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Stochastic modeling of finite populations with individual heterogeneity in vital parameters

Thesis for the degree of Philosophiae Doctor

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Preface

I have enjoyed the years in Trondheim working with this thesis, thanks to a number of people. Firstly, I would like to thank my advisors, Bernt-Erik Sæther from the Department of Biology, and Steinar Engen from the Department of Mathematical Sciences, for their knowledge, inspiration and support since I was a master student. I feel very lucky to have had both as advisors.

I am especially grateful for the collaboration with Martijn van de Pol, which has been very inspiring. We have had many nice discussions, and I liked working with empirical data since much of my work so far is purely theoretical.

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Trondheim, November 4, 2010

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Summary

Natural populations show large variation among individuals in patterns of survival and reproduction over time, that can often be associated with differences in state variables such as age, size or spatial location. Some of the variation is random, due to environmental fluctuations and inherent stochasticity in the processes of survival and reproduction. Several mechanisms can give rise to individual heterogeneity in natural populations, including spatial heterogeneity in the environment, maternal effects, cohort effects, and physiological differences. In this thesis I investigate how such heterogeneity affects properties of stochastic population dynamics, how it affects the fixation probability of slightly beneficial alleles, and how it influences effects of climate change on population dynamics. A demographic modeling framework for heterogeneous populations is developed based on stochastic matrix modeling and integral projection modeling, and I focus especially on (small) finite populations that are often of conservation concern.

One can never be sure to have detected all sources of heterogeneity in a natural population, and individual-based data are often not available. Therefore an important question is whether estimates of parameters describing long-term population dynamics and population viability will be biased due to hidden heterogeneity, and if so in which direction and to which extent. Results given in this thesis indicate that while estimates of the expected population growth rate are not affected, estimates of the demographic and environmental variance of the population growth will be biased if the reproductive value varies between individuals. These results highlight the importance of reproductive value in stochastic models of structured populations, as it is not differences in survival or reproduction *per se* that affect the long-term stochasticity in population growth, but differences in reproductive value.

Individual heterogeneity may affect the rate of evolution via the fixation probability of slightly beneficial alleles. Finding this probability is a classical problem in population genetics, dating from the work of Haldane in the 1920s. Here some earlier results are extended to include overlapping generations (individual heterogeneity) and stochastic fluctuations in a population with finite size (demographic stochasticity). The fixation probability of a slightly beneficial allele is shown to depend on the reproductive value of the individual(s) carrying the allele and the demographic variance of the population growth, in addition to the selective advantage of the allele and the population size. The reproductive value and demographic variance both depend on individual heterogeneity and can reflect general life history properties of the population. If the reproductive value of the individual(s) carrying the allele is low and the demographic variance is high, the probability of ultimate fixation will be low.

In the presence of climate change individual heterogeneity can influence predictions of future population dynamics, because the effect of climatic variables on vital parameters can depend on individual state. Both the mean and variability of climatic variables are predicted to change in the future, so it is also important to assess their relative influence on population dynamics. Using data from a population of long-lived eurasian oystercatchers (*Haematopus ostralegus*) and a stochastic stage structured matrix model, we investigated effects of mean and variability in an important climatic variable (winter temperature) and predicted future population dynamics for different climate scenarios. The mean and variability of winter temperature had opposite effects on survival and fecundity, and the median time to extinction was most sensitive to changes in vital parameters of breeders in high-quality habitats. The population dynamics were overall more sensitive to changes in survival rates than in fecundity, in line with predictions from life-history theory for long-lived species. We hypothesize that general life history properties may be used to predict effects of changes in mean and variability in climatic variables. This study illustrates that if we want to understand how climate change affects future population dynamics, it is crucial to consider individual-level processes.

The thesis is based on the following papers:

I **Vindenes, Y.**, S. Engen, and B.-E. Sæther. 2008. Individual heterogeneity in vital parameters and demographic stochasticity. American Naturalist 171:455–467.[1]

II **Vindenes, Y.**, S. Engen, and B.-E. Sæther (Accepted manuscript). Integral projection models for finite populations in a stochastic environment. Ecology.[2]

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

IV Van de Pol, M., **Y. Vindenes**, B.-E. Sæther, S. Engen, B. J. Ens, K. Oosterbeek, and J. Tinbergen. 2010. Effects of climate change and variability on population dynamics in a long-lived shorebird. Ecology 91:1192–1204.[4]

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[1] SE and BES initiated the project. YV developed the model and wrote the paper with contributions from the coauthors.

[2] YV initiated the project, developed the model with contributions from SE, and wrote the paper with comments from the coauthors.

[3] SE initiated the project and contributed to the analyses. AML did the analysis for infinite population size using branching processes, and performed calculations for the example. YV did the analysis for finite population size, performed computer simulations and wrote the paper with comments from the coauthors.

[4] MVDP and YV initiated the project and developed the population dynamical model, with comments from SE and BES. MVDP estimated the model parameters from data and YV performed the simulations. MVDP wrote the paper with comments from the coauthors. BJE, KO, JT, and MVDP contributed to fieldwork and the continuity of the long-term oystercatcher study.

Introduction

> “This uniqueness of biological individuals means that we must approach groups of biological entities in a very different spirit from the way we deal with groups of identical inorganic entities. This is the basic meaning of population thinking.”
>
> Ernst Mayr (1982, The growth of biological thought, p. 46)

Individual heterogeneity in natural populations

Individual variation is ubiquitous in natural populations, whether it occurs in morphological traits, behavior, or other properties (McNamara and Houston, 1996). During their lifetime, individuals experience different external conditions that together with other mechanisms can affect their survival and reproduction (Coulson et al., 2001; Benton et al., 2006). Such differences can influence several population-dynamical and evolutionary processes, and finding the causes and consequences of individual heterogeneity is therefore a central theme in population ecology and evolutionary biology (Wilson and Nussey, 2010).

Individual heterogeneity can arise from a number of different mechanisms (Hutchings et al., 2000a; Conner and White, 1999; Kendall and Fox, 2002; Wilson and Nussey, 2010; Clutton-Brock and Sheldon, 2010). Age can often explain much of the observed variation in a population (Caswell, 2001). In most species individuals go through several ontogenetic stages and physiological changes during their lifetime, even in a constant environment, and in many animals individuals can gain experience over time or increase their social status (Sæther, 1990; Forslund and Pärt, 1995). Some species show very distinct life cycle stages, such as egg-larvae-pupae-adult in many insects (e.g., seed beetles; Fox and Mousseau, 1996), and the differences in survival and reproduction are then often better described by stage than by age (Lefkovitch, 1965). In many populations, however, individual differences are not well explained by either age or life cycle stage, or by age or stage alone (Conner and White, 1999; Easterling et al., 2000; Caswell, 2001).

Spatial heterogeneity in the environment can be an important factor creating variation among individuals (Stewart et al., 2000). Sessile organisms, like plants, that occur in areas with spatial heterogeneity can show permanent differences in traits affecting survival and reproduction, due to different local conditions at the growing sites (e.g., Fitter et al., 2000; Hutchings et al., 2000b; Rees et al., 2000; Hesse et al., 2008). However, by phenotypic plasticity some organisms can adapt their phenotype to a range of environmental conditions, reducing the differences in vital parameters (Via and Lande, 1985; Sibly, 1995; Deng and Hazel, 2010). In non-sessile organisms spatial heterogeneity in the environment can still affect vital parameters via quality of habitats and territories (e.g., Nilsen et al., 2004; Carrete et al., 2006; van de Pol et al., 2006b; Byholm et al., 2007).

Environmental conditions can also fluctuate in time, either periodically or randomly. This can affect individual vital parameters in several ways, with both immediate and long-term effects on individuals and their offspring. In addition, the influence of environmental conditions can depend on the age, life cycle stage, or some other state variable of the individual. Effects of conditions experienced during early development seem especially important in determining future life history properties of an individual (Lindström, 1999; Metcalfe and Monaghan, 2001; Monaghan, 2008; Hamel et al., 2009; Reid et al., 2010). An important example is cohort effects, referring to long-lasting differences among cohorts that may even be transferred across generations (Beckerman et al., 2002, 2003; Lindström and Kokko, 2002). Such effects have been demonstrated in several populations of ungulates (e.g., Albon et al., 1987; Rose et al., 1998; Gaillard et al., 1997; Forchhammer et al., 2001; Solberg et al., 2004) as well as other organisms (e.g., Landis et al., 2005; Jensen et al., 2006; Reid et al., 2003; Descamps et al., 2008).

During their early development individuals can also be affected by other factors than environmental conditions. Maternal effects can be defined as all influences of a parent's phenotype on the offspring phenotype beyond additive genetic effects (Bernardo, 1996; Mousseau and Fox, 1998), and several examples have been found in different organisms (e.g., Price, 1998; Hastings and Testa, 1998; LaMontagne and McCauley, 2001; McAdam et al., 2002; Benton et al., 2008; Venturelli et al., 2010). They can have a large impact on the future vital parameters of offspring, and thereby create long-lasting differences both within and between clutches. In addition, maternal effects can be modified by environmental conditions. For instance, differential allocation of resources by parents may produce long-lasting differences within clutches, that are enhanced when food availability is low (Smiseth et al., 2003; Reed et al., 2009). Similar effects where the environment enhances individual differences have also been found for the performance of first-time breeders in some long-lived bird species (Newton, 1998; Barbraud and Weimerskirch, 2005; Nevoux et al., 2008).

Dispersal is an important process in many species that is often affected by natal conditions (Verhulst et al., 1997; Reid et al., 2006; Benard and McCauley, 2008). Individual heterogeneity can give rise to differences in dispersal (Hawkes, 2009), and can itself also result from differences among individuals in dispersal status (e.g., Rees et al., 2000; Pärn et al., 2009; Pakanen et al., 2010; Bouwhuis et al., 2010). Consistent differences among individuals in other types of behavior can also affect vital parameters, and could arise from physiological differences (Dall et al., 2004; Biro and Stamps, 2010), social status, or grouping of individuals (McDonald and Fitzpatrick, 1996; Packer et al., 2005; Clutton-Brock, 2009; Ratikainen et al., 2010).

Although individual heterogeneity in vital parameters can occur without any genetic causes, several mechanisms exist to maintain genetic variation in traits over time (Roff, 1996; Kruuk, 2004). However, the heritability of most life-history traits is often small in natural populations (Mousseau and Roff, 1987; Price and Schluter, 1991; Kruuk et al., 2000).

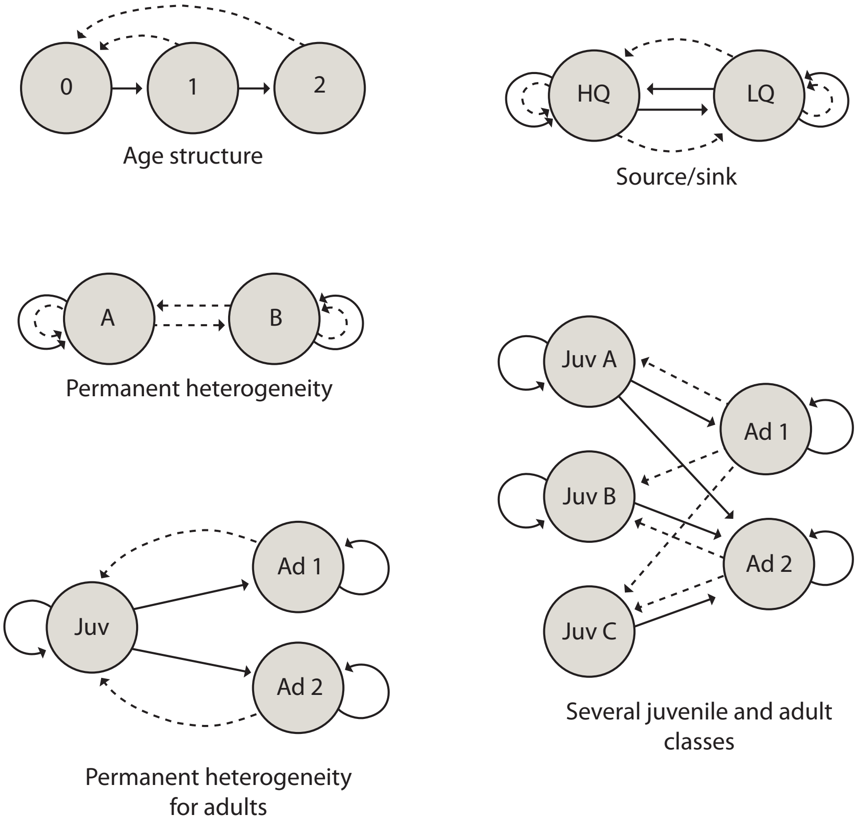
These studies and others indicate that many, if not most, natural populations are likely to show some type of individual heterogeneity. Independently of the causes, such variation in vital parameters can affect several processes at the population level. Recently such effects have received an increasing interest in ecological literature (Bjørnstad and Hansen, 1994; Conner and White, 1999; Kendall and Fox, 2002; Fox and Kendall, 2002; Fox, 2005; Tuljapurkar et al., 2009; Caswell, 2009; Zuidema et al., 2009). The question is important because we will never be able to identify all sources of heterogeneity in a population (Yashin et al., 2008). In population viability analysis, for instance, we need to know if hidden heterogeneity can bias estimates of extinction risk.

Stochastic life cycles

The life cycle of an individual is the description of how its vital parameters change over the lifetime (Caswell, 2001). At a given time these parameters can depend on individual state (e.g., age, size, spatial location), population density, and environmental conditions, and govern the stochastic processes of survival and reproduction. Parameters that describe transitions in individual state over time are also important elements of an individual's life cycle. Such transitions may be deterministic or stochastic, depending on the state variable(s). Figure 1 shows some examples of simple life cycles for some discrete cases of individual heterogeneity.

The processes underlying survival and reproduction of an individual are stochastic processes. Fluctuations in environmental conditions can affect the vital parameters of all individuals at the same time, assuming they experience the same environment, and give rise to environmental stochasticity (May, 1973; Lande et al., 2003). The realized survival and reproduction of an individual at a given time (when vital parameters are given) are also stochastic. This type of stochasticity is referred to as demographic stochasticity, and assumed to act independently among individuals (May, 1973).

Conditional on the individual state and environment, individual survival during a time interval is a binomial process, described by a survival probability. By contrast, the distribution of number of offspring in a reproductive event is generally not given, especially since the definition of an offspring differs between studies (Kendall and Wittmann, 2010). However, the mean and variance in number of offspring can be described without knowledge of the distribution. The survival and reproduction of an individual at a given time may also covary (Engen et al., 1998). If positive, such covariation is often attributed to permanent "quality" differences among individuals (Wilson and Nussey, 2010), and if negative it may indicate a trade-off between survival and reproduction (Reznick et al., 2000).



Age structure

Source/sink

Permanent heterogeneity

Several juvenile and adult classes

Permanent heterogeneity for adults

Figure 1: Some examples of simple life cycles in populations with various types of individual heterogeneity (for the discrete case). Arrows indicate transitions of adults (solid lines), which are conditional on survival, and transitions of offspring (dashed lines), which are conditional on reproduction. Vital parameters of survival and reproduction are not shown on this illustration.

The next state of an individual is often a stochastic variable, which can depend on the current state of the individual and environment. The state of an offspring can also depend on the state of its parent and the environment (McNamara and Houston, 1996). Stochasticity in state transitions is also a kind of demographic stochasticity, and has recently been referred to as dynamic heterogeneity (Tuljapurkar et al., 2009), or individual stochasticity (Caswell, 2009). For a population of kittiwakes (*Rissa tridactyla*), Steiner et al. (2010) showed that this type of stochasticity could produce the same observed variation in lifetime number of offspring as when differences among individuals were assumed to be fixed at birth (permanent heterogeneity).

Figure 2 shows a schematic illustration of the relationship between individual state, environment, vital parameters, transition parameters and realized survival and reproduction of an individual, assuming no density dependence. Sources of demographic and environmental stochasticity are also indicated. At the individual level, it is not possible to distinguish between the two types of stochasticity in realized survival and reproduction, but at the population level they have different effects.

Here I use the general term *individual heterogeneity* for differences among individuals in survival and reproduction that are not completely random. This definition is general and also includes age structure, but most of the questions considered in this thesis deal with cases where individuals show different life cycles (stochasticity in transition between states of adults and/or offspring). In a heterogeneous population at least some individuals will show temporal autocorrelation in one or more of the vital parameters, because the next state value depends on the current value. Otherwise, if the subsequent state of an individual is always independent of its current state, all differences among individuals in survival and reproduction will be random. Thus, individual heterogeneity is likely to play a more important role in the dynamics of long-lived species than in those of short-lived species.

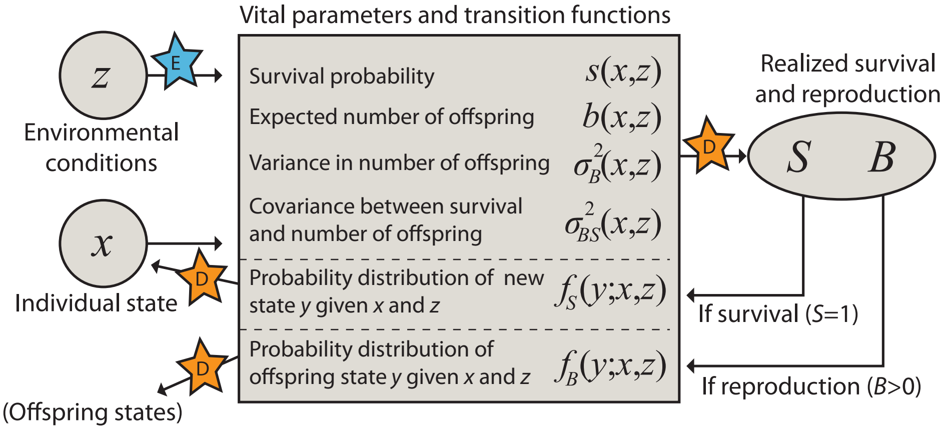


Figure 2: An overview of the underlying processes affecting the realized survival and reproduction of an individual at a given time, with indications of the sources of demographic (orange stars with D) and environmental (blue star with E) stochasticity in (density-independent) population dynamics. Environmental conditions are summarized by a variable z which may vary stochastically between years and give rise to temporal fluctuations in the vital parameters and transition functions. The state variable x of the individual represents factors that influence vital parameters and transition functions, such as age, size or spatial location. The realized survival and number of offspring produced in a given year are stochastic variables governed by the vital parameters. If the individual survives, it can obtain a new state value according to the transition parameters. If it produces any offspring, these will also obtain state values that may depend on the parent's current state and the environment. Stochasticity in transition between states also gives rise to demographic stochasticity in the population dynamics.

Stochastic population dynamics

Stochasticity in the survival and reproduction of individuals (figure 2) will create stochastic fluctuations in population size over time (Lande et al., 2003). Because stochasticity is an inherent property in the underlying processes that determine dynamics of wild populations, a stochastic modeling framework is crucial for population viability analysis (Sæther and Engen, 2002). The amount of stochasticity in the population growth depends on life history properties of the organism as well as properties of the environment (Lande et al., 2003). It is common to distinguish between two main types of stochasticity: environmental stochasticity and demographic stochasticity (May, 1973; Keiding, 1975; Engen et al., 1998). Figure 2 indicates where these types of stochasticity arise in the underlying processes affecting survival and reproduction of an individual. However, it is only at the population level that the different consequences of the two appears.

The effects of demographic stochasticity on long-term population growth levels off with population size, and can be ignored in large populations (May, 1973; Keiding, 1975). Environmental stochasticity is assumed to affect the vital parameters of all individuals at the same time (May, 1973; Roughgarden, 1975; Turelli, 1977), and its effects on on population dynamics are then independent of population size (May, 1973; Keiding, 1975). The amount of stochasticity in population growth can be measured by the demographic and environmental variance, which are constant parameters in a density-independent model. For an unstructured population, Engen et al. (1998) demonstrated that the variance in next year's population size is given by

$$\mathrm{Var}(N + \Delta N | N) = \sigma_d^2 N + \sigma_e^2 N^2, \tag{1}$$

where N is the current population size. The constant σ_d^2 is the demographic variance, which is the expected variance of an individual contribution (survival and reproduction) to next year's population size. The environmental variance σ_e^2 is the between-year variance of the expected individual contribution (Engen et al., 1998).

The demographic variance can reflect general life-history properties of the population, and tends to be lower in long-lived species with few offspring per reproductive event (Sæther et al., 2004).

Equation (1) shows how the effects of the two types of stochasticity scale differently with population size. On logarithmic scale, the stochastic population growth rate of this model is given by $s = r - \frac{1}{2}\sigma_e^2 - \frac{1}{2N}\sigma_d^2$ (Lande et al., 2003), where r is the growth rate of the logarithm of the expected population size. This formula shows that both types of stochasticity will generally reduce the population growth rate. In addition, it shows that for many populations a critical population size may exist below which demographic stochasticity causes the growth rate to become negative and extinction becomes a certain event (a stochastic Allee-effect; Lande, 1998).

For an age structured population with environmental stochasticity and no demographic stochasticity, Tuljapurkar (1982) showed that the stochastic growth rate (on log scale) is approximately $s \approx r - \frac{1}{2}\sigma_e^2$, and gave an expression for the environmental variance as function of the covariances of different age specific vital rates. Lande and Orzack (1988) demonstrated that this expected growth rate and environmental variance could be used to define a diffusion approximation of the population dynamics, assuming small fluctuations in population size. The accuracy of the approximation demonstrates that these two parameters contain all relevant information about long-term population dynamics. Later, this diffusion approximation was extended to include demographic stochasticity as well as environmental stochasticity for an age structured model (Engen et al., 2005b).

The role of individuals in population models

In evolutionary biology individual (phenotypic) variation has always been a key element in the models, as a prerequisite for natural selection and determinant of genetic drift (Lenormand et al., 2009). By contrast, in population biology a large part of the theory is based on the assumption that individuals are equal. Since population biologists are primarily interested in the fate of populations and not of individuals, many population models, dating from the early deterministic exponential growth model of Malthus (1798) and the logistic growth model described by Verhulst (1838), ignore individual-level processes. Today time-series analysis is often used to describe and predict stochastic dynamics, without knowledge of individual properties (Roughgarden, 1975; Royama, 1992; Turchin, 2003; Clark and Bjørnstad, 2004). The advantages of such models are that they can include density-dependent dynamics and environmental fluctuations, and do not require detailed individual-based data. However, this top-down approach yields few insights into how population dynamics depend on the life history of the organism. In addition, the link to evolutionary processes is unclear when individual-level processes are ignored.

Demographic population models represent a more mechanistic approach where the population dynamics are derived from individual-level processes of survival and reproduction, but individuals are still grouped into state categories and assumed to be equal within each state (Caswell and John, 1992). Keeping in mind that all population models are simplifications of reality, demographic models provide more insight into how individual life histories affect population dynamics and evolution. However, they can often be complex and empirical studies require more detailed, individual-based data (Caswell, 2001; Clutton-Brock and Sheldon, 2010).

Four major types of demographic modeling frameworks have been developed, depending on whether time and individual state are treated as discrete or continuous variables (Caswell and John, 1992; Easterling et al., 2000). Partial differential equation models apply when both time and state are continuous variables (Metz and Diekmann, 1986), and delay-differential equation models can be used when time is continuous and state is discrete (Nisbet and Gurney, 1982). Matrix models are used when both time and individual state are treated as discrete variables (Caswell, 2001). They were introduced to population ecology by Leslie (1945, 1948), who considered age structured populations. Age is by far the most common state variable in demographic models, and age structure has been studied since the deterministic models of Euler (1760), Lotka (1907, 1939) and Fisher (1930). Later, Lefkovitch (1965) introduced matrix models for more general stage structured populations. Today matrix modeling is probably the most commonly used demographic approach, because of the many analytical advantages (Caswell and John, 1992).

