari Olsen	Dr. scient Botany	Gravitropism in roots of <i>Pisum sativum</i> and <i>Arabidopsis thaliana</i>
1982	Dag Dolmen	Dr. philos Zoology	Life aspects of two sympatric species of newts ( <i>Triturus, Amphibia</i> ) in Norway, with special emphasis on their ecological niche segregation
1984	Eivind Røskaft	Dr. philos Zoology	Sociobiological studies of the rook <i>Corvus frugilegus</i>
1984	Anne Margrethe Cameron	Dr. scient Botany	Effects of alcohol inhalation on levels of circulating testosterone, follicle stimulating hormone and luteinizing hormone in male mature rats
1984	Asbjørn Magne Nilsen	Dr. scient Botany	Alveolar macrophages from expectorates – Biological monitoring of workers exposed to occupational air pollution. An evaluation of the AM-test
1985	Jarle Mork	Dr. philos Zoology	Biochemical genetic studies in fish
1985	John Solem	Dr. philos Zoology	Taxonomy, distribution and ecology of caddisflies ( <i>Trichoptera</i> ) in the Dovrefjell mountains
1985	Randi E. Reinertsen	Dr. philos Zoology	Energy strategies in the cold: Metabolic and thermoregulatory adaptations in small northern birds
1986	Bernt-Erik Sæther	Dr. philos Zoology	Ecological and evolutionary basis for variation in reproductive traits of some vertebrates: A comparative approach
1986	Torleif Holthe	Dr. philos Zoology	Evolution, systematics, nomenclature, and zoogeography in the polychaete orders <i>Oweniimorpha</i> and <i>Terebellomorpha</i> , with special reference to the Arctic and Scandinavian fauna
1987	Helene Lampe	Dr. scient Zoology	The function of bird song in mate attraction and territorial defence, and the importance of song repertoires
1987	Olav Hogstad	Dr. philos Zoology	Winter survival strategies of the Willow tit <i>Parus montanus</i>
1987	Jarle Inge Holten	Dr. philos Botany	Autecological investigations along a coast-inland transect at Nord-Møre, Central Norway
1987	Rita Kumar	Dr. scient Botany	Somaclonal variation in plants regenerated from cell cultures of <i>Nicotiana glauca</i> and <i>Chrysanthemum morifolium</i>

1987	Bjørn Åge Tømmerås	Dr. scient. Zoolog	Olfaction in bark beetle communities: Interspecific interactions in regulation of colonization density, predator - prey relationship and host attraction
1988	Hans Christian Pedersen	Dr. philos Zoology	Reproductive behaviour in willow ptarmigan with special emphasis on territoriality and parental care
1988	Tor G. Heggberget	Dr. philos Zoology	Reproduction in Atlantic Salmon ( <i>Salmo salar</i> ): Aspects of spawning, incubation, early life history and population structure
1988	Marianne V. Nielsen	Dr. scient Zoology	The effects of selected environmental factors on carbon allocation/growth of larval and juvenile mussels ( <i>Mytilus edulis</i> )
1988	Ole Kristian Berg	Dr. scient Zoology	The formation of landlocked Atlantic salmon ( <i>Salmo salar</i> L.)
1989	John W. Jensen	Dr. philos Zoology	Crustacean plankton and fish during the first decade of the manmade Nesjø reservoir, with special emphasis on the effects of gill nets and salmonid growth
1989	Helga J. Vivås	Dr. scient Zoology	Theoretical models of activity pattern and optimal foraging: Predictions for the Moose <i>Alces alces</i>
1989	Reidar Andersen	Dr. scient Zoology	Interactions between a generalist herbivore, the moose <i>Alces alces</i> , and its winter food resources: a study of behavioural variation
1989	Kurt Ingar Draget	Dr. scient Botany	Alginate gel media for plant tissue culture
1990	Bengt Finstad	Dr. scient Zoology	Osmotic and ionic regulation in Atlantic salmon, rainbow trout and Arctic charr: Effect of temperature, salinity and season
1990	Hege Johannesen	Dr. scient Zoology	Respiration and temperature regulation in birds with special emphasis on the oxygen extraction by the lung
1990	Åse Krøkje	Dr. scient Botany	The mutagenic load from air pollution at two work-places with PAH-exposure measured with Ames Salmonella/microsome test
