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# Stochastic Modeling of Mating Systems and their Effect on Population Dynamics and Genetics

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# Preface

This thesis is the end product of four years of hard work. These years have been somewhat exhausting, but more importantly they have been enjoyable and very rewarding. I have learned a lot, not only about science, but also about myself.

Many people have been involved in this endeavor of mine and have supported me along the way. I am extremely grateful to my advisors, Bernt-Erik Sæther and Steinar Engen, for all their support, inspiration and knowledge. I feel truly privileged to have worked with them. I therefore also wish to thank two people who helped to bring this about; Vidar Grøtan for suggesting that I contact Bernt-Erik about a possible Master's project, and Per Hag for convincing my (then future) advisors that I had the mathematical skills required for the project in question.

Vidar has also been my R support, and his help, combined with that of Ivar Herfindal, is probably what has saved my computer from being smashed against the wall. Yngvild Vindenes, my fellow theoretician, has provided me with stimulating discussions, and has been an excellent travel companion on several conference trips. I have had nice office mates during my time at NTNU, and would like to thank Børge, Lars Erik and Gine for making the office a fun place to be.

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Finally, I would like to thank my family for being the best family I could ever have wished for. Their love and support means the world to me. I want to thank mommy for introducing me to the wonders of nature and biology, and daddy for encouraging my interest in math and showing me just how much fun it can be. And most importantly of all I want to thank them for teaching me to believe in myself and my own abilities.

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# Summary

In sexually reproducing species, individuals are dependent on finding one or more mates in order to produce offspring. There are different ways of achieving this, and a wide variety of mating systems exist in natural populations. However, the process of pair formation is often ignored in demographic models, which typically only look at the female segment of populations.

In this thesis a set of stochastic models is developed with the goal of describing and analyzing mating systems and their effect on population dynamics and genetics. It is shown that sex ratio is a factor that should not be ignored when attempting to study and compare different mating systems. Combinations of mating system and sex ratio are shown to have a large influence on the demographic variance of populations. Demographic stochasticity is known to decrease the growth rate of (usually small) populations and increase their extinction risk. Here it is found that combinations of mating system and sex ratio influence this effect. In particular, polygynous populations are shown to be more vulnerable to demographic stochasticity than monogamous ones. A stochastic Allee effect is also demonstrated to be amplified by polygyny.

Different aspects of mating systems can affect genetic processes as well, including sexual selection, fixation of slightly beneficial mutations, and genetic drift. Levels of genetic drift are here shown to be affected by persistent individual differences in male mating success, and by combinations of age at reproductive maturity and juvenile survival.

In general, it is important to examine the mechanisms behind observed patterns of interest, rather than simply recording the realized outcome. For example, it is shown here that different mating systems can give rise to different distributions of mating and/or reproductive success, without the variance of the distribution differing. This variance is a frequently used measure for quantifying inequalities in reproductive success, but it does not contain information about these differences. Also, when studying how age at first reproduction affects the ratio of effective population size to

census population size ($N_e/N$), the definition of $N$ used can influence the results substantially. In fact, using different definitions of census population size can result in opposite patterns of change being observed in the ratio $N_e/N$, even though there is no difference in actual levels of genetic drift. The explanation for this lies in the age distribution (juveniles vs. adults) and how changes in it affect the adult population size but not the total population size. Effects of this type are easily overlooked if one is focused only on the end results of the processes of interest, rather than on the processes themselves.

These results demonstrate that mating system, sex ratio and demographic stochasticity play important roles in population dynamics and genetics. These factors become particularly influential at small population sizes, and may therefore have consequences for conservation efforts.

## This thesis is based on the following papers:

I  **Lee, A.M.**, S. Engen, B.-E. Sæther. 2008. Understanding mating systems: A mathematical model of the pair formation process. Theoretical Population Biology 73:112-124. [1]

II  **Lee, A.M.**, B.-E. Sæther, S. Engen. 2011. Demographic stochasticity, Allee effects and extinction: The influence of mating system and sex ratio. American Naturalist 177(3):301-313. [2]

III  Vindenes, Y., **A.M. Lee**, S. Engen, B.-E. Sæther. 2010. Fixation of slightly beneficial mutations: Effects of life history. Evolution 64(4):1063-1075 [3]

IV  **Lee, A.M.**, S. Engen, B.-E. Sæther. The influence of persistent individual differences and age at maturity on effective population size. Proceedings of the Royal Society B: Biological Sciences (Manuscript accepted in slightly revised version.) [4]

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[1] SE and BES initiated the project. SE and AML developed the model. AML performed all analyses, simulations and calculations and wrote the paper with comments from BES and SE.

[2] SE and BES initiated the project. AML developed the model, performed all analyses and wrote the paper with comments from BES and SE.

[3] SE initiated the project and contributed to the analyses. AML performed the analysis and calculations for the new method of approximating fixation probability in large populations. YV performed the analyses and simulations for finite populations and wrote the paper with contributions from AML and comments from SE and BES.

[4] SE and AML initiated the project. AML developed the model, performed all analyses and wrote the paper with comments from SE and BES.

# Introduction

Reproduction is a fundamental goal of all living organisms. In sexually reproducing species, changes in both population size and allele distribution are dependent on the processes of pair formation and offspring production. For many years, population biologists have been working to gain a better understanding of the dynamics and genetics of populations. Theoretical models are useful tools in this venture. Traditionally, demographic models have tended either to not distinguish between the sexes, or to focus only on the female segment of populations (assuming that any fluctuations in the number of males present would have no effect on the vital parameters of females). However, males and females do differ, and (in species with sexual reproduction) successful procreation requires finding a mate.

Typically, females produce energy rich eggs while males produce relatively cheap sperm (Wallace et al., 1996). Because of this difference, female reproductive success is usually limited by access to resources for egg production, whereas male reproductive success is often limited by access to mates (Bateman, 1948). A single male has the capacity to produce large numbers of gametes and fertilize the eggs of many females. As a result of this, females are often assumed to be choosy when selecting mates, whereas males are expected to mate with as many females as possible (Bateman, 1948). The resulting sexual conflict, working within the boundaries of ecological factors and physiological constraints of different species, has led to an astounding variety of mating systems (Trivers, 1972).

Basic distinctions among mating systems include the number of mates individuals of each sex may have in a breeding season (Thornhill and Alcock, 1983), how pair formation takes place (Emlen and Oring, 1977), and how much individuals of each sex invest in parental care (Trivers, 1972; Krebs and Davies, 1993). Several attempts have been made at developing rigorous classifications of mating systems based on these factors (Emlen and Oring, 1977; Gregorius and Hattemer, 1987; Shuster and Wade, 2003). Probably the most well-known way of classifying mating systems is

based solely on the number of mates that individuals of each sex obtain. When individuals form exclusive pair bonds and only have one mate per season (or reproductive event) we call it monogamy (Thornhill and Alcock, 1983). The more common situation in which males have multiple mates while females do not is called polygyny. Polyandry describes a situation where females are the ones obtaining multiple matings. And finally, in promiscuous systems individuals of both sexes mate with multiple mates. Monogamy is often associated with birds, polygyny is considered to be the most common mating system in mammals, and promiscuity is often mentioned in relation to fish (Krebs and Davies, 1993). However, there is a wide variety of mating systems within different taxa, and in some cases even within the same species or population. In addition, the definitions are not as clear-cut as they may seem. Genetic mating systems do not necessarily reflect the social mating system. For example, social monogamy is quite common in birds, with couples raising young together (Lack, 1968), but extra pair copulations are often frequent in both sexes, making genetic monogamy much rarer (Bennett and Owens, 2002).

In 1977, Emlen and Oring proposed a classification of mating systems based on the monopolizability of mates, as well as the behavior involved in such monopolization (e.g. harem defense or resource defense). This classic paper also introduced the important concept of operational sex ratio (OSR), defined as the average ratio of sexually receptive females to sexually active males. Sex ratio has a substantial influence on the distribution of matings in a population. As an example, consider a polygynous population with an OSR equal to one. For every male with $k$ mates, there must be $k - 1$ males with no mates at all (Shuster and Wade, 2003). On the other hand, a similar population with a female-biased sex ratio is likely to have a more even distribution of matings among the males.

Quantifying inequalities in mating or reproductive success among individuals in a population is an important step in describing mating systems and studying processes such as sexual selection. One proposed way of achieving this is to use one of

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several suggested reproductive skew indices (see Kokko et al., 1999; Nonacs, 2003, for a review). However, compressing information about the distribution of mating success into a single value index may cause important information to be lost.

Effects of the OSR on reproductive success have been investigated in a number of species. A common pattern seems to be that the average male mating and/or reproductive success is lower in populations with a more male-biased OSR, while the variance among males is higher (and the reverse in more female-biased populations). Evidence for this has been found in bank voles (Klemme et al., 2007; Mills et al., 2007), red deer (Clutton-Brock et al., 1997), newts (Jones et al., 2004), field crickets (Souroukis and Cade, 1993), poison-dart frogs (Pröhl, 2002), and several types of fish (Keenleyside, 1985; Kodric-Brown, 1988; Itzkowitz, 1990; Kvarnemo et al., 1995). Thus, as expected from theory (Emlen and Oring, 1977), male-biased sex ratios are often found to coincide with high levels of sexual selection and genetic drift. It is, however, still relatively unclear how such patterns may affect the overall dynamics of populations. In addition, not all systems seem to conform to the above pattern. Wang et al. (2009) found that the bug *Nysius huttoni* obtained increased male mating success at male-biased OSRs compared to an even sex ratio. A male-biased OSR has also been shown to decrease the variance in male mating success in water striders (Arnqvist, 1992; Krupa and Sih, 1993) and the European bitterling (Mills and Reynolds, 2003). In addition to this, female fecundity has been shown to be affected by the OSR in several systems (e.g. Lawrence, 1986; Arnqvist, 1992; Magurran and Seghers, 1994; Marchesan, 2002; Solberg et al., 2002; Le Galliard et al., 2005; Rossi et al., 2010). The direction of this effect varies from system to system. Still other studies have found little or no effect of the OSR on mating success or productivity (Lawrence, 1986; Singh and Sisodia, 1999; White et al., 2001). Sex ratios vary greatly in nature, but some general patterns have been found. Male-biased sex ratios are quite common in wild bird populations (Donald, 2007) but uncommon in mammals (Bessa-Gomes et al., 2004; Donald, 2007). A study of data from birds, primates and ungulates also revealed

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that the sex ratio is often female-biased in polygynous populations and male-biased in monogamous ones (Bessa-Gomes et al., 2004).

Sex ratios, survival, offspring production and pair formation all involve a certain amount of randomness, or stochasticity. There are two main types of stochasticity that affect the dynamics of populations (Lande et al., 2003). Environmental stochasticity is caused by random fluctuations in the environment, and affects all individuals in a population simultaneously (May, 1973; Shaffer, 1981; Lande et al., 2003). Demographic stochasticity, on the other hand, is caused by randomness in individual survival and reproduction events, and works independently among individuals in a population (May, 1973; Roughgarden, 1975; Lande et al., 2003). All the stochastic factors mentioned above are thus examples of demographic stochasticity. Since demographic stochasticity operates independently among individuals, its effect on population dynamics will be small in large populations. Large numbers of independent, random survival and reproduction events will tend to sum to zero. In small populations, however, demographic stochasticity can have a significant impact on population growth (Lande et al., 2003). It is therefore especially important to consider possible effects of demographic stochasticity when dealing with conservation of small, endangered populations. The models and analyses presented in this thesis all incorporate demographic stochasticity from several sources.

Population size and growth rate are clearly of the utmost importance in determining the extinction risk of populations. Stochastic effects tend to cause a decrease in the population growth rate (Tuljapurkar, 1982; Lande, 1998; Sæther and Engen, 2003). For this reason the work in this thesis focuses on the stochastic growth rate (also known as the long-run growth rate) (Tuljapurkar and Orzack, 1980; Tuljapurkar, 1982; Lande et al., 2003), rather than the deterministic one. In other words, effects of demographic stochasticity are accounted for when calculating the growth rates. But growth rate alone is not sufficient to ensure a healthy population. Small populations are vulnerable to loss of genetic variation, and inbreeding. This can

decrease a population's ability to respond to environmental change, increase receptivity to parasitism and disease, and cause inbreeding depression (Halliburton, 2004). Random changes in allele frequency from one generation to the next is termed genetic drift, and can have a substantial impact in small populations (Allendorf and Luikart, 2007). In a diploid population of constant size with discrete, nonoverlapping generations and reproduction by random sampling of gametes, the expected rate of genetic drift and loss of selectively neutral heterozygosity is expected to be $1/(2N)$ per generation. A common way of quantifying genetic drift in other types of populations is to use the concept of effective population size ($N_e$). Effective population size is defined as the size of an ideal population (such as the one described above) that would experience the same amount of genetic drift as the population being studied (Wright, 1931).

Genetic drift is not the only force involved in changed allele frequencies. Mutation rates and selection also play an important role, and the actual allele frequencies observed in populations are an outcome of the combined effects of all three forces. The outcome depends on the mutation rate, strength of selection, and the population size (Halliburton, 2004).

Understanding the mechanisms that cause changes in population size and allele frequency is necessary in order to be able to monitor and improve the viability of populations.

# Aims

The main goal of this thesis is to develop a set of stochastic models to describe and analyze mating systems, and to use these models to examine how mating systems affect population dynamics and genetics. More specifically, the thesis addresses the following issues.

## 1. Understanding the pair formation process (Paper I)

In this first part of the thesis I aim to develop a way of describing the pair formation process using a very limited number of parameters. Several different aspects of mating systems have previously been described through models. For example, there are a number of models that look at mate choice (Janetos, 1980; Parker, 1983; Hubbell and Johnson, 1987; Real, 1990; McNamara et al., 2003), as well as several different approaches involving encounter rates and individual compatibilities or preferences (Gimelfarb, 1988 $a,b$; Møller and Legendre, 2001; Bessa-Gomes et al., 2003 $a,b$). Many of these models are purely deterministic, and thus do not account for randomness in mating events. In addition it is most common to model special cases (e.g. strict monogamy and polygyny with a set harem size), using separate models. It would be useful to have a single model that could deal with a whole range of mating systems by varying the parameters. The stochastic processes involved in pair formation and offspring production should be accounted for, since it is known that demographic stochasticity can influence results of demographic studies.

The idea of this first part of the thesis is to develop a very basic stochastic model that can cover a continuous range of mating systems (from strict monogamy to extreme polygyny). This model can then be used to examine the variance in male mating success in different cases. This represents a mechanistic approach to this question, and can be considered an alternative to the use of reproductive skew indices which describe the outcome without considering the underlying mechanisms.

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## 2. Mating systems and demographic stochasticity (Papers II, III)

How do mating systems affect the demographic variance, and how does this in turn affect growth, extinction risk and genetic changes in populations?

It has previously been shown that polygynous populations experience higher levels of demographic stochasticity than monogamous ones when the sex ratio is even (1:1) and it is assumed that all females get to mate (Engen et al., 2003). It is known that demographic stochasticity has a negative effect on the long-term dynamics of populations (May, 1973; Lande et al., 2003) and can cause extinction in (usually small) populations even when their deterministic growth rate is positive (Sæther and Engen, 2003). Thus, there is reason to believe that differences in demographic stochasticity caused by mating system could influence the growth and extinction risk of populations. In fact, several theoretical studies have found that monogamous populations should experience a higher extinction risk than polygynous ones (Legendre et al., 1999; Bessa-Gomes et al., 2004; Sæther et al., 2004). This prediction fits well with data from passerine introductions in New Zealand (Legendre et al., 1999) and with a study of extinction risk in large mammals in nature reserves in Ghana (Brashares, 2003). However, other empirical studies have failed to find any systematic connection between mating system and extinction risk (Bessa-Gomes et al., 2003 *b*; Morrow and Pitcher, 2003; Thomas et al., 2006).

Bessa-Gomes et al. (2004) demonstrated that the number of pairs formed in a given mating system will depend on the sex ratio, and that this can affect population dynamics. Despite this, studies comparing different mating systems routinely assume a 1:1 sex ratio (e.g. Legendre et al., 1999; Møller and Legendre, 2001; Bessa-Gomes et al., 2003*b*; Engen et al., 2003; Sæther et al., 2004). Using a modified version of the model developed for the first section of the thesis, I examine the combined effects of mating system and sex ratio on the demographic variance of populations. The next step is to show how this affects population growth and extinction risk.

The demographic variance also plays a role in genetic processes. Athreya

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(1993) found that the fixation probability of a slightly beneficial allele in an infinitely large age-structured population depends on the demographic variance, as well as the reproductive value of the individual(s) in which the mutation first occurred, and the fitness benefit of the mutation. This result is asymptotically exact as the selective advantage of the mutation approaches zero. In this thesis I develop a method for calculating a fixation probability that remains accurate for mutations with larger selective advantages.

## 3. Population size, sex ratio and mating system (Papers I, II)

How do population size and sex ratio influence the effects of mating systems?