Recently, a new demographic modeling approach called integral projection modeling (IPM) has been developed, for the case of discrete time and continuous state (Easterling et al., 2000; Ellner and Rees, 2006). This approach retains many of the analytical advantages of matrix models, but uses different methods of parameterization (Ellner and Rees, 2006). Integral projection modeling has received increasing interest in ecological literature, and has already been applied in several studies of demography and evolution (Easterling et al., 2000; Rees and Rose, 2002; Rees et al., 2004; Rees and Ellner, 2009; Ellner and Rees, 2006, 2007; Childs et al., 2004; Kuss et al., 2008; Hesse et al., 2008; de Valpine, 2009; Zuidema et al., 2010; Coulson et al., 2010; Ozgul et al., 2010). Because they are parameterized by regression techniques, IPMs can be a better option than matrix models in small populations (Ramula et al., 2009).

Individual-based modeling (Lomnicki, 1988, 1999; Uchmanski, 1999; Grimm and Railsback, 2005) is another modeling approach that is different from demographic modeling. Individual-based models are more or less complex computer simulation models that keep track of each individual separately, and can include several factors that influence survival, reproduction and other individual-level processes. For instance, various kinds of interaction between individuals can be included (Grimm and Railsback, 2005). These models can be very useful for studies of given populations, but results are difficult to analyze and generalize to other systems. Individual-based modeling have been used to study effects of individual heterogeneity on population dynamics and evolution in specific populations (e.g., Jager, 2001).

Aims of the thesis

The overall aim of this thesis is to further our understanding of the links between demography, environmental conditions, population dynamics and evolutionary processes within a stochastic framework. I focus especially on (small) populations of finite size, that are often of conservation concern. Specific questions are:

1. How does individual heterogeneity affect properties of population growth and extinction risk (Paper I, II)? Some earlier studies suggest that the demographic variance of population growth and thereby the extinction risk will be reduced by individual heterogeneity (Conner and White, 1999; Kendall and Fox, 2002; Fox and Kendall, 2002; Kendall and Fox, 2003; Fox and Kendall, 2002), but other studies based on simulation (e.g., Jager, 2001) show contrasting results. It is important to find the potential consequences of ignoring individual heterogeneity, as we may never know all sources of heterogeneity in a natural population (Yashin et al., 2008). Demographic modeling approaches (matrix modeling and integral projection modeling) provide a general framework for studying populations with individual heterogeneity. The demographic and environmental variance can be derived as function of the state-specific vital parameters, and used in a diffusion approximation to study population dynamics and viability.

2. How can individual heterogeneity affect rates of evolution (Paper III)? Studies of rates of evolution have revealed large differences among organisms with different life histories (Britten, 1986; Bromham, 2002; Rodriguez-Trelles et al., 2006; Nabholz et al., 2007; Smith and Donoghue, 2008; Lanfear et al., 2010), but the underlying mechanisms for how life history affects evolutionary rates are still not clearly understood. Two main processes are the rate of formation of beneficial alleles, and the rate of fixation of such alleles (Bromham, 2009). Finding the fixation probability of a slightly beneficial allele is a classical problem in population genetics, dating from the well-known result by Haldane (1927) that if the selective advantage of the allele is s, its probability of ultimate fixation is approximately $2s$. This result was based on the assumption of infinite population size, non-overlapping generations and Poisson distributed contributions of an individual to the next generation. Several generalizations of this result have been made, such

as finite (but constant) population size (Kimura, 1957, 1962) or other types of offspring distribution than Poisson (Gillespie, 1974, 1975; Leigh, 1990). For an age structured population with infinite size, Athreya (1993) showed using branching process theory that the fixation probability depends on the reproductive value of the individual carrying the allele as well as the demographic variance of the population growth. The aim of this part of the thesis is to extend this result to finite populations, based on diffusion approximation and some recent results from stochastic demography (Engen et al., 2005a, 2007).

3. How does individual heterogeneity affect population dynamics in presence of climate change (Paper IV)? Predicting changes in demography and population dynamics due to future climate change is currently an important challenge in population ecology (Jenouvrier et al., 2009; Miller-Rushing et al., 2010; Hunter et al., 2010). It is well-known that climate change can affect the dynamics of populations (Coulson et al., 2001; Boyce et al., 2006), but most studies use phenomenological approaches relating changes in climatic variables directly to changes in population size (e.g., McLaughlin et al., 2002; Drake, 2005; Tyler et al., 2008), or consider only part of the life cycle (e.g., McMahon and Burton, 2005; Nevoux et al., 2008). With the former approach one risks missing important information on how vital parameters respond to climatic variables, whereas the latter approach cannot be used to predict future population dynamics. It is therefore important to consider effects on vital rates across the entire life-cycle of the organism (e.g., Hunter et al., 2010). Another challenge is to assess relative effects of changes in the mean and variability of climatic variables (Boyce et al., 2006; Morris et al., 2008), as both aspects are predicted to change in the future.

Methods

The first part of this section includes a description of linear matrix models and integral projection models, with definition of the expected growth rate, stable structure and reproductive values in the two cases. This is followed by a brief description of diffusion approximations and sensitivity analysis. The last part presents study species and data that are used in Paper IV.

Matrix modeling

The dynamics of a density-independent (linear) matrix model are given by $\mathbf{n}_{t+1} = \mathbf{A}_t \mathbf{n}_t$, where $\mathbf{n}_t$ is the population vector at time t and $\mathbf{A}_t$ is the projection matrix at the time, which can be deterministic or stochastic (Caswell, 2001). The elements of $\mathbf{A}_t$ describe the contributions of individuals in different stages to the population growth, depending on the vital parameters and transition parameters. In a stochastic matrix model, the expectation of the stochastic projection matrix corresponds to a deterministic projection matrix, and describes the expected population growth. Both environmental and demographic stochasticity can be included in a stochastic projection matrix (Engen et al., 2005b).

In linear matrix models, eigenanalysis of the (expected) projection matrix yields several important population parameters, provided that the Perron-Frobenius theorem for non-negative, ergodic matrices holds (Caswell, 2001). First, this theorem guarantees the existence of a real, dominant eigenvalue λ, which corresponds to the expected population growth rate. Second, the right eigenvector $\mathbf{u}$ associated with λ, scaled so that $\sum_i u_i = 1$, corresponds to the stable stage structure of the population. In a deterministic model, when the stage structure is reached the population size will grow exponentially with rate λ. In stochastic age structured models the stage distribution will fluctuate around the stable distribution due to demographic and environmental stochasticity. Finally, the left eigenvector $\mathbf{v}$ associated with λ, scaled so that $\mathbf{vu} = 1$, contains the stage-specific reproductive values (Caswell, 2001).

The reproductive value was first introduced by Fisher (1930) for a deterministic, age structured population. Fisher's model had continuous time, and his results were derived for a matrix model by Leslie (1948). For an individual of a given age (or stage), the reproductive value describes its (expected) relative contribution to future population growth, compared to individuals of other ages.

The total reproductive value V is defined as the sum of reproductive values of all individuals in the population. Fisher (1930) demonstrated for the deterministic model that this parameter will grow exponentially with rate λ, even if the population does not have the stable age distribution. In stochastic structured models, the expected total reproductive value also has this property (Engen et al., 2007). The reproductive values therefore act as a filter for the population process, removing fluctuations that are due to deviations from the stable stage distribution. The total reproductive value follows a process which is approximately Markovian (Engen et al., 2007, 2009), so its dynamics can be described by a diffusion approximation. Properties of long-term population growth (the demographic and environmental variance) should therefore be derived based on the dynamics of the total reproductive value rather than population size.

Integral projection modeling

Integral projection models (IPM) are the continuous-state analogue to matrix models (Easterling et al., 2000; Ellner and Rees, 2006). In these models vital parameters are described as smooth functions of a continuous state variable, which can usually be estimated by regression techniques (e.g., Metcalf et al., 2003). IPMs that include environmental stochasticity have been developed (Ellner and Rees, 2007; Rees and Ellner, 2009), but to my knowledge demographic stochasticity has so far not been included.

For a deterministic, density-independent IPM the dynamics can be written as $n(y, t+1) = \int_\Omega k(y, x)n(x, t)\mathrm{d}x$, where Ω defines the state space (depending on the state variable), $n(x, t)$ is the distribution of population size at time t, and $k(y, x)$ is the projection function, or kernel, which is the analogue to the projection matrix in a matrix model (Easterling et al., 2000). The projection function is defined by the vital parameter functions and the transition functions. As in linear matrix models, eigenanalysis of $k(y, x)$ provides important population parameters, and similar conditions apply to guarantee the existence of the growth rate λ and stable state distribution (Ellner and Rees, 2006). However, it is important to pay attention to model assumptions concerning what happens outside observed state values (Ellner and Rees, 2006).

The stable state distribution $u(x)$ is a function defined by the recursion $\lambda u(y) = \int_\Omega k(y,x)u(x)\mathrm{d}x$ (Haccou et al., 2005), and scaled so that $\int_\Omega u(x)\mathrm{d}x = 1$. The reproductive value as function of state is defined by the recursion $\lambda v(x) = \int_\Omega v(y)k(y,x)\mathrm{d}y$ (Haccou et al., 2005), and scaled so that $\int_\Omega v(x)u(x)\mathrm{d}x = 1$. The parameter λ and functions $u(x)$ and $v(x)$ can be found numerically (Ellner and Rees, 2006). The total reproductive value is defined as $V = \int_\Omega v(x)n(x)\mathrm{d}x$, and has the same dynamical properties as in the discrete case.

Diffusion approximation

A diffusion process is continuous in time and state, and characterized only by its infinitesimal mean and infinitesimal variance (describing the change of the process in a very small time interval), and boundary conditions. Mathematically it is defined as the solution of a stochastic differential equation (e.g., Karlin and Taylor, 1981). Several properties of diffusion processes can often be derived analytically, such as the expected time until the process reaches a given state (first passage time).

In population ecology, diffusion approximation is used to describe and study extinction processes and spatial dynamics (Lande et al., 2003). Diffusion approximation is also an important tool in population genetics, especially to study the spread of a gene in a population (Kimura, 1957; Crow and Kimura, 1970). If the population dynamics are (approximately) Markovian, the expectation and variance of the change in population size can be expressed as functions of the current size. This conditional mean and variance may then be used as approximations for the infinitesimal mean and variance of the diffusion process (Itô approximation; Karlin and Taylor, 1981). The accuracy of this approximation depends on the amount of variability in the process. If the fluctuations in population size are very large, the diffusion approximation will break down.

In structured populations with no density dependence, the dynamics of the total reproductive value are approximately Markovian (Engen et al., 2007, 2009). The expected population growth rate λ, demographic variance σ_d^2, and environmental variance σ_e^2 can then be used to define a diffusion approximation for the population growth (Lande and Orzack, 1988; Engen et al., 2005b, 2009). Hence, provided that we can find appropriate expressions for these parameters, complex dynamics of many structured populations can be described by diffusion approximation with only three parameters.

Perturbation and sensitivity analysis

Perturbation analysis is used to determine how the dynamics of a given model respond to changes in a parameter (Caswell, 2001). In linear structured models we can use sensitivity analysis to analyze how population dynamics respond to changes in the different vital parameters (Caswell, 1978). In a deterministic, density-independent, stage structured model, the sensitivity of the growth rate λ with respect to element a_{ij} of the projection matrix $\mathbf{A}$, is given by $\frac{\partial \lambda}{\partial a_{ij}} = v_i u_j$ (Caswell, 1978, with scaling of $\mathbf{v}$ as defined above).

Stochastic sensitivity analysis requires a different approach (Tuljapurkar, 1990; Caswell, 2001). In an age structured population with environmental stochasticity, the sensitivity of the stochastic growth rate as approximated by Tuljapurkar (1982) can be found with respect to both the mean and variance of a vital parameter. The approach is described by Caswell (1996). With density dependent population dynamics, however, Tuljapurkar's approximation cannot be used. By simulation we can still investigate the sensitivity of the median time to extinction T (or some other measure of persistence) to the mean and variability of vital parameters.

The effects of changes in underlying parameters (for instance some climatic variable) affecting the vital rates can also be considered. In a life-table response experiment (LTRE) analysis the effects of a variable on the population growth rate (or other population parameter) is decomposed into effects on each vital parameter across the life cycle (Caswell, 2001, 2010). Letting w represent a climatic variable with mean μ_w and standard deviation σ_w, and assuming w follows a stationary process with no temporal autocorrelation, the sensitivity in T to changes in w can be written as

$$\mathrm{d}T = \frac{\partial T}{\partial \mu_w}\,\mathrm{d}\mu_w + \frac{\partial T}{\partial \sigma_w}\,\mathrm{d}\sigma_w. \tag{2}$$

Thus, the change in T can be separated into a component due to changes in the mean and a component due to changes in the variability of w. By the chain rule, this equation can be further decomposed into how the effects of w on each vital rate in the life cycle contribute to the change in T, i.e.

$$\mathrm{d}T = \left(\sum_{ij} \frac{\partial T}{\partial a_{ij}} \frac{\partial a_{ij}}{\partial \mu_w}\right) \mathrm{d}\mu_w + \left(\sum_{ij} \frac{\partial T}{\partial \sigma_{ij}} \frac{\partial \sigma_w}{\partial \sigma_{ij}}\right) \mathrm{d}\sigma_w, \tag{3}$$

where a_{ij} is the mean of an element in the stochastic projection matrix, and σ_{ij} is the standard deviation.

Study species and data (Paper IV)

The analysis of Paper IV is based on data from a long-term study of oystercatchers in the Dutch Wadden Sea island Schiermonnikoog, which was initiated in 1983. Oystercatchers are long-lived (>40 years) shore-birds with high site-fidelity of breeders and a despotic territorial system (Heg et al., 1993; Ens et al., 1996; Safriel et al., 1996). The species is monogamous with biparental care, and there are few differences between the sexes in vital parameters (van de Pol et al., 2006b, 2007). Oystercatchers depend strongly on inter-tidal mudflats as food-source. During the last decades their number in the Dutch Wadden Sea has declined strongly (van de Pol, 2006).

There are two main types of breeding territory of oystercatchers, depending on where the nest is located relative to the feeding area (Safriel et al., 1996; Ens et al., 1992). High-quality territories are adjacent to the mudflats so that parents can take their chicks to the food, whereas low-quality territories are separated from the feeding grounds and parents spend much energy transporting food to the chicks. Oystercatchers show clear stage structure with six stages (fledglings, one-year old juveniles, two-year old juveniles, adult non-breeders, high-quality breeders, and low-quality breeders) (van de Pol et al., 2006a). The population dynamics are also density dependent, mainly due to the limited number of territories.

The standard monitoring protocol is described in detail by Ens et al. (1992) and Heg et al. (2000). All non-breeders, breeders, and offspring of the study population are marked with color rings. During each breeding season (May–August) of the study period from 1984-2007 population numbers were counted as well as the stage and reproductive output of individuals (∼300 marked individuals and ∼100 breeding territories annually).

The main climatic variables affecting the oystercatcher population are winter temperature (mean of December-March), food abundance (density of main prey species at the peak of egg hatching; van de Pol, 2006) and flooding events (van de Pol et al., 2010). The time series of winter temperature are provided by the Royal Netherlands Meteorological Institute, and ranges from 1907-2007.

Key Results and Discussion

Population dynamical consequences of individual heterogeneity (Paper I, II)

A discrete stage structured matrix model (Paper I) and a continuous-state integral projection model (Paper II) were defined and used to derive the demographic variance σ_d^2 (Paper I, II) and the environmental variance σ_e^2 (Paper II)), which describe the stochastic properties of the population dynamics. Both models assume no density dependence.

For a general stage structured matrix model the demographic variance (Paper I) is given by

$$\sigma_d^2 = \sum_l u_l \sigma_{dl}^2 = \sum_l u_l (\mu_{sl}^2 \sigma_{Sl}^2 + \mu_{bl}^2 \sigma_{Bl}^2 + 2\mu_{sl}\mu_{bl}\sigma_{BSl}^2 + \sigma_{sl}^2 s_l + \sigma_{bl}^2 b_l), \qquad (4)$$

where for an individual in stage l, s_l is the survival probability, $\sigma^2_{Sl} = s_l(1 - s_l)$, b_l is the expected number of offspring, σ^2_{Bl} is the variance in offspring number, and σ^2_{BSl} is the covariance between survival and reproduction. The parameters μ_{sl} and σ^2_{sl} are the mean and variance, respectively, of next year's reproductive value for a surviving adult from stage l. Similarly, μ_{bl} and σ^2_{bl} are the mean and variance of next year's reproductive value for an offspring from the stage. These are found from the transition probabilities of adults and offspring, respectively (Paper I).

For a continuous state-structured integral projection model, the expression for the demographic variance is (Paper II)

$$\begin{aligned}\sigma^2_d &= \int_\Omega u(x)\sigma^2_d(x)\mathrm{d}x \\ &= \int_\Omega u(x)(\mu^2_s(x)\sigma^2_S(x) + \mu^2_b(x)\sigma^2_B(x) + 2\mu_s(x)\mu_b(x)\sigma^2_{BS}(x) + \sigma^2_s(x)s(x) + \sigma^2_b(x)b(x))\mathrm{d}x,\end{aligned} \tag{5}$$

where the notation follows that of equation (4), with x describing individual state. For instance, $s(x)$ is the survival probability of an individual with state x.

Equations (4) and (5) define the demographic variance of a heterogeneous population. They can be used to find consequences of individual heterogeneity in vital parameters of both survival and reproduction, as well as of different structures for transition between states. Depending on the type of heterogeneity, the demographic variance can increase or decrease compared to when we assume a homogeneous population (Paper I). Thus, the indication of some earlier studies that heterogeneity would lead to a reduced demographic variance (Conner and White, 1999; Kendall and Fox, 2002; Fox and Kendall, 2002; Fox, 2005) does not hold in general, the demographic variance will in some cases also increase.

The effects of heterogeneity on demographic variance demonstrate the importance of the concept of reproductive value in structured population models. If we ignore individual heterogeneity, any error in the demographic variance occurs because we assume that all individuals have the same reproductive value. If individuals have different survival and reproduction but the same reproductive value, the assumption of no heterogeneity has no consequence. As the reproductive values do not affect the expected growth rate λ, this explains why ignoring heterogeneity will not affect the estimates of λ (Paper I).

In a population with continuous state-structure, the environmental variance is given by (Paper II)

$$\sigma_e^2 = \int_\Omega \int_\Omega u(x)u(y)c(x,y)\mathrm{d}x\mathrm{d}y, \tag{6}$$

where $c(x,y)$ is the covariance between the expected contributions of an individual in state x and an individual in state y to the total reproductive value (generated by a fluctuating environment). For a discrete, stage structured population the corresponding parameter would be $\sigma_e^2 = \sum_{ij} u_i u_j C_{ij}$, where C_{ij} is the covariance between (expected) contributions of individuals in stage i and j to the total reproductive value next year. To the first order, the environmental variance is approximately the variance of the growth rate $\lambda(Z)$ with respect to the environmental variable Z (Paper II).

Equation (6) shows that individual heterogeneity can also affect the environmental variance, via covariances between contributions from individuals in different states generated by the fluctuating environment. One way to estimate this parameter is to estimate the demographic variance based on individual contributions and then subtract this from the total variance in population growth (Engen et al., 2001; Lande et al., 2003). If we ignore heterogeneity this approach can lead to two mistakes. First, errors in the estimate of demographic variance will be transferred to estimates of the environmental variance (Engen et al., 2001). Second, the total variance in the population growth will include transient fluctuations due to the heterogeneity, and is therefore larger than the variance in total reproductive value (which we should have used if we knew about the population structure). Thus, estimates of both the environmental and demographic variance can be affected if we ignore individual heterogeneity.

Fixation of a slightly beneficial allele (Paper III)

Individual heterogeneity can affect the fixation probability of alleles via two parameters (Paper III), the reproductive value of the individual(s) carrying the allele, and the demographic variance for a subpopulation of individuals with the allele. In the haploid case the demographic variance σ_d^2 is defined as in Papers I and II. For a diploid population, the demographic variance of the subpopulation will also contain variance in the inheritance of the allele and is therefore denoted σ_{dg}^2. In Paper III we show how this parameter can be found for a two-sex population with individual heterogeneity, assuming a polygynous mating system.

If v_i is the reproductive value of an individual in stage i that carries the allele, and s is the (small) selective advantage of individuals carrying the allele, then based on a diffusion approximation the probability of ultimate fixation is approximately given by (Paper III)

$$\frac{1 - e^{-2sv_i/\sigma_{dg}^2}}{1 - e^{-4sN/\sigma_{dg}^2}}, \tag{7}$$

where N is the current population size. As $N \to \infty$ equation (7) reduces to $2sv_i/\sigma_{dg}^2$, which was derived by Athreya (1993) using a multitype branching process model.

Equation (7) shows that the probability of fixation increases with the reproductive value v_i of the individual carrying the allele, and decreases with the demographic variance σ_{dg}^2. In age structured populations the reproductive value of different ages is to some extent related to general life history properties (Charlesworth, 1994). In species with many offspring produced per reproductive event and low juvenile survival, the reproductive value of a newborn individual is generally low compared to that of adults. In species with few offspring per reproductive event and higher survival of young, for instance due to more parental care, the reproductive value of newborn compared to adults may be higher.

The model is not limited to study mutations occurring in newborn individuals. For instance, equation (7) can be used to calculate the probability of fixation given that the individual carrying the allele has reached a certain age or stage. If several individuals carry the allele, we can find the fixation probability by replacing v_i in equation 7 by the total reproductive value of these individuals. The allele can be introduced to the population by mutation, or by an immigrant from some other population. In that case, the fixation probability will depend on the reproductive value of the immigrant individual in the population where it settles.

The demographic variance summarizes stochastic properties of the life history. It tends to be low in long-lived species with few offspring per reproductive event and high in species with many offspring per reproductive event (Sæther et al., 2004). For most taxa, however, the demographic variance has never been estimated and we can only speculate on its magnitude. For instance, in many fish individuals can produce a large number of offspring, of which only a few survive to adulthood. Our results suggest that the probability of fixation of a mutation occurring in a newborn should be very low in such cases. However, the number of mutations that occur is also likely to increase with number of offspring, so that the total effect on the rate of evolution is difficult to predict from the fixation probability alone.

Individual heterogeneity and effects of climate change (Paper IV)

Using a density-dependent stochastic stage structured matrix model we explored effects of predicted changes in the mean and variability of winter temperature on long-term population viability of the oystercatcher population, accounting for other known sources of environmental variability and residual environmental stochasticity.

Overall, the expected persistence of the population increased with increasing mean winter temperature and with decreasing standard deviation of winter temperature. However, winter temperature had different and in some cases opposite effects on the vital rates across the life cycle. All vital rates were associated with winter temperature, either directly or indirectly. The survival probability in different stages all showed a positive correlation with winter temperature. The fecundities of high- and low-quality breeders were negatively correlated with winter temperature, presumably because winter temperature has a negative effect on the abundance of the major prey species of oystercatchers during summer (the reproductive season). Thus, an increase in mean winter temperature was predicted to have a negative effect on reproductive output in the population, but a positive effect on survival. The sensitivity analysis showed that the population dynamics were overall sensitive to changes in survival than in fecundity, so that the predicted negative effects on fecundity are likely to be overcome by positive effects on survival. The highest sensitivities of population growth to vital parameters were found in the stage of high quality breeders.

The environmental canalization hypothesis states that vital rates to which the population dynamics are more sensitive should be less sensitive to changes in the environment (Pfister, 1998). In this study juvenile survival showed a high sensitivity to changes in the winter temperature, but had very little influence on the population dynamics, whereas adult survival rates showed the opposite pattern. Thus, our results for oystercatchers are in line with the theory of environmental canalization and with results from other long-lived species (Sæther and Bakke, 2000; Gaillard and Yoccoz, 2003).