1990	Arne Johan Jensen	Dr. philos Zoology	Effects of water temperature on early life history, juvenile growth and prespawning migrations of Atlantic salmon ( <i>Salmo salar</i> ) and brown trout ( <i>Salmo trutta</i> ): A summary of studies in Norwegian streams
1990	Tor Jørgen Almaas	Dr. scient Zoology	Pheromone reception in moths: Response characteristics of olfactory receptor neurons to intra- and interspecific chemical cues
1990	Magne Husby	Dr. scient Zoology	Breeding strategies in birds: Experiments with the Magpie <i>Pica pica</i>
1991	Tor Kvam	Dr. scient Zoology	Population biology of the European lynx ( <i>Lynx lynx</i> ) in Norway
1991	Jan Henning L'Abête Lund	Dr. philos Zoology	Reproductive biology in freshwater fish, brown trout <i>Salmo trutta</i> and roach <i>Rutilus rutilus</i> in particular
1991	Asbjørn Moen	Dr. philos Botany	The plant cover of the boreal uplands of Central Norway. I. Vegetation ecology of Sølendet nature reserve; haymaking fens and birch woodlands
1991	Else Marie Løbersli	Dr. scient Botany	Soil acidification and metal uptake in plants
1991	Trond Nordtug	Dr. scient Zoology	Reflectometric studies of photomechanical adaptation in superposition eyes of arthropods
1991	Thyra Solem	Dr. scient Botany	Age, origin and development of blanket mires in Central Norway
1991	Odd Terje Sandlund	Dr. philos Zoology	The dynamics of habitat use in the salmonid genera <i>Coregonus</i> and <i>Salvelinus</i> : Ontogenic niche shifts and polymorphism
1991	Nina Jonsson	Dr. philos	Aspects of migration and spawning in salmonids

1991 Atle Bones	Dr. scient Botany	Compartmentation and molecular properties of thioglucoside glucohydrolase (myrosinase)
1992 Torgrim Breiehagen	Dr. scient Zoology	Mating behaviour and evolutionary aspects of the breeding system of two bird species: the Temminck's stint and the Pied flycatcher
1992 Anne Kjersti Bakken	Dr. scient Botany	The influence of photoperiod on nitrate assimilation and nitrogen status in timothy ( <i>Phleum pratense</i> L.)
1992 Tycho Anker-Nilssen	Dr. scient Zoology	Food supply as a determinant of reproduction and population development in Norwegian Puffins <i>Fratercula arctica</i>
1992 Bjørn Munro Jenssen	Dr. philos Zoology	Thermoregulation in aquatic birds in air and water: With special emphasis on the effects of crude oil, chemically treated oil and cleaning on the thermal balance of ducks
1992 Arne Vollan Aarset	Dr. philos Zoology	The ecophysiology of under-ice fauna: Osmotic regulation, low temperature tolerance and metabolism in polar crustaceans.
1993 Geir Slupphaug	Dr. scient Botany	Regulation and expression of uracil-DNA glycosylase and O <sup>6</sup> -methylguanine-DNA methyltransferase in mammalian cells
1993 Tor Fredrik Næsje	Dr. scient Zoology	Habitat shifts in coregonids.
1993 Yngvar Asbjørn Olsen	Dr. scient Zoology	Cortisol dynamics in Atlantic salmon, <i>Salmo salar</i> L.: Basal and stressor-induced variations in plasma levels and some secondary effects.
1993 Bård Pedersen	Dr. scient Botany	Theoretical studies of life history evolution in modular and clonal organisms
1993 Ole Petter Thangstad	Dr. scient Botany	Molecular studies of myrosinase in Brassicaceae
1993 Thrine L. M. Heggberget	Dr. scient Zoology	Reproductive strategy and feeding ecology of the Eurasian otter <i>Lutra lutra</i> .
1993 Kjetil Bevanger	Dr. scient. Zoology	Avian interactions with utility structures, a biological approach.
1993 Kåre Haugan	Dr. scient Bothany	Mutations in the replication control gene trfA of the broad host-range plasmid RK2
1994 Peder Fiske	Dr. scient. Zoology	Sexual selection in the lekking great snipe ( <i>Gallinago media</i> ): Male mating success and female behaviour at the lek
1994 Kjell Inge Reitan	Dr. scient Botany	Nutritional effects of algae in first-feeding of marine fish larvae
1994 Nils Røv	Dr. scient Zoology	Breeding distribution, population status and regulation of breeding numbers in the northeast-Atlantic Great Cormorant <i>Phalacrocorax carbo carbo</i>
1994 Annette-Susanne Hoepfner	Dr. scient Botany	Tissue culture techniques in propagation and breeding of Red Raspberry ( <i>Rubus idaeus</i> L.)