Population size and density are known to affect many population processes. Density dependent regulation around a carrying capacity is a well-known process in large populations. Of more importance for extinction risk, are density effects at small population sizes. Many populations show positive density dependence in the per capita growth rate at low population density (Courchamp et al., 2008). This is referred to as the Allee effect (Allee et al., 1949; Odum and Allee, 1954; Courchamp et al., 2008). Allee effects are proving to be practically ubiquitous in nature (Courchamp et al., 2008), and can drive populations to extinction in a short amount of time if the number of individuals falls below a critical threshold (Odum and Allee, 1954; Wang and Kot, 2001; Dennis, 2002). In addition to this, the decrease in log-scale stochastic growth rate caused by demographic stochasticity is inversely proportional to population size (Lande et al., 2003), and population size is also known to affect genetic processes, like drift (Allendorf and Luikart, 2007).

As mentioned in section 2 above, the sex ratio will affect the number of pairs formed, given a particular mating system. This can in turn influence population dynamics (Bessa-Gomes et al., 2004) and genetics (Wright, 1931; Nomura, 2002). In addition, fluctuations in the sex ratio are an important component of the demographic variance (Engen et al., 2003).

This part of the thesis examines how population size and sex ratio affect distributions of mating success in a single season, and how they influence the effects of different mating systems on population growth and extinction risk.

## 4. Mating system and effective population size (Paper IV)

How do persistent individual differences in mating success affect genetic drift?

Variation in reproductive success is an important factor in determining effective population size (Wright, 1938; Crow and Kimura, 1970). As mating success becomes less evenly distributed among individuals in a population, levels of genetic drift increase and the effective population size decreases (Nunney, 1991, 1993; Briton et al., 1994; Nomura, 2002; Balloux and Lehmann, 2003). Nunney (1991, 1993) found that this effect all but disappeared when the generation time was long. The effective population size converged toward half the census population size as the generation time was increased, regardless of mating system. This was postulated to be caused by a decrease in the variance in male mating success as generation time was lengthened. But this explanation assumes that male mating success is independent among years. This part of the thesis therefore examines how this relationship is influenced by the presence of persistent individual differences in male mating success. There are a number of studies that suggest that persistent differences of this kind can be found in natural populations (McVey, 1988; Höglund and Alatalo, 1995; McElligott and Hayden, 2000; Pelletier et al., 2006).

Another factor that affects the effective population size, is the age at which reproduction first takes place. According to some previous theoretical studies, delayed reproductive maturity should increase the effective population size (Nunney, 1993; Waite and Parker, 1996). Furthermore, Waite and Parker (1996) showed that the effects of generation time presented by Nunney (1993) were dependent on the prereproductive stage constituting a small proportion of the total life span. When age at maturity was increased in relation to the adult lifespan, they found that the ratio of

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effective population size to census population size increased linearly. Census population size was here defined as the number of adults in the population. All individuals were assumed to survive to maturity. In nature, juvenile survival rates vary substantially among species (e.g. Buettner et al., 2007; Iverson, 2007; Neff and Lister, 2007; Kostecke and Cimprich, 2008). Therefore, this section of the thesis will also examine how the effect that age at maturity has on genetic drift is influenced by juvenile survival.

# Models

## Model 1

Paper I presents a stochastic model of the pair formation process in a single season. The basic idea of the model is that males each have a number of tokens, representing their probability of obtaining mates. Females each choose a token at random (without replacement), and mate with the male owner of the token they have chosen. This assumes that females mate only once each. Only potential breeders are included in the model, so each male starts out with a single token. Additional tokens represent opportunities for multiple mating. In monogamous systems there are no additional tokens, and males can mate only once each. In this situation, once a given male's token has been chosen by a female, he has no more tokens in the system, and thus no more chances of mating. In polygynous systems a number of additional "popularity" tokens are assigned, giving males a chance of mating with multiple females. The number of tokens in the model can be seen as a measure of the potential for polygyny in the system. This number can be deterministic (as in Paper I), or stochastic (Paper II). If all males in a population are equal in their ability to obtain mates, the popularity tokens would be assigned at random. But males in a breeding population are seldom identical. Differences in phenotypic traits can translate into differences in mating probability. Therefore, males are assigned "quality" values. These quality values could be based on popularity among the females, searching or fighting ability, or any other

characteristics that influence a male's probability of success in obtaining mates. These quality values are here assumed to have a Dirichlet distribution, and thus sum to one for all males in the population. The shape parameter of the Dirichlet distribution can be seen as a measure of the effective equality of males. When it is large, males are essentially equal. As it approaches zero, a single male gets a quality value of one, while all the other males have quality values of zero. The popularity tokens are then distributed according to a multinomial distribution with the quality values as probabilities. The more tokens a male has compared to other males, the higher his chance of obtaining mates.

In this way, mating systems are described using two main parameters, potential for polygyny and effective equality of males. Varying the (expected) number of popularity tokens in the model allows the degree of polygyny to be adjusted in a continuous manner.

## Model 2

Paper II uses a modified version of Model I to examine stochastic population dynamics in populations with non-overlapping generations. When generations are non-overlapping, only those females that mate can contribute to the future population. This paper focuses on population dynamics, and ignores genetic factors. Assuming that the distribution underlying the number of offspring produced is the same for all mated females, the number of mated females is the measure that holds information about the size of the population at the next time step. Because of this, the subpopulation of mated females is tracked over time, in place of the total population size. This model uses the same token system as in Model I. However, since genetic factors are being ignored, the identity of individual fathers is not important. The number of matings available to the female subpopulation is the determining factor. The number of tokens in the system is assumed to be one monogamy token per male, plus a Poisson distributed number of popularity tokens. If the total number of tokens

exceeds the number of females, all females are assumed to mate. Otherwise, the number of tokens determines how many females mate. In this model there are three stochastic steps. The number of offspring produced per mated female is assumed to have a Poisson distribution, the sex of these offspring is determined through a binomial process, and the number of tokens follows a Poisson distribution.

**Model 3**

In Paper III a method of calculating an approximation of the fixation probability of slightly beneficial alleles is presented. This method provides a more accurate approximation than the equation found by Athreya (1993). The calculations involve using the cumulant-generating function for the distributions of contributions among classes to obtain a set of equations with the fixation probabilities of mutations arising in different classes as unknowns. These equations can then be solved using the fixed point method.

**Model 4**

A very useful way to study genetic drift is to study the dynamics of a subpopulation of individuals carrying a rare allele (Engen et al., 2005). This can be done with the help of a stochastic matrix model (Caswell, 2001; Engen et al., 2005). In a model of this type, a population vector is used to tabulate the number of individuals present in different classes at a given time. The classes represent groups of individuals that are assumed to have similar vital rates (Caswell, 2001). Age and developmental stage are commonly used groupings (Leslie, 1945; Lefkovitch, 1965). The population vector at the next time step is obtained from the current vector by matrix multiplication with a (stochastic) projection matrix containing vital parameters and transition probabilities (Caswell, 2001). In Paper IV a stochastic matrix model is developed for a diploid population with two sexes. The male subpopulation is divided into classes on the basis of mating success. Adult females are assumed to mate once each, and are therefore

grouped together in a single class. If the age at first reproduction is higher than one, prereproductive individuals are entered into the model in age classes. Probabilities in the projection matrix are based on survival rates, offspring production, and mating probabilities.

In order to obtain mating probabilities resulting in a certain variance in male mating success, Model 1 is used. An additional parameter is introduced to control the presence of persistent individual differences in mating success. When such differences are present, each male has an increased probability of obtaining the same number, one more, or one less female than in the previous season. This parameter can be adjusted from the case of independent mating seasons, and up to the situation in which all males are guaranteed to be within one mating class of where they were at the previous time step. It is assumed that reproduction and survival are independent.

A model of this type provides us with the growth rate, stable stage structure, reproductive value, generation time, and demographic variance of the subpopulation studied. The demographic variance in this case includes genetic components (caused by Mendelian segregation). By combining information about the generation time and the demographic variance, the ratio of effective population size to census population size, $N_e/N$, can be found (Engen et al., 2005).

# Results and discussion

## 1. Understanding the pair formation process (Paper I)

The urn and token model presented in Paper I (Model 1) describes the pair formation process through two main parameters, the effective equality of males and the potential for polygyny (or interdependence of mating events). Simulations of mating systems with different combinations of parameter values result in distributions of male mating success that correspond with expectations. As the effective equality of males increases, mating success becomes more evenly distributed. As the potential for polygyny

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increases, the distribution becomes more skewed. This latter change is more pronounced when there are "quality" differences among males.

Results from this model reveal that different combinations of parameters (i.e. different mating systems) can produce the same variance in male mating success. The actual distribution of male mating success, however, may differ markedly. Most reproductive skew indices that have been suggested are based on the variance in reproductive success (Kokko et al., 1999). Since different mating systems that lead to different distributions of mating success can still have the same variance in reproductive success, the descriptive function of such indices is limited. Thus, using a mechanistic model such as the one presented in Paper I could in many cases be a more useful way of describing mating systems and their outcomes.

## 2. Mating systems and demographic stochasticity (Papers II, III)

Using a simulation model with stochasticity at several levels (Model 2), we show that combinations of mating system (degree of polygyny) and adult sex ratio affect the demographic variance (Paper II). The highest variances are found in highly polygynous populations with female-biased sex ratios. The lowest levels are found in monogamous systems with even sex ratios. Milner-Gulland et al. (2003) reported a case of population collapse in the Saiga antelope (*Saiga tatarica tatarica*). When the sex ratio in this population became extremely female-biased, fecundity was reduced. Concern has also been raised about other species in similar situations (Bergerud, 1974; Dobson and Poole, 1998). Our results show that a very high demographic variance could be expected in a population in this situation, and it is possible that this can have contributed to the collapse.

The stochastic growth rate is also shown to depend on both the mating system and the sex ratio (Paper II). Demographic stochasticity causes the growth rate to decrease (Lande et al., 2003). Here, the magnitude of this decrease is shown to be the greatest when the expected number of females in the population is equal to the

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expected number of male matings available. The sex ratio at which this is the case varies for different mating systems. Our results show that polygynous populations in general tend to show a greater vulnerability to demographic stochasticity, than monogamous ones. This is reflected in the decreases in growth rate and increases in extinction risk caused by demographic stochasticity in the different systems. However, comparisons between mating systems will garner different results depending on the sex ratio at which they are compared. At the even (1:1) sex ratio, monogamous populations experience a greater decrease from demographic stochasticity than do polygynous ones. This is consistent with the results of previous studies that have compared mating systems at even sex ratios only (Legendre et al., 1999). Model 2 assumes non-overlapping generations. Overlapping generations can cause positive correlations in the sex ratio over time. This makes it difficult to predict how the results obtained from this model might differ when generations overlap.

These results show that it is important to take both demographic stochasticity and sex ratio into account, when comparing different mating systems and their effects on population dynamics.

It has previously been shown that demographic variance and reproductive value are important parameters for studying the fixation probability of slightly beneficial alleles (Athreya, 1993). In paper III a method is presented for calculation of this probability in large populations with age-structure and two sexes. A simulation study shows that this new method is quite a bit more accurate than the approximation presented by Athreya (1993), as the selective advantage of the mutation moves away from zero. As shown in paper II, the demographic variance is influenced by the mating system, as is the reproductive value of different classes. Thus, mating system may be an important factor in the fixation of slightly beneficial alleles.

**3. Population size, sex ratio and mating system (Papers I, II)**

*Population size*

As the population size increases (holding all other parameters constant), the variance in male mating success obtained from Model 1 increases towards a limit (Paper I). This is a general characteristic of the statistical variance, and is experienced by most reproductive skew indices as well. This is often considered to be an undesirable trait, as it makes it difficult to compare populations and test for nonrandom mating (Ruzzante et al., 1996; Kokko et al., 1999). However, it can be argued that the higher variance found in larger populations is an important feature of the realized inequality in male mating success.

Population size seems to be particularly important when it becomes small. Using Model 2, it is found that demographic stochasticity can cause an Allee effect, and that this Allee effect is amplified by polygyny (Paper II). As previously mentioned, demographic stochasticity can in itself cause a substantial decrease in growth rate at low population size. Stephens et al. (1999) and Stephens and Sutherland (1999) argued that this should not be considered an Allee effect as long as no specific component of individual fitness is decreased. Dennis (2002) makes a similar distinction between mechanisms that affect the expected growth rate, as opposed to affecting only the variance in the growth rate. A fluctuating sex ratio is still considered a legitimate Allee effect mechanism under this restricted definition (Courchamp et al., 2008). The demographic variance in our model has several components (number of offspring produced, sex ratio, and pair formation). The Allee effect that it causes is however mainly due to a decrease in the expected growth rate, and therefore falls within the bounds of what Dennis (2002) calls "real" biological Allee effects.

As the population size becomes very small, the sex ratio that gives the highest population growth is shifted closer to the even sex ratio. This corroborates the statement by Legendre (2004) that the sex ratio that maximizes the (deterministic) growth rate usually differs from the sex ratio that minimizes extinction risk, and that

the difference is dependent on the mating system.

*Sex ratio*

As shown in section 2 above, sex ratio plays a very important role in determining the demographic variance and stochastic growth rate in populations with different mating systems. In addition, the variance in male mating success found in Model 1 increases when the proportion of females increases (Paper I). This effect is stronger than the previously mentioned effect of population size. Similarly to the population size effect, this effect of sex ratio can be viewed either as an undesirable statistical artefact (Ruzzante et al., 1996; Tsuji and Kasuya, 2001), or as a true reflection of a biological phenomenon (Nonacs, 2003).

The opportunity for sexual selection, measured as the variance in mating success divided by the mean mating success squared $(\mathrm{Var}(X)/\bar{X}^2)$, is a frequently cited measure that sets an upper limit for the intensity of sexual selection (Crow, 1958; Wade and Arnold, 1980; Arnold and Wade, 1984). In Model 1, when the number of females per male increases, the opportunity for sexual selection in males decreases. This is consistent with the theory of Emlen and Oring (1977) that states that sexual selection is more intense when there is a shortage of mates.

## 4. Mating system and effective population size (Paper IV)

Persistent individual differences in mating success among males cause the effective population size to converge to a lower value when the generation time becomes long, than when such persistent differences are absent. In populations with overlapping generations, it is the variance in *lifetime* reproductive success that is important when determining the effective population size (Hill, 1972). When the same males retain an advantage throughout their lives, the variance in lifetime reproductive success increases, thus decreasing the effective population size. However, the effective size of populations with different mating systems still converge as the generation time

becomes long. As shown by Engen et al. (2005), the effective population size can be obtained from a fraction that has both the demographic variance of a subpopulation of individuals carrying a rare allele, and the generation time, in the denominator. Lengthening the generation time therefore causes a convergence of the effective population size even if the demographic variance stays constant.

The effect that age at maturity has on genetic drift is here shown to vary with different rates of juvenile survival. The effect that this has on the ratio of effective population size to census population size is, however, dependent on which census population size one uses. Using the adult population as their census population, Waite and Parker (1996) found that $N_e/N$ increased as the age at maturity increased. However, if the total population size is used instead, the ratio is found to decrease. This can be explained by changes in the proportion of prereproductive individuals present in the population as the age at maturity is shifted. Unless juvenile survival is very high, delayed maturation (with a constant expected adult lifespan) causes an increase in both the genetic drift per timestep (measured as the demographic variance of a subpopulation of individuals with a rare allele) and the generation time. Both of these factors are expected to decrease the effective population size, $N_e$. However, when $N$ is defined as the number of adults in the population, the accompanying decrease in the proportion of individuals present as adults still causes the ratio $N_e/N$ to increase linearly. This emphasizes the need for a consensus on what definition of $N$ should be used, to make results transferrable. It also highlights once again the importance of understanding the mechanisms behind the quantities being measured.

## Future prospects

In this thesis I examine some effects of mating system and demographic stochasticity on population dynamics and genetics. Mating system and demographic stochasticity are factors that are often ignored when studying population processes, but that can be influential, especially in small populations. Also, as has been shown here, sex ratio

needs to be considered when mating systems are studied. Models such as the ones developed here, can be useful tools for investigating effects of mating systems. However, there is still quite a bit that can be done to make them more serviceable.

The model upon which much of the work in this thesis is based (Model 1) is a very basic model. It has a lot of potential for being extended in different ways. It can be made more general by allowing for multiple mating among females. This would make it adjustable for polyandry and promiscuity, in addition to monogamy and polygyny. It would also be possible to model female choice separately from other aspects of male "quality". In a version with polyandrous females it would be natural to allow for male choosiness, and eventually also mutual mate choice and assortative mating. Another natural next step is to estimate the parameters of the model from population data, and examine ways of tailoring it to specific species. For example, linking "quality" values to specific male traits (or suites of traits). In addition, testing some of the model predictions in an experimental setup would be extremely useful.

In nature it is common for populations to have overlapping generations. Using non-overlapping generations such as in Model 2 is a useful simplification, but results cannot be uncritically extrapolated to the case of overlapping generations. It will therefore be important to examine how the results from Paper II are affected by the addition of overlapping generations.

In Paper I it is shown that different mating systems can give rise to different distributions of mating success with the same variance. The variance in reproductive success is used in many contexts, and it would be interesting to see if such a difference in distribution would affect, for example, genetic processes.