Some recent work in stochastic demography have suggested that increased climatic variability may sometimes increase population persistence, depending on the relationship between climatic variables and vital rates (Drake, 2005; Morris et al., 2008). In oystercatchers fecundity is a convex function of winter temperature, whereas survival probability is a concave function. In this case increasing variability in winter temperature is expected to increase the mean fecundity but decrease the mean survival probability (due to Jensen's inequality; Ruel and Ayres, 1999). We think this may be the case for most long-lived species, whereas in short-lived species with many offspring per reproductive event the vital parameters may show the opposite pattern relationship with climatic variables.

Based on our results we also propose that changes in mean climatic variables may generally have a larger effect on population dynamics than changes in variability. The sensitivity analysis showed that a change in mean winter temperature had an overall larger and opposite effect on the persistence time than the same change in standard deviation. In addition, climate models predict that changes in mean winter temperature will be much larger than changes in the standard deviation.

This study highlights the importance of using a demographic model including individual heterogeneity as well as stochasticity in the environment and dynamics.

Future prospects

The work of this thesis highlights only some aspects of effects of individual heterogeneity on stochastic population dynamics and evolution. Future research on individual heterogeneity will likely include more empirical studies, although such studies require detailed individual-based data. However, several long-term datasets that have so far (mostly) been used to study questions in relation to age structure can probably be used to explore effects of individual heterogeneity. In a recent review, Clutton-Brock and Sheldon (2010) mention several examples of such long-term individual-based studies of birds and mammals.

Another challenge for future studies is to explore possible interactions between density-dependence and heterogeneity. In many populations individuals likely respond differently to changes in density, due to variation in competitive ability or other factors. As a result, the amount of heterogeneity itself may depend on density. Some individuals could experience a reduced survival and/or fertility at high density, whereas others could be less affected. Density dependence and individual heterogeneity is challenging to study analytically, as the models will be non-linear. Unless the population is very small, however, the assumption of no density dependence will generally not hold in natural populations.

Most of the questions considered in this thesis are studied with models assuming asexual or female populations. One of the models used to find the fixation probability of a slightly beneficial allele is based on two sexes and a polygynous mating system where differences among both males and females can be included. However, other kinds of mating systems exist (Lee et al., 2008; Jenouvrier et al., 2010) and it could be interesting to study how effects of individual heterogeneity on population dynamics depend on mating system.

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Paper I

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Individual Heterogeneity in Vital Parameters and Demographic Stochasticity

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ABSTRACT: Most population models assume that individuals have equal opportunities for survival and reproduction, although many natural populations consist of individuals with different vital parameters that remain different over time. Individual heterogeneity in vital parameters, which may depend on age or stage, can alter many population characteristics compared with a homogeneous population, affecting both deterministic and stochastic properties of the population process. Demographic variance is an important parameter influenced by heterogeneity. However, whether heterogeneity leads to increased or decreased demographic variance has been an unresolved question, except for special cases. Here, we present a general stochastic matrix model for a heterogeneous population that allows us to examine effects of heterogeneity on population dynamics, even when the degree of heterogeneity depends on age. Using this model, we found that the demographic variance may increase, decrease, or remain unaltered compared with a homogeneous comparison model, depending on the vital parameter values and on how these are distributed among individuals at each time step. Furthermore, if the reproductive value is the same for all individuals, heterogeneity has no effect on the demographic variance. Thus, we provide a general theoretical framework for analyzing how individual heterogeneity caused by different biological mechanisms affects fluctuations of especially small populations.

Keywords: individual heterogeneity, demographic stochasticity, demographic variance, stochastic matrix population models, vital parameters.

The theoretical foundation for population ecology is based on deterministic models in which all individuals are equal (May 1981). A large and important step toward greater biological realism was achieved when stochastic models, incorporating random variation among individuals in survival and reproduction, appeared in the ecological literature (e.g., Bartlett 1960). Under the influence of such demographic stochasticity, individual contributions to the next population size are independent and identically distributed random variables. These early models were followed by models with only environmental stochasticity (e.g., Lewontin and Cohen 1969; May 1973; Turelli 1977) that, at a given time, affects survival and reproduction of all individuals simultaneously, generating dependence between the contributions. All such unstructured models rely on the assumption that individuals have equal opportunities for survival and reproduction. Different stochastic age or stage-structured models have also been developed, incorporating demographic stochasticity (Goodman 1967; Pollard 1973), environmental stochasticity (Cohen 1977, 1979; Lande and Orzack 1988; Tuljapurkar 1990; Caswell 2001), or both types of stochasticity (Lande et al. 2003; Engen et al. 2005*b*), all assuming that individuals are equal within each age or stage class. Nevertheless, except for these well-studied cases of age or stage structure, other cases of individual heterogeneity have been largely ignored in stochastic population models.

Recent evidence based on long-term demographic analyses covering a large variety of taxa suggests that the assumption of no individual heterogeneity is often not justified. Many mechanisms have now been identified that can contribute to such demographic variation in a population. First, considerable additive genetic variance is often present in life history (Mousseau and Roff 1987; Roff 1997; Merilä and Sheldon 2000; Kruuk 2004) as well as in morphological traits (e.g., Jensen et al. 2003 and references therein) that are closely associated with individual variation in fitness. Furthermore, the genetic covariances

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among fitness-related traits may also be positive (Bell and Koufopanou 1986; Roff 1996). As a consequence, individual heterogeneity can be maintained over generations. Second, maternal effects—that is, when the phenotype of the mother affects the phenotype of the offspring beyond additive genetic effects (Mousseau and Fox 1998)—also generate large individual differences in vital parameters (see examples in Mousseau and Fox 1998; Kruuk 2004). Third, spatial heterogeneity in the environment is an important source of individual heterogeneity. This is well illustrated by plants with random seed dispersal, in which the vital parameters of seedlings depend on the characteristics of the site where the seed happens to land (e.g., Beckage and Clark 2003). Other examples are found in many vertebrates, where quality of territory or home range often explains a high proportion of the variance among individuals in reproductive success, and these differences may be consistent over several years (e.g., Arlt and Pärt 2007; Byholm et al. 2007). Finally, temporal variation in environment may also generate individual heterogeneity in demography (Beckerman et al. 2002). In particular, environmental conditions experienced at early ontogenetic stages in life are important (Albon et al. 1987; Solberg and Sæther 1994; Coltman et al. 1999; Lindström 1999; Solberg et al. 1999; Metcalfe and Monaghan 2001; Reid et al. 2003, 2006).

The mechanisms for generating differences in vital parameters are not mutually exclusive, and individual heterogeneity can arise from complex interactions between different processes. For instance, Postma and van Noordwijk (2005) found consistent differences in clutch size among great tits *Parus major* living on the east and west side of the small island Vlieland on the coast of the Netherlands. Females born on the west side, as well as immigrants from the mainland, tended to have larger clutch size than birds on the east side. By contrast, females born on the east side had twice as high survival. Because immigration was lower to the east side, eastern birds were probably more adapted, due to microevolutionary processes, to the prevailing conditions at Vlieland (Postma and van Noordwijk 2005). A very similar pattern was also found in the same species in a forest outside Oxford in England (Garant et al. 2005).

The effects of individual heterogeneity have received considerable theoretical attention (Bjørnstad and Hansen 1994; Grimm 1999; Grimm et al. 1999; Pfister and Stevens 2003; Morris et al. 2006), mainly through analyses of deterministic models that introduce either spatial (Lomnicki 1988; Ginzburg 1998; Uchmanski 2000; Grimm and Uchmanski 2002) or temporal variation (DeAngelis et al. 1993; Lindström and Kokko 2002; De Roos et al. 2003) in demographic characteristics. Effects of individual heterogeneity on population dynamics should, however, be studied within a stochastic framework, since realized differences among individuals arise from an interaction of deterministic and stochastic processes.

Population dynamics are determined by stochastic events of individual survival and reproduction, of which the expectation and variance are given by the vital parameters (survival probability, expected number of offspring, variance in number of offspring, and covariance between survival and number of offspring). These vital parameters may vary in time, under influence of environmental stochasticity or in a seasonal environment. In the simplest stochastic population models, all individuals have equal vital parameters, so that any differences in realized survival or reproduction are completely random. In stochastic age- and stage-structured models, vital parameters change according to age or stage, so that realized differences are partly due to age/stage differences and are partly random. However, many other kinds of population structure also exist (Caswell 2001).

Here, we define individual heterogeneity as differences among individuals in vital parameters that are not completely random. At one extreme, individuals may have different vital parameters and stay different for their entire lives. Such consistent individual heterogeneity was analyzed by Conner and White (1999) using an individual-based simulation model. At the other extreme, if individuals randomly change vital parameters each time step independently of their current parameters, all realized differences are completely random. This is equivalent to an unstructured modeled with equal vital parameters. Between these two extremes, we find all cases of individual heterogeneity in which future vital parameters of an individual depend on, but are not necessarily equal to, its current ones. Then, in a constant environment, the population has a consistent structure even if the vital parameters are not consistent for a given individual. In a heterogeneous population, realized differences in survival and reproduction are partly random and are partly due to differences in vital parameters. Age and stage structure are special cases of individual heterogeneity because the future vital parameters of individuals depend on current ones.

In this article we will develop a stochastic matrix population model that includes individual heterogeneity in vital parameters. We will use this model to examine how such heterogeneity affects demographic stochasticity compared with a homogenous population. With this approach, we can determine how more- or less-consistent heterogeneity affects important characteristics such as the expected lifetime of the population (Lande 1998; Lande et al. 2003; Sæther et al. 2004*b*; Engen et al. 2005*b*) and genetical population dynamics (Engen et al. 2005*a*), because these are processes strongly influenced by demographic stochasticity.

Definitions of Stochastic Components of Population Dynamics

Early literature on stochastic population dynamics (e.g., Bartlett 1960) defined birth and death processes in discrete time by the assumption that individual contributions to the next population size, N_{t+1}, were independent when conditioned on current population size, N_t. As a consequence, the population size at the next discrete time step is a stochastic variable with variance proportional to current population size, say, $\sigma_d^2 N_t$. In general, the demographic variance σ_d^2 may be a density-dependent function of N_t (Sæther et al. 1998). In order to perform exact calculations in such models, the distribution of next year's population size must be specified. However, the diffusion approximation, which is based only on the mean and variance of yearly change in population size, has proved to work well for models with small and moderate fluctuations between years (Engen et al. 2003, 2005*b*). This makes the variance an important biological parameter containing practically all information about the stochasticity of the dynamics.

Studies of real populations, however, have shown that between-year fluctuations in population size are also affected by fluctuations in the biological and physical environment (e.g., Cappuccino and Price 1995; Sæther 1997; Newton 1998; Sibly et al. 2003; Sæther et al. 2005). Such fluctuations make the individual contributions dependent, as the environment affects all individuals simultaneously. These external forces create another variance component, $\sigma_e^2 N_t^2$ (May 1973; Keiding 1975; Turelli 1977; Lande et al. 2003), so that the total variance now becomes $\sigma_e^2 N_t^2 + \sigma_d^2 N_t$. Although the environmental variance σ_e^2 is usually much smaller than σ_d^2 (Sæther et al. 2004*a*), the environmental term will always dominate for large populations. For small populations approaching extinction, however, the demographic variance may often dominate, and the environmental term can be ignored (Lande 1993).

Engen et al. (1998) mathematically formalized the concepts of environmental and demographic variance for the female segment of an unstructured population, with overlapping generations and no shortage of males. Let **z** be a vector of all environmental components affecting the vital parameters, and let B be the number of offspring of an individual and J its survival ($J = 1$ for survival and 0 for death). Then $W = B + J$ is the individual fitness, that is, the contribution of individuals to the next generation (Lande et al. 2003). On an absolute scale, the demographic variance is defined as $\sigma_d^2 = \mathrm{E}\,[\mathrm{Var}\,(W|\mathbf{z})]$, where the expectation is taken with respect to **z** and the variance refers to variation among individuals (Engen et al. 1998). Similarly, the environmental variance is defined as $\sigma_e^2 = \mathrm{Var}\,[\mathrm{E}(W|\mathbf{z})]$, where the variance refers to **z** and the expectation is the theoretical mean among individuals in a given environment. With these definitions, the variance of the annual change in population size becomes $\sigma_e^2 N_t^2 + \sigma_d^2 N_t$, whereas the variance of the change in log population size is, to the first order, $(\sigma_e^2 + \sigma_d^2/N_t)\lambda^{-2}$, where λ is the multiplicative population growth rate. When working on the log scale, the factor λ^{-2} is usually included in the definitions of the variances, so that $\mathrm{Var}\,(\Delta \ln N) \approx \sigma_e^2 + \sigma_d^2/N_t$, a definition we adopt from now on.

Various important extensions of this simple model have shown that the main stochastic properties of age-structured populations are also described by only two parameters, the demographic and environmental variance. Generally, structured populations will show complex transient fluctuations given by other parameters (Caswell 2001). These fluctuations, however, have no impact on future population sizes except over a very short timescale (Engen et al. 2007). In contrast to the simple model with no age structure, stochastic age-structured models were first analyzed including only the concept of environmental stochasticity (Cohen 1977, 1979; Tuljapurkar 1982). An important contribution was provided by Lande and Orzack (1988), who showed how the environmental variance in such models, σ_e^2, could be applied in a diffusion approximation to give accurate approximations for the distribution of future population size as well as time to extinction. Later, Engen et al. (2005*b*) extended these results by defining a demographic variance, σ_d^2, for the age-structured model. This variance is generated by individual variation in survival and reproduction within a year, so that the infinitesimal variance in an accurate diffusion approximation is $\sigma_e^2 N_t^2 + \sigma_d^2 N_t$.

The demographic and environmental variance for age-structured populations are most easily defined, interpreted, and understood intuitively by using the concept of total reproductive value (Engen et al. 2007). Writing $\mathbf{n} = [n_1, \ldots, n_k]'$ for the vector of number of individuals in the k age classes with time index t when required, the deterministic Leslie model is given by $\mathbf{n}_{t+1} = \ell \mathbf{n}_t$, where ℓ is the deterministic Leslie matrix. Let λ be the dominant eigenvalue of ℓ. The existence of a real and nonnegative λ is guaranteed by the Perron-Frobenius theorem for nonnegative, primitive matrices (Caswell 2001). Without stochasticity, the population will grow exponentially with rate $r = \ln \lambda$. The right (column) and left (row) eigenvectors, $\mathbf{u} = [u_1, \ldots, u_k]'$ and $\mathbf{v} = [v_1, \ldots, v_k]$, are defined by $\ell \mathbf{u} = \lambda \mathbf{u}$ and $\mathbf{v}\ell = \lambda \mathbf{v}$. We scale the eigenvector **u** by the sum of the components being 1 so that **u** is the stable age distribution in the corresponding deterministic model. Furthermore, **v** is scaled so that $\mathbf{vu} = 1$. The components of **v** are the reproductive values of different age classes, and the total reproductive value at time t is $V_t = \mathbf{vn}_t$. In the absence of density regulation and in a constant environment, the expected value of this quantity will grow exactly exponentially, with no transient fluctuations in the initial phase, since

$$\mathrm{E}(V_{t+1}|V_t) = \mathbf{v}\ell_t\mathbf{n}_t = \lambda\mathbf{v}\mathbf{n}_t = \lambda V_t. \quad (1)$$

This occurs even if the population vector starts far from the stable age distribution (Fisher 1958; Caswell 2001; Lande et al. 2003).

Engen et al. (2007) used the same representation in the case of a stochastic Leslie model, given by $\mathbf{n}_{t+1} = \mathbf{L}_t\mathbf{n}_t$, where the elements of the stochastic Leslie matrix $\mathbf{L}_t$ are under influence of both demographic and environmental stochasticity. We write $\mathbf{L}_t = \ell + \boldsymbol{\varepsilon}_t$, where $\boldsymbol{\varepsilon}_t$ is the matrix of stochastic deviations with zero expectations, giving $V_{t+1} = \mathbf{v}(\ell + \boldsymbol{\varepsilon}_t)\mathbf{n}_t = \lambda V_t + \mathbf{v}\boldsymbol{\varepsilon}_t\mathbf{n}_t$. Ignoring second-order terms by approximating $\mathbf{n}_t$ in the stochastic term by a vector proportional to the stable age distribution, Engen et al. (2007) showed that

$$V_{t+1} = \lambda V_t(1 + \lambda^{-1}\mathbf{v}\boldsymbol{\varepsilon}_t\mathbf{u}). \quad (2)$$

The important conclusion to be drawn from this simple expression is that $\ln V_{t+1}$ is $(r + \ln V_t)$ plus a stochastic variable $\ln(1 + \lambda^{-1}\mathbf{v}\boldsymbol{\varepsilon}_t\mathbf{u})$, depending on the environment in year t only. Hence, if there is no temporal autocorrelation in the environment, $\ln V_t$ follows a simple additive process. With only environmental stochasticity, the added term has the same distribution each year, and the process is a random walk. By contrast, $\ln N_t$ follows a much more complex stochastic process with temporal autocorrelation in the noise. Writing $\ln V_t = \ln N_t + X_t$, Engen et al. (2007) showed that the deviation X_t is a stationary process fluctuating around 0 with a memory of only a few generations. Hence, all relevant information about the future is contained in the total reproductive value V_t.

The variance of the growth in total reproductive value is $\mathrm{Var}(V_{t+1}|V_t) = V_t^2\mathrm{Var}(\mathbf{v}\boldsymbol{\varepsilon}\mathbf{u}) = V_t^2\sigma_V^2$, where

$$\sigma_V^2 = \sum_{ij}\sum_{kl} v_i u_j v_k u_l \mathrm{Cov}[L_{ij}(\mathbf{z}), L_{kl}(\mathbf{z})]. \quad (3)$$

The long-run growth rate of the total reproductive value, defined as the expected growth rate for the log of total reproductive value, is given by

$$\begin{aligned} s &= \mathrm{E}(\ln V_{t+1} - \ln V_t|\ln V_t) \\ &= r + \mathrm{E}\ln(1 + \lambda^{-1}\mathbf{v}\boldsymbol{\varepsilon}_t\mathbf{u}) \\ &\approx r - \frac{1}{2}\lambda^{-2}\sigma_V^2, \end{aligned}$$

where $\sigma_V^2 = \mathrm{Var}(\mathbf{v}\boldsymbol{\varepsilon}\mathbf{u})$. The process of the total reproductive value can then simply be written in the form

$$\ln V_{t+1} \approx \ln V_t + s + \eta_t,$$

where η_t has mean 0 and variance $\mathrm{Var}[\ln(1 + \lambda^{-1}\mathbf{v}\boldsymbol{\varepsilon}_t\mathbf{u})] \approx \lambda^{-2}\sigma_V^2$, assuming that the term $\lambda^{-1}\mathbf{v}\boldsymbol{\varepsilon}\mathbf{u}$ is small and using a linear approximation of ln. With only environmental stochasticity, the above results are equal to the well-known results of Cohen (1977, 1979) and Tuljapurkar (1982) for stochastic growth of age-structured populations in a random environment.

Equation (2) may also be applied to study purely demographic stochasticity as well as both types of stochasticity operating jointly. Consider a finite age-structured population with no density regulation in a constant environment. Next year's population vector is still described by a matrix multiplication, $\mathbf{n}_{t+1} = \mathbf{L}_t\mathbf{n}_t$, but the elements of $\mathbf{L}_t$ are now the within-year means of the indicators of survival and number of offspring in each age class (Pollard 1966; Engen et al. 2005*b*, 2007). For example, next year's number of individuals in the third age class is the current number of individuals in the second age class multiplied by the mean indicator of survival for these individuals, say, $\bar{J}_2$. If $\bar{B}_i$ is the mean number of offspring of individuals in age class i, their contribution to the first age class is $\bar{B}_i$ times the number of individuals in class i. We write $\sigma_{B_i}^2$ for the variance in number of offspring per individual in age class i, $\sigma_{J_i}^2 = p_i(1 - p_i)$ for the variance of the survival indicators, and $\sigma_{BJ_i}^2$ for the covariance between number of offspring and the survival indicator. Equation (3) represents the variance on log scale, in the form $\lambda^{-2}\sigma_V^2 = \sigma_d^2/N_t$. For age-structured populations without environmental stochasticity, the demographic variance, which is approximately constant, is given by

$$\sigma_d^2 = \lambda^{-2}\sum_{i=1}^{k} u_i(v_1^2\sigma_{B_i}^2 + v_{i+1}^2\sigma_{J_i}^2 + 2v_1v_{i+1}\sigma_{BJ_i}^2) \quad (4)$$

(Engen et al. 2005*b*).

Modeling Individual Heterogeneity

Populations with individual heterogeneity can be modeled using a more general stochastic matrix model. In short, the population is divided in k groups with different vital parameters. These groups are generally not age classes or stages in the life cycle, and they could represent spatial heterogeneity or any other type of individual heterogeneity (see the introduction to this article). Each time step, offspring and adults from each group are distributed among the groups according to given offspring and adult transition probabilities.

By adjusting these transition probabilities, we can obtain different kinds of population structure. For instance, if the transition probabilities of adults and offspring are independent of their current group, the model becomes equivalent to a homogeneous model of equal vital parameters. A model of consistent individual heterogeneity is obtained if adults cannot move between the groups. Age and stage structure are modeled by letting all offspring be born into one group, while adults move only to the subsequent group. If individuals have a higher probability of leaving some groups than others, and vital parameters are positively correlated with the probability of leaving, we get a model with source/sink dynamics. By adjusting the transition probabilities, we can also model individual heterogeneity as an increasing or decreasing function of age (see Pfister and Stevens 2002 for examples of both types of functional relationship). Since the model is flexible, it could be a useful tool for studying different population structures. Here, however, the main purpose is to explore the effects of individual heterogeneity on demographic stochasticity. We will focus on cases of consistent heterogeneity but also consider some other cases.

To assess the effects of individual heterogeneity, we define a homogeneous comparison model assuming equal vital parameters. This model has the same expected dynamics as the heterogeneous model, so if there was no stochasticity, the two would be equal. In the heterogeneous model, for a given individual, events of survival and reproduction are dependent between time steps. In the homogeneous model, these events are assumed to be independent. For instance, consider five individuals who produce a number of offspring one year, say, 0, 0, 1, 4, and 3. Next year, the same individuals produce 0, 0, 2, 5, and 3 offspring, respectively. From the two samples, it seems that some individuals consistently produce more offspring than others. In the heterogeneous model, the two samples are correlated because individuals have different vital parameters. In the homogeneous model, however, any similarity between the samples is a coincidence, because individuals have equal vital parameters.

Both models assume no environmental variance, no density dependence, and no other population structure than the one under study, and they consider only female populations with no shortage of males. Events of survival and reproduction are assumed to happen independently among individuals; that is, there is no demographic covariance (Engen et al. 1998).

Heterogeneous Model

Consider a population of size N that is divided into k groups with different vital parameters. At each time step, for each individual in group i, let J_i be an indicator variable for survival, and let B_i represent the number of offspring. Hence, (J_i, B_i) is a random variable taking values in $(0, 1) \times (0, 1, 2, 3, \ldots)$ with mean (p_i, f_i) and covariance matrix

$$\begin{bmatrix} \sigma^2_{J_i} & \sigma^2_{BJ_i} \\ \sigma^2_{BJ_i} & \sigma^2_{B_i} \end{bmatrix},$$

where $\sigma^2_{J_i} = p_i(1 - p_i)$. The means, variances, and covariances of J_i and B_i constitute the vital parameters of an individual in group i. A summary of the variables and parameters used in the model is given in table 1. At a given time step, the proportion of survivors in group i is $\overline{J}_i$, whereas the mean number of offspring per individual is $\overline{B}_i$.