1994 Inga Elise Bruteig	Dr. scient Bothany	Distribution, ecology and biomonitoring studies of epiphytic lichens on conifers
1994 Geir Johnsen	Dr. scient Botany	Light harvesting and utilization in marine phytoplankton: Species-specific and photoadaptive responses
1994 Morten Bakken	Dr. scient Zoology	Infanticidal behaviour and reproductive performance in relation to competition capacity among farmed silver fox vixens, <i>Vulpes vulpes</i>
1994 Arne Moksnes	Dr. philos Zoology	Host adaptations towards brood parasitism by the Cuckoo
1994 Solveig Bakken	Dr. scient Bothany	Growth and nitrogen status in the moss <i>Dicranum majus</i> Sm. as influenced by nitrogen supply
1994 Torbjørn Forseth	Dr. scient Zoology	Bioenergetics in ecological and life history studies of fishes.

1995 Olav Vadstein	Dr. philos Botany	The role of heterotrophic planktonic bacteria in the cycling of phosphorus in lakes: Phosphorus requirement, competitive ability and food web interactions
1995 Hanne Christensen	Dr. scient Zoology	Determinants of Otter <i>Lutra lutra</i> distribution in Norway: Effects of harvest, polychlorinated biphenyls (PCBs), human population density and competition with mink <i>Mustela vison</i>
1995 Svein Håkon Lorentsen	Dr. scient Zoology	Reproductive effort in the Antarctic Petrel <i>Thalassoica antarctica</i> ; the effect of parental body size and condition
1995 Chris Jørgen Jensen	Dr. scient Zoology	The surface electromyographic (EMG) amplitude as an estimate of upper trapezius muscle activity
1995 Martha Kold Bakkevig	Dr. scient Zoology	The impact of clothing textiles and construction in a clothing system on thermoregulatory responses, sweat accumulation and heat transport
1995 Vidar Moen	Dr. scient Zoology	Distribution patterns and adaptations to light in newly introduced populations of <i>Mysis relicta</i> and constraints on Cladoceran and Char populations
1995 Hans Haavardsholm Blom	Dr. philos Bothany	A revision of the <i>Schistidium apocarpum</i> complex in Norway and Sweden
1996 Jorun Skjærmo	Dr. scient Botany	Microbial ecology of early stages of cultivated marine fish; impact fish-bacterial interactions on growth and survival of larvae
1996 Ola Ugedal	Dr. scient Zoology	Radiocesium turnover in freshwater fishes
1996 Ingibjörg Einarsdottir	Dr. scient Zoology	Production of Atlantic salmon ( <i>Salmo salar</i> ) and Arctic charr ( <i>Salvelinus alpinus</i> ): A study of some physiological and immunological responses to rearing routines
1996 Christina M. S. Pereira	Dr. scient Zoology	Glucose metabolism in salmonids: Dietary effects and hormonal regulation
1996 Jan Fredrik Børseth	Dr. scient Zoology	The sodium energy gradients in muscle cells of <i>Mytilus edulis</i> and the effects of organic xenobiotics
1996 Gunnar Henriksen	Dr. scient Zoology	Status of Grey seal <i>Halichoerus grypus</i> and Harbour seal <i>Phoca vitulina</i> in the Barents sea region
1997 Gunvor Øie	Dr. scient Bothany	Eevaluation of rotifer <i>Brachionus plicatilis</i> quality in early first feeding of turbot <i>Scophthalmus maximus</i> L. larvae
1997 Håkon Holien	Dr. scient Botany	Studies of lichens in spruce forest of Central Norway. Diversity, old growth species and the relationship to site and stand parameters
1997 Ole Reitan	Dr. scient. Zoology	Responses of birds to habitat disturbance due to damming
1997 Jon Arne Grøttum	Dr. scient. Zoology	Physiological effects of reduced water quality on fish in aquaculture
1997 Per Gustav Thingstad	Dr. scient. Zoology	Birds as indicators for studying natural and human-induced variations in the environment, with special emphasis on the suitability of the Pied Flycatcher
1997 Torgeir Nygård	Dr. scient Zoology	Temporal and spatial trends of pollutants in birds in Norway: Birds of prey and Willow Grouse used as Biomonitor
1997 Signe Nybø	Dr. scient. Zoology	Impacts of long-range transported air pollution on birds with particular reference to the dipper <i>Cinclus cinclus</i> in southern Norway
1997 Atle Wibe	Dr. scient. Zoology	Identification of conifer volatiles detected by receptor neurons in the pine weevil ( <i>Hyllobius abietis</i> ), analysed by gas chromatography linked to electrophysiology and to mass spectrometry