Finally, the study of age at maturity and effective population size in Paper IV assumes that males and females become sexually mature at the same age. However, there are a number of species in which this is not the case (e.g. Andersson, 1994; St Clair, 1998; Khonsue et al., 2001; Setchell et al., 2005). An interesting question for future study is therefore how the effective size would be influenced by differences

between the sexes in age at first reproduction.

Theoretical results of this type should be combined with empirical work, in order to get as complete a picture as possible of the processes being studied. Some empirical work has already been carried out on the topics discussed here (as mentioned throughout the thesis). However, there is still a definite need for more research in this area.

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# Paper I

# Understanding mating systems: A mathematical model of the pair formation process

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## Abstract

Mechanisms generating inequalities among males in reproductive success are key to understanding the evolutionary significance of sexual selection. This paper develops a stochastic model to quantitatively describe and analyze mating systems on a continuous scale from strict monogamy to extreme polygyny. The variance in male mating success is shown to increase with increased differences among males, with decreased interdependence of mating events, with increased population size, and with an increased number of females per male. The latter condition decreases the opportunity for sexual selection. It is found that different combinations of mating system characteristics can lead to the same variance in male mating success, although the distribution differs. This emphasizes the importance of using a model of this type to study mating systems, rather than relying solely on the variance in reproductive success as a descriptor of different systems.
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*Keywords:* Mating systems; Pair formation; Reproductive skew; Reproductive success; Sexual selection; Stochastic model

## 1. Introduction

The differences between males and females within animal species are many and diverse. One major difference is that females produce energy rich eggs while males produce relatively cheap sperm (Wallace et al., 1996). Therefore, a single male has the capacity to produce large numbers of gametes and fertilize the eggs of many females. A female only needs one or a few mates to accomplish fertilization of her eggs. This means that female reproductive success is usually limited by access to resources, whereas male reproductive success is often limited by access to mates (Bateman, 1948). Because of this, females are assumed to be choosy when selecting mates, whereas males are expected to mate with as many females as possible (Bateman, 1948). The resulting sexual conflict, working within the boundaries of ecological factors and physiolo-

gical constraints of different species, has led to a wide variety of mating systems (Trivers, 1972). It has, however, been shown that a large variance in mating success among males does not necessarily indicate non-random mating (Sutherland, 1985). The most basic distinction among mating systems is the number of mates individuals of each sex may have in a breeding season (Thornhill and Alcock, 1983), how the pair formation takes place (Emlen and Oring, 1977), and how much individuals of each sex invest in parental care (Trivers, 1972; Krebs and Davies, 1993).

Although mating systems vary significantly in most taxa (e.g. Davies, 1991), the processes involved in generating the differences are still poorly understood. The contributing factors seem to be many and complicated (Andersson, 1994). In one influential paper, Emlen and Oring (1977) suggested that an important cause of the variation in mating systems is the extent to which potential mates are economically monopolizable. They hypothesized that the average ratio of sexually receptive females to sexually active males present in a population at any given time (termed the operational sex ratio, OSR) can be used as a measure of the monopolizability of mates, and thus of the

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degree of polygamy (polygyny or polyandry) in the population.

In the present paper it is proposed that the potential degree of polygamy can be modeled by the strength of interdependence of matings. If individuals that have already mated once have no possibility of mating again, interdependence of matings is very strong and the mating system is monogamous. At the other extreme, a population in which mating events are totally independent will have the potential for extreme polygamy. In this case the mating chances of individuals will not be affected at all by the number of matings they have already participated in. This concept is closely related to the economic monopolizability of mates described by Emlen and Oring (1977).

Differences in mating systems are intimately linked with the intensity of sexual selection (Emlen and Oring, 1977), described by Darwin (1875, p. 209) as "the advantage which certain individuals have over others of the same sex and species solely in respect of reproduction". Sexual selection is an important source of evolutionary change in natural populations (Shuster and Wade, 2003). The potential reproductive rate (PRR) of males and females has been suggested as a predictor of the direction of sexual selection, and is defined as the maximum number of independent offspring an individual of a given sex can produce per unit time (Clutton-Brock and Vincent, 1991). A frequently used measure of the opportunity for sexual selection is the variance in mating success divided by the mean mating success squared ($\mathrm{Var}(X)/\bar{X}^2$) (Crow, 1958; Wade and Arnold, 1980). This measure sets an upper limit for the intensity of sexual selection (Wade and Arnold, 1980; Arnold and Wade, 1984).

Darwin (1875) pointed out that in order for sexual selection to act in monogamous species, some individuals must gain a reproductive advantage over others with the same number of mates. Darwin (1875) and Fisher (1958) suggested that superior males gain access to the first females ready to mate in a season, and that these females should be more vigorous, and thus produce more offspring than later breeding females, thereby allowing the superior males a reproductive advantage. Generalizing this idea, a decomposition of mating systems by Arnold and Duvall (1994) and Møller (1994b) identified two main paths of sexual selection: differential mating success and differential fecundity per mate. Each of these pathways has a number of contributing factors (e.g. search and handling time, parental investment and infanticide). The concept of male mating success is more complicated than it may appear on the surface. Multiple mating by females and sperm competition is common in natural populations (Birkhead and Møller, 1998). Gaining access to mates may therefore not guarantee a male paternity.

One proposed way of quantifying inequalities in reproductive success is with a reproductive skew index. Several suggestions for such an index have been made (see Kokko et al., 1999; Nonacs, 2003, for a review). However, important information may be lost when the variation in reproductive success is expressed as a single value. Crespi and Yanega (1995) pointed out that very different distributions of reproduction can produce the same skew index value, while populations with the same social system could end up with significantly different values if they, for example, differ in patterns of mortality without this being properly accounted for. An alternative way of studying mating systems and sexual selection is to develop theoretical models which may be able to describe the mechanisms involved in producing the observed distributions of reproductive success, and thus retain and explain more information about the systems being studied. In addition to sexual selection, mating system models may be used to study the effect of mating systems on, for example, genetic drift and extinction dynamics.

A number of models representing different aspects of mating systems have been developed. For example, mate choice has been extensively modeled (e.g. Janetos, 1980; Parker, 1983; Hubbell and Johnson, 1987; Real, 1990). Mating rates and mating probabilities have been studied through several different models (Taylor, 1975; Gimelfarb, 1988a, b; Møller and Legendre, 2001; Bessa-Gomes et al., 2003, 2004), all focusing on different contributing factors. The majority of these models are purely deterministic, not allowing for any random events in the mating system. This limits their realism. Different types of mating systems are often modeled separately (e.g. separate models for monogamous populations, populations with a specific harem size, etc.), and some models allow changes in only one mating system characteristic at a time.

The purpose of this paper is to present a general, stochastic model of the pair formation process. This model uses two basic factors, interdependence of mating events and effective equality of male mating probabilities, to describe a continuous range of mating systems from strict monogamy to extreme polygyny. It will be used to investigate how these two mating system characteristics affect the distribution of male mating success and the opportunity for sexual selection in populations with different numbers of males and females.

## 2. The model

Consider a population of $m$ potentially breeding males and $f$ potentially breeding females. Assume that females mate only once each and that all pair formation/mating takes place at roughly the same time and with no carry-over effects from previous breeding seasons. Fig. 1 gives a schematic overview of how this system is being modeled.

Males in a breeding population will seldom be identical. Differences in phenotypic traits can translate into differences in mating probability, mainly through the influence of male–male competition and female mate choice (Andersson, 1994). In order to model this inequality, each male in the model is assigned a value chosen independently and at random from a gamma distribution with shape parameter $k$. These values are then scaled by dividing each
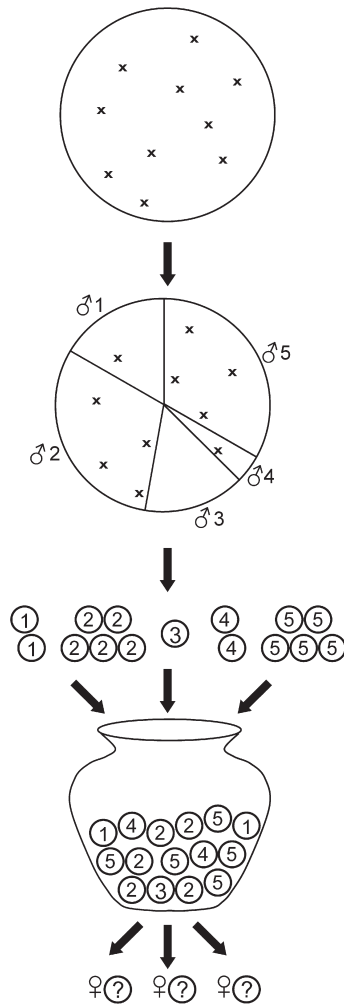
Fig. 1. Basic model setup for five males and 10 popularity tokens. The males are each given a probability, $p_i$ (a fraction of the circle). These are Dirichlet distributed and sum to one. The 10 popularity points are randomly distributed in the circle. Males each have one token (ball) to start with, and receive an extra token for each point that lands within their wedge. All tokens are placed in an urn from which females each draw one token at random (without replacement) and mate with the male owner of this token.

one by the sum of all the values. The resulting set of scaled values, $p_i$ ($i = 1, 2, \ldots, m$), sums to one, and has a Dirichlet distribution. This is a multivariate generalization of the beta distribution (see Evans et al., 2000). The marginal distribution (and due to symmetry also the distribution of $p_i$ values within a population) is a beta distribution with parameters $k$ and $k(m - 1)$. The shape parameter $k$ controls the variance, $(m - 1)/m^2(mk + 1)$, of the $p_i$ values (around an expected value of $1/m$), and can thus be said to describe how different the males of the population are

expected to be. This $k$ is one of the two main parameters of the model, and can be called the effective equality of males. The Dirichlet distribution is such that when $k$ is large, the males end up with very similar $p_i$ values. As $k$ approaches infinity, the $p_i$ values become identical (at $1/m$). On the other hand, as $k$ becomes small, the values will become more uneven. As $k$ tends to zero one male will have a value approaching one, while the values of all other males approach zero. The stochasticity of this process allows for some randomness in the level of inequality found in the population.

The $p_i$ value assigned to a male can be seen as a measure of his "quality" relative to other males in the population. The term quality is here (and in the rest of this paper) used very loosely to mean any characteristic which can increase a male's chances of mating. This "quality" needs to be translated into mating probability.

In most populations, each mate a male obtains decreases his probability of gaining another one. This is caused mainly by time and energy constraints. Representing male mating probabilities by numbers of tokens in an urn allows this decrease to be modeled. Picture a setup where the males each put one or more tokens into an urn, after which the females each choose one random token from the urn (without replacement) and mate with the male owner of the token they have chosen (Fig. 1). Each draw of a token and subsequent mating is considered a mating event. The number of tokens a male places in the urn relative to the total number (the sum of all the males' tokens) represents the mating probability of that male. After a token has been drawn and its owner rewarded with a mate, the token is removed from the model. Thus, for the next draw that male has one token less than before and therefore a lower mating probability.

The assignment of tokens to the males is accomplished through a multinomial process in which the $p_i$ values are the males' probabilities of receiving each token. The tokens are assigned independently of each other (i.e., the number of tokens already received by a male does not affect his probability of getting another one). In this way each male in the model is given an initial mating probability based on his relative "quality" and the effects of random events. It is important to understand that this model is not individual based, but rather focuses on how quality and success are distributed in the male population.

The total number of tokens in the system reflects the degree of interdependence of mating events. In a system with a large number of tokens, the mating events are practically independent, with the mating probabilities of each male changing little between each event. When the number of tokens is low, the mating probabilities will change significantly each time a token is removed. In the extreme case of complete monogamy, each male should have exactly one token. No males can ever have less than that, since the model only considers potential breeders. For this reason, each male receives a "monogamy token"

before the other "popularity tokens" are assigned. Thus, the urn contains $m$ monogamy tokens and a number, $n_p$, of popularity tokens. When the average number of tokens per male is high, there will be a possibility for one or more males to obtain multiple matings. The measure $n_p/m$ can thus be said to describe the potential for polygyny in the population, and is the second main parameter of the model. The potential for polygyny is mainly determined by how much time and energy males spend on activities connected with each mating, like courting, copulation, mate guarding and parental care. If each mating requires high investments in terms of time or energy, the potential for multiple mating is decreased. The presence of the $m$ monogamy tokens ensures that no matter how small $k$ is, and how unevenly the popularity tokens are distributed, each male in the model will have at least one token. Hence, in a population with a low polygyny potential most males will get one female, even if the differences in male quality are high. A completely monogamous system has no popularity tokens, leaving just the monogamy tokens, and a polygyny potential ($n_p/m$) equal to zero. The monogamy tokens also permit the model to accommodate systems in which some males (e.g. young ones) have an extremely low probability of mating compared to others, but still should be considered potential breeders. Having only one token among males with large numbers of tokens leads to a low mating probability. However, due to the stochasticity of the model, even males with very small probabilities of mating may on occasion be successful. Fig. 2 shows the joint effect of the two parameters on the number and distribution of tokens in the urn, and thus on the resulting mating system.

It is assumed that all females mate, unless there are fewer tokens than there are females, in which case ($n_p + m$) females will mate. The sex ratio in the model is equivalent to the OSR defined by Emlen and Oring (1977), since the model only includes potential breeders and describes a single pair formation process. Individuals not sexually receptive at the time of the given pair formation process are excluded.

When the whole model is assembled, it gives the distribution of females (matings) among the males of a population. The number of females obtained by the $i$th male is denoted by $X_i$. In most cases the subscript will be left off, since all males initially (unconditional of $p_i$ values) have the same expected values and variances.

The marginal distribution of $X$ (from Appendix A) is

$$f_X(x) = \sum_{n_i=0}^{n_p} \binom{n_p}{n_i} \frac{\mathrm{B}(k+n_i, n_p+k[m-1]-n_i)}{\mathrm{B}(k, k[m-1])}$$
$$\times \frac{\binom{1+n_i}{x}\binom{m+n_p-1-n_i}{f-x}}{\binom{m+n_p}{f}}, \quad (1)$$
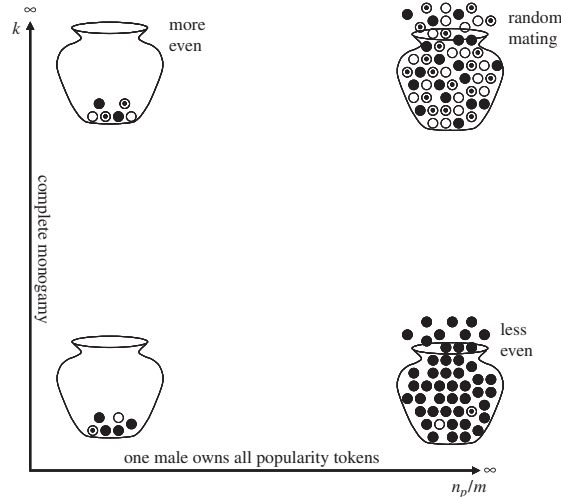


Fig. 2. Joint effect of the two model parameters, $k$ (effective equality of males) and $n_p/m$ (potential for polygyny). All urns in this figure contain three monogamy tokens (one for each male). When $k$ is low, the ownership of popularity tokens is unevenly distributed among the males (here ownership is illustrated by color), whereas high values of $k$ give an even distribution. The value of $n_p/m$ determines the number of popularity tokens in the system. When both parameters approach infinity (top right) the result is random mating; $n_p/m = 0$ gives complete monogamy; while $k = 0$ means that one male owns all the popularity tokens.

where $n_i$ denotes the number of popularity tokens received by the male in question, $f$ is the number of females, and $\mathrm{B}(\cdot)$ denotes a beta function. Because all males have the same parameter $k$ and thus the same (marginal) distribution, the distribution of the number of mates per male in a population will be equivalent to the marginal distribution for each of the males.

By the formula for unconditional variance (Appendix B), the variance of this distribution is

$$\mathrm{Var}(X) = \mathrm{Var}[\mathrm{E}(X \mid n_i)] + \mathrm{E}[\mathrm{Var}(X \mid n_i)]$$
$$= \frac{f(m-1)\left[(m+n_p-f) + \dfrac{n_p(f-1)(n_p+mk)}{(m+n_p)(1+mk)}\right]}{m^2(m+n_p-1)}.$$
$$(2)$$

If there are more females than there are tokens in the model, $f$ is replaced by ($n_p + m$) in this expression.

When the number of popularity tokens approaches infinity (while the population size remains small), the distribution of females per male simply becomes a binomial distribution with probability $p_i$ (in other words, each male's "quality" decides his mating probability directly). If $k$ also approaches infinity (i.e., all males become equal), the probability of success becomes $1/m$ (still with a binomial distribution). This constitutes random mating in a finite population. And finally, also letting the number of

males and females approach infinity causes the distribution to become Poisson, with variance and mean equal to $f/m$.

When the population size (with $m = f$) approaches infinity, but the average number of tokens per male stays constant, the variance tends towards the limit

$$\lim_{m=f \to \infty} \text{Var}(X) = \frac{2ks + ks^2 + s^2}{2ks + ks^2 + k}, \tag{3}$$

where $s = n_p/m$.