In addition to the vital parameters, each group is characterized by transition probabilities that determine how its individuals are redistributed between the groups for each time step, after survival and reproduction have taken place. We distinguish between offspring and adult transitions, and we assume that transitions are independent between individuals. Let the probability of moving from group j to i be q_{ij} and r_{ij} for offspring and adults, respectively. Since all surviving individuals have to end up somewhere after each time step, we have $\sum_{i=1}^{k} q_{ij} = \sum_{i=1}^{k} r_{ij} = 1$. Accordingly, $\overline{Q}_{ij}$ and $\overline{R}_{ij}$ are the proportions of offspring and adults, respectively, moving from j to i. Then the joint

Table 1: Parameters and variables used in the models

Label	Definition
J_i	Indicator of survival for individual in group i equal to 1 if it survives and 0 otherwise
p_i	Independent probability of survival for each individual in group i
$\sigma^2_{J_i} = p_i(1 - p_i)$	Variance of the random variable J_i
$\overline{J}_i$	Proportion of survivors in group i
B_i	Number of offspring of an individual in group i
f_i	Expected value of the random variable B_i
$\sigma^2_{B_i}$	Variance of the random variable B_i
$\sigma^2_{BJ_i}$	Covariance of the random variables J_i and B_i
$\overline{B}_i$	Mean number of offspring per individual in group i
q_{ij}	Probability that an offspring from group j is assigned to group i
r_{ij}	Probability that a surviving adult from group j moves to group i
$\overline{Q}_{ij}$	Proportion of offspring from group j assigned to group i
$\overline{R}_{ij}$	Proportion of surviving adults from group j moving to group i

distributions of the offspring and adults moving from j to the different groups are multinomial.

The population dynamics are given by $\mathbf{n} + \Delta\mathbf{n} = \mathbf{Mn}$, where $\mathbf{n} = (n_1, \ldots, n_k)'$ is the vector of population sizes and $\mathbf{M}$ is a stochastic projection matrix (Caswell 2001) given by

$$\mathbf{M} = \begin{bmatrix} \overline{J}_1\overline{R}_{11} + \overline{B}_1\overline{Q}_{11} & \overline{J}_2\overline{R}_{12} + \overline{B}_2\overline{Q}_{12} & & \cdots & \overline{J}_k\overline{R}_{1k} + \overline{B}_k\overline{Q}_{1k} \\ \overline{J}_1\overline{R}_{21} + \overline{B}_1\overline{Q}_{21} & \overline{J}_2\overline{R}_{22} + \overline{B}_2\overline{Q}_{22} & & \cdots & \overline{J}_k\overline{R}_{2k} + \overline{B}_k\overline{Q}_{2k} \\ \vdots & & \ddots & & \\ \overline{J}_1\overline{R}_{k1} + \overline{B}_1\overline{Q}_{k1} & \overline{J}_2\overline{R}_{k2} + \overline{B}_2\overline{Q}_{k2} & & \cdots & \overline{J}_k\overline{R}_{kk} + \overline{B}_k\overline{Q}_{kk} \end{bmatrix}.$$

Each entry in $\mathbf{M}$ represents the proportion of group j contributed to group i. After one time step, the number of individuals in group i is the sum of the contributions from all k groups to group i, giving

$$n_i + \Delta n_i = \sum_{j=1}^{k} n_j(\overline{J}_j\overline{R}_{ij} + \overline{B}_j\overline{Q}_{ij}).$$

All covariances between elements from different columns in $\mathbf{M}$ are 0 because of the assumption that events of survival, reproduction, and transition are independent between individuals.

The expected dynamics are determined by a deterministic matrix $\mathbf{K} = \mathrm{E}(\mathbf{M})$, by analogy with the stochastic age-structured model (Engen et al. 2005*b*) described in the second section. This matrix is the equivalent of the Leslie matrix ℓ, and its elements are given by $K_{ij} = p_j r_{ij} + f_j q_{ij}$. Although they do not have the same structure, $\mathbf{K}$ and ℓ share many important properties. The expected growth rate λ is the dominant eigenvalue of $\mathbf{K}$, the stable group structure is given by the scaled right eigenvector $\mathbf{u}$, and the reproductive values are given by the scaled left eigenvector $\mathbf{v}$, as described in the section "Definitions of Stochastic Components of Population Dynamics." The expected growth rate is given by $\lambda = \sum_{i=1}^{k} u_i w_i$, where $w_i = f_i + p_i$ is the expected individual fitness in group i.

The derivation of the demographic variance for this model is shown in appendix A in the online edition of the *American Naturalist*. It is given by

$$\sigma_d^2 = \lambda^{-2} \sum_l u_l(\alpha_l^2\sigma_{J_l}^2 + \beta_l^2\sigma_{B_l}^2 + 2\alpha_l\beta_l\sigma_{BJ_l}^2 + \gamma_l p_l + \delta_l f_l), \tag{5}$$

where $\alpha_l = \sum_{i=1}^{k} v_i r_{il}$, $\beta_l = \sum_{i=1}^{k} v_i q_{il}$,

$$\gamma_l = \begin{cases} \sum_{ij} v_i v_j r_{il}(1 - r_{il}), & i = j \\ -\sum_{ij} v_i v_j r_{il} r_{jl}, & i \neq j \end{cases},$$

and

$$\delta_l = \begin{cases} \sum_{ij} v_i v_j q_{il}(1 - q_{il}), & i = j \\ -\sum_{ij} v_i v_j q_{il} q_{jl}, & i \neq j \end{cases}.$$

Homogeneous Comparison Model

To construct the homogeneous comparison model, we consider an underlying heterogeneous population with k groups and then assume that it is homogeneous. In a homogenous population, survival and reproduction of each individual are given by the random variable (J, B), with expectation (p, f) and covariance matrix

$$\begin{bmatrix} \sigma_J^2 & \sigma_{BJ}^2 \\ \sigma_{BJ}^2 & \sigma_B^2 \end{bmatrix},$$

where $\sigma_J^2 = p(1 - p)$. From year to year, the variable (J, B) of a given individual is independent, in contrast to the heterogeneous model. Hence, these are the parameters we would estimate from data if observations, also those made on the same individual, are assumed to be independent between years.

We wish to relate the parameters of this model to those of the heterogeneous model. By the law of large numbers, if the heterogeneous population has stable group distribution $\mathbf{u}$, the probability that a randomly chosen individual belongs to group i is u_i. Hence, the survival probability in the homogeneous model is $p = \sum_{i=1}^{k} p_i u_i$, and the expected number of offspring is $f = \sum_{i=1}^{k} f_i u_i$. Similarly, σ_B^2, σ_J^2, and σ_{BJ}^2 are given by

$$\sigma_B^2 = \sum_{i=1}^{k} u_l[\sigma_{B_i}^2 + (f_i - f)^2],$$

$$\sigma_J^2 = \sum_{i=1}^{k} u_l[\sigma_{J_i}^2 + (p_i - p)^2],$$

and

$$\sigma_{BJ}^2 = \sum_{l=i}^{k} u_i[\sigma_{BJ_i}^2 + (p_l - p)(f_i - f)].$$

The expected growth rate is $\lambda = p + f$, which is the same as in the heterogeneous model. The stochastic properties, however, are generally different in the two models.

The demographic variance in a homogeneous population is given by $\sigma_d^2 = \lambda^{-2}\mathrm{Var}(J + B)$ (Engen et al. 1998).

Hence, using the parameters defined above, the demographic variance of this model is given by

$$\sigma_d^{2*} = \lambda^{-2}\sum_{i=1}^{k} u_i[\sigma_{B_i}^2 + \sigma_{J_i}^2 + 2\sigma_{BJ_i}^2 + (f_i - f)^2 + (p_i - p)^2 + 2(p_l - p)(f_l - f)]. \quad (6)$$

Comparison of the Models

As a measure of the degree of individual heterogeneity, we use the between-group variance in expected individual fitness, given by

$$\mathrm{Var}(w) = \sum_{i=1}^{k} u_i[(f_i - f)^2 + (p_i - p)^2 + 2(p_i - p)(f_i - f)]. \quad (7)$$

This variance increases with increasing differences in survival probability or increasing differences in expected number of offspring. If the expected individual fitness is the same in all groups, the variance is 0. In order to compare the demographic variances (eqq. [5], [6]) in the two models, we use the relative difference, $\beta = (\sigma_d^2 - \sigma_d^{2*})/\sigma_d^{2*}$.

Different Effects of Heterogeneity on the Demographic Variance

The demographic variance (eq. [5]) can either increase, decrease, or remain unaltered compared with that of the homogeneous comparison model (eq. [6]). For increasing heterogeneity (eq. [7]), the effect on the demographic variance depends on the vital parameter values of the different groups as well as on the transition probabilities of adults and offspring. In order to get a more thorough understanding of these rather general patterns, we will examine cases where either the p_i's or the f_i's (and $\sigma_{B_i}^2$) are altered while other parameters, as well as the growth rate λ, are kept constant. In many populations, the variance $\sigma_{B_i}^2$ is a function of the f_i's (e.g., Sæther and Bakke 2000). In the following examples, we assume $\sigma_{B_i}^2 = f_i$ and $\sigma_{BJ_i}^2 = 0$. We also consider different scenarios for the transition probabilities. This approach enables us to examine several of the general patterns of individual heterogeneity.

First, we consider cases with consistent heterogeneity, that is, where the adult transition probabilities are given by $r_{ij} = 1$ for $i = j$ and 0 otherwise. We also let the offspring be randomly distributed among groups. This type of model applies to populations of sessile organisms, such as plants or mussels, or other populations in heterogeneous environments where individuals do not migrate as adults. It can also be used to model populations where individuals experience long-lasting or irreversible effects from the environment during early development. In this case, for increasing heterogeneity in the p_i's, the demographic variance ultimately decreases compared with that of the homogeneous comparison model (fig. 1*A*). However, for certain combinations of parameter values and a relatively low degree of heterogeneity, the demographic variance increases (fig. 1*A*). Figure 2*A* shows the demographic variance for one of these cases. By contrast, for increasing heterogeneity in the f_i's, the demographic variance ultimately increases compared with that of the ho-

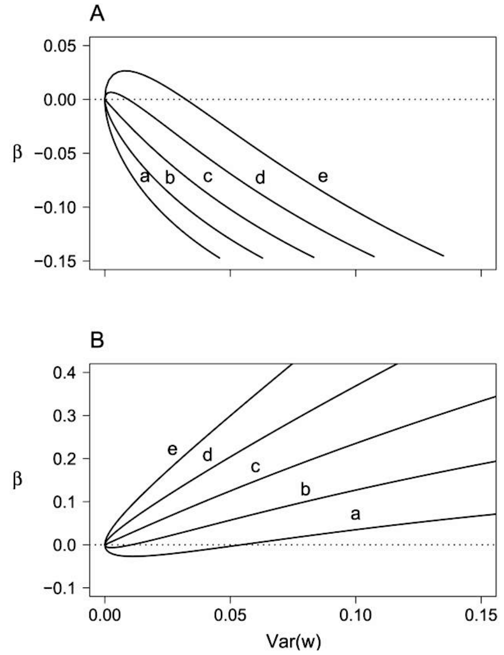

Figure 1: Relative difference in demographic variance, $\beta = (\sigma_d^2 - \sigma_d^{2*})/\sigma_d^{2*}$, as a function of variance in expected individual fitness, Var(*w*), in a population with two groups. *A*, Survival probability p_1 decreases and p_2 increases, whereas expected numbers of offspring f_1 and f_2 are constant. *B*, Values of p_1 and p_2 are constant, whereas f_1 decreases and f_2 increases. In both panels, the expected growth rate $\lambda = 1$, offspring transition probability $q_{11} = q_{22} = 0.5$, adult transition probability $p_{11} = p_{22} = 1$, variance in number of offspring $\sigma_{B_i}^2 = f_i$, and covariance between survival and number of offspring $\sigma_{BJ_i}^2 = 0$. Curves correspond to different initial values: *a*: $p_1 = 0.4$, $p_2 = 0.6$, $f_1 = 0.6$, $f_2 = 0.4$; *b*: $p_1 = 0.45$, $p_2 = 0.55$, $f_1 = 0.55$, $f_2 = 0.45$; *c*: $p_1 = 0.5$, $p_2 = 0.5$, $f_1 = 0.5$, $f_2 = 0.5$; *d*: $p_1 = 0.55$, $p_2 = 0.45$, $f_1 = 0.45$, $f_2 = 0.55$; *e*: $p_1 = 0.6$, $p_2 = 0.4$, $f_1 = 0.4$, $f_2 = 0.6$.

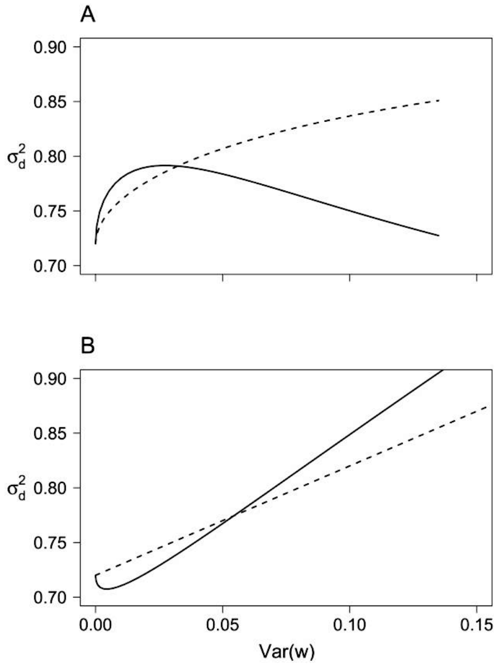

Figure 2: Demographic variance σ_d^2, in the heterogeneous (*solid lines*) and homogeneous (*dashed lines*) model, as a function of variance in expected individual fitness, Var(w), in a population with two groups. *A*, Survival probability p_1 decreases and p_2 increases from $p_1 = 0.6$ and $p_2 = 0.4$, whereas expected numbers of offspring $f_1 = 0.4$ and $f_2 = 0.6$ are constant. *B*, $p_1 = 0.4$ and $p_2 = 0.6$ are constant, whereas f_1 decreases and f_2 increases from $f_1 = 0.6$ and $f_2 = 0.4$. In both panels, expected growth rate $\lambda = 1$, offspring transition probabilities $q_{11} = q_{22} = 0.5$, adult transition probabilities $p_{11} = p_{22} = 1$, variance in number of offspring $\sigma_{B_i}^2 = f_i$, and covariance between survival and number of offspring $\sigma_{BJ_i}^2 = 0$.

mogeneous model (fig. 1*B*). Again, for low degrees of heterogeneity, certain parameter values lead to the opposite result of a smaller demographic variance in the heterogeneous model (fig. 2*B*).

Next, we examine how these patterns are affected by altering the offspring transition probabilities so that offspring are not randomly distributed. In other words, we introduce positive or negative correlation between offspring and parents. This kind of model applies, for instance, to populations with maternal effects or sessile organisms with nonrandom dispersal. If for all groups, offspring have a higher probability of remaining in their birth group, the demographic variance increases compared with the above cases where the offspring transition probabilities were equal (fig. 3). Correspondingly, if offspring have a higher probability of leaving their birth group, the demographic variance decreases compared with when the probabilities are equal (fig. 3).

We then consider cases of less consistent heterogeneity, that is, where adults do not always remain in one group and assume random distribution of offspring. Such a model applies to spatially structured populations, for instance, with source/sink structure (Pulliam 1988), or when adults move among habitat patches of different quality, such as in many metapopulations of butterflies (Hanski 1998). In such cases, the effect on demographic variance depends on whether the increasing heterogeneity occurs in the p_i's or the f_i's. For increasing heterogeneity in the p_i's, the demographic variance increases with the probability of leaving a patch (fig. 4*A*). By contrast, for increasing heterogeneity in the f_i's, the demographic variance decreases as the probability of leaving a patch increases (fig. 4*B*).

An important special case of the heterogeneous model is when all individuals have the same reproductive value, leading to equal demographic variance in the heterogeneous model and the homogeneous comparison model. Hence, in this case, it is possible for individuals to have different vital parameters without any effect on the demographic variance compared with that of the homogenous model. We emphasize that this result is valid regardless of the values of transition probabilities, variances in number of offspring, and covariances between survival and number of offspring.

Our model may also be used to study complex but perhaps more biologically realistic situations. For instance, individual heterogeneity can show age-specific variation (Pfister and Stevens 2002). In appendix B in the online edition of the *American Naturalist*, we show examples of such models where the degree of individual heterogeneity increases or decreases with age. Here, the comparison model has stages but is homogeneous within each stage. The results show that heterogeneity in either of the stages may alter the demographic variance compared with that of the homogenous model. Hence, including other types of structure does not change the main result, that heterogeneity may increase, decrease, or have no effect on the demographic variance.

Discussion

Our results show that it is generally not possible to predict the effects of individual heterogeneity in only one of the vital parameters, say, the survival probability, without some specification or assumption of the other vital parameters and transition probabilities. The special case of equal reproductive values shows that it is possible to have individual heterogeneity that does not affect the demographic variance, but for all other cases, knowledge of the vital parameters and transition probabilities is important for assessing the population dynamic consequences of individual heterogeneity. For instance, if there is a positive correlation between the vital parameters of parents and offspring, we have seen that the demographic variance increases compared with the cases where there is no such correlation.

Demographic stochasticity most strongly affects the dynamics of small populations (Lande 1998; Lande et al. 2003), which are often the central focus in population viability analysis (Beissinger and McCullough 2002). Our results show that it is important to include individual heterogeneity in viability models because it can affect estimates of extinction probability and extinction time. Generally, increasing demographic variance leads to a higher probability of extinction before a certain time and a shorter expected time to extinction (Lande et al. 2003). We have shown that in some cases, heterogeneity can be beneficial for the population, whereas in other cases it can be detrimental (figs. 1, 3, 4). Thus, for small, threatened populations, it is important to gain knowledge of heterogeneity in vital parameters as well as of the mechanisms maintaining the heterogeneity. Using a stochastic population-modeling framework, our approach provides a theoretical foundation for examining quantitatively how individual heterogeneity affects the dynamics of small populations (Holmes et al. 2007).

Different biological mechanisms can give rise to the same type of heterogeneous model. We gave some examples of such mechanisms in the previous section. Populations where survival and reproduction are dependent among individuals, however, are not included in our model. Such demographic covariance (Engen et al. 1998), as well as density dependence, can be created by intraspecific interactions such as contest competition (Birch 1957) or territoriality (e.g., Fretwell 1972). Density regulation is usually modeled by allowing the expected survival and reproduction to be functions of population density. For weak density regulation, our results are still likely to apply, whereas strong density regulation requires more complex analyses, taking eigenvalues other than the dominant one into account (Lande et al. 2006). However, the assumption of no density dependence is reasonable for most small populations, for which demographic stochasticity is most important.

We also assumed a constant environment in the derivation of the demographic variance. Environmental stochasticity can be included, again using methods developed for the age-structured model (Engen et al. 2005*b*). The matrix model would essentially be the same, but the vital parameters would have to be redefined as between-years means. For instance, the parameter $\sigma^2_{B_i}$ would be replaced by the between-years mean of the within-year variances in number of offspring in group i (Engen et al. 2005*b*). The offspring assignment probabilities could also fluctuate in time due to environmental stochasticity or seasonal variation in the environment. This would enable us to model the effects of individual heterogeneity among cohorts (Lindström and Kokko 2002) on the population dynamics.

Other studies of individual heterogeneity have used different methods than matrix modeling, from individual-based simulation models (e.g., Conner and White 1999; Jager 2001) to more analytical approaches (e.g., Kendall and Fox 2002; Fox 2005). Our matrix modeling approach represents an extension of these models and allows ex-

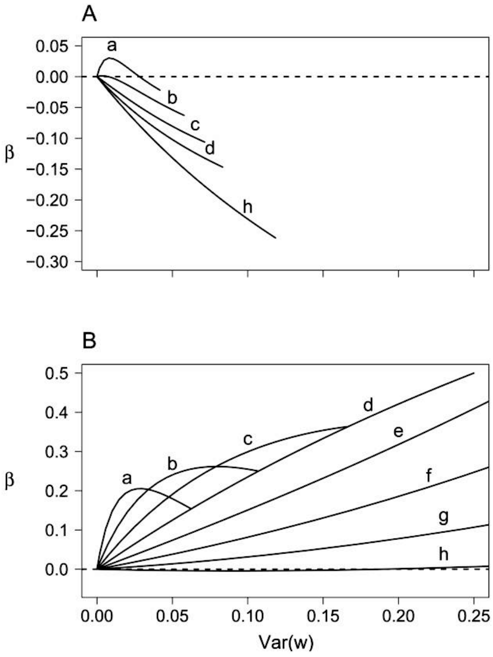

Figure 3: Relative difference in demographic variance $\beta = (\sigma^2_d - \sigma^{2*}_d)/\sigma^{2*}_d$ as a function of variance in expected individual fitness Var(w) in a population with two groups. Curves correspond to different values of offspring transition probabilities, $q_{11} = q_{22}$: *a*: $q_{11} = 0.8$; *b*: $q_{11} = 0.7$; *c*: $q_{11} = 0.6$; *d*: $q_{11} = 0.5$; *e*: $q_{11} = 0.4$; *f*: $q_{11} = 0.3$; *g*: $q_{11} = 0.2$; *h*: $q_{11} = 0.1$. *A*, Survival probability p_1 decreases and p_2 increases from $p_1 = p_2 = 0.5$, whereas expected number of offspring $f_1 = f_2 = 0.5$ is constant. *B*, $p_1 = p_2 = 0.5$ is constant, whereas f_1 decreases and f_2 increases from $f_1 = f_2 = 0.5$. In both panels, expected growth rate $\lambda = 1$, adult transition probabilities $p_{11} = p_{22} = 1$, variance in number of offspring $\sigma^2_{B_i} = f_i$, and covariance between survival and number of offspring $\sigma^2_{BJ_i} = 0$.

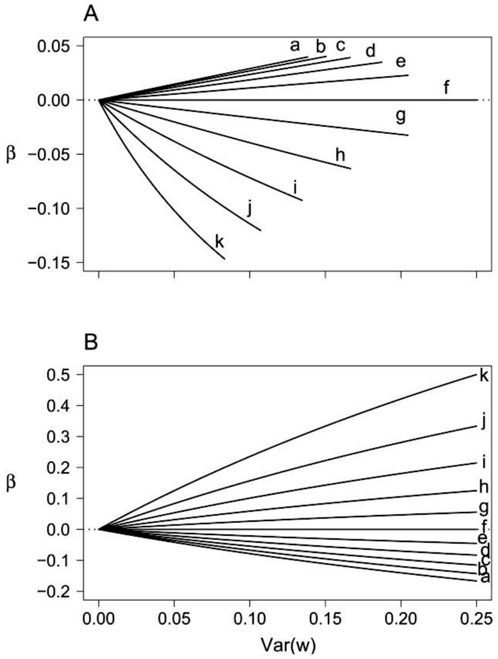

Figure 4: Relative difference in demographic variance $\beta = (\sigma_d^2 - \sigma_d^{2*})/\sigma_d^{2*}$ as a function of variance in expected individual fitness $\mathrm{Var}\,(w)$ in a population with two groups. Curves correspond to different values of adult transition probabilities, $r_{11} = r_{22}$: *a*: $r_{11} = 0$; *b*: $r_{11} = 0.1$; *c*: $r_{11} = 0.2$; *d*: $r_{11} = 0.3$; *e*: $r_{11} = 0.4$; *f*: $r_{11} = 0.5$; *g*: $r_{11} = 0.6$; *h*: $r_{11} = 0.7$; *i*: $r_{11} = 0.8$; *j*: $r_{11} = 0.9$; *k*: $r_{11} = 1$. *A*, Survival probability p_1 decreases and p_2 increases from $p_1 = p_2 = 0.5$, whereas expected number of offspring $f_1 = f_2 = 0.5$ is constant. *B*, $p_1 = p_2 = 0.5$ is constant, whereas f_1 decreases and f_2 increases from $f_1 = f_2 = 0.5$. In both panels, expected growth rate $\lambda = 1$, offspring transition probability $q_{11} = q_{22} = 0.5$, variance in number of offspring $\sigma_{B_i}^2 = f_i$, and covariance between survival and number of offspring $\sigma_{BJ_i}^2 = 0$.

amination of population dynamics with individual heterogeneity as well as of stochastic effects. Furthermore, because our model is based on relatively few parameters, we can explicitly examine the dynamic consequences of various kinds of individual heterogeneity by varying only certain parameters.