1997 Rolv Lundheim	Dr. scient Zoology	Adaptive and incidental biological ice nucleators

1997 Arild Magne Landa	Dr. scient Zoology	Wolverines in Scandinavia: ecology, sheep depredation and conservation
1997 Kåre Magne Nielsen	Dr. scient Botany	An evolution of possible horizontal gene transfer from plants to soil bacteria by studies of natural transformation in <i>Acinetobacter calcoaceticus</i>
1997 Jarle Tufto	Dr. scient Zoology	Gene flow and genetic drift in geographically structured populations: Ecological, population genetic, and statistical models
1997 Trygve Hesthagen	Dr. philos Zoology	Population responses of Arctic charr ( <i>Salvelinus alpinus</i> (L.)) and brown trout ( <i>Salmo trutta</i> L.) to acidification in Norwegian inland waters
1997 Trygve Sigholt	Dr. philos Zoology	Control of Parr-smolt transformation and seawater tolerance in farmed Atlantic Salmon ( <i>Salmo salar</i> ) Effects of photoperiod, temperature, gradual seawater acclimation, NaCl and betaine in the diet
1997 Jan Østnes	Dr. scient Zoology	Cold sensation in adult and neonate birds
1998 Seethaledsumy Visvalingam	Dr. scient Botany	Influence of environmental factors on myrosinases and myrosinase-binding proteins
1998 Thor Harald Ringsby	Dr. scient Zoology	Variation in space and time: The biology of a House sparrow metapopulation
1998 Erling Johan Solberg	Dr. scient. Zoology	Variation in population dynamics and life history in a Norwegian moose ( <i>Alces alces</i> ) population: consequences of harvesting in a variable environment
1998 Sigurd Mjøen Saastad	Dr. scient Botany	Species delimitation and phylogenetic relationships between the Sphagnum recurvum complex (Bryophyta): genetic variation and phenotypic plasticity
1998 Bjarte Mortensen	Dr. scient Botany	Metabolism of volatile organic chemicals (VOCs) in a head liver S9 vial equilibration system in vitro
1998 Gunnar Austrheim	Dr. scient Botany	Plant biodiversity and land use in subalpine grasslands. – A conservation biological approach
1998 Bente Gunnveig Berg	Dr. scient Zoology	Encoding of pheromone information in two related moth species
1999 Kristian Overskaug	Dr. scient Zoology	Behavioural and morphological characteristics in Northern Tawny Owls <i>Strix aluco</i> : An intra- and interspecific comparative approach
1999 Hans Kristen Stenøien	Dr. scient Bothany	Genetic studies of evolutionary processes in various populations of nonvascular plants (mosses, liverworts and hornworts)
1999 Trond Arnesen	Dr. scient Botany	Vegetation dynamics following trampling and burning in the outlying haylands at Sølendet, Central Norway
1999 Ingvar Stenberg	Dr. scient Zoology	Habitat selection, reproduction and survival in the White-backed Woodpecker <i>Dendrocopos leucotos</i>
1999 Stein Olle Johansen	Dr. scient Botany	A study of driftwood dispersal to the Nordic Seas by dendrochronology and wood anatomical analysis
1999 Trina Falck Galloway	Dr. scient Zoology	Muscle development and growth in early life stages of the Atlantic cod ( <i>Gadus morhua</i> L.) and Halibut ( <i>Hippoglossus hippoglossus</i> L.)
1999 Marianne Giæver	Dr. scient Zoology	Population genetic studies in three gadoid species: blue whiting ( <i>Micromisistius poutassou</i> ), haddock ( <i>Melanogrammus aeglefinus</i> ) and cod ( <i>Gradus morhua</i> ) in the North-East Atlantic
1999 Hans Martin Hanslin	Dr. scient Botany	The impact of environmental conditions of density dependent performance in the boreal forest bryophytes <i>Dicranum majus</i> , <i>Hylocomium splendens</i> , <i>Plagiochila asplenigides</i> , <i>Ptilium crista-castrensis</i> and <i>Rhytidiadelphus lukeus</i>



1999 Ingrid Bysveen Mjølnerød	Dr. scient Zoology	Aspects of population genetics, behaviour and performance of wild and farmed Atlantic salmon ( <i>Salmo salar</i> ) revealed by molecular genetic techniques
1999 Else Berit Skagen	Dr. scient Botany	The early regeneration process in protoplasts from <i>Brassica napus</i> hypocotyls cultivated under various g-forces
1999 Stein-Are Sæther	Dr. philos Zoology	Mate choice, competition for mates, and conflicts of interest in the Lekking Great Snipe