Because the number of mating females in the model is finite and fixed, males are not independent of each other in the number of matings they obtain. The dependence between any two males in the model will be the same. The total number of females mated, $\sum_{i=1}^{m} X_i$, is a constant and thus has zero variance. Using the fact that the variance of a sum is the sum of the individual variances plus the sum of all possible covariances, this leads to the simple relationship

$$\text{Cov}(X_i, X_j) = \frac{-\text{Var}(X)}{m-1}. \tag{4}$$

Wade and Shuster (2004) showed that the variance in male mating success can be partitioned into two components: variance between the mean number of mates of mated and unmated males, and variance among the males within each of these groups. Thus,

$$\text{Var}(X) = \frac{f}{m}\left(H - \frac{f}{m}\right) + \frac{(f/m)\text{Var}(X_H)}{H}, \tag{5}$$

where $H$ is the mean number of mates per mating male and $\text{Var}(X_H)$ is the variance in number of mates among mated males.

In this model, the opportunity for sexual selection (Crow, 1958; Wade and Arnold, 1980) is

$$\frac{\text{Var}(X)}{\bar{X}^2} = \frac{m^2}{f^2}\text{Var}(X). \tag{6}$$

Darwin (1875) emphasized that in order for sexual selection to play a role in evolution, individuals with a higher mating success must also leave more offspring. In order to investigate the reproductive success of males, a distribution of offspring per female ($Z_f$) needs to be included in the model. The shape of this distribution will vary among species, and should therefore be chosen with a particular population in mind, not as a general feature of the model. However, the relationship between the variance in number of offspring per female and the variance in number of offspring per male (male reproductive success) will be a general result. The variance in offspring number per male, $\text{Var}(Z_m)$, can be partitioned into one component describing the variance among males with the same number of females, and one component describing the variance caused by males having different numbers of mates. Thus,

$$\begin{aligned}
\text{Var}(Z_m) &= \text{E}[\text{Var}(Z_m \mid X)] + \text{Var}[\text{E}(Z_m \mid X)] \\
&= \text{E}\left[\text{Var}\left(\sum_{j=1}^{X} Z_{f_j}\right)\right] + \text{Var}\left[\text{E}\left(\sum_{j=1}^{X} Z_{f_j}\right)\right] \\
&= \text{E}[X\,\text{Var}(Z_f)] + \text{Var}[X\,\text{E}(Z_f)] \\
&= \frac{f}{m}\text{Var}(Z_f) + \text{Var}(X)[\text{E}(Z_f)]^2. \tag{7}
\end{aligned}$$

This assumes that the number of offspring produced by a female is independent of the numbers of offspring produced by other females. The result in Eq. (7) has previously been reported by Wade (1979) and Shuster and Wade (2003). Eq. (7) shows that a more variable distribution of offspring per female (increased $\text{Var}[Z_f]$) also increases the variance in offspring numbers among males ($\text{Var}[Z_m]$). It also shows that if the variance in female reproductive success and the sex ratio are held constant, changes in the variance of male mating success parallel changes in the variance in male reproductive success. Thus, the variance in male mating success may be used as a basis for studying the effects of mating system on sexual selection in this simple case of monogamous females with independent numbers of offspring.

## 3. Results

Using the model to simulate populations with different levels of male equality ($k$) and potential extent of polygyny ($n_p/m$) for several population sizes has revealed the following general pattern of mate distributions. Populations with males that differ substantially in "quality" (populations with small values of $k$) have a more uneven mate distribution than populations with more similar males (larger values of $k$). This effect is stronger when the polygyny potential ($n_p/m$) is high. Populations in which the interdependence of mating events is high and hence the potential for polygyny is low have a more even mate distribution than those with a higher polygyny potential. The effect is stronger when $k$ is low. Theoretical analyses have been carried out to further examine the behavior of the model.

The variance in mating success among the males of a population (Eq. (2)) increases with an increasing potential for polygyny ($n_p/m$) and with a decreasing $k$ (effective equality of males) (Fig. 3), thus confirming the results obtained from the simulations. In addition, $\text{Var}(X)$ increases with a growing population size when $k$ and $n_p/m$ are held constant (Fig. 3). This is a consequence of the way statistical variance is defined, and its dependence on the range of possible values. When the population size approaches infinity (still with an even sex ratio), the variance approaches the limit presented in Eq. (3) (Fig. 3).

An increased sex ratio, $f/m$, (more females per male) leads to a higher variance in mating success among the males (Fig. 4). The effect is greater for smaller values of $k$
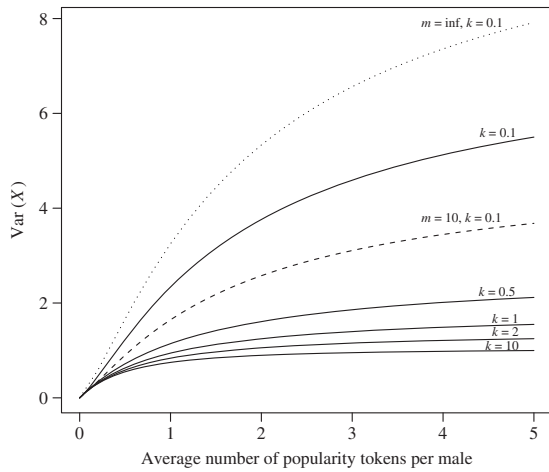
Fig. 3. Variance among males in the number of mates obtained, Var($X$), as a function of the average number of popularity tokens per male ($n_p/m$) in the population. Results are shown for different values of $k$ (effective equality of males) in a population with 25 males and 25 females (solid lines). In addition, results for $k = 0.1$ are shown in a population with 10 individuals of each sex (dashed line) and in a population with a size approaching infinity (dotted line).
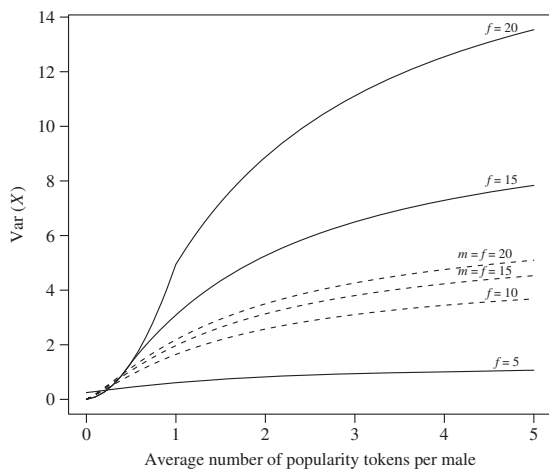


Fig. 4. Variance in the number of mates obtained by males, Var($X$), in relation to the average number of popularity tokens per male ($n_p/m$) at different sex ratios. All populations have a medium level of equality among males ($k = 0.1$). The numbers of females in the populations are labeled on the graph. The number of males is 10 unless otherwise specified. Dashed lines indicate even sex ratios.

(not shown in the figure), and is closely connected to the previously mentioned effect of population size. In a population with more females per male, the benefits of being popular are higher, leading to more pronounced differences among males and therefore a higher variance.

In fact, a population with 10 males and 20 females has a higher variance in mating success among males than a population with an infinite population size and an even sex ratio (assuming $k$ and $n_p/m$ are the same) (compare Figs. 3 and 4). In cases where there are more females than the total number of tokens ($f$ larger than $[n_p + m]$), all males will get to mate with at least one female (since all tokens will be used, and every male has one monogamy token). Then the variance among males is due solely to the differences in numbers of tokens received, without the added variance created by only some of the tokens being chosen by females. This causes an extra drop in the variance below the point where $f$ is equal to $(n_p + m)$ (see Fig. 4).

When there are fewer females than males the variance is low (Fig. 4), partly because the maximum number of females a male can obtain is small, and partly because the number of tokens required for a male to win the majority of the females becomes very large. However, this situation increases the opportunity for sexual selection (Eq. (6)), whereas an increased sex ratio ($f/m$) decreases the opportunity for sexual selection (Fig. 5). The drop in the variance caused by an $f$ larger than the total number of tokens creates a corresponding drop in the opportunity for sexual selection (Fig. 5).

One important feature of this model is that several different combinations of the two parameters $k$ and $n_p/m$, and population size, can result in the same variance in mating success (see e.g. Fig. 3). Simultaneous increases (or decreases) in both $k$ and $n_p/m$, an increase in $n_p/m$ while the population size decreases, and an increase in $k$ while the population size increases, can all preserve the original variance in mating success (Fig. 6). Furthermore, the distribution of females among the males changes as the
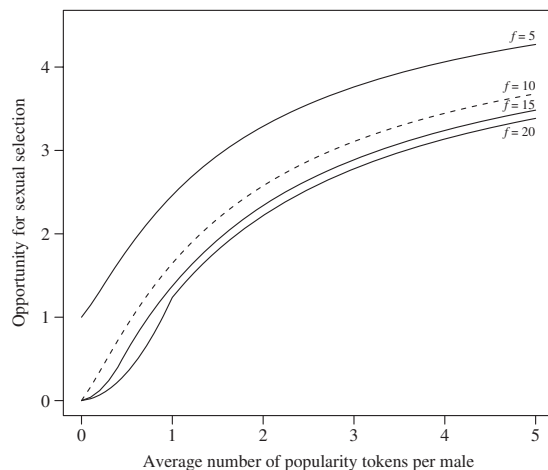


Fig. 5. The opportunity for sexual selection (Eq. (6)) in relation to the average number of popularity tokens per male ($n_p/m$) at different sex ratios. All populations have a medium level of equality among males ($k = 0.1$). Populations consist of 10 males and a number of females labeled on the graph. The dashed line indicates an even sex ratio.
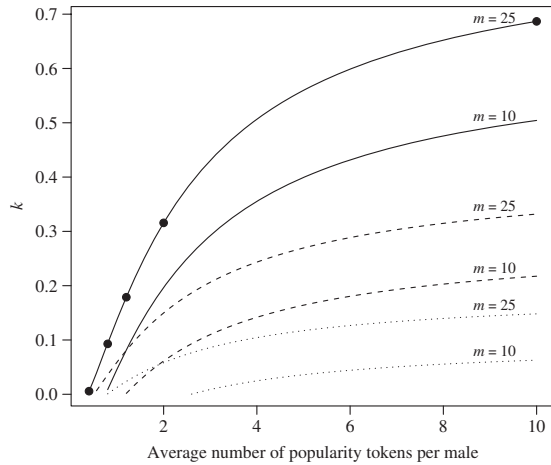
Fig. 6. Relationship between the two parameters $k$ (effective equality of males) and $n_p/m$ (average number of popularity tokens per male, or potential for polygyny) when the variance, Var($X$), is held constant at 2 (solid lines), 3 (dashed lines) and 5 (dotted lines). Two different population sizes (even sex ratio) are shown for each variance. The dots on the top curve are placed at $n_p/m$ = 0.4, 0.8, 1.2, 2.0, and 10.

parameters are varied, even when the variance is constant (Fig. 7).

As $k$ and $n_p/m$ increase, maintaining a constant variance, the proportion of unmated males in the population, and the mean number of females per mating male ($H$) both increase (Fig. 7). In other words, the variance between the classes of mated and unmated males (the first term in Eq. (5)) increases, and the variance within the mated class (second term) decreases. Gradually, a stable distribution is approached (compare Figs. 7e and f). The pattern described here is general, and is found for different population sizes and different variances.

## 4. Discussion

The model presented in this paper describes the process behind the distribution of reproductive success (mainly represented by mating success) among males in a population. This is done using just two main parameters (in addition to the required parameters of male and female numbers), namely the effective equality of males ($k$), and the interdependence of mating events ($n_p/m$). By varying these parameters, the model can be used to describe a continuous range of mating systems, from monogamy to polygyny, including the special cases of strict monogamy, random mating, and a single male mating with all the females.

A male's ability to obtain mates can be affected by a number of factors. For example, male attractiveness to females is often closely correlated with phenotypic traits, like body size or ornamentation (Andersson, 1994), while in systems with direct male–male combat over mates

fighting ability is decisive (Darwin, 1875). In other instances, arrival time at the breeding ground may determine access to potential mates (e.g. Møller, 1994a; Mitrus, 2006), or the ability to locate females quickly in scramble competition may be a major factor (Thornhill and Alcock, 1983). The combined effect of all such components is described by the model parameter called effective equality of males ($k$). This parameter can be said to jointly represent all male traits that may be acted on by sexual selection.

The second parameter of the model describes the level of interdependence among mating events. When mating events are strongly interdependent, it means that the mating probability of a male decreases significantly with each mate he obtains. This limits the number of mates a single male can have, thus reducing the impact of male inequalities on the distribution of mates. In systems with completely independent mating events, on the other hand, males with a high mating probability retain their advantage throughout the whole pair formation process. This allows the inequality of males to be fully realized in their mating success. This parameter is closely connected to the potential for polygyny, since it affects the probabilities of males obtaining multiple mates. In most systems a decrease in mating probability with increasing numbers of previous matings can be attributed to time and energy constraints. This can be related directly to the economic monopolizability of mates described by Emlen and Oring (1977). The PRR of males is not specified directly in the model, but rather arises as a result of the chosen set of parameters.

The model is based on a number of assumptions. All females are assumed to mate, but only once each. This means that all the offspring of a given female are assumed to be fathered by the same male. Therefore the model is most appropriate for studying monogamous through to polygynous systems, rather than polyandrous or promiscuous ones. Sexual monogamy in females seems to be relatively rare in the wild (Birkhead and Møller, 1998), making this assumption somewhat unrealistic. However, this simplification makes a useful starting point for modeling. The assumptions may later be relaxed as the model is extended.

In the simplest form of the model all females are considered to be identical. Using number of mates to quantify male reproductive success is a frequently applied simplification (e.g. Höglund and Alatalo, 1995; Forstmeier, 2002; Lappin and Husak, 2005) which may give good approximations in some situations (see Eq. (7) and associated text). However, in addition to number of mates, mate quality can play an important role in male reproductive success (e.g. Domb and Pagel, 2001). The inclusion of a distribution of offspring number among females, as demonstrated earlier in this paper (Eq. (7) and associated text), is a first simple step in allowing variance in female quality.

The model describes pair formation in one season only. Pair formation is here assumed to be a discrete process
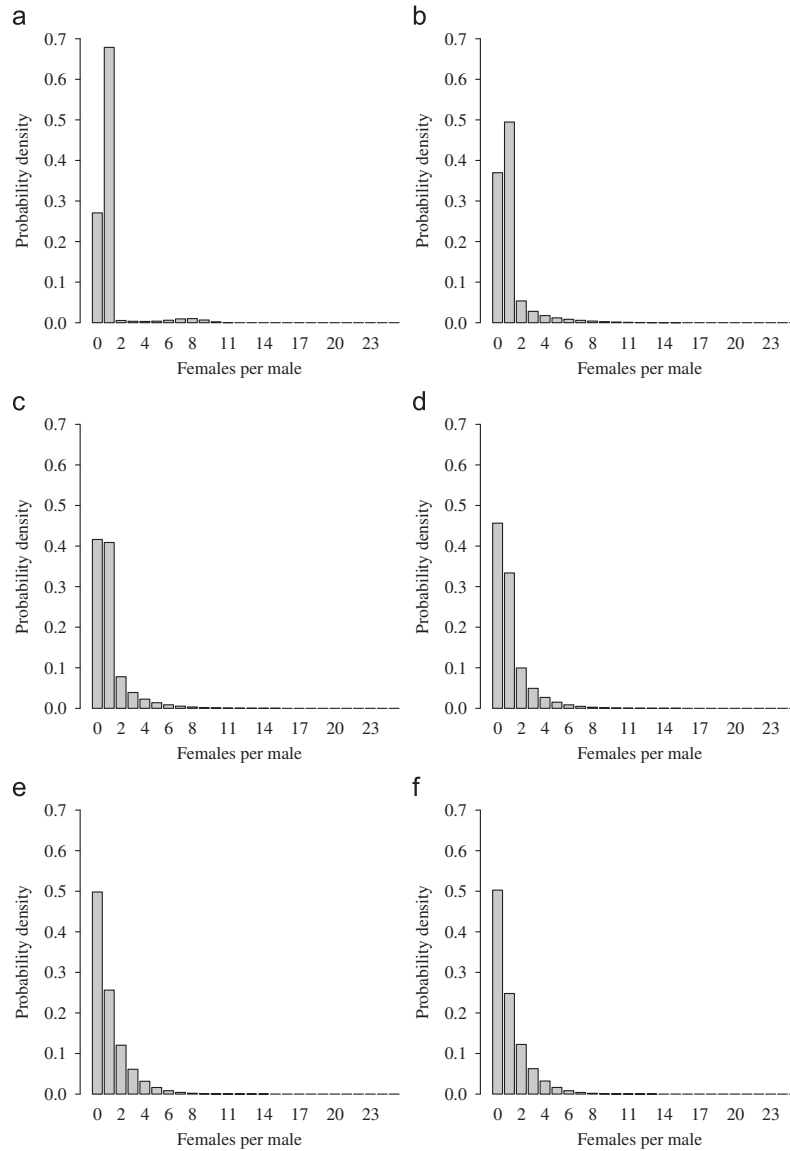
Fig. 7. Probability distribution of the number of females per male in populations with 25 males, 25 females and a constant variance of 2. The average number of popularity tokens per male in the systems are $n_p/m =$ (a) 0.4, (b) 0.8, (c) 1.2, (d) 2, (e) 10 and (f) 20. Values of $k$ (effective equality of males) are 0.006, 0.093, 0.179, 0.316, 0.687 and 0.762. The parameter values of (a)–(e) correspond to the dots in Fig. 6. The probability of a male having more than one mate becomes $P(X>1) = 0.051, 0.136, 0.175, 0.210, 0.246$ and 0.249. All numbers are rounded off.

independent from pair formation in previous seasons. Carry-over effects from previous seasons are known to exist in some systems, and can be either positive or negative (e.g. Krebs and Davies, 1993). Similarly, age effects in reproductive success are found in many species (Clutton-Brock, 1988). Because of the potential lack of independence between breeding seasons, lifetime reproductive success may not always follow the same pattern as

reproductive success in a single season (McCauley, 1983; Nunney, 1993). In addition, reproductive lifespan generally has a large effect on lifetime reproductive success (Newton, 1989), further complicating the situation. This means that any extrapolations of model results must be carried out with care.