However, our conclusions seem to differ from those of previous analyses of the effects of individual heterogeneity. Kendall and Fox (2002) showed that increasing heterogeneity in survival probability reduces the variance in total number of survivors. We have here generalized these analyses to show that the effect of heterogeneity in survival depends on the other parameters as well. If these are equal, with consistent heterogeneity and random distribution of offspring, we obtain a similar situation to the one described by Kendall and Fox (2002; e.g., curve *c* in fig. 1*A*). However, this is only one of many possible combinations of vital parameter values and transition probabilities. Other combinations can lead to increased demographic variance (e.g., fig. 2*A*). The same is true regarding the effect of heterogeneity in expected number of offspring. It depends on the other parameters, and the demographic variance may decrease or increase compared with a homogeneous population (figs. 1*B*, 2*B*).

In another model, Conner and White (1999) developed an individual-based simulation model including consistent individual heterogeneity, and they found that small populations persisted longer at high levels of heterogeneity. Individual probabilities of death and of giving birth to a maximum of one offspring per year were modeled as functions of normally distributed variables, and the variances of these normal distributions measured the degree of consistent individual heterogeneity (Conner and White 1999). Generally, individual-based models are considered more realistic than state-based models, as detailed information on each individual can be included (Lomnicki 1999). Interactions producing demographic covariance and density dependence can also be included in these models. However, the high level of detail can make it difficult to separate different causes of the results (Grimm 1999). In addition, results based only on simulations are often hard to generalize, since all parameter ranges may not have been explored. Regarding population viability, the results of some individual-based simulation models have not been consistent with others.

The general nature of our modeling approach can also be used to clarify seemingly contrasting results of the effects of individual heterogeneity on population dynamics. For example, Jager (2001) used a biologically detailed individual-based model for white sturgeon (*Acipenser transmontanus*), with individual variation in age of maturity. The probability of population extinction before 1,000 years did not increase when nonheritable variation in this trait was increased, in contrast to the conclusions of Conner and White (1999). Our results provide a possible explanation for these seemingly contrasting results, showing that it is possible to obtain increased demographic variance with increasing variance in life-history traits associated with fitness. Although the individual-based model of Jager (2001) is very complex and includes density dependence, among other things, perhaps the chosen parameter values used in this model are found within one of the ranges leading to an increased demographic variance. Because Conner and White (1999) assumed that individuals produced a maximum of one offspring per year, the demographic variance could only decrease in their model.

We have based our approach on analyses of stochastic projection matrices, extending the theory of Engen et al. (2005*b*, 2007). Another approach to studying individual heterogeneity, by using branching process theory, was provided by Fox (2005). Increasing differences among individuals in extinction risk (probability of leaving 0 descendants after t generations) reduced the extinction risk of the total population compared with a population of identical individuals. This model assumes that individuals inherit the lineage extinction probability from their parent with perfect fidelity (Fox 2005). In our model, correlation between offspring and parents is measured through the offspring assignment probabilities q_{ij}. If all offspring are randomly distributed between the groups, there is no correlation between offspring and parents, but individual heterogeneity can still exist. If offspring inherit vital parameters from their parents with perfect fidelity and adults remain in their groups with the probability of 1, we obtain the situation modeled by Fox (2005). In this special case, there are no interactions among the groups, so eventually the group with highest expected individual fitness will constitute the whole population. Thus, the individual heterogeneity is not maintained over time, so the demographic variance can only decrease, compared with the initial population. This situation is also known as the frailty effect (Vaupel and Yashin 1985).

Our model represents a generalization of previous approaches that allows us to examine how individual heterogeneity affects the demographic variance and hence the population fluctuations. The stage-structured examples in appendix B show that even if heterogeneity is present in only one stage in the life cycle, the demographic variance can be altered compared with a population with no heterogeneity in the stages. Because demographic variance strongly affects the dynamics of especially small populations (Lande 1998; Lande et al. 2003), our model can be used to examine important characteristics such as expected time to extinction and genetic drift.

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Appendix A from Y. Vindenes et al., “Individual Heterogeneity in Vital Parameters and Demographic Stochasticity”

(Am. Nat., vol. 171, no. 4, p. 455)

Derivation of the Demographic Variance in the Heterogeneous Model

Here, we derive the demographic variance of the heterogeneous model, described in the section “Modeling Individual Heterogeneity.” As for age-structured models, we consider the dynamics of the total reproductive value V (see “Definitions of Stochastic Components of Population Dynamics”). For heterogeneous populations, the analogue of equation (3) is given by

$$\frac{\sigma_d^2}{N} = \lambda^{-2}\sum_{ij}\sum_{ml} v_i u_j v_m v_l \,\mathrm{Cov}\,(M_{ij}, M_{ml}).$$

Because the covariances between elements from different columns in $\mathbf{M}$ are all 0, $j = l$ in the above expression, which reduces to

$$\frac{\sigma_d^2}{N} = \lambda^{-2}\sum_{l} u_l^2 \sum_{ij} v_i v_j \,\mathrm{Cov}\,(M_{il}, M_{jl}).$$

The second sum in the above expression can be rewritten as $\mathrm{Var}\,(\sum_{i=1}^{k} v_i M_{il})$. Let J_{Tl} be the total number of survivors, and let B_{Tl} be the total number of offspring, in group l. Then, this variance can be expressed as

$$\mathrm{Var}\left(\sum_{i=1}^{k} v_i M_{il}\right) = \mathrm{E}\left[\mathrm{Var}\left(\sum_{i=1}^{k} v_i M_{il} | J_{Tl}, B_{Tl}\right)\right] + \mathrm{Var}\left[\mathrm{E}\left(\sum_{i=1}^{k} v_i M_{il} | J_{Tl}, B_{Tl}\right)\right].$$

In the first term, the expression $\mathrm{Var}\,(\sum_{i=1}^{k} v_i M_{il} | J_{Tl}, B_{Tl})$ is given by

$$\mathrm{Var}\left(\sum_{i=1}^{k} v_i M_{il} | J_{Tl}, B_{Tl}\right) = \frac{J_{Tl}}{n_l^2}\gamma_l + \frac{B_{Tl}}{n_l^2}\delta_l,$$

because transitions of parents and offspring are independent, where

$$\gamma_l = \begin{cases} \sum_{i=1}^{k}\sum_{j=1}^{k} v_i v_j r_{il}(1 - r_{il}), & i = j \\ -\sum_{i=1}^{k}\sum_{j=1}^{k} v_i v_j r_{il} r_{jl}, & i \neq j \end{cases},$$

$$\delta_l = \begin{cases} \sum_{i=1}^{k}\sum_{j=1}^{k} v_i v_j q_{il}(1 - q_{il}), & i = j \\ -\sum_{i=1}^{k}\sum_{j=1}^{k} v_i v_j q_{il} q_{jl}, & i \neq j \end{cases}.$$

Taking the expectation of the above variance, the first term of $\mathrm{Var}\,(\sum_{i=1}^{k} v_i M_{il})$ is given by

$$\mathrm{E}\left[\mathrm{Var}\left(\sum_{i=1}^{k} v_i M_{il} | J_{Tl}, B_{Tl}\right)\right] = \frac{1}{n_l}(p_l\gamma_l + f_l\delta_l).$$

Next, consider the second term, $\mathrm{Var}\,[\mathrm{E}(\sum_{i=1}^{k} v_i M_{il} | J_{Tl}, B_{Tl})]$. The expectation is given by

$$\mathrm{E}\left(\sum_{i=1}^{k} v_i M_{il} | J_{Tl}, B_{Tl}\right) = \frac{1}{n_l}\sum_{i=1}^{k} v_i (J_{\mathrm{T}l} r_{il} + B_{\mathrm{T}l} q_{il}).$$

Taking the variance of the above expression, we obtain

$$\mathrm{Var}\left(\mathrm{E}\left[\sum_{i=1}^{k} v_i M_{il} | J_{Tl}, B_{Tl}\right]\right) = \frac{1}{n_l}(\alpha_l^2 \sigma_{J_l}^2 + \beta_l^2 \sigma_{B_l}^2 + 2\alpha_l \beta_l \sigma_{BJ_l}^2),$$

where $\alpha_l = \sum_{i=1}^{k} v_i r_{il}$ and $\beta_l = \sum_{i=1}^{k} v_i q_{il}$. Hence, the unconditional variance is given by

$$\mathrm{Var}\left(\sum_{i=1}^{k} v_i M_{il}\right) = \frac{1}{n_l}[\alpha_l^2 \sigma_{J_l}^2 + \beta_l^2 \sigma_{B_l}^2 + 2\alpha_l \beta_l \sigma_{BJ_l}^2 + (p_l \gamma_l + f_l \delta_l)].$$

Finally, using the approximation $n_i \approx u_i N$ and inserting the resulting expression in the first equation, the demographic variance is given by

$$\sigma_{\mathrm{d}}^2 = \lambda^{-2} \sum_l u_l [\alpha_l^2 \sigma_{J_l}^2 + \beta_l^2 \sigma_{B_l}^2 + 2\alpha_l \beta_l \sigma_{BJ_l}^2 + \gamma_l p_l + \delta_l f_l].$$

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Appendix B from Y. Vindenes et al., "Individual Heterogeneity in Vital Parameters and Demographic Stochasticity"

(Am. Nat., vol. 171, no. 4, p. 455)

Examples of Where Heterogeneity Changes with Age

The matrix model for individual heterogeneity may also be used to study populations where individual heterogeneity is a function of age (Pfister and Stevens 2002). Here, we present two such examples. In both, we consider a population with two stages, where individuals are heterogeneous (two groups) in one of the stages and homogeneous (one group) in the other, so that in total there are three groups in the model. In both examples we assume that the expectation and variance in number of offspring are equal and that the covariance between survival and number of offspring is 0, for all groups.

Figure B1*A* shows possible transitions for adults and offspring in the example where heterogeneity increases with age, with corresponding probabilities. Here, all individuals are born into group 1; hence, they are equal at birth, with survival probability $p_1 = 0.3$ and expected number of offspring $f_1 = 0$. From this group adults may move to either group 2 or group 3, each with probability 0.15, and then remain in these groups. Individuals in group 3 have higher expected fitness than individuals in group 2, with $p_2 = 0.3$, $p_3 = 0.6$, $f_2 = 0.5$, and $f_3 = 6.5$. Since individuals in groups 2 and 3 tend to be older than individuals in group 1, we obtain the situation where heterogeneity increases with age. With these parameters, the expected growth rate is $\lambda \approx 0.991$; the stable group structure is $u_1 \approx 0.847$, $u_2 \approx 0.055$, and $u_3 \approx 0.098$; and the reproductive values are $v_1 \approx 0.40$, $v_2 \approx 0.29$, and $v_3 \approx 6.63$. The homogenous model has two groups, assuming that the numbers of individuals in groups 2 and 3 are equal. For the parameter values given above, parameters in the homogeneous model are $p_1^* = 0.3$, $p_2^* \approx 0.492$, $f_1^* = 0$, and $f_2^* \approx 4.332$. Here, the stable structure is $u_1^* \approx 0.847$ and $u_2^* \approx 0.153$, while the reproductive values are $v_1^* \approx 0.460$ and $v_2^* \approx 3.99$. The demographic variance of the heterogeneous model is $\sigma_d^2 \approx 2.76$, whereas in the homogeneous model it is $\sigma_d^{2*} \approx 1.86$. Figure B2*A* shows quantiles from simulations of the heterogeneous and homogeneous model in this example. It is clear that the variance is larger in the heterogeneous models and that the heterogeneous processes tend to die out before the homogeneous processes.

Figure B1*B* shows possible transitions of adults and offspring for the example where heterogeneity decreases with age, with corresponding probabilities. Individuals are born in either group 1 or group 2 with equal probability 0.5; hence, they are not equal at birth. Parameters in these groups are $p_1 = 0.9$, $p_2 = 0.18$, $f_1 = 0$, and $f_2 = 0.4$, and adults may not move between them. From groups 1 and 2, adults may move to group 3 with probability 0.3, then remain there. Hence, older individuals will tend to assimilate in group 3, where they obtain equal vital parameters $p_3 = 0.15$ and $f_3 = 1.6$. With these parameter values, the expected growth rate is $\lambda \approx 0.992$; the stable group structure is $u_1 \approx 0.566$, $u_2 \approx 0.237$, and $u_3 \approx 0.197$; and the reproductive values are $v_1 \approx 1.08$, $v_2 \approx 0.44$, and $v_3 \approx 1.44$. In this case, the homogeneous model assumes that groups 1 and 2 are equal in size, and parameters are $p_1^* \approx 0.688$, $p_2^* = 0.15$, $f_1^* \approx 0.118$, and $f_2^* = 1.6$. Here, the stable structure is $u_1^* \approx 0.803$ and $u_2^* \approx 0.197$, while the reproductive values are $v_1^* \approx 0.849$ and $v_2^* \approx 1.61$. The demographic variance of the heterogeneous model is $\sigma_d^2 \approx 0.453$, whereas in the homogeneous model it is $\sigma_d^{2*} \approx 0.64$. Figure B2*B* shows quantiles from simulations of the heterogeneous and homogeneous models for this case. Now the variance is larger in the homogeneous model, and the heterogeneous processes tend to die out later than the homogeneous processes.

These examples show that even if individual heterogeneity increases or decreases with age, it can alter the demographic variance compared with that of a homogeneous population. The demographic variances found in these examples depend on the vital parameter values chosen. In both cases, however, it is possible to find other parameter values that would make the demographic variance either larger or smaller in the heterogeneous model than in the homogeneous model.

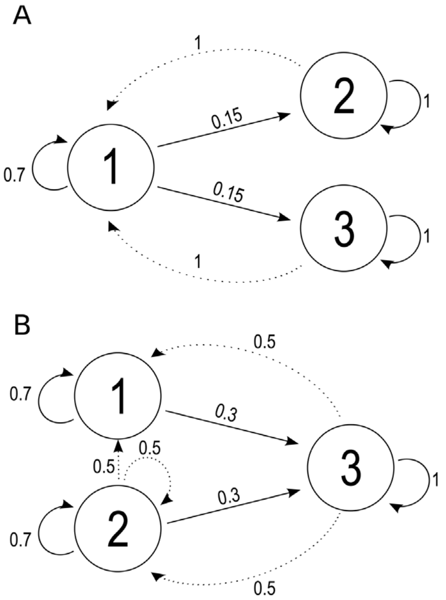

Figure B1: Illustration of possible transitions in a population with three groups, for the examples used in appendix B. Solid lines represent adult transitions, while dotted lines represent offspring transitions. *A*, An example where individual heterogeneity increases with age. All offspring are born into group 1; groups 2 and 3 are absorbing. *B*, An example where individual heterogeneity decreases with age. Individuals are born into groups 1 and 2 with equal probability; group 3 is absorbing.

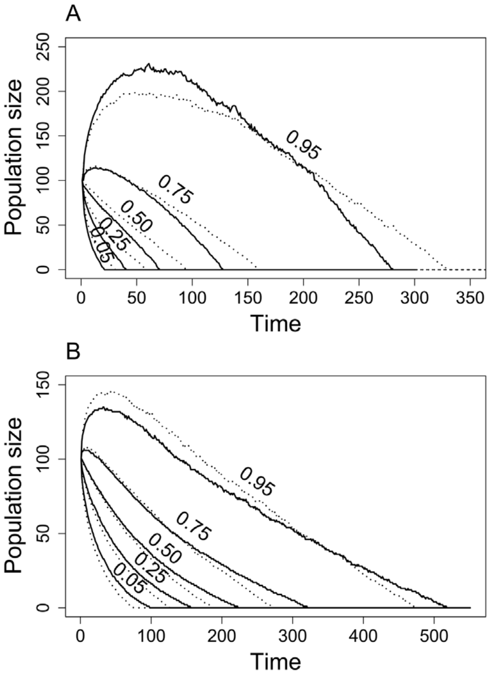

Figure B2: Quantiles from 10,000 simulations of the heterogeneous (*solid line*) and homogeneous (*dotted line*) models for the examples in appendix B. See figure B1 for values of transition probabilities. *A*, Heterogeneity increases with age. Parameters (see table 1) are $p_1 = 0.3$, $p_2 = 0.3$, $p_3 = 0.6$, $f_1 = 0$, $f_2 = 0.5$, $f_3 = 6.5$, $\sigma^2_{B_i} = f_i$, $\sigma_{BJ_i} = 0$ for $i = 1, 2, 3$. *B*, Heterogeneity decreases with age. Parameters are $p_1 = 0.9$, $p_2 = 0.18$, $p_3 = 0.15$; $f_1 = 0$, $f_2 = 0.4$, $f_3 = 1.6$; $\sigma^2_{B_i} = f_i$, $\sigma_{BJ_i} = 0$ for $i = 1, 2, 3$.

Paper II

Integral projection models for finite populations in a stochastic environment

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Running head: Continuously structured populations

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Abstract

Continuous types of population structure occur when continuous variables such as body size or habitat quality affect the vital parameters of individuals. These structures can give rise to complex population dynamics, and interact with environmental conditions. Here we present a model for continuously structured populations with finite size, including both demographic and environmental stochasticity in the dynamics. Using recent methods developed for discrete age structured models we derive the demographic and environmental variance of the population growth as functions of a continuous state variable. These two parameters, together with the expected population growth rate, are used to define a one-dimensional diffusion approximation of the population dynamics. Thus, a substantial reduction in complexity is achieved as the dynamics of the complex structured model can be described by only three population parameters. We provide methods for numerical calculation of the model parameters, and demonstrate the accuracy of the diffusion approximation by computer simulation of specific examples. The general modeling framework makes it possible to analyze and predict future dynamics and extinction risk of populations with various types of structure, and to explore consequences of changes in demography caused by e.g. climate change or different management decisions. Our results are especially relevant for small populations that are often of conservation concern.

Keywords: Structured populations, demographic stochasticity, environmental stochasticity, diffusion approximation, individual heterogeneity.

Introduction

Long-term individual-based studies from different taxa have shown that the causes of observed population dynamics may be highly complex, due to temporal and spatial fluctuations in the environment as well as inherent life history properties of the species (Coulson et al., 2001; Benton et al., 2006). At the individual level, there is often a large variability in outcomes of survival and reproduction. Some of this variation is explained by age, size, and/or other structuring variables, whereas the rest of the variation is random, due to demographic and environmental stochasticity. Recently, integral projection modeling has arisen as a powerful method for studying populations with complex structure (Easterling et al., 2000; Ellner and Rees, 2006, 2007). In contrast to matrix models, an integral projection model (IPM) is not based on a limited number of classes or stages. It can be used when population structure arises from continuously distributed variables, and retains practically all the analytical advantages of a matrix model (Ellner and Rees, 2006). IPMs assume that smooth, functional relationships exist between the vital parameters (e.g., survival probability) and the structuring variable. These functions can usually be estimated with regression techniques (e.g., Metcalf et al., 2003). As parameters of matrix models are generally estimated independently for each class, IPMs make more efficient use of data and may therefore be a better option for studying small populations (Ramula et al., 2009).

Integral projection modeling has so far been successfully applied to study how vital parameters of plant populations vary with size, quality and age, as well as how demographic structure affects evolutionary strategies of flowering (Rees and Rose, 2002; Metcalf et al., 2003; Childs et al., 2004; Kuss et al., 2008). IPMs including environmental stochasticity have also been developed, and used to derive expressions for the long-term (stochastic) population growth rate and its sensitivities (Ellner and Rees, 2007; Rees and Ellner, 2009). Environmental stochasticity arises from environmental fluctuations and acts simultaneously on all individuals in a population, creating covariance between individuals in their survival and reproduction at a given time (May, 1973; Lande et al., 2003).

A large shortcoming with the current theory of integral projection modeling is that the other main source of stochasticity in population dynamics, demographic stochasticity, has to our knowledge so far been ignored. This type of stochasticity acts independently between individuals each year (Lande et al., 2003). Although both types of stochasticity have a negative effect on the long-term population growth, the effects of demographic stochasticity level off as population size increases, and are negligible for large populations (Lande et al., 2003). For small to moderate population sizes, however, it may have a large effect on population dynamics and extinction risk. Thus, in order to fully understand the population dynamical consequences of stochasticity in structured populations, we need a modeling framework including both types of stochasticity.

For an age structured population model with only environmental stochasticity, Lande and Orzack (1988) showed that the environmental variance and the expected population growth rate could be used to define an accurate diffusion approximation of the population dynamics, as long as the fluctuations in population size are not very large. This diffusion approximation was later extended to include the demographic variance of age structured populations (Engen et al., 2005). The main advantage of the diffusion approximation, besides having well known mathematical properties, is that the dynamics of complex structured population models may be described by a one-dimensional diffusion process with only a few parameters. Thus, it also tells us which population parameters are important to consider and to estimate for correctly describing the population dynamics (Lande et al., 2003).

Here we will define an IPM for a continuously structured population that includes both demographic and environmental stochasticity. An important difference from other IPM's is that the number of individuals is finite, so that the realized state distribution each year is discrete. Figure 1 presents an illustration of how the realized state distribution can change over time in a finite population with both types of stochasticity present. With only environmental stochasticity or no stochasticity, one must either assume that the population is infinite or work with the distribution of population size rather than the population size. When demographic stochasticity is included, an individual either survives or not, and produces an integer number of offspring, so that the population size is naturally restricted to be an integer.

In the following, we will start by describing the model, including some important population parameters found from the dynamics of the expected population size. Then we will consider the dynamics of the total reproductive value, and briefly review how the demographic and environmental variance can be used to define a one-dimensional diffusion approximation to the density-independent dynamics of a structured model. In the Results section we will derive expressions for the demographic and environmental variance as functions of the continuous state variable. Using computer simulation of given examples, we will demonstrate the accuracy of the diffusion approximation, as well as how it can be used to estimate extinction risk.

Methods

Model description and assumptions

Consider a population with density-independent growth, which is structured by a continuous state variable x. This state, which is defined on a state space Ω, includes all parameters that may affect the survival and reproduction of an individual (McNamara and Houston, 1996), and may be multivariate (a vector of different variables) or univariate. The fluctuating environment is represented by a variable z, which may also be multivariate. We assume that this variable follows a stochastic stationary process with no temporal autocorrelation. Each year, a new value of z is drawn from a probability density function (or probability distribution if z is discrete) $f(z)$. While individuals generally have different values of the state x, the environment z is common for all individuals at any time. Figure 2 illustrates how individual state could change over time, for two different examples. In the first example (fig. 2A and 2B), x represents body mass, where individuals show stochastic growth over time. In the second example, x represents the amount of some resource available to individuals. Plants at different spatial locations, for instance, could experience different base levels of nitrogen in the soil, with some fluctuation over time at each location.

In general, all vital parameters of individuals, such as survival probability, may depend on both individual state x and environment z. Figure 3 presents an illustration of how a vital rate (the survival probability) might change with environmental condition as a function of state. In this example, an individual in state x_B experiences a larger change in survival probability as the environment changes than an individual in state x_A, and in opposite direction. Such interactions between state and environment can occur for example due to differences among individuals in resource acquisition ability (Lomnicki, 1988). Individuals with poor ability to obtain resources such as food may have a harder time in years of low resource availability, with potentially larger reduction in survival probability.