1999 Katrine Wangen Rustad	Dr. scient Zoology	Modulation of glutamatergic neurotransmission related to cognitive dysfunctions and Alzheimer's disease
1999 Per Terje Smiseth	Dr. scient Zoology	Social evolution in monogamous families: mate choice and conflicts over parental care in the Bluethroat ( <i>Luscinia s. svecica</i> )
1999 Gunnbjørn Bremset	Dr. scient Zoology	Young Atlantic salmon ( <i>Salmo salar</i> L.) and Brown trout ( <i>Salmo trutta</i> L.) inhabiting the deep pool habitat, with special reference to their habitat use, habitat preferences and competitive interactions
1999 Frode Ødegaard	Dr. scient Zoology	Host specificity as parameter in estimates of arthropod species richness
1999 Sonja Andersen	Dr. scient Bothany	Expressional and functional analyses of human, secretory phospholipase A2
2000 Ingrid Salvesen, I	Dr. scient Botany	Microbial ecology in early stages of marine fish: Development and evaluation of methods for microbial management in intensive larviculture
2000 Ingar Jostein Øien	Dr. scient Zoology	The Cuckoo ( <i>Cuculus canorus</i> ) and its host: adaptations and counteradaptations in a coevolutionary arms race
2000 Pavlos Makridis	Dr. scient Botany	Methods for the microbial econtrol of live food used for the rearing of marine fish larvae
2000 Sigbjørn Stokke	Dr. scient Zoology	Sexual segregation in the African elephant ( <i>Loxodonta africana</i> )
2000 Odd A. Gulseth	Dr. philos Zoology	Seawater tolerance, migratory behaviour and growth of Charr, ( <i>Salvelinus alpinus</i> ), with emphasis on the high Arctic Dieset charr on Spitsbergen, Svalbard
2000 Pål A. Olsvik	Dr. scient Zoology	Biochemical impacts of Cd, Cu and Zn on brown trout ( <i>Salmo trutta</i> ) in two mining-contaminated rivers in Central Norway
2000 Sigurd Einum	Dr. scient Zoology	Maternal effects in fish: Implications for the evolution of breeding time and egg size
2001 Jan Ove Evjemo	Dr. scient Zoology	Production and nutritional adaptation of the brine shrimp <i>Artemia</i> sp. as live food organism for larvae of marine cold water fish species
2001 Olga Hilmo	Dr. scient Botany	Lichen response to environmental changes in the managed boreal forest systems
2001 Ingebrigt Uglem	Dr. scient Zoology	Male dimorphism and reproductive biology in corkwing wrasse ( <i>Symphodus melops</i> L.)
2001 Bård Gunnar Stokke	Dr. scient Zoology	Coevolutionary adaptations in avian brood parasites and their hosts
2002 Ronny Aanes	Dr. scient	Spatio-temporal dynamics in Svalbard reindeer ( <i>Rangifer tarandus platyrhynchus</i> )
2002 Mariann Sandsund	Dr. scient Zoology	Exercise- and cold-induced asthma. Respiratory and thermoregulatory responses
2002 Dag-Inge Øien	Dr. scient Botany	Dynamics of plant communities and populations in boreal vegetation influenced by scything at Sølendet, Central Norway
2002 Frank Rosell	Dr. scient Zoology	The function of scent marking in beaver ( <i>Castor fiber</i> )
2002 Janne Østvang	Dr. scient Botany	The Role and Regulation of Phospholipase A <sub>2</sub> in Monocytes During Atherosclerosis Development

2002 Terje Thun	Dr.philos Biology	Dendrochronological constructions of Norwegian conifer chronologies providing dating of historical material
2002 Birgit Hafjeld Borgen	Dr. scient Biology	Functional analysis of plant idioblasts (Myrosin cells) and their role in defense, development and growth
2002 Bård Øyvind Solberg	Dr. scient Biology	Effects of climatic change on the growth of dominating tree species along major environmental gradients
2002 Per Winge	Dr. scient Biology	The evolution of small GTP binding proteins in cellular organisms. Studies of RAC GTPases in <i>Arabidopsis thaliana</i> and the Ral GTPase from <i>Drosophila melanogaster</i>
2002 Henrik Jensen	Dr. scient Biology	Causes and consequences of individual variation in fitness-related traits in house sparrows
2003 Jens Rohloff	Dr. philos Biology	Cultivation of herbs and medicinal plants in Norway – Essential oil production and quality control
2003 Åsa Maria O. Espmark Wibe	Dr. scient Biology	Behavioural effects of environmental pollution in threespine stickleback <i>Gasterosteus aculeatur</i> L.