Search and encounter dynamics are ignored. If the probability of a male encountering a female and mating

with her is determined primarily by his searching ability (e.g. Nahrung and Allen, 2004), this could be included in the $p_i$-values, as a component of male "quality". However, the probability of a male mating after an encounter, may depend on which female he encounters. In this case, more complex modeling is required (e.g. Gimelfarb, 1988b).

Simulations of mating systems with different combinations of parameter values show that the distribution of mating success among males becomes more even as the males become more similar ($k$ increases), and as the potential for polygyny ($n_p/m$) decreases. These results make biological sense, complying with our expectations for the distribution of matings in different systems. This indicates that the model is successful at describing mating systems, at least at a basic level, and lends support to the validity of the above assumptions.

The theoretical variance of reproductive success in the model has been shown to increase when differences between the males become more pronounced ($k$ decreases) and when the potential for polygyny increases ($n_p/m$ increases) (Fig. 3). This further supports the conclusions drawn from the simulations. As the number of popularity tokens ($n_p$) increases, the variance gradually stabilizes. The situation at the limit (when $n_p$ becomes infinite) is one in which mating events are completely independent of each other, so a given male has the same probability of mating with each female, regardless of how many females he has mated with previously. If a population like this has one male with a very strong competitive advantage over the other males ($k$ close to zero), there is a possibility of that male obtaining all the females. If, at the other extreme, all the males are equal ($k$ approaches infinity), they each have the same probability ($1/m$) of mating with each of the females. This describes random mating in a finite population. Allowing the population size to approach infinity (with an even sex ratio) turns the male mating distribution into a Poisson distribution. This is as expected for a large, randomly mating population (easily extrapolated from the discussion on the Poisson distribution in Larsen and Marx, 2001). Thus, the model lends itself well to these special cases.

When the number of popularity tokens is zero, the population is completely monogamous. As long as the number of females equals or exceeds that of males, the distribution of mating success in this system will be completely even. However, male reproductive success may not be equal for all males if females differ in quality. Therefore it will be important to specify a distribution of offspring among females when studying monogamous populations.

In addition to the two main parameters, $k$ and $n_p/m$, the numbers of males and females in the population also influence the outcome of the model. Assuming a constant sex ratio, it has been shown that an increase in the number of males (with a proportional increase in female number) increases the variance in reproductive success among males (Fig. 3). This effect of population size can make it difficult

to compare the variance in reproductive success across populations. Most skew indices developed for studying mating systems also experience this dependence on population size. If one is attempting to measure how likely it is that a given mating distribution has arisen by chance (in a system with random mating), a dependence on population size is an undesirable trait. This has been discussed in several papers (e.g. Ruzzante et al., 1996; Kokko et al., 1999). On the other hand, if the goal is to describe the realized inequality in male mating success, and possible evolutionary effects of this, it can be argued that the higher variance found in larger populations is a real phenomenon that should be recognized.

Increasing the number of females per male, $f/m$, also causes an increase in the variance in male mating success (Fig. 4). The variance in male reproductive success experiences an even greater effect of the sex ratio (Eq. (7)). The effect caused by a change in the sex ratio is stronger than the previously mentioned population size effect. Given a population with an even sex ratio, adding a number of extra females increases the variance in mating success more than adding the same number of individuals equally divided among males and females, or adding the extra females plus an equal number of males. As the population size increases (with an even sex ratio and a constant number of tokens per male), the variance approaches the limit in Eq. (3) (Fig. 3). On the other hand, when the sex ratio ($f/m$) increases, the variance continues to grow towards infinity (assuming that the number of tokens available allows all females to mate). The sex ratio effect is, however, limited by the number of tokens per male, making it difficult to separate the effects of sex ratio from the effects of the polygyny potential.

Similar to the effect of population size, changes due only to the sex ratio can either be viewed as an undesirable statistical effect (see e.g. Ruzzante et al., 1996; Tsuji and Kasuya, 2001), or as an appropriate reflection of the biological system (Nonacs, 2003). Either way, it is important to be aware of the effects that the population size and sex ratio have on the variance in reproductive success, when trying to explain patterns seen in nature.

Under the assumptions of this paper, the opportunity for sexual selection (Eq. (6)) only differs from the variance when the sex ratio deviates from one. When the number of females per male increases, the opportunity for sexual selection on males decreases (Fig. 5). This is consistent with the relationship between the sexes, described by Emlen and Oring (1977, p. 215), "when one sex becomes a limiting factor for the other, the result is an increase in intrasexual competition among members of the available sex for access to mates of the limiting sex. The greater the 'shortage' of one sex, the more intense the sexual selection.". As the ratio of females to males increases, the number of females becomes less of a limiting factor, and the intensity of sexual selection decreases.

Different combinations of the two model parameters can result in the same variance in male mating success, despite

different distributions of matings (Figs. 6 and 7). This clearly shows that studying the variance in reproductive success is not enough to attain a good understanding of mating systems and how they work. The majority of the skew indices that have been suggested for studying mating systems are based on this variance (Kokko et al., 1999), so that populations with the same variance are assigned the same index value, regardless of how different their distributions of male mating success may be. Thus, the information that can be extracted about a mating system from such an index value is severely limited. In order to gain an understanding of how mating systems function, one must look beyond the variance to the many interacting factors which underlie the mating distribution. These factors need to be disentangled, and links between them and the resulting distribution uncovered. The model presented in this paper does just that, describing the connections between two fundamental factors of mating systems (effective equality of males and interdependence of mating events) and the distribution of male mating success.

Understanding the mechanisms of mating systems and sexual selection are of interest both in evolutionary biology and in population ecology. In addition, this model can have uses in conservation biology. Variance in reproductive success has been shown to be closely linked to genetic drift (Frankham, 1995; Ramakrishnan et al., 2004) and demographic stochasticity (Lande et al., 2003). These processes are in turn closely connected to the extinction dynamics of populations (Lande and Barrowclough, 1987; Lande et al., 2003). Predicting effects of different changes in mating system characteristics on the reproductive variance, can thus be crucial for conservation efforts, for example in situations with captive breeding. This model gives a basis for such predictions.

One advantage of this model over many of the earlier mating system models is its stochastic structure. Stochasticity is built into the model at all levels where random events can occur in natural systems (male quality, mating probability and mating success). This makes the model more realistic than many previous ones. In addition, the model describes a continuous range of mating systems, including extreme cases, but not limited to them. The model is well suited for analyzing variances, parameters, and their relationships through analytical expressions (see Eqs. (1)–(7)).

The assumptions of the model are a bit limiting, especially the supposition that females are monogamous. An important future step will therefore be to extend the model to accommodate a wider range of populations and situations, including age/stage structure, females that mate more than once, and mutual mate choice. The model will then be a useful tool for analyzing how variation in mating systems affects population dynamics and genetics. Furthermore, it will be useful to develop statistical methods with which the model parameters can be estimated in populations for which data on the distribution of reproductive success is available. This will increase our understanding of the specific characteristics of the populations examined, and also of mating system mechanisms in general.

## Appendix A. Marginal distribution

The number of popularity tokens received by a particular male, $n_i$, is decided by a binomial process with $n_p$ trials, in which the probability of success, $p_i$, is itself a beta variate with parameters $k$ and $k(m-1)$. The resulting distribution is beta binomial (Evans et al., 2000, p. 42) with probability function

$$g(n_i) = \binom{n_p}{n_i} \frac{B(k+n_i, n_p + k[m-1] - n_i)}{B(k, k[m-1])}, \tag{8}$$

where $B(\cdot)$ denotes a beta function, defined by

$$B(v, w) = \frac{\Gamma(v)\Gamma(w)}{\Gamma(v+w)} = \int_0^1 u^{v-1}(1-u)^{w-1}\, du, \tag{9}$$

with

$$\Gamma(v) = \int_0^\infty \exp(-u)u^{v-1}\, du. \tag{10}$$

The number of females a male with a given $n_i$ gets to mate with, depends on how many of his $(1 + n_i)$ tokens are chosen by females. This is a hypergeometric process with

$$P(X = x \mid n_i) = \frac{\binom{1 + n_i}{x} \binom{m + n_p - 1 - n_i}{f - x}}{\binom{m + n_p}{f}}. \tag{11}$$

By the law of total probability, the probability of a male mating with $x$ females becomes

$$
\begin{aligned}
f_X(x) &= \sum_{n_i=0}^{n_p} g(n_i) P(X = x \mid n_i) \\
&= \sum_{n_i=0}^{n_p} \binom{n_p}{n_i} \frac{B(k + n_i, n_p + k[m - 1] - n_i)}{B(k, k[m - 1])} \\
&\quad \times \frac{\binom{1 + n_i}{x} \binom{m + n_p - 1 - n_i}{f - x}}{\binom{m + n_p}{f}}.
\end{aligned}
\tag{12}
$$

## Appendix B. Finding the variance of $X$

As explained in Appendix A, the number of popularity tokens a male receives follows a beta binomial distribution. The expected value and variance of this distribution are (Evans et al., 2000, p. 42)

$$E(n_i) = \frac{n_p k}{k + k(m - 1)} = \frac{n_p}{m}, \tag{13}$$

$$
\begin{aligned}
Var(n_i) &= \frac{n_p k^2 (m - 1)(n_p + mk)}{(mk)^2 (1 + mk)} \\
&= \frac{n_p (m - 1)(n_p + mk)}{m^2 (1 + mk)}.
\end{aligned}
\tag{14}
$$

The number of females a male mates with, given the number of popularity tokens he has, is the result of a hypergeometric process. There are $(m + n_p)$ tokens in the model, of which $(1 + n_i)$ are owned by the male in question. The number of tokens drawn is $f$. Thus

$$E(X \mid n_i) = \frac{f(1 + n_i)}{m + n_p}, \tag{15}$$

$$
\begin{aligned}
Var(X \mid n_i) &= \left[\frac{m + n_p - f}{m + n_p - 1}\right] \left[\frac{f(1 + n_i)}{m + n_p}\right] \left[1 - \frac{1 + n_i}{m + n_p}\right] \\
&= \left[\frac{(m + n_p - f)f + (m + n_p - f)fn_i}{(m + n_p - 1)(m + n_p)}\right] \left[\frac{m + n_p - 1 - n_i}{m + n_p}\right] \\
&= \frac{f(m + n_p - f)[(m + n_p - 1)(1 + n_i) - n_i - n_i^2]}{(m + n_p - 1)(m + n_p)^2}.
\end{aligned}
\tag{16}
$$

From this the expressions needed to use the law of total variance (see below) can be found.

$$
\begin{aligned}
VarE(X \mid n_i) &= \left(\frac{f}{m + n_p}\right)^2 Var(n_i) \\
&= \left(\frac{f}{m + n_p}\right)^2 \frac{n_p (m - 1)(n_p + mk)}{m^2 (1 + mk)},
\end{aligned}
\tag{17}
$$

$$\mathrm{E\,Var}(X \mid n_i) = \frac{f(m+n_p-f)[(m+n_p-1)[1+\mathrm{E}(n_i)] - \mathrm{E}(n_i) - (\mathrm{Var}(n_i)+[\mathrm{E}(n_i)]^2)]}{(m+n_p-1)(m+n_p)^2}$$

$$= \frac{f(m+n_p-f)\left[(m+n_p-1)\left(1+\frac{n_p}{m}\right)-\frac{n_p}{m}-\frac{n_p(m-1)(n_p+mk)}{m^2(1+mk)}-\left(\frac{n_p}{m}\right)^2\right]}{(m+n_p-1)(m+n_p)^2}$$

$$= \frac{f(m+n_p-f)\left[\left(1+\frac{n_p}{m}\right)\left(m+n_p-1-\frac{n_p}{m}\right)-\frac{n_p(m-1)(n_p+mk)}{m^2(1+mk)}\right]}{(m+n_p-1)(m+n_p)^2} \tag{18}$$

Using the law of total variance, this gives the variance of $X$:

$$\mathrm{Var}(X) = \mathrm{E\,Var}(X \mid n_i) + \mathrm{Var\,E}(X \mid n_i)$$

$$= \frac{f(m+n_p-f)\left[\left(1+\frac{n_p}{m}\right)\left(m+n_p-1-\frac{n_p}{m}\right)-\frac{n_p(m-1)(n_p+mk)}{m^2(1+mk)}\right]}{(m+n_p-1)(m+n_p)^2} + \frac{f^2 n_p(m-1)(n_p+mk)}{m^2(1+mk)(m+n_p)^2}$$

$$= \frac{f(m+n_p-f)\left(1+\frac{n_p}{m}\right)\left(m+n_p-1-\frac{n_p}{m}\right) + [f^2(m+n_p-1)-f(m+n_p-f)]\left[\frac{n_p(m-1)(n_p+mk)}{m^2(1+mk)}\right]}{(m+n_p-1)(m+n_p)^2}$$

$$= \frac{f(m+n_p-f)\frac{1}{m^2}(m+n_p)^2(m-1) + f(f-1)(m+n_p)\left[\frac{n_p(m-1)(n_p+mk)}{m^2(1+mk)}\right]}{(m+n_p-1)(m+n_p)^2}$$

$$= \frac{f(m-1)\left[(m+n_p-f)+\frac{n_p(f-1)(n_p+mk)}{(m+n_p)(1+mk)}\right]}{m^2(m+n_p-1)}. \tag{19}$$

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# Paper II

# Paper III

# Paper IV

# The influence of persistent individual differences and age at maturity on effective population size.

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Ratios of effective populations size, $N_e$, to census population size, $N$, are used as a measure of genetic drift in populations. Several life history parameters have been shown to affect these ratios, including mating system and age at sexual maturation. Using a stochastic matrix model we examine how different levels of persistent individual differences in mating success among males may affect $N_e/N$, and how this relates to generation time. Individual differences of this type are shown to cause a lower $N_e/N$ ratio than would be expected when mating is independent among seasons. Examining the way in which age at maturity affects $N_e/N$, we find that both the direction and magnitude of the effect depends on the survival rate of juveniles in the population. In particular, when maturation is delayed, lowered juvenile survival causes higher levels of genetic drift. In addition, predicted shifts in $N_e/N$ with changing age at maturity are shown to be highly dependent on which of the commonly used definitions of census population size, $N$, is employed. Our results demonstrate that patterns of mating success, as well as juvenile survival probabilities, have substantial effects on rates of gentic drift.

2

# Introduction

Genetic diversity is of central importance in evolutionary biology and conservation. Random genetic drift is a major cause of loss of this diversity, and a lot of studies have focused on the rates at which this loss can be expected to occur in natural populations (reviewed in [1]). Wright [2] introduced the concept of effective population size, $N_e$, defined as the size of an ideal population that would experience the same amount of genetic drift as the population in question. An ideal population refers to a population of constant size with discrete, nonoverlapping generations and reproduction by random sampling of gametes. In a diploid population the expected rate of allele frequency change due to drift, and the loss of (selectively neutral) heterozygosity, is proportional to $1/(2N_e)$ per generation.

Most real populations have an effective population size that is lower than their census size ($N$), and thus experience higher levels of genetic drift [3, 4, 5, 6]. It has proven difficult to find any general relationship between the effective population size and the actual size of populations [4], but a number of factors that influence the effective population size have been identified. Some of the most important of these are fluctuations in population size [2, 4], variation in reproductive success [7, 8], and unequal sex ratios [2, 9]. Different mating systems give rise to different patterns of male mating success. When the distribution of mating success is skewed, like in harem polygyny, the effective population size is lower. This has been demonstrated both theoretically [7, 8, 9, 10, 11, 12] and experimentally [13]. Other factors that affect the variance in reproductive success, and thus $N_e$, are multiple paternity within broods [14], population subdivision [15], and variance in female fecundity [16, 17, 18]. Nunney [16] examined different types of variation in female fecundity and found that consistent individual effects decreased the effective population size more than random effects or age-related effects. The effects of mating system on $N_e$ can be influenced by other factors [19, 20, 21, 22], and may often be overwhelmed by stronger effects, such as fluctuating population size [23]. However, many species have life history characteristics that allow $N_e$ to be substantially affected by mating system [5, 23, 24, 25].