For an individual with state x, let S_x be a stochastic indicator variable for survival, equal to 1 if the individual survives at a given time and 0 otherwise. The survival probability of the individual is given by a function $s(x, z)$. The number of offspring produced by the individual is given by a stochastic variable B_x, with expectation $b(x, z)$ and variance $\sigma_B^2(x, z)$. The covariance between B_x and S_x is given by a function $\sigma_{BS}^2(x, z)$. Next year, if the individual has survived it will obtain a new state value Y_{sx}, according to some probability density function $f_s(y; x, z)$. If the individual reproduces we let Y_{bxi} represent the state of offspring number i, for $i = 1, ..., B_x$. The probability density function of Y_{bxi} is given by $f_b(y; x, z)$, and the Y_{bxi} are independent for a given B_x.

The total population size in this model is given by $N = \int_\Omega \mathrm{d}n(x)$. If demographic stochasticity is included we define the integrator $\mathrm{d}n(x)$ to be equal to 1 whenever the state of an individual lies within the small interval $[x, x + \mathrm{d}x]$, and 0 otherwise. Then, the above integral (a Lebesgue-Stieltjes integral; e.g. Mikosch, 1998) defining population size N corresponds to the sum of all individuals in the population. If demographic stochasticity is not included we define $\mathrm{d}n(x) = n(x)\mathrm{d}x$, where $n(x)$ is a continuous function.

The dynamics of the expected population size correspond to those of a deterministic IPM, from which we can find several important model parameters, especially the expected growth rate λ, the stable state structure $u(x)$ and the reproductive value $v(x)$ (Easterling et al., 2000; Ellner and Rees, 2006). The expectation of next year's population size given this year's size N can be written as

$$\mathrm{E}[N + \Delta N | N] = \int_\Omega \int_\Omega n(x) k(y, x)\, \mathrm{d}x \mathrm{d}y, \tag{1}$$

where ΔN is the yearly change in population size, and $k(y, x)$ is the mean projection function. This function is given by $k(y, x) = \int k(y, x, z) f(z) \mathrm{d}z$, where

$k(y,x,z) = s(x,z)f_s(y;x,z) + b(x,z)f_b(y;x,z)$ is the projection function in a given environment z. The mean projection function $k(y,x)$ is also known as a kernel function, and equivalent to the projection matrix in discrete models (Easterling et al., 2000). The expected contribution from an individual with state x to a small state interval $[y, y + \mathrm{d}y]$ in the next time step, is given by $k(y,x)\mathrm{d}y$. In matrix models, the existence of a unique multiplicative growth rate λ and a stable stage structure is guaranteed by the Perron-Frobenius theorem for non-negative and ergodic matrices (Caswell, 2001). Similar conditions apply for the projection function, and are described by Ellner and Rees (2006).

The stable state distribution $u(x)$ is defined by the recursion $\lambda u(y) = \int_\Omega k(y,x)u(x)\mathrm{d}x$ (Haccou et al., 2005), and scaled so that $\int_\Omega u(x)\mathrm{d}x = 1$. The function $v(x)$ defines the reproductive value as function of state x, and is determined by the recursion $\lambda v(x) = \int_\Omega v(y)k(y,x)\mathrm{d}y$ (Haccou et al., 2005), scaled so that $\int_\Omega v(x)u(x)\mathrm{d}x = 1$. If an individual is drawn at random from the population at its stable state distribution, the probability that it has a state value within some subinterval $U \subset \Omega$ is given by $\int_U u(x)\mathrm{d}x$. The reproductive value $v(x)$ describes the expected contribution of an individual with state x to future population growth, relative to other individuals in the population. The total reproductive value of the population is defined as $V = \int_\Omega v(x)\mathrm{d}n(x)$. If the population has the exact stable state distribution, then $N = V$ and $n(x) = u(x)N$. Otherwise, we will use the approximations $N \approx V$ and $n(x) \approx u(x)N$ (Engen et al., 2007). The parameters λ, $u(x)$, and $v(x)$ are all easily found numerically (see appendix A).

Dynamics of total reproductive value and diffusion approximation

Fisher (1930) demonstrated for a density-independent, deterministic age structured model that the total reproductive value will grow exponentially even if the population does not have the stable age distribution. Recently, Engen et al. (2007) showed for a stochastic age structured model that the total reproductive value is approximately a Markovian process, and that its dynamics can be approximated by a one-dimensional diffusion process. The population size, which is not a Markovian process, will fluctuate around the total reproductive value with larger magnitude of the fluctuations. The reproductive value can be seen as a filter for the population process, removing the part of the fluctuations that are due to stochastic deviations from the stable distribution. Thus, in structured, stochastic population models the parameters describing the long-term population growth should be derived based on the dynamics of the total reproductive value, rather than the dynamics of the population size (Engen et al., 2007, 2009).

In an age structured population with both types of stochasticity, the variance in next year's total reproductive value is given by (Engen et al., 2007)

$$\sigma_V^2 = \mathrm{Var}(V + \Delta V | V) \approx \sigma_e^2 V^2 + \sigma_d^2 V, \tag{2}$$

where the constant σ_e^2 is the environmental variance and σ_d^2 is the demographic variance.

With diffusion approximations it is common to work on the log scale because the variance of population change is more stable on this scale (Cohen, 1977; Tuljapurkar, 1982). We can write next year's total reproductive value as $V + \Delta V = \lambda V + \varepsilon$, where ε is a stochastic term with mean zero and variance σ_V^2. On log scale, the change is then given by $\Delta \ln V = \ln \lambda + \ln(1 + \varepsilon/(\lambda V))$ (Engen et al., 2009). By second order approximation, the expectation of this change is given by $\ln \lambda - 1/(2\lambda^2)(\sigma_e^2 + \sigma_d^2/V)$, and by first order approximation the variance is $\lambda^{-2}(\sigma_e^2 + \sigma_d^2/V)$. These are the infinitesimal mean and variance for the diffusion approximation on log scale. Assuming that the yearly change in total reproductive value is not very large, the diffusion approximation will work well for all population sizes all the way down to extinction (Lande et al., 2003). Here we will show that it can be used also for continuously structured populations, once the appropriate expressions for σ_e^2 and σ_d^2 have been found.

Results

In this section we will first consider the special case with only demographic stochasticity, followed by the special case with only environmental stochasticity. By deriving the demographic and environmental variance for these special cases first, the terminology is kept simpler and the concepts of demographic and environmental stochasticity in this model are easier to study when first considered separately. Finally, we will derive the demographic and environmental variance in the general case where both types of stochasticity are present. The formulas for demographic and environmental variance are then essentially the same as in the special cases where each type of stochasticity is considered alone, but the parameters entering the formulas are redefined. The analytical results are illustrated by a numerical example with simulations at the end of each subsection. Methods for numerical calculation are described in Appendix, and as supplementary material we also provide the programming script (Rcode.txt) that we used to perform the numerical calculations and simulations with the software R (R Development Core Team, 2009). The derivation of our results largely follows the approach of Engen et al. (2009) for a discrete age structured population. In order to see the structural similarities as well as differences between that model and the continuous case presented here, we have listed some main parameters and results from the two models in table 1.

Demographic stochasticity alone

Assuming a constant environment, we can now omit the environmental variable z from the vital parameter functions. To derive the demographic variance as function of the vital parameters, we consider the contribution of an individual with state x to next year's total reproductive value. This contribution consists of two main parts, a survival component and a reproduction component. If the individual survive to obtain state variable Y_{sx} next year, its reproductive value will be $v(Y_{sx})$ next year (a stochastic variable). Since survival is given by the indicator variable S_x, the total survival contribution of the individual is given by $S_x v(Y_{sx})$. Similarly, if the individual produces B_x offspring with states Y_{bsi} (for $i = 1, 2, ...B_x$), then offspring number i will have reproductive value $v(Y_{sbi})$ next year. Adding up these contributions, the total contribution of the individual can be written as

$$W_x = S_x v\left(Y_{sx}\right) + \sum_{i=1}^{B_x} v\left(Y_{bxi}\right). \tag{3}$$

The expected contribution of the individual is then $\mathrm{E}\left[W_x\right] = \int_\Omega v(y)[s(x)f_s(y;x)$ $+b(x)f_b(y;x)]\mathrm{d}y = \lambda v(x)$, which is in accordance with Fisher's definition of reproductive value (Fisher, 1930), and in analogue with the results of Engen et al. (2009) for the discrete age structured model.

To simplify notation, we write the expectation and variance of $v(Y_{sx})$ as $\mu_{vs}(x)$ and $\sigma^2_{vs}(x)$, respectively. This expectation is given by $\mu_{vs}(x) = \int_\Omega v(y)f_s(y;x)\mathrm{d}y$, and the variance is given by $\sigma^2_{vs}(x) = \mu^*_{vs}(x) - \mu^2_{vs}(x)$, where $\mu^*_{vs}(x) = \int_\Omega v^2(y)f_s(y;x)\mathrm{d}y$.

Similarly, we write the expectation and variance of $v(Y_{bxi})$ (for $i = 1, ..., B_x$) as $\mu_{vb}(x)$ and $\sigma^2_{vb}(x)$, respectively. Using this, the variance of W_x is given by

$$\begin{aligned}\mathrm{Var}\left(W_x\right) =&\sigma^2_d(x) = \mathrm{E}\left[\mathrm{Var}\left(W_x|S_x, B_x\right)\right] + \mathrm{Var}\left(\mathrm{E}\left[W_x|S_x, B_x\right]\right)\\ =&s(x)\sigma^2_{vs}(x) + b(x)\sigma^2_{vb}(x) + \mu^2_{vs}(x)\sigma^2_S(x) + \mu^2_{vb}(x)\sigma^2_B(x) + 2\sigma^2_{BS}(x)\mu_{vs}(x)\mu_{vb}(x),\end{aligned} \tag{4}$$

where $\sigma^2_S(x) = s(x)[1 - s(x)]$. Assuming that the contributions of different individuals are independent, the variance of next year's total reproductive value is $\sigma^2_V = \int_\Omega \sigma^2_d(x)\mathrm{d}n(x)$, corresponding to the sum over all individuals currently in the population. Using the approximation $\mathrm{d}n(x) \approx Nu(x)\mathrm{d}x \approx Vu(x)\mathrm{d}x$ we see that σ^2_V is proportional to V. The demographic variance, which in the absence of environmental noise is defined as σ^2_V/V in accordance with equation (2), is consequently given by

$$\sigma^2_d \approx \frac{\sigma^2_V}{V} = \int_\Omega u(x)\sigma^2_d(x)\mathrm{d}x. \tag{5}$$

This is the continuous analogue to the demographic variance of an age structured population (Engen et al., 2009). The formula shows that if an individual is drawn at random from the population, σ^2_d is the expected variance of its contribution to the total reproductive value the next year.

As an example, consider a population structured according to a continuous state variable such as body mass, living in a constant environment. We assume that both survival and fecundity are functions of this state (fig. 4A). There is no heritability, and the body mass of offspring follows a normal distribution (truncated at zero). Next year's body mass of a surviving individual is also normally distributed, but includes a growth term in the mean that depends on the current body mass x, and levels off as x increases so that for larger individuals the change in body mass is approximately random. The resulting mean projection function surface, showing the expected contribution from individuals in different states to next year's population, is shown in figure 4B. By numerical calculations (Appendix) for this example, we find the expected growth rate $\lambda \approx 1.007$ and demographic variance $\sigma_d^2 \approx 0.82$, assuming Poisson distributed number of offspring and no covariance between survival and reproduction. The stable distribution $u(x)$ and reproductive value function $v(x)$ are shown in figure 4C. We performed simulations of the diffusion approximation for this model, using the calculated values of λ and σ_d^2 (with $\sigma_e^2 = 0$) to find the infinitesimal mean and variance (given in Methods). These simulations were compared to simulations of the full structured population dynamics (fig. 4D), demonstrating that the diffusion approximation is fairly accurate for this model.

Environmental stochasticity alone

We now assume that the population is large enough to ignore demographic stochasticity. The environmental variable is then the only stochastic element in the model, and we denote it by a capital Z. This variable, which is a parameter in the dynamic model in a given year, will take a new value $Z = z$ each year according to the distribution $f(z)$. To find the environmental variance expressed by the vital parameters, we first consider the contribution of an individual with state x to the total reproductive value the next year,

$$w(x, Z) = \int_\Omega v(y) k(y, x, Z) \mathrm{d}y, \tag{6}$$

where $k(y, x, Z)$ is the projection function associated with the stochastic environmental variable Z, and is stochastic between years. Next year's total reproductive value is given by $\int_\Omega w(x, Z) \mathrm{d}n(x)$. Again, using the approximation $n(x) \approx V u(x)$ together with equation (2), the environmental variance is given by

$$\sigma_e^2 \approx \frac{\sigma_V^2}{V^2} \approx \frac{1}{N^2} \operatorname{Var}\left(\int_\Omega w(x,Z) N u(x)\,\mathrm{d}x \right)$$
$$= \int_\Omega \int_\Omega u(x) u(y) c(x,y) \mathrm{d}x \mathrm{d}y, \tag{7}$$

where $c(x,y) = \operatorname{Cov}(w(x,Z), w(y,Z))$. This formula is in analogue with the environmental variance for age structured populations (Engen et al., 2009). It shows that the environmental variance can also be described as the expected covariance of the contributions of two randomly selected individuals from the population. The covariances entering equation (7) may be difficult to find, both analytically and numerically. However, in appendix A describing numerical methods, we demonstrate that by using a first order Taylor approximation the environmental variance can be approximated by the variance in the population growth rate $\lambda(Z)$ with respect to environment, simplifying the numerical calculation of this parameter.

To evaluate the accuracy of the parameters in this model, we again consider a population which is structured according to a continuous trait, this time with no demographic stochasticity. We assume that the environment is discrete uniformly distributed from $z = -0.5$ to $z = 0.5$, with 100 possible values. In this example the environmental variable can only affect the survival probability and fecundity, as shown in figure 5A. The mean projection function surface over all environments (fig. 5B) is similar to the previous example. The expected growth rate is $\lambda \approx 1.024$, and the environmental variance is $\sigma_e^2 \approx 0.038$. These values were used to specify the infinitesimal mean and variance of the diffusion approximation (defined in Methods). Comparison of results from simulation of the diffusion process to simulations of the full structured model (fig. 5D), confirm that the parameters of this model describe the population dynamics with good accuracy.

Demographic and environmental stochasticity together

When the population dynamics are influenced by both demographic and environmental stochasticity at the same time, the variance of an individual contribution, as well as the total variance in next year's total reproductive value, can be decomposed to a demographic and environmental component (Engen et al., 2009). Because of Jensen's inequality the values of the vital parameters in the mean environment are generally not the same as their mean values with respect to environment (Ruel and Ayres, 1999). Therefore, we cannot find the demographic variance by setting the environmental variable equal to its mean and use equation (5). Instead, we must calculate the mean vital parameter functions first. The covariances entering the environmental variance must also be redefined when both types of stochasticity occur.

The variance of the individual contribution W_x to next year's total reproductive value is now given by $\mathrm{Var}(W_x) = \mathrm{E}\left[\mathrm{Var}\left(W_x|Z\right)\right] + \mathrm{Var}\left(\mathrm{E}\left[W_x|Z\right]\right)$. The first term corresponds to the demographic component $\mathrm{E}\left[\sigma_d^2(x,Z)\right]$, which is found by replacing all vital parameter functions in equation (4) with their expectations with respect to the environmental variable. For instance, the expected survival probability function is given by $\mathrm{E}[s(x,Z)] = \int s(x,z)f(z)\mathrm{d}z$ (if the probability distribution $f(z)$ of the environmental variable is discrete, the integral should be replaced by a sum). The second term of the variance in W_x is the environmental component of the variance in the individual contribution.

The variance in next year's total reproductive value is given by $\sigma_V^2 = \mathrm{E}\left[\mathrm{Var}\left(V + \Delta V|Z\right)\right] + \mathrm{Var}\left(\mathrm{E}\left[V + \Delta V|Z\right]\right)$. The first term is the demographic component, describing the expected within-year variation, and is given by

$$\int_\Omega \mathrm{E}\left[\sigma_d^2(x,Z)\right]\mathrm{d}n(x) \approx V\int_\Omega u(x)\mathrm{E}\left[\sigma_d^2(x,Z)\right]\mathrm{d}x = \sigma_d^2 V, \tag{8}$$

which defines the demographic variance σ_d^2 of this model. The main difference between this case and the case of demographic stochasticity alone is that the vital rates occuring in equation (4) are now replaced by their expectations with respect to environment. In addition, the functions $u(x)$ and $v(x)$ are found from the overall mean (within and between-year) projection function.

The second term of the variance in next year's total reproductive value is the environmental component, describing the between-year variation of within-year expectations. It is given by

$$\operatorname{Var}\left(\int_\Omega Vu(x)\mathrm{E}\left[W_x|Z\right]\mathrm{d}x\right) = V^2\int_\Omega\int_\Omega u(x)u(y)c(x,y)\mathrm{d}x\mathrm{d}y = \sigma_e^2V^2, \tag{9}$$

where $c(x,y) = \operatorname{Cov}\left(\mathrm{E}\left[W_x|Z\right], \mathrm{E}\left[W_y|Z\right]\right) = \operatorname{Cov}\left(w(x,Z), w(y,Z)\right)$. Thus, the environmental variance σ_e^2 of this model is given by essentially the same formula as (7), but the covariances of the individual contributions are now replaced with the covariances of the expected contributions.

To evaluate the accuracy of this model and demonstrate how it can be used to estimate extinction risk, we consider a new example of population structured according to a continuously distributed phenotypic trait. The number of offspring per individual is Poisson distributed, and transition of adults and offspring to new states were modeled as in the example with only demographic stochasticity (fig. 4). The environmental variable is the same as in the previous example (fig. 5), and the survival probability $s(x,z)$ and fecundity $b(x,z)$ are shown in figure 6A, for $z = -0.5$, $z = 0$ and $z = 0.5$. Using the numerical methods given in appendix A we find the expected growth rate $\lambda \approx 0.99$, environmental variance $\sigma_e^2 \approx 0.007$, and demographic variance $\sigma_d^2 \approx 0.83$, which were used to define the infinitesimal mean and variance of the diffusion approximation described in Methods. We performed simulations of the full structured model as well as of the diffusion approximation, and comparison of the simulation quantiles (fig. 6B) indicated that the model parameters are accurate. Density estimates for the time to extinction (fig. 6C), as well as the cumulative probability of extinction (fig. 6D) were estimated from the same realizations. Thus, using the diffusion approximation with the calculated parameters from the model we can predict extinction risk with good accuracy.

Discussion

We have derived the demographic (8) and environmental variance (9) for a continuously structured population, demonstrated that these parameters accurately describe the population dynamics (figs. 4-6), and shown how they can be used to evaluate extinction risk (fig. 6). This model extends the theory of integral projection modeling to finite populations by including demographic stochasticity. Although we make several simplifying assumptions (no density dependence, small fluctuations, female or asexual population, and no demographic covariance between individuals) this modeling framework can be used to study many ecological and evolutionary questions relating to structured populations.

Our examples (figs. 4-6) were based on a population structured according to body mass, but many other types of continuous structure exist. Individual state may represent any morphological trait, as well as external properties such as spatial location or resource availability. The resulting population structure will often be continuous, and integral projection modeling is then a natural choice as modeling tool. Due to the generality of this model it can easily be extended to include discrete stages in addition to continuous structure, as described by Ellner and Rees (2006) for deterministic IPMs.

One of the largest advantages with the method presented here compared to pure simulation studies is that we achieve a substantial reduction in complexity. The one-dimensional diffusion approximation shows us that the dynamics of a complex structured model can be accurately described by only three parameters; the expected growth rate λ, the demographic variance σ_d^2 and the environmental variance σ_e^2. Thus, provided that the assumptions of density-independence and small fluctuations hold, these parameters summarize all the important aspects of the life history (including stochastic properties) of a structured population. In empirical studies, λ, σ_d^2 and σ_e^2 are the parameters we should strive to estimate from data when we want to understand and predict the dynamics. In addition, because we separate the demographic and environmental variance of the population growth, we can evaluate at which population size demographic stochasticity starts to contribute significantly to extinction risk, and whether the stochastic growth rate can fall below zero (a critical population size). Finally, the analytical approach enables us to evaluate at which state values individuals contribute more (or less) to the population growth, which could provide valuable insights for making efficient management decisions.

Recently, the question of how individual or demographic heterogeneity affects population dynamics has received much interest in ecological literature (Conner and White, 1999; Kendall and Fox, 2002; Vindenes et al., 2008; Tuljapurkar et al., 2009; Caswell, 2009). Many mechanisms exist that can create such heterogeneity in natural populations (Kendall and Fox, 2002; Vindenes et al., 2008). These include spatial heterogeneity in the environment combined with limited movement of individuals (e.g. plants; Beckage and Clark, 2003) or with territoriality (e.g. oystercatchers (*Haematopus ostralegus*); van de Pol et al., 2006), social rank and grouping of individuals (e.g. lions (*Panthera leo*); Packer et al., 2005), and also genetic causes (Roff, 1996; Kruuk et al., 2008). Temporal fluctuations in the environment can create cohort effects (Beckerman et al., 2003), and interact with maternal effects (Mousseau and Fox, 1998), in both cases giving rise to individual heterogeneity. For instance, differential allocation of resources by parents may produce long-lasting differences within clutches, that may be enhanced when food availability is low (Smiseth et al., 2003). Although it seems likely that most types of individual heterogeneity will produce continuous types of population structures, analytical approaches to this question have so far been based on matrix modeling (e.g., Vindenes et al., 2008; Tuljapurkar et al., 2009; Caswell, 2009). The modeling framework given here can provide an even more natural choice to study effects of heterogeneity on population dynamics, that may be useful for empirical investigation of such effects in natural populations.

Integral projection modeling has many advantages compared to matrix models. It is a more general modeling class, with discrete structure as a special case. The largest advantage is probably that fewer parameters need to be estimated from data. As the vital parameters are assumed to be smooth functions of the structuring variable(s), they can be estimated by standard regression procedures (Rees and Ellner, 2009). Although such estimation is not always straightforward, data can be used more efficiently than in matrix models, in which the parameters of each stage are usually estimated independently (Easterling et al., 2000). In addition, the number of stages in a matrix model may be limited by the uncertainty of estimation. IPMs may therefore especially perform better for small populations where the amount of data is limited (Ramula et al., 2009). However, to evaluate extinction risk and develop management strategies for such small populations it is also vital to consider effects of demographic stochasticity, which this modeling framework enables.

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Table 1: Parameters and main results from the discrete age structured model by Engen *et al.* (2009) and the continuously structured model (see main text for definition of parameters). In the age structured case, $\tau_{eij} = \mathrm{Cov}(\mathrm{E}[W_i|Z], \mathrm{E}[W_j|Z])$, where i and j refer to age classes.

	Discrete age model	**Continuous model**
Total reproductive value V	$\sum_i n_i v_i$	$\int_\Omega v(x)\mathrm{d}n(x)$
Individual contribution to $V + \Delta V$	$W_i = S_i v_{i+1} + B_i v_1$	$W(x) = S_x v(Y_{sx}) + \sum_{i=1}^{B_x} v(Y_{bxi})$
Demographic variance σ_d^2	$\sum_i u_i \mathrm{E}\left[\sigma_{di}^2(Z)\right]$	$\int_\Omega u(x)\mathrm{E}\left[\sigma_d^2(x, Z)\right]\mathrm{d}x$
Environmental variance σ_e^2	$\sum_{ij} u_i u_j \tau_{eij}$	$\int_\Omega \int_\Omega u(x)u(y)c(x, y)\mathrm{d}x\mathrm{d}y$

Figure legends

Figure 1.Illustration of how the realized distribution of a continuous state such as body size might change over time, in a small population with both demographic and environmental stochasticity present. Although the underlying state variable is continuous, the number of individuals, and therefore the realized state distribution, are discrete.