2003 Dagmar Hagen	Dr. scient Biology	Assisted recovery of disturbed arctic and alpine vegetation – an integrated approach
2003 Bjørn Dahle	Dr. scient Biology	Reproductive strategies in Scandinavian brown bears
2003 Cyril Lebogang Taolo	Dr. scient Biology	Population ecology, seasonal movement and habitat use of the African buffalo ( <i>Syncerus caffer</i> ) in Chobe National Park, Botswana
2003 Marit Stranden	Dr.scient Biology	Olfactory receptor neurones specified for the same odorants in three related Heliothine species ( <i>Helicoverpa armigera</i> , <i>Helicoverpa assulta</i> and <i>Heliothis virescens</i> )
2003 Kristian Hassel	Dr.scient Biology	Life history characteristics and genetic variation in an expanding species, <i>Pogonatum dentatum</i>
2003 David Alexander Rae	Dr.scient Biology	Plant- and invertebrate-community responses to species interaction and microclimatic gradients in alpine and Arctic environments
2003 Åsa A Borg	Dr.scient Biology	Sex roles and reproductive behaviour in gobies and guppies: a female perspective
2003 Eldar Åsgard Bendiksen	Dr.scient Biology	Environmental effects on lipid nutrition of farmed Atlantic salmon ( <i>Salmo Salar</i> L.) parr and smolt
2004 Torkild Bakken	Dr.scient Biology	A revision of Nereidinae (Polychaeta, Nereididae)
2004 Ingar Pareliussen	Dr.scient Biology	Natural and Experimental Tree Establishment in a Fragmented Forest, Ambohitantely Forest Reserve, Madagascar
2004 Tore Brembu	Dr.scient Biology	Genetic, molecular and functional studies of RAC GTPases and the WAVE-like regulatory protein complex in <i>Arabidopsis thaliana</i>
2004 Liv S. Nilsen	Dr.scient Biology	Coastal heath vegetation on central Norway; recent past, present state and future possibilities
2004 Hanne T. Skiri	Dr.scient Biology	Olfactory coding and olfactory learning of plant odours in heliothine moths. An anatomical, physiological and behavioural study of three related species ( <i>Heliothis virescens</i> , <i>Helicoverpa armigera</i> and <i>Helicoverpa assulta</i> )
2004 Lene Østby	Dr.scient Biology	Cytochrome P4501A (CYP1A) induction and DNA adducts as biomarkers for organic pollution in the natural environment
2004 Emmanuel J. Gerreta	Dr. philos Biology	The Importance of Water Quality and Quantity in the Tropical Ecosystems, Tanzania
2004 Linda Dalen	Dr.scient Biology	Dynamics of Mountain Birch Treelines in the Scandes Mountain Chain, and Effects of Climate Warming

2004 Lisbeth Mehli	Dr.scient Biology	Polygalacturonase-inhibiting protein (PGIP) in cultivated strawberry ( <i>Fragaria x ananassa</i> ): characterisation and induction of the gene following fruit infection by <i>Botrytis cinerea</i>
2004 Børge Moe	Dr.scient Biology	Energy-Allocation in Avian Nestlings Facing Short-Term Food Shortage
2005 Matilde Skogen Chauton	Dr.scient Biology	Metabolic profiling and species discrimination from High-Resolution Magic Angle Spinning NMR analysis of whole-cell samples
2005 Sten Karlsson	Dr.scient Biology	Dynamics of Genetic Polymorphisms
2005 Terje Bongard	Dr.scient Biology	Life History strategies, mate choice, and parental investment among Norwegians over a 300-year period
2005 Tonette Røstelién	ph.d Biology	Functional characterisation of olfactory receptor neurone types in heliothine moths
2005 Erlend Kristiansen	Dr.scient Biology	Studies on antifreeze proteins
2005 Eugen G. Sørmo	Dr.scient Biology	Organochlorine pollutants in grey seal ( <i>Halichoerus grypus</i> ) pups and their impact on plasma thyrid hormone and vitamin A concentrations
2005 Christian Westad	Dr.scient Biology	Motor control of the upper trapezius
2005 Lasse Mork Olsen	ph.d Biology	Interactions between marine osmo- and phagotrophs in different physicochemical environments
2005 Åslaug Viken	ph.d Biology	Implications of mate choice for the management of small populations
2005 Ariaya Hymete Sahle Dingle	ph.d Biology	Investigation of the biological activities and chemical constituents of selected <i>Echinops</i> spp. growing in Ethiopia
2005 Anders Gravbrøt Finstad	ph.d Biology	Salmonid fishes in a changing climate: The winter challenge
2005 Shimane Washington Makabu	ph.d Biology	Interactions between woody plants, elephants and other browsers in the Chobe Riverfront, Botswana
2005 Kjartan Østbye	Dr.scient Biology	The European whitefish <i>Coregonus lavaretus</i> (L.) species complex: historical contingency and adaptive radiation
2006 Kari Mette Murvoll	ph.d Biology	Levels and effects of persistent organic pollutants (POPs) in seabirds  Retinoids and $\alpha$ -tocopherol – potential biomarkers of POPs in birds?