Values of $N_e/N$ have been reported for a number of populations of different species (see e.g. [3, 4, 6]). The range of values reported is extensive (studies reviewed by Frankham [4] include values of $N_e/N$ from $10^{-6}$ to 1.07), and techniques for obtaining these estimates vary [3, 4, 26]. One problem with these numbers is that several different definitions of $N$ are used [3]. Sometimes $N$ is reported as the census size of the entire population, sometimes it refers to the adult population only, and sometimes only breeding individuals are counted. Nunney & Elam [3] discussed this issue, and concluded with a recommendation that $N$ be counted as the number of adults in the population.

There are two main types of effective population size. Inbreeding effective size focuses on the rate of increase of identity by descent, whereas the variance effective size is concerned with the sampling variance in allele frequency from one generation to the next [27, 28]. These two types of effective population size can differ substantially in populations of increasing or decreasing size [8, 29], but are identical when populations are of constant size with stable stage distributions, as is the case in this paper [30].

The study of effective population size is often complicated by the presence of overlapping generations [1, 31]. Several authors have addressed this point, and presented formulas for calculating the effective population size in populations in which generations overlap ([10, 11, 31, 32, 33, 34, 35, 36], among others). As shown by Hill [32], it is the variance in *lifetime* reproductive success that matters when determining effective size in such populations. Fluctuations in age-structure make the problem even more complex. Engen *et al.* [37] showed how diffusion theory and matrix models can be used to derive the effective population size in populations subject to fluctuations in age structure. Studying a subpopulation of individuals carrying a selectively neutral allele allows calculation of the sampling variance in the frequency of this allele per time step [37]. Thus, this method can be used to study genetic drift per time step, and when it is combined with the generation time, it gives $N_e/N$ per generation.

Generation time has been shown to influence the effects of other factors on the effective population size. For example, a skewed sex ratio tends to cause $N_e/N$ to decrease more

when the generation time is short than when it is long [10, 38]. Also, Nunney [10, 11] found that although some mating systems have the potential to lower $N_e/N$ significantly, this effect all but disappeared as the generation time in their model was lengthened, and $N_e$ approached $N/2$ regardless of mating system. This was explained by a decrease in the variance in male mating success as the generation time increased. When each male participated in several mating seasons they had more chances to be successful, and reproductive success could even out among them. This assumes that male mating success is independent each season, which is not necessarily the case. Several recent studies have highlighted the importance of recognizing that populations consist of individuals with different vital parameters, and that the individual differences may be persistent over time [39, 40, 41, 42, 43, 44, 45, 46, 47]. Mating success is one area in which persistent individual differences may exist in some species [e.g. 44, 48, 49, 50], thus potentially causing correlations in individual success from year to year.

Delayed maturity has been shown to increase the effective population size [11, 51, 52, 53]. In fact, Waite & Parker [51] found that the convergence of $N_e/N$ to 0.5 at long generation times reported by Nunney [11] was dependent on a low ratio of age at maturity to adult lifespan. When the age at maturity was increased in relation to the adult lifespan, $N_e/N$ was found to increase linearly. Both age at maturity, adult lifespan, and the relationships between the two vary among species and taxonomic groups, making this particularly relevant [51].

In this paper we use a stochastic matrix model to investigate how the effective population size is influenced by the presence of persistent individual differences in mating success among males, and how this may depend on generation time. We also examine how juvenile survival rates influence the effects of delayed maturity. In addition we demonstrate that the definition of $N$ used to calculate $N_e/N$ when studying age at maturity has the potential to influence the results in ways not previously considered.

# The model

Consider a diploid population with two sexes. Based on well-known theory, we use a matrix model to study a subpopulation of heterozygote individuals carrying a certain rare allele [see e.g. 8, 37, 54, 55]. The number of individuals in this subpopulation will be called $X$. Prereproductive individuals are divided into classes according to age and sex. Adult males are classed according to mating success (number of mates, from 0 to $d$), and adult females are assumed to all have the same individual parameters (survival probability and expected number of offspring) and are therefore collected in a single group. This means that there are a total of $(r_m + d + r_f)$ classes in the model, where $r_m$ is the age at sexual maturity of males, $d$ is the maximum number of mates a single male can obtain, and $r_f$ is the female age at maturity. The population vector can then be written as $\mathbf{X} = (X_{ym1}, ..., X_{ym(rm-1)}, X_{am0}, ..., X_{amd}, X_{yf1}, \ldots, X_{yf(rf-1)}, X_{af})^T$, where the superscript $T$ indicates matrix transposition. Subscripts denote young (prereproductive) males of age 1 to $r_m - 1$ $(ym1, ..., ym(rm - 1))$, adult males who obtain 0 to $d$ mates $(am0, ..., amd)$, young females of age 1 to $r_f - 1$ $(yf1, ..., yf(rf - 1))$, and adult females $(af)$. Note that offspring are not included in the model until they reach one year of age (any individuals that die before that age are ignored). The population vector for the next time step is obtained from the current population vector by matrix multiplication with the stochastic projection matrix $\mathbf{G}$. Thus, $\mathbf{X}_{t+1} = \mathbf{G}\mathbf{X}_t$. The stochastic projection matrix can be partitioned into four parts,

$$
G = \begin{bmatrix} G_{mm} & G_{mf} \\ G_{fm} & G_{ff} \end{bmatrix},
$$

where $G_{mm}$ is the contribution from the male part of the population to next time step's males, $G_{mf}$ is the contribution from females to males, $G_{fm}$ from males to females, and $G_{ff}$ is the contribution from females to next time step's females.

If all individuals become sexually mature at age one $(r_m = r_f = 1)$, the stochastic projection matrix can be written as a composite of the following submatrices,

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$$\mathbf{G}_{mm} = \begin{bmatrix} \bar{S}_{am0}\bar{T}_{am0,am0} & \bar{S}_{am1}\bar{T}_{am0,am1} + \bar{Z}_{am1}\bar{A}_{am0,am1} & \bar{S}_{am2}\bar{T}_{am0,am2} + \bar{Z}_{am2}\bar{A}_{am0,am2} & \cdots & \bar{S}_{amd}\bar{T}_{am0,amd} + \bar{Z}_{amd}\bar{A}_{am0,amd} \\ \bar{S}_{am0}\bar{T}_{am1,am0} & \bar{S}_{am1}\bar{T}_{am1,am1} + \bar{Z}_{am1}\bar{A}_{am1,am1} & \bar{S}_{am2}\bar{T}_{am1,am2} + \bar{Z}_{am2}\bar{A}_{am1,am2} & \cdots & \bar{S}_{amd}\bar{T}_{am1,amd} + \bar{Z}_{amd}\bar{A}_{am1,amd} \\ \bar{S}_{am0}\bar{T}_{am2,am0} & \bar{S}_{am1}\bar{T}_{am2,am1} + \bar{Z}_{am1}\bar{A}_{am2,am1} & \bar{S}_{am2}\bar{T}_{am2,am2} + \bar{Z}_{am2}\bar{A}_{am2,am2} & \cdots & \bar{S}_{amd}\bar{T}_{am2,amd} + \bar{Z}_{amd}\bar{A}_{am2,amd} \\ \vdots & & & \ddots & \vdots \\ \bar{S}_{am0}\bar{T}_{amd,am0} & \bar{S}_{am1}\bar{T}_{amd,am1} + \bar{Z}_{am1}\bar{A}_{amd,am1} & \bar{S}_{am2}\bar{T}_{amd,am2} + \bar{Z}_{am2}\bar{A}_{amd,am2} & \cdots & \bar{S}_{amd}\bar{T}_{amd,amd} + \bar{Z}_{amd}\bar{A}_{amd,amd} \end{bmatrix}$$

$$\mathbf{G}_{mf} = \left( \bar{Z}_{af}\bar{A}_{am0,af}, \bar{Z}_{af}\bar{A}_{am1,af}, \bar{Z}_{af}\bar{A}_{am2,af}, \ldots, \bar{Z}_{af}\bar{A}_{amd,af} \right)^T$$

$$\mathbf{G}_{fm} = \left( 0, \bar{Z}_{am1}\bar{A}_{af,am1}, \bar{Z}_{am2}\bar{A}_{af,am2}, \ldots, \bar{Z}_{amd}\bar{A}_{af,amd} \right)$$

$$\mathbf{G}_{ff} = \bar{S}_{af} + \bar{Z}_{af}\bar{A}_{af,af}.$$

In these matrices

$$\bar{S}_i = \frac{1}{x_i} \sum_{k=1}^{x_i} S_{i,k} \qquad \text{where } S_{i,k} \text{ is an indicator variable for survival of individual } k \text{ in group } i,$$

$$\bar{T}_{i,j} = \frac{1}{S_j} \sum_{k=1}^{S_j} T_{i,j,k} \qquad \text{where } T_{i,k} \text{ is an indicator variable indicating which of the } S_j \text{ survivors}$$

$$\text{from group } j \text{ move to group } i,$$

$$\bar{Z}_i = \frac{1}{x_i} \sum_{k=1}^{\alpha_i x_i} Z_{i,k} \qquad \text{where } Z_{i,k} \text{ is the number of offspring produced by individual } k \text{ in group } i,$$

$$\bar{A}_{i,j} = \frac{1}{Z_j} \sum_{k=1}^{Z_j} A_{i,j,k} \qquad \text{where } A_{i,j,k} \text{ is an indicator variable indicating which of the } Z_j \text{ offspring}$$

$$\text{from group } j \text{ move to group } i \text{ (based on presence of the rare allele,}$$

$$\text{sex, and mating probability).}$$

We assume a constant environment, so the stochastic projection matrix $\mathbf{G}$ includes demographic stochasticity but not environmental stochasticity. Adult males are assumed to have a survival probability $s_m$ ($s_f$ for females). The probability of a male obtaining $\nu$

mates, and thus being in class $am\nu$ is called $t_\nu$. Since the variance effective population size is defined by the variance in allele frequency, the actual distribution of females among males does not need to be known. It is the variance in reproductive success among males (or females) that matters. In order to find $t$-values that give a particular variance in male mating success, we have used the model from Lee *et al.* [56]. The $t$-values represent the probability of a new male in the population ending up in a certain class (and mating a certain number of times) in his first season. If there are no permanent individual differences among males, these are also the probabilities of surviving males moving to each class in later seasons. However, the mating probability of a male in a given season is not necessarily independent from his mating success in previous seasons. This is incorporated by introducing a parameter $c$. This parameter can increase the probability of obtaining the same number, one more or one less mate than the previous season. At the limits, if $c = 0$ mating is independent among seasons. If $c = 1$ a surviving male is guaranteed to end up in the same class, or one of the neighboring classes (one more or one less mate) the next season. The adjusted probabilities of these three classes are $E(\bar{T}_{am\nu,am\omega}) = t_\nu(1-c) + c/3$ (for $\nu = \omega - 1, \omega, \omega + 1$). The only exception is the group of unmated males, where we assume that $c$ affects only the probability of staying unmated the next season (without increasing the probability of obtaining a single mate). Thus, $E(\bar{T}_{am0,am0}) = t_0(1-c) + c$. All other classes have an adjusted probability of $E(\bar{T}_{am\nu,am\omega}) = t_\nu(1-c)$. In this way the ratio between the other classes is not altered. It would also be possible for $c$ to be negative, but we have not considered that here.

We assume that survival and reproduction are independent within years, and can therefore treat the survival and reproduction terms separately. We also assume independence among columns since we are studying a small group of individuals found in a much larger population. Within columns, however, there must be some covariance. To see this, consider the surviving males from adult class one at a given time step. At the next time step, each of these survivors will be in one and only one of the $d$ classes of

adult males. A single individual cannot move to more than one class. Thus, survival terms in $\mathbf{G}_{mm}$ have a multinomial distribution in which the $S_{am\omega}$ survivors from group $j = am\omega$ have probabilities $\mathrm{E}(\bar{T}_{am\nu,am\omega})$ of ending up in each of the $d+1$ classes of adult males. Equivalently, the reproduction terms also have a multinomial distribution in which the $Z_j$ offspring from class $j$ have a probability $\mathrm{E}(\bar{A}_{am\nu,j}) = \frac{1}{2}(1-q)t_\nu$ of ending up in class $i = am\nu$ (this is the probability of an offspring having the rare allele, being male, and ending up in quality group $am\nu$), as well as a probability $\mathrm{E}(\bar{A}_{af,j}) = \frac{1}{2}q$ of being female. Assuming that females produce a mean of $\mu_z$ offspring each, the number of offspring produced in group $j$ can be written as $\mathrm{E}(Z_j) = \mathrm{E}\left(\sum_{k=1}^{\alpha_j x_j} Z_{j,k}\right) = \mu_z x_j \alpha_j$, where $\alpha_j$ is equal to $\nu$ for $am\nu, \nu = 0, \ldots, d$ and equal to one for adult females. For simplicity we assume that the number of offspring produced per female per time step has a Poisson distribution. The total number of offspring produced in the population at a given time step, and the total number of offspring produced by a single female over her entire lifetime, are then also Poisson distributed.

When $r_m$ and/or $r_f$ are greater than one, offspring of each sex are born into a single class. Male offspring pass through $r_m - 1$ prereproductive classes (and females pass through $r_f - 1$ prereproductive classes) before entering an adult class. Survival probability in these prereproductive classes is called $s_{ym}$ for males and $s_{yf}$ for females. The projection matrix $\mathbf{G}$ for this case is presented in appendix 1.

Ignoring environmental stochasticity, the demographic variance of the subpopulation of heterozygotes with the rare allele can be written as [37]

$$\sigma_{d,g}^2 = \frac{X}{\lambda^2} \sum_{ijk} v_i v_k u_j^2 \, \mathrm{E}\,\mathrm{Cov}(G_{ij}, G_{kj}), \tag{1}$$

where $\lambda$ is the growth rate of the subpopulation, found as the dominant eigenvalue of the expected projection matrix, $v_i$ is the reproductive value of class $i$ (found from the left eigenvector), $u_j$ is the proportion of individuals found in class $j$ once a stable stage distribution has been reached (found from the right eigenvector), and $G_{ij}$ is the entry in the $i$'th row and $j$'th column of $\mathbf{G}$. The stable stage distribution is scaled such that

$\sum u_j = 1$, and the reproductive values are scaled to get $\sum u_j v_j = 1$. We use $u_{ad}$ to denote the proportion of a population that is found in adult classes (as opposed to prereproductive classes).

Assuming $x_j = X u_j$, equation (1) becomes

$$\sigma^2_{d,g} = \frac{1}{\lambda^2} \sum_{ijk} v_i v_k u_j \, \text{Cov}(G_{ij}, G_{kj}) x_j. \tag{2}$$

Expressions for $\text{Cov}(G_{ij}, G_{kj})$ in the different cases described above can be found in appendix 2. These covariances are all proportional to $1/x_j$, causing the $x_j$'s in equation (2) to cancel out. Thus, $\sigma^2_{d,g}$ is independent of the size of the subpopulation, $X$.

As shown by Engen *et al.* [37], the ratio of effective population size to census population size can be calculated as

$$\frac{N_e}{N} = \frac{1}{\sigma^2_{d,g} T}, \tag{3}$$

where $T$ is the generation time (defined as the average age of parents of newborn offspring), and $N$ is the total population size. The average generation time, $T$, can be written as $T = (T_m + T_f)/2$, where

$$
\begin{aligned}
T_m &= (1 - q) \sum_{i=r_m}^{\infty} i s_{ym}^{r_m - 1} s_m^{i - r_m} \lambda^{-i} \mu_z \frac{q}{1 - q} \\
&= \mu_z q \sum_{i=r_m}^{\infty} i s_{ym}^{r_m - 1} s_m^{i - r_m} \lambda^{-i}
\end{aligned}
$$

and

$$T_f = \mu_z q \sum_{i=r_f}^{\infty} i s_{yf}^{r_f - 1} s_f^{i - r_f} \lambda^{-i},$$

[33, 37, 54].

In equation (3) $N$ is the total number of individuals in the population. In order to find $N_e/N$ for an alternate definition of $N$ (e.g. only adults or only mated individuals), one can simply multiply equation (3) by $N/N_{alt}$. This ratio can be found from the relevant values of $u_j$ (the stable stage distribution).

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This model is used here to study genetic drift by looking at the sampling variance in allele frequency per time step, and the effective population size (per generation). The growth rate of the subpopulation $X$ is held constant at $\lambda = 1$ at all times. The effect of persistent differences in mating probability among individual males is examined by adjusting the parameter $c$ while holding all other parameters constant. We look at three specific cases, with $c = 0$, 0.5 and 1, which span the gradient from completely independent mating success among seasons ($c = 0$) to permanent individual differences ($c = 1$). We also look at four different levels of variance in male mating success (1, 2, 5 and 10). By increasing survival probabilities we also investigate the effect of generation time on these populations. As survival is increased, female fecundity is decreased such that the growth rate stays constant at one. As long as female fecundity is assumed to have a Poisson distribution this adjustment does not affect the ratio of variance in male reproductive success to expected male reproductive success. With a Poisson distributed number of offspring per female we have the following relationship

$$
\begin{aligned}
\frac{\text{Var(mRS)}}{\text{E(mRS)}} &= \frac{\mu_z \, \text{E(mMS)} + \mu_z \, \text{Var(mMS)}}{\mu_z \, \text{E(mMS)}} \\
&= 1 + \frac{\text{Var(mMS)}}{\text{E(mMS)}},
\end{aligned} \tag{4}
$$

where mRS is male reproductive success and mMS is male mating success. Thus, as long as the mean and variance in male mating success are held constant, the mean over variance ratio of male reproductive success will stay constant as well.