Figure 2. Illustration of how individual state x can change over time, when the state represents body mass (A and B) and when state represents the amount of a resource available (C and D). A: Stochastic growth of three individuals starting with different body mass and at different times. For example, the dashed and dotted lines may represent offspring of the individual represented by the solid line. B: Seven realizations of stochastic growth of an individual, starting at the same initial body mass. C: Change in the amount of resource (e.g., nitrogen for plants) over time for three individuals, starting at different times and with different initial values, representing parent and offspring as in A. D: Seven realizations of change in the amount of resource for an individual, starting at the same initial value.

Figure 3. Illustration of how survival probability might change as function of state in two different environmental conditions, represented by solid and dashed lines. An individual with state x_A experiences a slight decrease in survival probability with change in environmental condition (from solid to dashed line), whereas an individual with state x_B experiences an increase in survival probability with the same change in the environmental condition.

Figure 4. Example with only demographic stochasticity ($\sigma_e^2 = 0$). Expected growth rate

is $\lambda \approx 1.007$ and demographic variance is $\sigma_d^2 \approx 0.82$. Offspring numbers are Poisson distributed, with zero covariance between survival and reproduction. Offspring body mass is normally distributed with mean 10 and standard deviation 1. Next year's body mass of an adult with current mass x is normally distributed with mean $x + 5e^{-0.2x}$ and standard deviation 1, implying larger growth rate for small individuals. A: Survival probability $s(x)$ and fecundity $b(x)$. B: Contours of the projection function $k(y, x)$. C: Stable state distribution $u(x)$ and reproductive value function $v(x)$. D: Quantiles based on 10000 simulated realizations of the full structured dynamics (solid lines), and 10000 realizations of a diffusion approximation (dashed lines) using the calculated values of λ and σ_d^2.

Figure 5. Example with only environmental stochasticity ($\sigma_d^2 = 0$). Expected growth rate is $\lambda \approx 1.024$ and environmental variance is $\sigma_e^2 \approx 0.038$. There are 100 possible values of the environmental variable z, ranging from -0.5 to 0.5 and equally likely to occur. The environment can only affect survival probability and fecundity. A: Survival probability $s(x, z)$ shown for three sample environments. B: Fecundity $b(x, z)$ shown for three sample environments. C: Contours of the mean projection function $k(y, x)$. D: Simulation quantiles from 10000 simulated realizations of the full structured model (solid lines), and 10000 realizations of a diffusion approximation (dashed lines) of the population dynamics, using the calculated values of λ and σ_e^2.

Figure 6. Example with both demographic and environmental stochasticity. Expected growth rate is $\lambda \approx 0.99$, environmental variance is $\sigma_e^2 \approx 0.007$, and demographic variance is $\sigma_d^2 \approx 0.83$. All parameters except $s(x, z)$ and $b(x, z)$ are as described in figs. 3 and 4. A: Survival probability $s(x, z)$ and fecundity $b(x, z)$, for $z_1 = -.5$ (lowest curves), $z_2 = 0$ and $z_3 = 0.5$ (highest curves). B: Simulation quantiles from 10000 realizations

from the diffusion process (dashed lines) and 10000 realizations of the full structured model (solid lines). C: Density estimates of the times to extinction, from the same realizations of the diffusion (dashed line) and full structured model (solid line). D: Cumulative probability of extinction estimated from the same realizations of the diffusion (dashed line) and the full structured model (solid line).

Figure 1:

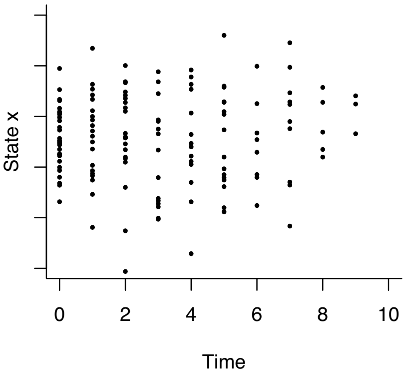


Figure 2:

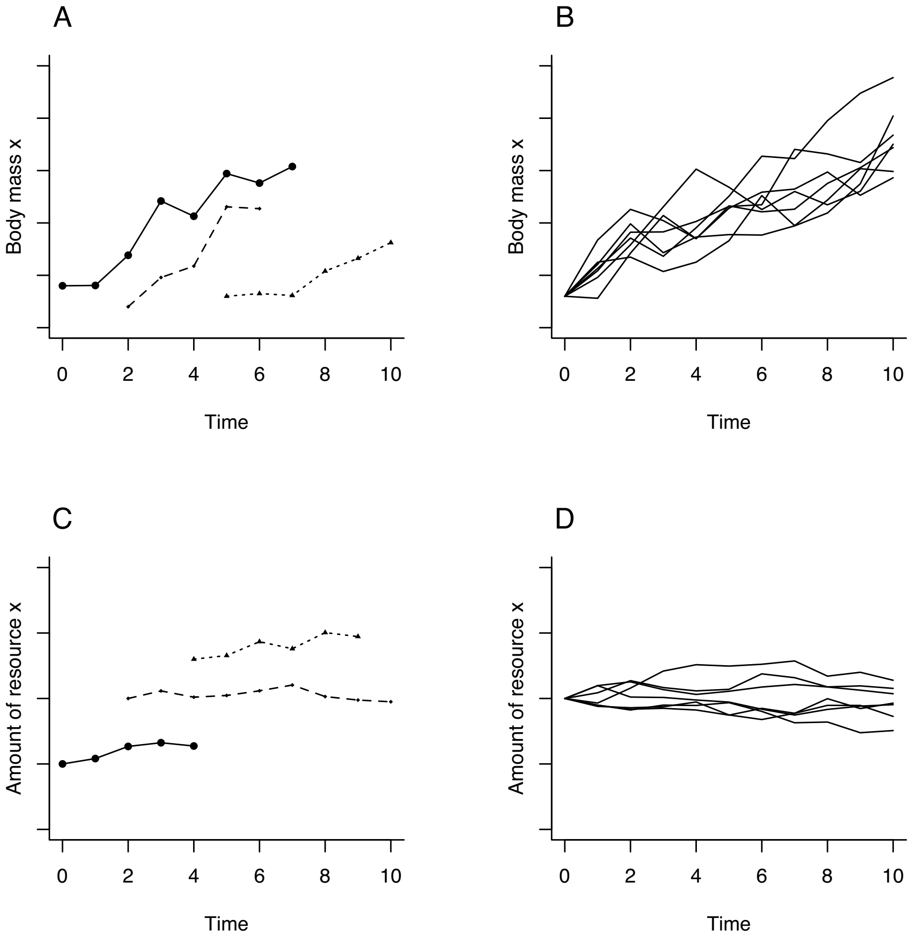

A
Body mass x
Time
0
2
4
6
8
10
B
Body mass x
Time
0
2
4
6
8
10
C
Amount of resource x
Time
0
2
4
6
8
10
D
Amount of resource x
Time
0
2
4
6
8
10

Figure 3:

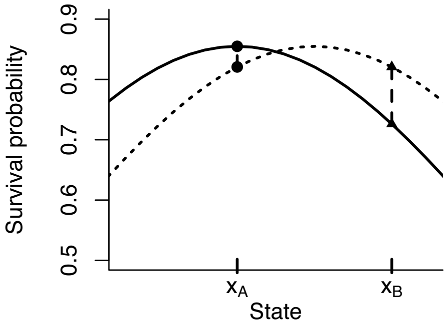


Figure 4:

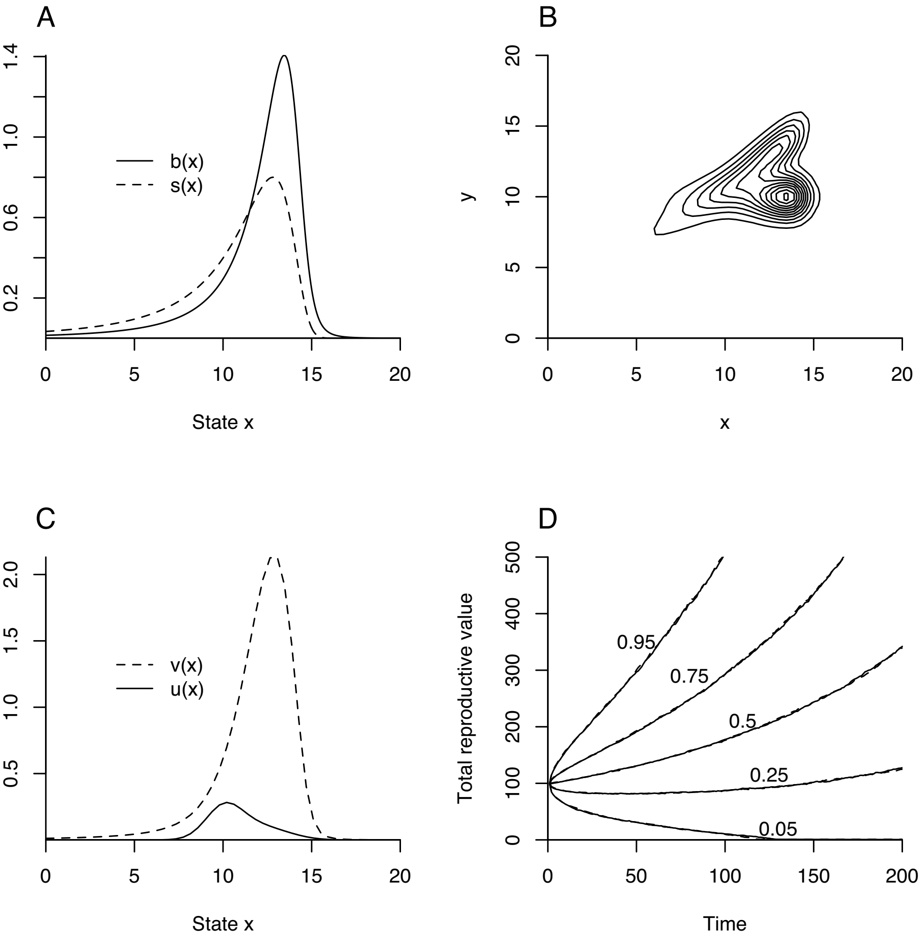

A
1.4
1.0
0.6
0.2
b(x)
s(x)
0
5
10
15
20
State x
B
20
15
10
5
0
y
0
5
10
15
20
x
C
2.0
1.5
1.0
0.5
v(x)
u(x)
0
5
10
15
20
State x
D
500
400
300
200
100
0
Total reproductive value
0.95
0.75
0.5
0.25
0.05
0
50
100
150
200
Time

Figure 5:

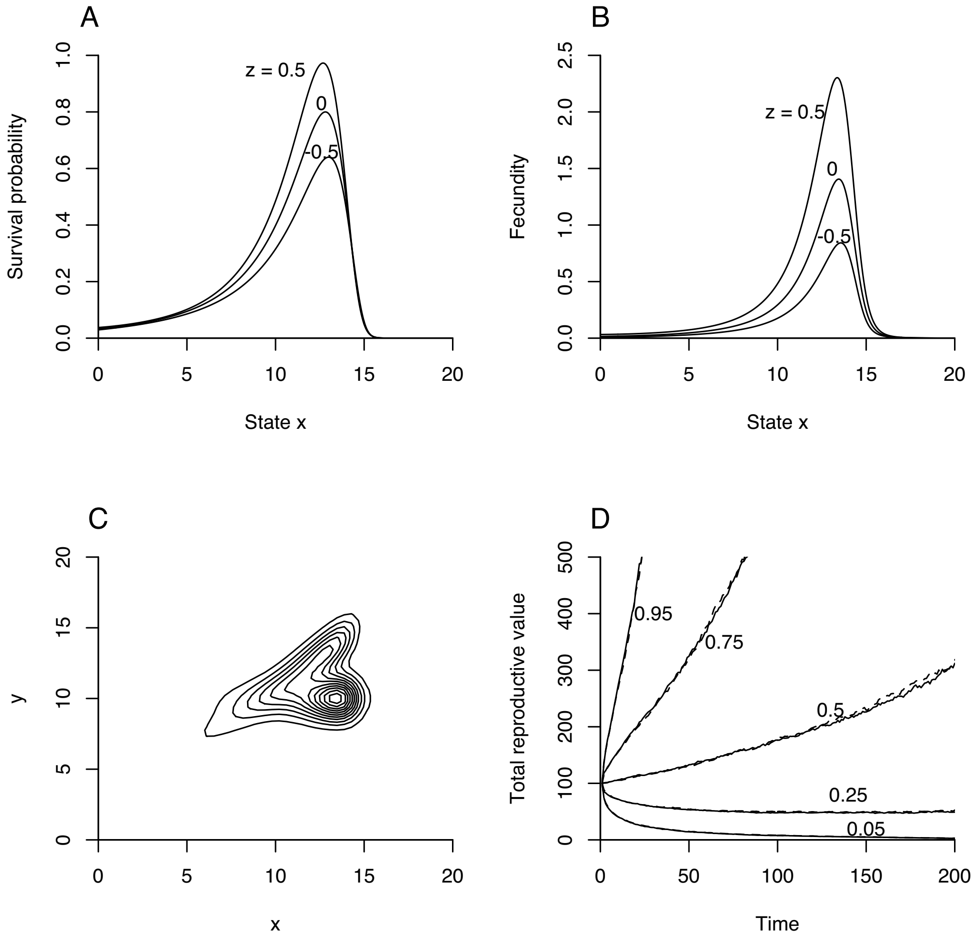
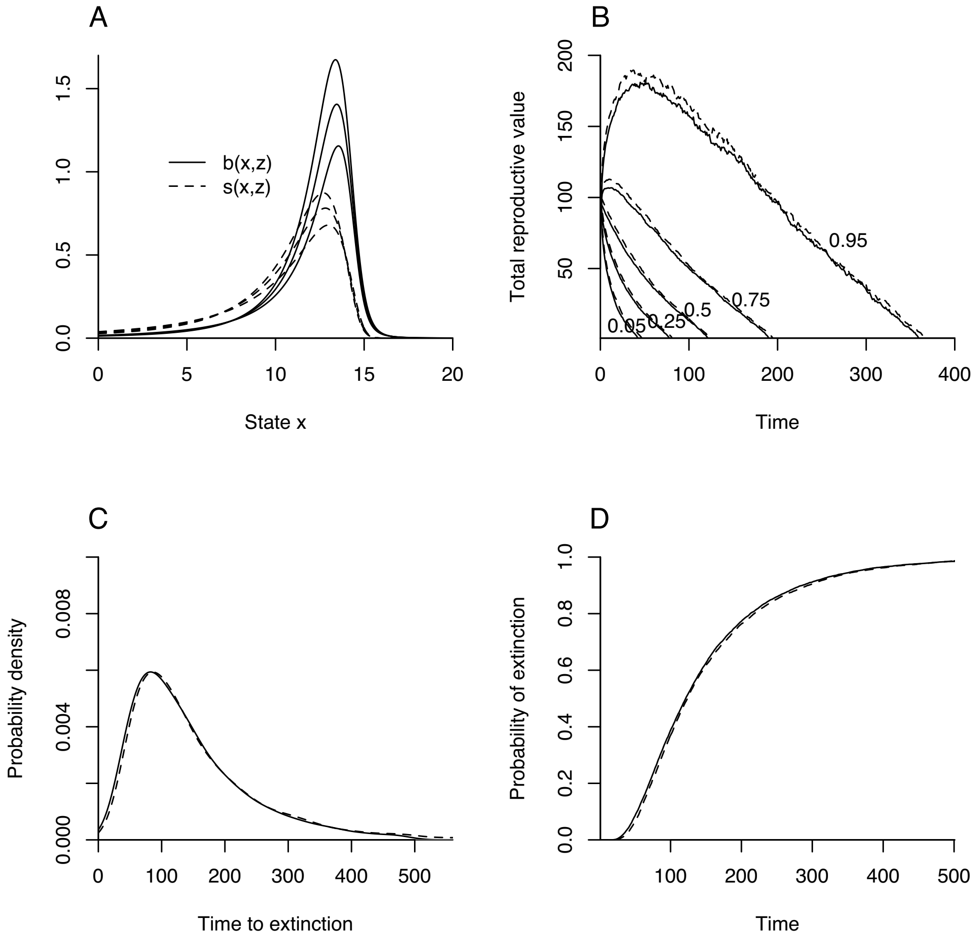

A
Survival probability
0.0
0.2
0.4
0.6
0.8
1.0
z = 0.5
0
-0.5
0
5
10
15
20
State x
B
Fecundity
0.0
0.5
1.0
1.5
2.0
2.5
z = 0.5
0
-0.5
0
5
10
15
20
State x
C
y
0
5
10
15
20
0
5
10
15
20
x
D
Total reproductive value
0
100
200
300
400
500
0.95
0.75
0.5
0.25
0.05
0
50
100
150
200
Time

Figure 6:


A
b(x,z)
s(x,z)
0.0
0.5
1.0
1.5
0
5
10
15
20
State x
B
Total reproductive value
50
100
150
200
0.95
0.75
0.5
0.25
0.05
0
100
200
300
400
Time
C
Probability density
0.000
0.004
0.008
0
100
200
300
400
500
Time to extinction
D
Probability of extinction
0.0
0.2
0.4
0.6
0.8
1.0
100
200
300
400
500
Time

Appendix: Numerical calculation of model parameters

Here we describe methods of numerical calculation of the parameters given in the main text. As supplementary material we also provide the programming script (Rcode.txt) that we used for numerical calculations as well as simulations, with the software R (R Development Core Team, 2009). The approach used here is essentially a second degree Newton-Cotes quadrature, which works well for our purposes but is just one of many possible methods for numerical integration.

The main idea behind the numerical calculation is to discretize the model, by dividing the state space Ω into a number of small intervals of length Δx. Let $\mathbf{x}$ denote the vector of the discretized state space. The accuracy of parameter values will increase as the interval Δx is made smaller. Similarly, for the cases with non-constant environment let $\mathbf{z}$ denote the vector of possible values for the environmental variable Z. The probability of choosing element z_i a given year is $P(Z = z_i)$ (we have $\sum_i P(Z = z_i) = 1$). Letting $k(y, x, z_i)$ denote the projection function in environment z_i, the mean projection function across environments is given by $k(y, x) = \sum_i k(y, x, z_i)P(Z = z_i)$. The mean survival probability function across environments is given by $\bar{s}(x) = \sum_i s(x, z_i)P(Z = z_i)$, and similar mean functions can be found for all other vital parameters (fecundity $b(x, z)$, variance in fecundity $\sigma^2_B(x, z)$, the covariance $\sigma^2_{BS}(x, z)$ the transition functions $f_s(y; x, z)$ and $f_b(y; x, z)$).

Expected growth rate, stable distribution and reproductive value

The growth rate λ, stable distribution $u(x)$ and reproductive value function $v(x)$, are found by discretizing the mean projection function $k(y, x)$ to obtain a (large) projection matrix $\mathbf{K}$ (Ellner and Rees, 2006). Then the discrete, deterministic model $\mathbf{n}_{t+1} = \mathbf{K}\mathbf{n}_t$ can be iterated, where $\mathbf{n}_t$ is the population vector giving the (expected) number of individuals in each state interval at time t. The initial population vector can be arbitrarily chosen, but must contain at least one reproducing individual. After some time steps, when the stable distribution is reached, the growth rate is given by $\lambda \approx \frac{N_{t+1}}{N_t}$, where N_t is the total population size at time t, and the stable distribution vector is given by $\mathbf{u} \approx \frac{\mathbf{n}_t}{N_t}$ (Caswell, 2001). To calculate the reproductive value function $v(x)$, we first iterate the transposed model $\mathbf{n}_{t+1} = \mathbf{K}^T\mathbf{n}_t$. The reproductive value vector $\mathbf{v}$ is then the stable distribution of this transposed model (Caswell, 2001), scaled so that $\mathbf{vu} = 1$. Based on interpolation of the data points in $\mathbf{u}$ and $\mathbf{v}$ and appropriate scaling, approximations for the functions $u(x)$ and $v(x)$ are obtained. Alternatively, λ can be found as the dominant eigenvalue of $\mathbf{K}$, and $\mathbf{u}$ and $\mathbf{v}$ are the corresponding right and left eigenvectors, with the same scaling as above (Caswell, 2001). Let $\hat{\lambda}$, $\hat{u}(x)$ and $\hat{v}(x)$ denote the estimated values of λ, $u(x)$ and $v(x)$. Once these are found, they can be used further in the estimation of the demographic and environmental variance.

Demographic variance

With no environmental stochasticity, the demographic variance is given by equation (5), and when both types of stochasticity are included it is given by equation (8). In latter case, we must use the mean vital parameter functions over environments such as $\bar{s}(x)$ (see first paragraph). To estimate the demographic variance, we must first find the expectation and variance of the stochastic variables $v(Y_{sx})$ and $v(Y_{bx})$ (next year's reproductive value of an individual of state x and its offspring, respectively), for each element of the state vector. For an element x_i the expectation of $v(Y_{sx_i})$ is found as $\hat{\mu}_{vs_i} = \sum_j \bar{f}_s(x_j; x_i)\hat{v}(x_j)\Delta x$. Letting $\hat{\mu}^*_{vs_i} = \sum_j \bar{f}_s(x_j; x_i)\hat{v}^2(x_j)\Delta x$, the variance is given by $\hat{\sigma}^2_{vs_i} = \hat{\mu}^*_{vs_i} - \hat{\mu}^2_{vs_i}$. Similar estimates are found for the mean and variance of $v(Y_{bx})$. Finally, the estimate of the demographic variance is found by summing up all the elements entering the formula,

$$\hat{\sigma}_d^2 = \sum_j \hat{u}(x_j) \left[\bar{s}(x_j)\hat{\sigma}_{vs_i}^2 + \bar{b}(x_j)\hat{\sigma}_{vb_i}^2 + \hat{\mu}_{vs_j}^2 \bar{s}(x_j)(1 - \bar{s}(x_j)) + \hat{\mu}_{vb_j}^2 \bar{\sigma}_B^2(x_j) + 2\hat{\mu}_{vs_j}\hat{\mu}_{vb_j}\bar{\sigma}_{BS}^2(x_j)\right] \Delta x.$$

For the simpler case of a constant environment, replace $\bar{s}(x_j)$ by $s(x_j)$ etc. in the above formula.

Environmental variance

To calculate the environmental variance (equations 7 and 9), we first show that this parameter is approximately equal to the variance of the growth rate $\lambda(Z)$ with respect to the environmental variable Z. Let $k(y, x)$ be the mean projection function across environments as before, associated with the overall mean growth rate λ, the stable distribution $u(x)$ and the reproductive value $v(x)$. A first order Taylor approximation of $\lambda(Z)$ around λ gives

$$\begin{aligned}
\lambda(Z) &\approx \lambda + \int\int \frac{\partial\lambda}{\partial k(y,x)}[k(y,x,Z) - k(y,x)]\mathrm{d}y\mathrm{d}x \\
&= \int\int v(y)u(x)k(y,x,Z)\mathrm{d}y\mathrm{d}x \\
&= \int u(x)\mathrm{E}\left[W_x|Z\right]\mathrm{d}x.
\end{aligned}$$

This approximation works well as long as the environment shows small fluctuations, so that effects of the environment on the stable distribution and reproductive value function can be ignored. By using the Taylor approximation, the variance of $\lambda(Z)$ with respect to environment is given by

$$\begin{aligned}
\mathrm{Var}\left(\lambda(Z)\right) &\approx \mathrm{Var}\left(\int u(x)\mathrm{E}\left[W_x|Z\right]\mathrm{d}x\right) \\
&= \int\int u(x)u(y)c(x,y)\mathrm{d}y\mathrm{d}x,
\end{aligned}$$

where $c(x, y) = \mathrm{Cov}\left(\mathrm{E}\left[W_x|Z\right], \mathrm{E}\left[W_y|Z\right]\right)$. Thus, we see that the variance of $\lambda(Z)$ corresponds approximately to the environmental variance derived in the main text (equation 8).