2006 Ivar Herfindal	Dr.scient Biology	Life history consequences of environmental variation along ecological gradients in northern ungulates
2006 Nils Egil Tokle	ph.d Biology	Are the ubiquitous marine copepods limited by food or predation? Experimental and field-based studies with main focus on <i>Calanus finmarchicus</i>
2006 Jan Ove Gjershaug	Dr.philos Biology	Taxonomy and conservation status of some booted eagles in south-east Asia
2006 Jon Kristian Skei	Dr.scient Biology	Conservation biology and acidification problems in the breeding habitat of amphibians in Norway
2006 Johanna Järnegren	ph.d Biology	Acesta Oophaga and Acesta Excavata – a study of hidden biodiversity
2006 Bjørn Henrik Hansen	ph.d Biology	Metal-mediated oxidative stress responses in brown trout ( <i>Salmo trutta</i> ) from mining contaminated rivers in Central Norway
2006 Vidar Grøtan	ph.d Biology	Temporal and spatial effects of climate fluctuations on population dynamics of vertebrates
2006 Jafari R Kideghesho	ph.d Biology	Wildlife conservation and local land use conflicts in western Serengeti, Corridor Tanzania

2006 Anna Maria Billing	ph.d Biology	Reproductive decisions in the sex role reversed pipefish <i>Syngnathus typhle</i> : when and how to invest in reproduction
2006 Henrik Pärn	ph.d Biology	Female ornaments and reproductive biology in the bluethroat
2006 Anders J. Fjellheim	ph.d Biology	Selection and administration of probiotic bacteria to marine fish larvae
2006 P. Andreas Svensson	ph.d Biology	Female coloration, egg carotenoids and reproductive success: gobies as a model system
2007 Sindre A. Pedersen	ph.d Biology	Metal binding proteins and antifreeze proteins in the beetle <i>Tenebrio molitor</i> - a study on possible competition for the semi-essential amino acid cysteine
2007 Kasper Hancke	ph.d Biology	Photosynthetic responses as a function of light and temperature: Field and laboratory studies on marine microalgae
2007 Tomas Holmern	ph.d Biology	Bushmeat hunting in the western Serengeti: Implications for community-based conservation
2007 Kari Jørgensen	ph.d Biology	Functional tracing of gustatory receptor neurons in the CNS and chemosensory learning in the moth <i>Heliothis virescens</i>
2007 Stig Ulland	ph.d Biology	Functional Characterisation of Olfactory Receptor Neurons in the Cabbage Moth, ( <i>Mamestra brassicae</i> L.) (Lepidoptera, Noctuidae). Gas Chromatography Linked to Single Cell Recordings and Mass Spectrometry
2007 Snorre Henriksen	ph.d Biology	Spatial and temporal variation in herbivore resources at northern latitudes
2007 Roelof Frans May	ph.d Biology	Spatial Ecology of Wolverines in Scandinavia
2007 Vedasto Gabriel Ndibalema	ph.d Biology	Demographic variation, distribution and habitat use between wildebeest sub-populations in the Serengeti National Park, Tanzania
2007 Julius William Nyahongo	ph.d Biology	Depredation of Livestock by wild Carnivores and Illegal Utilization of Natural Resources by Humans in the Western Serengeti, Tanzania
2007 Shombe Ntaraluka Hassan	ph.d Biology	Effects of fire on large herbivores and their forage resources in Serengeti, Tanzania
2007 Per-Arvid Wold	ph.d Biology	Functional development and response to dietary treatment in larval Atlantic cod ( <i>Gadus morhua</i> L.) Focus on formulated diets and early weaning
2007 Anne Skjetne Mortensen	ph.d Biology	Toxicogenomics of Aryl Hydrocarbon- and Estrogen Receptor Interactions in Fish: Mechanisms and Profiling of Gene Expression Patterns in Chemical Mixture Exposure Scenarios
2008 Brage Bremset Hansen	ph.d Biology	The Svalbard reindeer ( <i>Rangifer tarandus platyrhynchus</i> ) and its food base: plant-herbivore interactions in a high-arctic ecosystem
2008 Jiska van Dijk	ph.d Biology	Wolverine foraging strategies in a multiple-use landscape
2008 Flora John Magige	ph.d Biology	The ecology and behaviour of the Masai Ostrich ( <i>Struthio camelus massaicus</i> ) in the Serengeti Ecosystem, Tanzania
2008 Bernt Rønning	ph.d Biology	Sources of inter- and intra-individual variation in basal metabolic rate in the zebra finch, ( <i>Taeniopygia guttata</i> )