We look at how age at maturity affects $\sigma_{d,g}^2$ and $N_e/N$, and how this effect may vary depending on the survival probability of prereproductive individuals. We assume that males and females mature at the same age ($r_m = r_f$), and adjust female fecundity in such a way that a stable population size is maintained. Finally, we examine whether the outcome of these analyses is dependent on the definition of $N$ used when calculating the ratio $N_e/N$.

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# Results

In the absence of persistent individual differences among males, the mating success of each individual male is independent among years. In this situation, the ratio of effective population size to adult or census population size becomes less affected by differences in mating system as the generation time increases (figure 1a). Age at maturity is set to one, so all individuals in the population are assumed to be adults. Differences in mating system are here defined by differences in the variance in male mating success. Mean male mating success is constant at one (the sex ratio is even and all females mate), and the ratio of variance in male reproductive success to mean male reproductive success is then solely dependent on the variance in male mating success (equation 4). Nunney [11] has previously shown that the ratio of effective population size to adult population size converges towards 0.5 as the generation time increases. This result was confirmed by Waite & Parker [51] and seems to be supported by our figure 1. However, if there are persistent individual differences among males $N_e/N$ approaches a lower value than 0.5 (figure 1b and 1c). Effects of mating system differences on $N_e/N$ still decrease with increasing generation time, and the speed with which this happens does not seem to differ much from the case with no persistent individual differences. The demographic variance, on the other hand converges much more slowly as individual differences become more persistent (top panel in figure 1). Thus, the fact that differences in mating system become less important as the generation time increases does not seem to be caused by a reduction in the variance in male reproductive success (as suggested by Nunney [11]). Such a reduction in the variance is expected when the mating success of males is independent from year to year, allowing different males to be successful at different times, thereby reducing the variance in lifetime reproductive success compared to the variance in reproductive success in a single season. However, even when the probability of the same males being successful year after year is very high, causing the demographic variance to stay high as the generation time is increased, $N_e/N$ still seems to converge (figure 1c). This suggests that the convergence is a result of the way the effective

population size is defined. This can be seen from equation (3). As $T$ becomes large, changes in $\sigma_{dg}^2$ become less influential. Analogously, when $\sigma_{dg}^2$ is large, changes in $T$ have less effect on $N_e/N$.

Increasing the age at maturity also affects $N_e/N$ (figure 2). The direction and magnitude of this effect depends on the survival probability of prereproductive individuals, $s_{ym}$, as well as the definition of $N$ used in the calculation of $N_e/N$. When the annual survival probability of juveniles is close to one, an increase in the age at maturity causes $\sigma_{dg}^2$ to decrease (figure 2). At lower juvenile survival probabilities, on the other hand, $\sigma_{dg}^2$ increases as the age at maturity increases (figure 2). This increase becomes greater as the survival probability decreases (figure 3). Changes in the age at maturity are also reflected in the average generation time, $T$. When $N$ is defined as the (total) census population size, changes in $\sigma_{dg}^2$ and $T$ described above cause $N_e/N$ to decrease as the age at maturity increases (figure 2). When $s_{ym}$ is close to one, the observed decrease in $N_e/N$ is very slight. On the other hand, if $N_{ad}$ denotes the size of the adult population only, $N_e/N_{ad}$ increases linearly with age at maturity. With this definition of population size, the ratio $N_e/N_{ad}$ is also not affected by changes in juvenile survival rate (figure 3). The substantial difference between the behaviour of the two ratios $N_e/N$ and $N_e/N_{ad}$ can be explained by the changes in stage structure that accompany changes in the age at maturity and/or juvenile survival rate. Since the denominator of $N_e/N_{ad}$ only includes adult individuals, changing the proportion of the population that is in the adult state ($u_{ad}$) will alter this ratio. Thus, a decrease in $u_{ad}$ causes $N_e/N_{ad}$ to increase with age at maturity, even when both $\sigma_{dg}^2$ and $T$ increase (figure 2). When juvenile survival is altered, the resulting change in $\sigma_{dg}^2$ is cancelled out by the change in $u_{ad}$, leaving $N_e/N_{ad}$ unchanged, while $N_e/N$ is shifted.

## Discussion

Effective population size, $N_e$, is influenced by a number of different factors, including mating system and generation time. In a study on the influence of mating systems on $N_e$,

Nunney [11] found that the effective population size should approach half the size of the adult population, $N_{ad}/2$, as generation time becomes large. Later, Waite & Parker [51] showed that the result of Nunney only held when the age at maturity was low compared to the adult life span. Using a matrix model, we have reexamined these ideas, taking persistent individual differences and juvenile survival probabilities into account.

Persistent individual differences in mating success among males cause $N_e/N$ to converge to a value lower than 0.5 as the generation time increases (figure 1). There is evidence to support the existence of such persistent individual differences in natural populations [e.g. 43, 44, 48, 49, 50, 57, 58]. Basically, when male mating success is dependent on certain male traits and the expression of these traits is not independent among breeding seasons, mating success will not be independent among seasons either. Some physical attributes that may affect mating success are permanent, like colour morph [57, 59, 60, 61], while the expression of other traits may vary from season to season but still be correlated. One such trait is male body weight. In species where males engage in physical combat over females or territories, body weight may be important in determining reproductive success. Accordingly, body weight (at birth or capture) is positively correlated with lifetime reproductive success of males in some studied populations [49, 62, 63, 64, 65, 66, 67]. If there is strong site fidelity in a population, the distribution of territories may cause correlations in reproductive success among years, even without persistent differences in fighting ability [48, 68, 69, 70].

A common pattern, especially in birds, is that lifespan is the main predictor of lifetime reproductive success [71, 72]. However, even in long-lived seabirds, a considerable part of the variation in lifetime reproductive success can be traced back to factors other than lifespan, and reproductive parameters are often found to be consistent between years [43]. Sometimes traits that increase annual reproductive success also promote longevity, intensifying the effect [44, 48, 50, 58, 73, 74]. In other cases reproduction is costly. This can cause negative correlation in reproductive success among years [75], or negative effects of reproduction on survival [76, 77, 78, 79]. The model presented in this paper

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can easily be extended to include both of these cases.

It has previously been demonstrated that increasing the age at maturity in relation to the adult life span causes an increase in $N_e/N$ [51]. We have shown that this result is very dependent on the definition of $N$ used. Waite & Parker [51] used the number of adults, $N_{ad}$, as their measure of population size, following recommendations from Nunney & Elam [3]. When the prereproductive part of the life cycle is lengthened compared to the adult part, the proportion of individuals found in the prereproductive state also increases. Thus, $N_{ad}$ then represents a smaller proportion of the population, and $N_e/N_{ad}$ increases. This does not necessarily mean, however, that the amount of genetic drift decreases. In fact, depending on the survival probability of juveniles, the genetic drift per time step (measured by $\sigma_{dg}^2$) may increase substantially (figure 2). This is reflected in $N_e/N$ if $N$ is counted as the total population size (both adults and juveniles).

The use of different definitions of $N$ when reporting values of $N_e/N$ has previously been discussed by Nunney & Elam [3]. They called attention to the fact that estimates of $N_e/N$ become impossible to compare when different definitions of $N$ are used. The total census number was deemed an impractical measure of population size because it is often difficult to obtain and is also prone to fluctuations (juvenile numbers are more likely to vary with seasonal conditions). Thus, practical considerations make the number of adults a better choice [3]. This is not a problem as long as the consequences of this choice are kept in mind. As we have shown, the definition of $N$ used is not only an issue when comparing ratios of $N_e/N$ from different studies. Results from theoretical analyses must also be interpreted in light of the definition used.

Waite & Parker [51] mention that having delayed maturity could restrict the genetic effects of a catastrophic (short-term) loss of adults. Any possible advantage of having a large proportion of the population in a juvenile state during catastrophic events is obviously dependent on the relative vulnerability of juveniles and adults to such events. In figure 3 we have shown that $\sigma_{dg}^2$ increases as the survival probability of juveniles decreases. Koons *et al.* [80] demonstrated that environmental uncertainty can drive

the evolution of delayed maturity in iteroparous populations if juveniles have a higher survival probability than adults. However, environmental uncertainty did not have the same effect in the more common case of juvenile survival being lower than that of adults.

In general, low juvenile survival would be expected to oppose the evolution of delayed maturation [81]. What would be considered "low" in this context is however dependent on the benefits that delayed maturation confer. In a study using data from 109 populations of snakes, lizards and turtles, Pike *et al.* [82] found that juvenile survival in these species did not differ substantially from adult survival. These are taxa in which the age at maturity is often quite high in relation to their lifespan [51]. Survival probabilities shown in our figure 3 are within the range presented by Pike *et al.* [82]. Thus, these combinations of age at maturity and juvenile survival rate seem to be realistic.

The model presented here assumes that survival rate and fecundity are independent of age once adulthood is reached. However, it is not uncommon for these parameters to be age-specific [e.g. 71], and there is a possibility that this may affect patterns of genetic drift. Although we have chosen not to include adult age classes as an additional complicating factor in this study, the model can easily be expanded to accommodate this.

As shown by Hill [32], it is the variance in *lifetime* reproductive success that is important when estimating the effective size of populations with overlapping generations, and most formulas for $N_e$ contain this parameter [e.g. 1, 11, 32, 83]. However, estimates are often available for reproductive success in single seasons only [11]. Using seasonal measures for estimating $N_e$ could be a problem if fecundity varies with age, but Nunney [11] and Nunney & Elam [3] demonstrated that corrections can be made to minimize this problem. Our results highlight another potential problem with using seasonal estimates. We have shown that persistent individual differences in mating success over time can have a strong influence on genetic drift. Establishing the presence or absence of such differences will therefore be an important step in the venture to quantify genetic drift in natural populations.

## Acknowledgments

## APPENDIX 1: Projection matrix for the case of delayed maturation

If one or both sexes have delayed maturation (i.e. $r_f$ or $r_m$, or both, are greater than one), the projection matrix $\mathbf{G}$ consists of the following submatrices

$$
G_{mm} = \begin{bmatrix}
0 & 0 & 0 & 0 & 0 & \bar{Z}_{am1}\bar{A}_{ym1,am1} & \bar{Z}_{am2}\bar{A}_{ym1,am2} & \cdots & \bar{Z}_{amd}\bar{A}_{ym1,amd} \\
\bar{S}_{ym1} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & \ddots & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & \bar{S}_{ym(r_m-2)} & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & \bar{S}_{ym(r_m-1)}\bar{T}_{am0,ym(r_m-1)} & \bar{S}_{am0}\bar{T}_{am0,am0} & \bar{S}_{am1}\bar{T}_{am0,am1} & \bar{S}_{am2}\bar{T}_{am0,am2} & \cdots & \bar{S}_{amd}\bar{T}_{am0,amd} \\
0 & 0 & 0 & \bar{S}_{ym(r_m-1)}\bar{T}_{am1,ym(r_m-1)} & \bar{S}_{am0}\bar{T}_{am1,am0} & \bar{S}_{am1}\bar{T}_{am1,am1} & \bar{S}_{am2}\bar{T}_{am1,am2} & \cdots & \bar{S}_{amd}\bar{T}_{am1,amd} \\
0 & 0 & 0 & \bar{S}_{ym(r_m-1)}\bar{T}_{am2,ym(r_m-1)} & \bar{S}_{am0}\bar{T}_{am2,am0} & \bar{S}_{am1}\bar{T}_{am2,am1} & \bar{S}_{am2}\bar{T}_{am2,am2} & \cdots & \bar{S}_{amd}\bar{T}_{am2,amd} \\
& & & \vdots & & & & \ddots & \vdots \\
0 & 0 & 0 & \bar{S}_{ym(r_m-1)}\bar{T}_{amd,ym(r_m-1)} & \bar{S}_{am0}\bar{T}_{amd,am0} & \bar{S}_{am1}\bar{T}_{amd,am1} & \bar{S}_{am2}\bar{T}_{amd,am2} & \cdots & \bar{S}_{amd}\bar{T}_{amd,amd}
\end{bmatrix}
$$

$$
G_{mf} = \begin{bmatrix}
0 & 0 & 0 & 0 & \bar{Z}_{af}\bar{A}_{ym1,af} \\
0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 \\
\vdots & & & & \vdots \\
0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0
\end{bmatrix}
$$

$$
G_{fm} = \begin{bmatrix}
0 & 0 & 0 & 0 & 0 & \bar{Z}_{am1}\bar{A}_{yf1,am1} & \bar{Z}_{am2}\bar{A}_{yf1,am2} & \cdots & \bar{Z}_{amd}\bar{A}_{yf1,amd} \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0
\end{bmatrix}
$$

$$
G_{ff} = \begin{bmatrix}
0 & 0 & 0 & 0 & \bar{Z}_{af}\bar{A}_{yf1,af} \\
\bar{S}_{yf1} & 0 & 0 & 0 & 0 \\
0 & \ddots & 0 & 0 & 0 \\
0 & 0 & \bar{S}_{yf(r_f-2)} & 0 & 0 \\
0 & 0 & 0 & \bar{S}_{yf(r_f-1)} & \bar{S}_{af}.
\end{bmatrix}
$$

Expected values of the entries in these submatrices are basically the same as in the case with $r_m = r_f = 1$, except that the survival and reproduction terms are separate. A

few things that must be noted are that prereproductive survival may differ from adult survival and that the mating success of male offspring does not come into play until they enter the adult population at age $r_m$. Thus, $\mathrm{E}(\bar{T}_{am\nu,ym(r_m-1)}) = t_\nu$. It would also be possible to let mating probabilities be lower for these first-year males.

# APPENDIX 2: Variances and Covariances of G

Survival and reproduction are assumed to be independent within years. We can therefore treat survival and reproduction terms separately.

$\mathrm{Var}(G_{i,j,survival} \times x_j)$ is simply the variance in a multinomial distribution in which the $x_j$ individuals from class $j$ have probabilities $s_j \mathrm{E}(\bar{T}_{i,j})$ of surviving and moving to class $i$. Here, $s_j$ is either $s_m$ (for males) or $s_f$ (for females). Thus,

$$\mathrm{Var}(G_{i,j,survival} \times x_j) = s_j \mathrm{E}(\bar{T}_{i,j})(1 - s_j \mathrm{E}(\bar{T}_{i,j}))x_j.$$

In order to calculate $\mathrm{Var}(G_{i,j,reproduction} \times x_j)$ we first find the conditional variance given $Z_j$ (the number of offspring produced in class $j$), and then use the law of total variance to get

$$\mathrm{Var}(G_{i,j,reproduction} \times x_j) = \mathrm{E}(\bar{A}_{i,j})(1 - \mathrm{E}(\bar{A}_{i,j})) \mathrm{E}(Z_j) + \mathrm{E}(\bar{A}_{i,j})^2 \mathrm{Var}(Z_j).$$

The expressions for $s_j$, $\mathrm{E}(Z_j)$, $\mathrm{Var}(Z_j)$, $\mathrm{E}(\bar{T}_{i,j})$ and $\mathrm{E}(\bar{A}_{i,j})$ for different values of $i$ and $j$ are all presented in the main text. Note that $\mathrm{E}(\bar{A}_{af,af}) = 1$.

Since the $x_j$ values are known, we have

$$\mathrm{Var}(G_{i,j}) = \frac{\mathrm{Var}(G_{i,j} \times x_j)}{x_j^2} = \frac{\mathrm{Var}(G_{i,j,survival} \times x_j) + \mathrm{Var}(G_{i,j,reproduction} \times x_j)}{x_j^2}$$

As explained in the main text, there are no covariances between columns. Within

columns we have

$$\text{Cov}\left(G_{i,j} \times x_j, G_{k,j} \times x_j | Z_j\right) = -s_j^2 x_j \,\text{E}\left(\bar{T}_{i,j}\right)\text{E}\left(\bar{T}_{k,j}\right) - Z_j\,\text{E}\left(\bar{A}_{i,j}\right)\text{E}\left(\bar{A}_{k,j}\right).$$

This means that

$$\text{Cov}\left(G_{i,j} \times x_j, G_{k,j} \times x_j\right)$$
$$= -s_j^2 x_j\,\text{E}\left(\bar{T}_{i,j}\right)\text{E}\left(\bar{T}_{k,j}\right) - \text{E}(Z_j)\,\text{E}\left(\bar{A}_{i,j}\right)\text{E}\left(\bar{A}_{k,j}\right) + \text{Var}(Z_j)\,\text{E}\left(\bar{A}_{i,j}\right)\text{E}\left(\bar{A}_{k,j}\right)$$
$$= -s_j^2 x_j\,\text{E}\left(\bar{T}_{i,j}\right)\text{E}\left(\bar{T}_{k,j}\right) + \text{E}\left(\bar{A}_{i,j}\right)\text{E}\left(\bar{A}_{k,j}\right)\left[\text{Var}(Z_j) - \text{E}(Z_j)\right]$$

and

$$\text{Cov}\left(G_{i,j}, G_{k,j}\right) = \frac{\text{Cov}\left(G_{i,j} \times x_j, G_{k,j} \times x_j\right)}{x_j^2}.$$

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# Figure captions

Figure 1. Effects of generation time, $T$, on the genetic drift per time step, $\sigma^2_{dg}$, and the ratio of effective population size to census population size, $N_e/N$, in populations with different mating systems. The variance in annual male mating success is equal to 1 (solid lines), 2 (long dash), 5 (short dash) and 10 (dotted). The parameter $c$, which describes the level of persistent individual differences in mating success among males, is (a) 0 (no persistent differences), (b) 0.5, and (c) 1. See the methods section for a more detailed description of this parameter. Generation time is increased by increasing the annual survival probability, $s$ from 0 ($T = 1$) to 0.8 ($T = 5$), simultaneously decreasing the expected number of offspring per female from 2 to 0.4. Other parameters are sex ratio at birth, $q = 0.5$, and age at maturity, $r = 1$.

Figure 2. Effects of age at maturity, $r$, on the genetic drift per time step, $\sigma^2_{dg}$, the ratio of effective population size to census population size, $N_e/N$, and the proportion of adults at stable stage structure, $u_{ad}$, in populations with different levels of juvenile survival. Annual survival probability of prereproductive individuals, $s_{ym} = s_{yf}$, is equal to 0.5 (solid lines) and 1 (dotted lines). In the middle panel the dashed line shows the ratio $N_e/N_{ad}$, where $N_{ad}$ is the adult population size, whereas the solid and dotted lines show $N_e/N$, where $N$ is the total population size. Variance in annual male mating success is equal to 2, the sex ratio, $q$, is equal to 0.5, and the expected number of offspring is adjusted to maintain a growth rate, $\lambda$, of one.

Figure 3. Effects of juvenile survival probability on the genetic drift per time step, $\sigma^2_{dg}$, the ratio of effective population size to census population size, $N_e/N$, and the proportion of adults at stable stage structure, $u_{ad}$. Parameters are age at maturity, $r = 5$, generation time, $T = 9$, and sex ratio, $q = 0.5$. Variance in annual male mating success is equal to 2. The expected number of offspring is adjusted to maintain a growth rate, $\lambda$, of one. The dashed line in the middle panel shows the ratio $N_e/N_{ad}$, where $N_{ad}$ is the adult
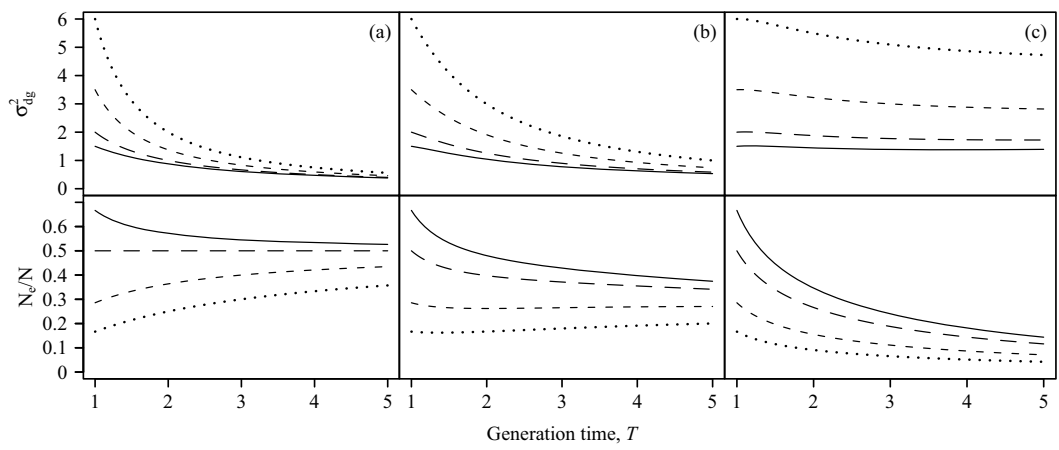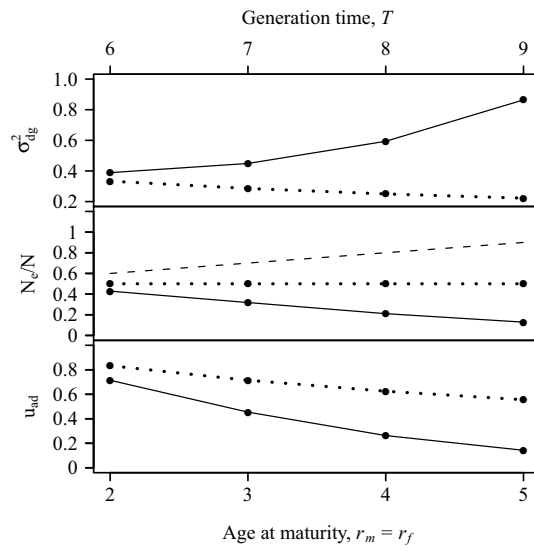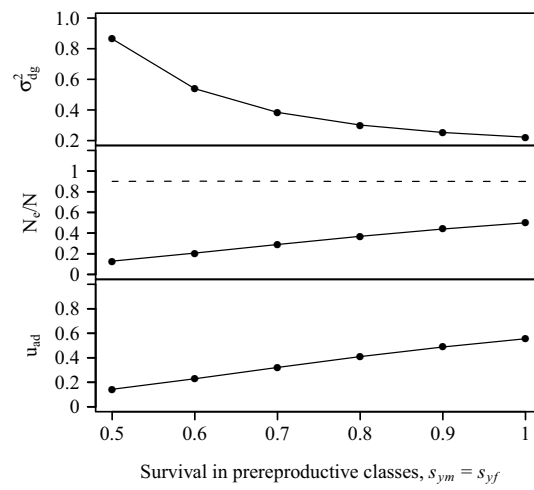
population size.

Figure 1:

30

Figure 2:

Figure 3:



Survival in prereproductive classes, $s_{ym} = s_{yf}$

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**Norwegian University of Science and Technology**

**Department of Biology**

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| 1978 | Egil Sakshaug | Dr.philos Botany | "The influence of environmental factors on the chemical composition of cultivated and natural populations of marine phytoplankton" |
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| 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 |
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|---|---|---|
| 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, *Vulpes vulpes* |
| 1994 Arne Moksnes | Dr. philos Zoology | Host adaptations towards brood parasitism by the Cockoo |
| 1994 Solveig Bakken | Dr. scient Bothany | Growth and nitrogen status in the moss *Dicranum majus* 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 *Lutra lutra* distribution in Norway: Effects of harvest, polychlorinated biphenyls (PCBs), human population density and competition with mink *Mustela vision* |
| 1995 Svein Håkon Lorentsen | Dr. scient Zoology | Reproductive effort in the Antarctic Petrel *Thalassoica antarctica*; 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 *Mysis relicta* and constraints on Cladoceran and Char populations |
| 1995 Hans Haavardsholm Blom | Dr. philos Bothany | A revision of the *Schistidium apocarpum* complex in Norway and Sweden |
| 1996 Jorun Skjærmo | Dr. scient Botany | Microbial ecology of early stages of cultivated marine fish; inpact fish-bacterial interactions on growth and survival of larvae |
| 1996 Ola Ugedal | Dr. scient Zoology | Radiocesium turnover in freshwater fishes |
| 1996 Ingibjørg Einarsdottir | Dr. scient Zoology | Production of Atlantic salmon (*Salmo salar*) and Arctic charr (*Salvelinus alpinus*): 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 *Mytilus edulis* and the effects of organic xenobiotics |
| 1996 Gunnar Henriksen | Dr. scient Zoology | Status of Grey seal *Halichoerus grypus* and Harbour seal *Phoca vitulina* in the Barents sea region |
| 1997 Gunvor Øie | Dr. scient Bothany | Eevalution of rotifer *Brachionus plicatilis* quality in early first feeding of turbot *Scophtalmus maximus* L. larvae |
| 1997 Håkon Holien | Dr. scient Botany | Studies of lichens in spurce 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 |

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| 1997 Jon Arne Grøttum | Dr. scient.<br>Zoology | Physiological effects of reduced water quality on fish in aquaculture |
| 1997 Per Gustav Thingstad | Dr. scient.<br>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<br>Zoology | Temporal and spatial trends of pollutants in birds in Norway: Birds of prey and Willow Grouse used as Biomonitors |
| 1997 Signe Nybø | Dr. scient.<br>Zoology | Impacts of long-range transported air pollution on birds with particular reference to the dipper *Cinclus cinclus* in southern Norway |
| 1997 Atle Wibe | Dr. scient.<br>Zoology | Identification of conifer volatiles detected by receptor neurons in the pine weevil (*Hylobius abietis*), analysed by gas chromatography linked to electrophysiology and to mass spectrometry |
| 1997 Rolv Lundheim | Dr. scient<br>Zoology | Adaptive and incidental biological ice nucleators |
| 1997 Arild Magne Landa | Dr. scient<br>Zoology | Wolverines in Scandinavia: ecology, sheep depredation and conservation |
| 1997 Kåre Magne Nielsen | Dr. scient<br>Botany | An evolution of possible horizontal gene transfer from plants to sail bacteria by studies of natural transformation in *Acinetobacter calcoacetius* |
| 1997 Jarle Tufto | Dr. scient<br>Zoology | Gene flow and genetic drift in geographically structured populations: Ecological, population genetic, and statistical models |
| 1997 Trygve Hesthagen | Dr. philos<br>Zoology | Population responces of Arctic charr (*Salvelinus alpinus* (L.)) and brown trout (*Salmo trutta* L.) to acidification in Norwegian inland waters |
| 1997 Trygve Sigholt | Dr. philos<br>Zoology | Control of  Parr-smolt transformation and seawater tolerance in farmed Atlantic Salmon (*Salmo salar*) Effects of photoperiod, temperature, gradual seawater acclimation, NaCl and betaine in the diet |
| 1997 Jan Østnes | Dr. scient<br>Zoology | Cold sensation in adult and neonate birds |
| 1998 Seethaledsumy Visvalingam | Dr. scient<br>Botany | Influence of environmental factors on myrosinases and myrosinase-binding proteins |
| 1998 Thor Harald Ringsby | Dr. scient<br>Zoology | Variation in space and time: The biology of a House sparrow metapopulation |
| 1998 Erling Johan Solberg | Dr. scient.<br>Zoology | Variation in population dynamics and life history in a Norwegian moose (*Alces alces*) population: consequences of harvesting in a variable environment |
| 1998 Sigurd Mjøen Saastad | Dr. scient<br>Botany | Species delimitation and phylogenetic relationships between the Sphagnum recurvum complex (Bryophyta): genetic variation and phenotypic plasticity |
| 1998 Bjarte Mortensen | Dr. scient<br>Botany | Metabolism of volatile organic chemicals (VOCs) in a head liver S9 vial  equilibration system in vitro |
| 1998 Gunnar Austrheim | Dr. scient<br>Botany | Plant biodiversity and land use in subalpine grasslands. – A conservtaion biological approach |
| 1998 Bente Gunnveig Berg | Dr. scient<br>Zoology | Encoding of pheromone information in two related moth species |
| 1999 Kristian Overskaug | Dr. scient<br>Zoology | Behavioural and morphological characteristics in Northern Tawny Owls *Strix aluco*: 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 *Dendrocopos leucotos* |
| 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 (*Gadus morhua* L.) and Halibut (*Hippoglossus hippoglossus* L.) |
| 1999 | Marianne Giæver | Dr. scient Zoology | Population genetic studies in three gadoid species: blue whiting (*Micromisistius poutassou*), haddock (*Melanogrammus aeglefinus*) and cod (*Gradus morhua*) 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 *Dicranum majus*, *Hylocomium splendens*, *Plagiochila asplenigides*, *Ptilium crista-castrensis* and *Rhytidiadelphus lokeus* |
| 1999 | Ingrid Bysveen Mjølnerød | Dr. scient Zoology | Aspects of population genetics, behaviour and performance of wild and farmed Atlantic salmon (*Salmo salar*) revealed by molecular genetic techniques |
| 1999 | Else Berit Skagen | Dr. scient Botany | The early regeneration process in protoplasts from *Brassica napus* 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 (*Luscinia s. svecica*) |
| 1999 | Gunnbjørn Bremset | Dr. scient Zoology | Young Atlantic salmon (*Salmo salar* L.) and Brown trout (*Salmo trutta* 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 spesificity as parameter in estimates of arhrophod 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 (*Cuculus canorus*) and its host: adaptions and counteradaptions 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 (*Loxodonta africana*) |
| 2000 | Odd A. Gulseth | Dr. philos Zoology | Seawater tolerance, migratory behaviour and growth of Charr, (*Salvelinus alpinus*), with emphasis on the high Arctic Dieset charr on Spitsbergen, Svalbard |

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| 2000 Pål A. Olsvik | Dr. scient Zoology | Biochemical impacts of Cd, Cu and Zn on brown trout (*Salmo trutta*) 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 *Artemia* 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 forset systems |
| 2001 Ingebrigt Uglem | Dr. scient Zoology | Male dimorphism and reproductive biology in corkwing wrasse (*Symphodus melops* 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 (*Rangifer tarandus platyrhynchus*) |
| 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 (*Castor fiber*) |
| 2002 Janne Østvang | Dr. scient Botany | The Role and Regulation of Phospholipase A$_2$ 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 *Arabidopsis thaliana* and the Ral GTPase from *Drosophila melanogaster* |
| 2002 Henrik Jensen | Dr. scient Biology | Causes and consequenses 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 *Gasterosteus aculeatur* 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 (*Syncerus caffer*) in Chobe National Park, Botswana |
| 2003 Marit Stranden | Dr.scient Biology | Olfactory receptor neurones specified for the same odorants in three related Heliothine species (*Helicoverpa armigera, Helicoverpa assulta* and *Heliothis virescens*) |
| 2003 Kristian Hassel | Dr.scient Biology | Life history characteristics and genetic variation in an expanding species, *Pogonatum dentatum* |

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|---|---|---|---|
| 2003 | David Alexander Rae | Dr.scient Biology | Plant- and invertebrate-community responses to species interaction and microclimatic gradients in alpine and Artic 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 (*Salmo Salar* 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 *Arabidopsis thaliana* |
| 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 (*Heliothis virescens, Helicoverpa armigera* and *Helicoverpa assulta*) |
| 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 (*Fragaria* x *ananassa*): characterisation and induction of the gene following fruit infection by *Botrytis cinerea* |
| 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 Røstelien | 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 (*Halichoerus grypus*) 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 |

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| 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 *Echinops* 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 *Coregonus lavaretus* (L.) species complex: historical contingency and adaptive radiation |
| 2006 | Kari Mette Murvoll | ph.d Biology | Levels and effects of persistent organic pollutans (POPs) in seabirds Retinoids and α-tocopherol –  potential biomakers 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 *Calanus finmarchicus* |
| 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 (*Salmo trutta*) 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 *Syngnathus typhle*: 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 *Tenebrio molitor* - 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 *Heliothis virescens* |
| 2007 | Stig Ulland | ph.d Biology | Functional Characterisation of Olfactory Receptor Neurons in the Cabbage Moth, (*Mamestra brassicae* 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 *(Gadus morhua* 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 (*Rangifer tarandus platyrhynchus*) 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 (Struthio camelus massaicus) 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, (*Taeniopygia guttata*) |
| 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 (*Gadus morhua*): 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 Bilogy | *Arabidopsis thaliana* Responses to Aphid Infestation |

| Year | Name | Degree/Field | Title |
|---|---|---|---|
| 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 *Cyclamen persicum.* 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 *Heliothis virescens:* 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 *Cuculus canorus* and *Fringilla* 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 (*Panthera leo*) in Tanzania |
| 2010 | Huy Quang Nguyen | ph.d Biology | Egg characteristics and development of larval digestive function of cobia (*Rachycentron canadum*) 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 *Arabidopsis* from Northern Europe |
| 2010 | Iddi Mihijai Mfunda | ph.d Biology | Wildlife Conservation and People's livelihoods: Lessons Learnt and Considerations for Improvements. Tha 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 *Eriophorum latifolium*, a Clonal Species in Rich Fen Vegetation |
| 2010 | Hilde Færevik | ph.d Biology | Impact of protective clothing on thermal and cognitive responses |
| 2010 | Ingerid Brænne Arbo | ph.d Medical technology | Nutritional lifestyle changes – effects of dietary carbohydrate restriction in healthy obese and overweight humans |

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|---|---|---|---|
| 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 |
| 2011 | Geir Hysing Bolstad | ph.d Biology | Evolution of Signals: Genetic Architecture, Natural Selection and Adaptive Accuracy |
| 2011 | Karen de Jong | ph.d Biology | Operational sex ratio and reproductive behaviour in the two-spotted goby (*Gobiusculus flavescens*) |
| 2011 | Ann-Iren Kittang | ph.d Biology | *Arabidopsis thaliana* L. adaptation mechanisms to microgravity through the EMCS MULTIGEN-2 experiment on the ISS:– The science of space experiment integration and adaptation to simulated microgravity |