2008 Sølvi Wehn	ph.d Biology	Biodiversity dynamics in semi-natural mountain landscapes. - A study of consequences of changed agricultural practices in Eastern Jotunheimen
2008 Trond Moxness Kortner	ph.d Biology	"The Role of Androgens on previtellogenic oocyte growth in Atlantic cod ( <i>Gadus morhua</i> ): Identification and patterns of differentially expressed genes in relation to Stereological Evaluations"
2008 Katarina Mariann Jørgensen	Dr.Scient Biology	The role of platelet activating factor in activation of growth arrested keratinocytes and re-epithelialisation
2008 Tommy Jørstad	ph.d Biology	Statistical Modelling of Gene Expression Data
2008 Anna Kusnierczyk	ph.d Biology	<i>Arabidopsis thaliana</i> Responses to Aphid Infestation
2008 Jussi Evertsen	ph.d Biology	Herbivore sacoglossans with photosynthetic chloroplasts
2008 John Eilif Hermansen	ph.d Biology	Mediating ecological interests between locals and globals by means of indicators. A study attributed to the asymmetry between stakeholders of tropical forest at Mt. Kilimanjaro, Tanzania
2008 Ragnhild Lyngved	ph.d Biology	Somatic embryogenesis in <i>Cyclamen persicum</i> . Biological investigations and educational aspects of cloning
2008 Line Elisabeth Sundt-Hansen	ph.d Biology	Cost of rapid growth in salmonid fishes
2008 Line Johansen	ph.d Biology	Exploring factors underlying fluctuations in white clover populations – clonal growth, population structure and spatial distribution
2009 Astrid Jullumstrø Feuerherm	ph.d Biology	Elucidation of molecular mechanisms for pro-inflammatory phospholipase A2 in chronic disease
2009 Pål Kvello	ph.d Biology	Neurons forming the network involved in gustatory coding and learning in the moth <i>Heliothis virescens</i> : Physiological and morphological characterisation, and integration into a standard brain atlas
2009 Trygve Devold Kjellsen	ph.d Biology	Extreme Frost Tolerance in Boreal Conifers
2009 Johan Reinert Vikan	ph.d Biology	Coevolutionary interactions between common cuckoos <i>Cuculus canorus</i> and <i>Fringilla</i> finches
2009 Zsolt Volent	ph.d Biology	Remote sensing of marine environment: Applied surveillance with focus on optical properties of phytoplankton, coloured organic matter and suspended matter
2009 Lester Rocha	ph.d Biology	Functional responses of perennial grasses to simulated grazing and resource availability
2009 Dennis Ikanda	ph.d Biology	Dimensions of a Human-lion conflict: Ecology of human predation and persecution of African lions ( <i>Panthera leo</i> ) in Tanzania
2010 Huy Quang Nguyen	ph.d Biology	Egg characteristics and development of larval digestive function of cobia ( <i>Rachycentron canadum</i> ) in response to dietary treatments -Focus on formulated diets
2010 Eli Kvingedal	ph.d Biology	Intraspecific competition in stream salmonids: the impact of environment and phenotype
2010 Sverre Lundemo	ph.d Biology	Molecular studies of genetic structuring and demography in <i>Arabidopsis</i> from Northern Europe

2010 Iddi Mihijai Mfunda	ph.d Biology	Wildlife Conservation and People's livelihoods: Lessons Learnt and Considerations for Improvements. The Case of Serengeti Ecosystem, Tanzania
2010 Anton Tinchov Antonov	ph.d Biology	Why do cuckoos lay strong-shelled eggs? Tests of the puncture resistance hypothesis
2010 Anders Lyngstad	ph.d Biology	Population Ecology of <i>Eriophorum latifolium</i> , a Clonal Species in Rich Fen Vegetation
2010 Hilde Færevik	ph.d Biology	Impact of protective clothing on thermal and cognitive responses
2010 Ingerid Brønne Arbo	ph.d Medical technology	Nutritional lifestyle changes – effects of dietary carbohydrate restriction in healthy obese and overweight humans
2010 Yngvild Vindenes	ph.d Biology	Stochastic modeling of finite populations with individual heterogeneity in vital parameters
2010 Hans-Richard Brattbakk	ph.d Medical technology	The effect of macronutrient composition, insulin stimulation, and genetic variation on leukocyte gene expression and possible health benefits