To find this variance numerically, we first find the growth rates $\lambda(z_i)$ for each value of the environmental vector, using the methods given above for each projection function $k(y, x, z_i)$. The numerical approximation of the environmental variance is then given by

$$\hat{\sigma}_e^2 \approx \sum_i (\lambda(z_i) - \hat{\lambda})^2 P(Z = z_i).$$

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Paper III

Paper IV

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Effects of climate change and variability on population dynamics in a long-lived shorebird

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Abstract. Climate change affects both the mean and variability of climatic variables, but their relative impact on the dynamics of populations is still largely unexplored. Based on a long-term study of the demography of a declining Eurasian Oystercatcher (*Haematopus ostralegus*) population, we quantify the effect of changes in mean and variance of winter temperature on different vital rates across the life cycle. Subsequently, we quantify, using stochastic stage-structured models, how changes in the mean and variance of this environmental variable affect important characteristics of the future population dynamics, such as the time to extinction. Local mean winter temperature is predicted to strongly increase, and we show that this is likely to increase the population's persistence time via its positive effects on adult survival that outweigh the negative effects that higher temperatures have on fecundity. Interannual variation in winter temperature is predicted to decrease, which is also likely to increase persistence time via its positive effects on adult survival that outweigh the negative effects that lower temperature variability has on fecundity. Overall, a 0.1°C change in mean temperature is predicted to alter median time to extinction by 1.5 times as many years as would a 0.1°C change in the standard deviation in temperature, suggesting that the dynamics of oystercatchers are more sensitive to changes in the mean than in the interannual variability of this climatic variable. Moreover, as climate models predict larger changes in the mean than in the standard deviation of local winter temperature, the effects of future climatic variability on this population's time to extinction are expected to be overwhelmed by the effects of changes in climatic means. We discuss the mechanisms by which climatic variability can either increase or decrease population viability and how this might depend both on species' life histories and on the vital rates affected. This study illustrates that, for making reliable inferences about population consequences in species in which life history changes with age or stage, it is crucial to investigate the impact of climate change on vital rates across the entire life cycle. Disturbingly, such data are unavailable for most species of conservation concern.

Key words: age structure; climatic variability; density dependence; environmental stochasticity; Eurasian Oystercatcher; Haematopus ostralegus; *nonlinearity; population viability analysis; Schiermonnikoog, The Netherlands; stochastic population dynamics; time to extinction; winter temperature.*

INTRODUCTION

Currently, the global climate changes at a rate much faster than experienced over most of earth's history, and this change is expected to continue in the future (IPCC 2007). Although it is well established that climate change can strongly affect population dynamics (e.g., Sæther et al. 2000, Coulson et al. 2001, McLaughlin et al. 2002), the general mechanisms causing climate-induced population change are still poorly understood. Four major unresolved questions are: (1) Does climate change mainly affect population dynamics through its effects on survival or fecundity, and how does this vary between species and environments (Lack 1954, Sæther et al. 2004)? (2) How important is the contribution of climate change to population fluctuations in comparison to other stochastic and deterministic processes (Lande et al. 2003)? (3) What is the relative importance of changes in the mean and variability of climatic drivers (Boyce et al. 2006, Morris et al. 2008)? (4) Does increased interannual climatic variability typically reduce population viability as predicted by classical stochastic population theory (Lewontin and Cohen 1969, Lande and Orzack 1988), or can it also improve population viability as more recently put forward (Drake 2005,

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Boyce et al. 2006, Morris et al. 2008)? Answering these questions and identifying the mechanisms involved are crucial for making general predictions about the population dynamical consequences of climate change and for identifying the species that are most at risk.

Most climate change studies either directly relate variation in climatic variables to changes in population size (e.g., McLaughlin et al. 2002, Drake 2005, Tyler et al. 2008) or examine how climate affects only one or a few vital rates (e.g., McMahon and Burton 2005, Nevoux et al. 2008, Votier et al. 2008). However, these approaches ignore the demographic mechanisms causing changes in population size. For example, does climate mainly act via an effect on fecundity or on survival? If we are to understand how climate change influences the population dynamics, we need to consider how different climatic variables affect the mean and variability of all major vital rates and then in turn how this will give rise to population changes (as advocated by Sillett et al. 2000, Ådahl et al. 2006, Morris et al. 2008, Visser 2008).

A demographic approach to the study of climate-induced changes of the population dynamics is a challenging task. First, it necessitates separation of deterministic from stochastic influences on population dynamics. This separation requires decomposition of how much of the temporal variation in, and covariation between, vital rates is explained by climatic variables, density dependence, demographic stochasticity, and (residual) environmental stochasticity (Lebreton 1990, Rotella et al. 1996, Dennis and Otten 2000). Furthermore, climatic responses of vital rates themselves may be density dependent (Turchin 1995, Coulson et al. 2001). Second, it requires identification of the major sources of age and stage structure in vital rates, as both age and stage structure can induce lagged responses to climatic variables (Lande et al. 2002). Third, climate change can manifest itself as changes in both the mean and variance of climatic variables (Easterling et al. 2001), which necessitates evaluation of their separate effects on each vital rate (Lande et al. 2003). Moreover, it requires examination of possible nonlinear dependencies between climatic variables and vital rates, as the shape of this relationship determines how increased environmental variability affects the means of vital rates (e.g., Ruel and Ayres 1999, Boyce et al. 2006). Fourth, quantifying all the abovementioned characteristics for vital rates over the entire life cycle requires detailed individual-based data. Additionally, such data must span long periods (typically decades for birds and mammals) in order to reliably decompose the temporal variance of the population process (Lande et al. 2003, Altwegg et al. 2006).

Recently, there is an increasing interest in the role of changes in climatic variability and the occurrence of catastrophic events (an extreme case of climatic variability; Boyce et al. 2006, Jentsch et al. 2007). Many studies have suggested that climatic variability can have important effects on population dynamics of a variety of animal and plant species (e.g., Sæther et al. 2000, Coulson et al. 2001, Green et al. 2003, Jenouvrier et al. 2003, Tews and Jeltsch 2007). However, to our knowledge no study has directly quantified the relative importance of changes in the mean versus changes in the interannual variability of climatic variables for population dynamics via their effect on each of the vital rates in the life cycle. Such a comparison is important, however, as it will help us to resolve the questions mentioned in the first paragraph.

Here we will investigate the impact of changes in the mean and variability of a major climatic variable (winter temperature) on the vital rates and population dynamics of Eurasian Oystercatchers (*Haematopus ostralegus*). This long-lived shorebird exhibits clear age, stage, and spatial structure, as well as density dependence in vital rates. Locally, mean winter temperatures are expected to increase, while interannual temperature variability is expected to decrease (van de Hurk et al. 2006). Interestingly, changes in winter temperature are expected not only to affect multiple vital rates in this species, but also to do so in opposing ways. Increasing winter temperature is predicted to enhance survival in all age and stage classes, because in warm winters oystercatchers have little problem meeting their daily energy requirements, while this is problematic in cold winters (Camphuysen et al. 1996, Atkinson et al. 2003). In contrast, warm winter temperatures are expected to adversely affect fecundity indirectly, because oystercatchers' main prey species during breeding are less abundant after warm winters (Beukema 1992, Philippart et al. 2003, Lawrence and Soame 2004). Furthermore, the effects of decreased interannual temperature variability on vital rates have not yet been investigated. Consequently, there is no a priori expectation for the direction and magnitude of the population dynamical consequences of climate change in this strongly declining species.

Using 24 years of data from the wild and a stage-structured stochastic population model, we will disentangle the relative importance of changes in climatic mean and variability for population dynamics. We will do this by quantifying whether a small change in mean winter temperature of X°C results in larger or smaller changes in time to extinction than a X°C change in the standard deviation of temperature. By further investigating the climatic effects on each vital rate we will investigate whether population consequences of climate change in oystercatchers are mainly caused by climate effects on survival or reproduction. More specifically, if an increase of X°C increases persistence time with Y years, how much of this increase in Y is caused by temperature effects on survival and how much by effects on fecundity? Finally, we will discuss when climatic variability is expected to improve or reduce population viability and how this might depend on the life history of a species and on the vital rates affected. Our modeling framework is general and can be adapted to other

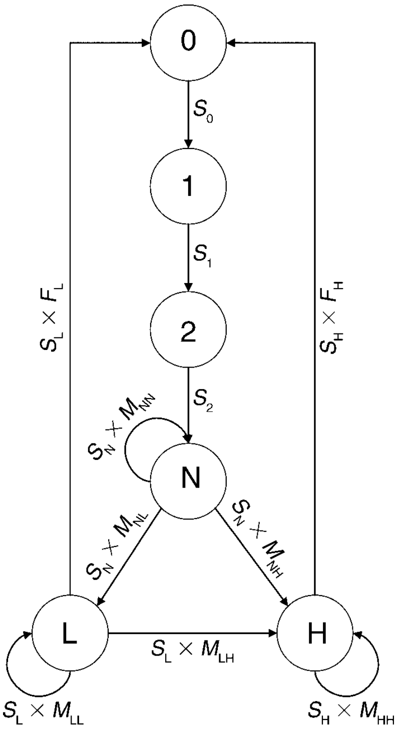

FIG. 1. Schematic view of the age-, stage- and spatially structured life cycle of the Eurasian Oystercatcher (*Haematopus ostralegus*) and the stage-dependent vital rates fecundity (*F*), survival (*S*), and movement probabilities between states (*M*). Six states are distinguished: 0, fledged offspring; 1, one-year-old juveniles; 2, two-year-old juveniles; N, adult nonbreeders; L, breeders in low-quality habitat; H, breeders in high-quality habitat. Note that $M_{NN} = 1 - M_{NL} - M_{NH}$, etc.

species with structured life cycles, provided that long-term individual-based data exist.

METHODS

Study species and population

Oystercatchers are long-lived monogamous shorebirds (>40 years), and their demography exhibits distinct age, stage, and spatial structure (e.g., van de Pol et al. 2007). Juveniles become sexually mature when they reach the age of three years; annual survival increases progressively from fledging to second year and remains approximately constant within adult stage classes. Due to the high site fidelity and despotic territorial system oystercatcher populations contain a surplus of adult nonbreeders that do not own a nesting territory; consequently delayed reproduction is common (age of first reproduction 3–12 years; Harris 1970, van de Pol et al. 2006). Oystercatcher populations typically exhibit a dichotomy in breeding habitat quality caused by permanent differences in the spatial organization of territories (Ens et al. 1992, Safriel et al. 1996). Some pairs have adjacent nesting and feeding territories, allowing them to take their chicks to the food, whereas other pairs have spatially separated nesting and feeding territories and are forced to spend much energy to bring every food item to their chicks (see Ens et al. 1992: Fig. 1). Consequently, adjacent territories consistently produce two to three times more offspring annually than split territories. Henceforth, adjacent and split territories are denoted high- and low-quality habitat, respectively (cf. Ens et al. 1992, Bruinzeel and van de Pol 2004). The six life stages (0, fledged offspring; 1, one-year-old juveniles; 2, two-year-old juveniles; N, adult nonbreeders; L, breeders in low-quality habitat; H, breeders in high-quality habitat) and the age, stage, and spatial structure of oystercatcher's vital rates fecundity (*F*), survival probability (*S*), and movement probability between stages (*M;* conditional on survival) are depicted in Fig. 1. Fecundity was defined as the number of fledglings (day 30 of age) a breeding pair produced in a year multiplied by 0.5 (reflecting a fledgling sex ratio of 0.5; Heg et al. 2000*a*).

From 1983 to 2007 we studied a breeding population of oystercatchers on the Dutch island of Schiermonnikoog (53°29′ N, 6°14′ W). This area is considered core breeding habitat for this species and is part of the international Wadden Sea estuary consisting of many other nearby barrier islands. An intensive color-ringing program was initiated to mark all nonbreeders, breeders, and their offspring. The standard monitoring protocol is described in detail elsewhere (Ens et al. 1992, Heg et al. 2000*b*). In short, during each breeding season (May–August) population numbers were counted and we recorded which individuals were alive and what their stage class status and reproductive output was (~300 marked individuals and ~100 breeding territories annually). Mortality occurred mainly in winter, with subsequent stage changes finalizing before the start of the breeding season. The study population declined ~5% per year over the 24-year study period (van de Pol 2006), comparable to Dutch national trends (van Dijk et al. 2007).

Climatic, environmental, and density covariates

Winter temperature (*w*; mean of December–March) has been measured at the local weather station (2 km from the study site). However, as this weather station is relatively new, we instead used historical data since 1907 from the Eelde weather station located 35 km away (Royal Netherlands Meteorological Institute). Winter temperatures at both weather stations were strongly correlated (Pearson's $r = 0.98$; $n = 33$). By combining the historical data with four different climate models specifically developed for this region (van de Hurk et al. 2006), projections of winter temperature trends were generated for 1990–2100 (Fig. 2A). Mean winter temperature is projected to continue to increase, whereas the interannual variability of winter temperature is projected to decrease in the future (Fig. 2A, B). Based

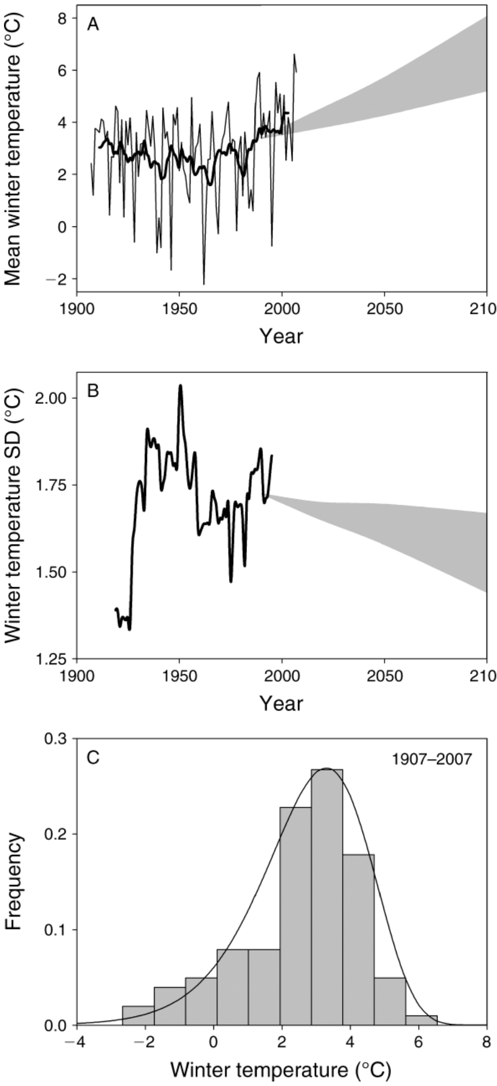

FIG. 2. Historical (1907–2007) and projected (1990–2100) changes in local winter temperature (data from the Royal Netherlands Meteorological Institute). (A) Mean winter temperature (thin line, annual fluctuations; thick line, 10-year running average; gray area, range of projections of mean temperature trends from four climate scenarios [van de Hurk et al. 2006]). (B) Standard deviation of winter temperature (thick line, 25-year running SD; gray area, range of projections of temperature standard deviance trends from four climate scenarios [van de Hurk et al. 2006]). (C) Distribution of historical mean winter temperature with a transformed lognormal distribution fitted to the data.

on the historical data we approximated winter temperature by a transformed lognormal process ($w \sim 10 - \text{lognormal}(\mu - 10, \sigma)$; Fig. 2C), with μ and σ chosen such that the mean and standard deviation of w are 3.7°C and 1.7°C, respectively (similar to the study period 1983–2007). The standard deviation of w decreases as a function of the mean for this transformed lognormal distribution, as is also predicted by all four future climate scenarios (Fig. 2A, B).

We also considered whether vital rates were associated with various other large-scale and local climatic variables besides winter temperature (summer and winter Northern Atlantic Oscillation index and summer temperature, precipitation, and flooding events). In addition, we explored how vital rates depend on food availability, as the abundances of oystercatchers' main prey species (shellfish and worms) are known to depend on winter temperature (Beukema 1992, Philippart et al. 2003, Lawrence and Soame 2004). Food abundance was measured as the density of each main prey species (ragworm [*Nereis diversicolor*], lugworm [*Arenicola marina*], Baltic tellin [*Macoma balthica*], and cockle [*Cerastoderma edule*]) on the mudflats in the study area during the birds' peak of egg-hatching (van de Pol 2006). We included only prey items that are accessible to oystercatchers (i.e., in the top 15 cm of the mudflats) and selected by oystercatchers (i.e., bivalves <10 mm were excluded).

Density dependence of fecundity and survival probabilities was investigated by including competitor numbers as a covariate (total population size [N_{pop}] or size of a stage class [e.g., N_{H}]). In addition, we specifically investigated possible interactions between climatic and density variables. The density dependence of movement probabilities between stages was investigated differently, because the limited amount of high- and low-quality habitat is the main factor regulating this population. Many adult nonbreeders are despotically excluded from breeding, and removal experiments have shown that when given the opportunity they can reproduce (Bruinzeel and van de Pol 2004). Movement probabilities from the nonbreeder stage to the high- or low-quality breeding stages are thus expected to be a function of both the number of vacant territories (due to deaths of breeders; $(1 - S_{\text{H}})N_{\text{H}}$ or $(1 - S_{\text{L}})N_{\text{L}}$) and the number of surviving nonbreeders that compete for these vacancies ($S_{\text{N}}N_{\text{N}}$). In addition, vacancies in high-quality habitat are much more likely to be occupied by nearby breeders from low-quality habitat than by nonbreeders (Heg et al. 2000*b*). Therefore, we expected the number of vacancies for nonbreeders also to be a function of the number of breeders moving from the low- to high-quality habitat breeding stage ($S_{\text{L}}M_{\text{LH}}N_{\text{L}}$). More specifically, we expected

$$M_{\text{NL}} \approx \frac{(1 - S_{\text{L}})N_{\text{L}} + S_{\text{L}}M_{\text{LH}}N_{\text{L}}}{S_{\text{N}}N_{\text{N}}}$$

$$M_{\text{NH}} \approx \frac{(1 - S_{\text{H}})N_{\text{H}} - S_{\text{L}}M_{\text{LH}}N_{\text{L}}}{S_{\text{N}}N_{\text{N}}}$$

$$M_{\text{LH}} \approx \frac{(1 - S_{\text{H}})N_{\text{H}}}{S_{\text{L}}N_{\text{L}}}.$$

Decomposition of variance in vital rates

We decomposed interannual variation in fecundity and survival rates over the 24-year study period into components due to demographic stochasticity, climatic and other environmental variables, density effects, and residual unexplained environmental stochasticity. The technical details of the estimation procedure will be described elsewhere; here we describe the major steps. As earlier studies showed no evidence for sex differences in vital rates (van de Pol et al. 2006, 2007), both sexes were pooled for parameter estimation. We decomposed temporal variation in each vital rate using generalized linear mixed models with year included as a random effect (intercept). We assumed that demographic heterogeneity in vital rates was sufficiently accounted for by the stage structure described in Fig. 1 and that the annual between-individual variation in fecundity and survival could be described by a Poisson and binomial probability distribution, respectively. Variation in fecundity was decomposed using a mixed model in program MLwiN 2.0 (Rasbash et al. 2004). Survival and movement probabilities were estimated simultaneously using a multistate mark–recapture–recovery model (model structure as in Fig. 1). Variance components were estimated in the global time-dependent model using the Bayesian Markov chain Monte Carlo random effects procedure implemented in program MARK (Burnham and White 2002). Selection between models with and without specific environmental and density covariates was based on the deviance information theoretic criterion (DIC, a hierarchical modeling generalization of the Akaike information criterion; Burnham and Anderson 2002).

Residual environmental covariation between fecundity and survival rates not caused by density, climatic, or other measured environmental variables was estimated using the shrinkage estimators of the annual residuals of each vital rate on either the log or logit scale (with base *e*). The 24 shrunken annual residuals of each vital rate were assumed to be normally distributed and residuals for each vital rate were used to calculate a variance–covariance matrix that describes the multivariate normally distributed residual environmental (co)variances among the vital rates (see Appendix).

Stochastic population model

Our stage-structured stochastic population model included demographic stochasticity, density dependence, the climatic effect of interest (i.e., winter temperature), other environmental effects, and residual environmental variance within and covariance between vital rates. The population model is asexual (i.e., tracks females only) with the following general form (Caswell 2001):

$$\mathbf{n}_{t+1} = \mathbf{A}_t \times \mathbf{n}_t \tag{1}$$

where $\mathbf{n}_t$ is the column vector of (female) stage sizes at time t and the elements of the projection matrix $\mathbf{A}_t$ are stochastic variables depending on the vital rates in the life cycle (cf. Fig. 1). We used a post-breeding census definition (each year birds first survive, then can move between stages, and finally reproduce) such that Eq. 1 becomes Eq. 2. The expressions determining the between-year expectation, variance, and covariances of the stochastic variables F, S, and M and their dependency on density, winter temperature, and other environmental variables are directly based on the statistical models, and parameter estimates are given in the Appendix. The observed sizes of stage classes in the last year of study were used as initial starting values in the simulations.

By assuming that individual fecundity and survival were generated by a Poisson and binomial process, respectively, the contribution of demographic stochasticity to temporal variation in each vital rate at a certain population size is given by the sampling variance of the specific distribution. Density regulation was modeled by including a ceiling for the number of high- and low-quality territories to account for the fact that breeding habitat is a limiting resource (cf. van de Pol et al. 2007; the ceiling was set to the maximum number of high- and low-quality territories from 1983 to 2007; $N_{\mathrm{H(max)}} = 60$, $N_{\mathrm{L(max)}} = 150$). A ceiling is based on the idea that at high density the breeding habitats become saturated and cannot be subdivided into smaller parts without their quality becoming below the territory acceptance threshold for nonbreeders (Kokko et al. 2001). Correspondingly, rates of recruitment to and breeding dispersal between high- and low-quality habitats (M_{NL}, M_{NH}, M_{LH}) were modeled as functions of the number of vacant breeding territories per competing nonbreeder. Moreover, breeders in low-quality habitat had priority over nonbreeders when competing for breeding vacancies in high-quality habitat (cf. Heg et al. 2000*b*). Although oystercatchers sometimes lose their territory ([M_{HN}, M_{HL}, M_{LN}] > 0), we did not model this explicitly, as these vacancies were typically reoccupied immediately and consequently this mainly concerns

$$\begin{pmatrix} n_0 \\ n_1 \\ n_2 \\ n_{\mathrm{N}} \\ n_{\mathrm{L}} \\ n_{\mathrm{H}} \end{pmatrix}_{t+1} = \begin{pmatrix} 0 & 0 & 0 & 0 & S_{\mathrm{L}}F_{\mathrm{L}} & S_{\mathrm{H}}F_{\mathrm{H}} \\ S_0 & 0 & 0 & 0 & 0 & 0 \\ 0 & S_1 & 0 & 0 & 0 & 0 \\ 0 & 0 & S_2 & S_{\mathrm{N}}(1 - M_{\mathrm{NL}} - M_{\mathrm{NH}}) & 0 & 0 \\ 0 & 0 & 0 & S_{\mathrm{N}}M_{\mathrm{NL}} & S_{\mathrm{L}}(1 - M_{\mathrm{LH}}) & 0 \\ 0 & 0 & 0 & S_{\mathrm{N}}M_{\mathrm{NH}} & S_{\mathrm{L}}M_{\mathrm{LH}} & S_{\mathrm{H}} \end{pmatrix}_t \begin{pmatrix} n_0 \\ n_1 \\ n_2 \\ n_{\mathrm{N}} \\ n_{\mathrm{L}} \\ n_{\mathrm{H}} \end{pmatrix}_t \tag{2}$$

individuals swapping stages and thus does not affect the stage distribution of the model. Similarly, although some permanent emigration and immigration of nonbreeders does occur (~4% annually; van de Pol 2006), we assumed immigration matched emigration and did not model migration explicitly (i.e., we focus on studying the local population dynamics).

Decomposing sensitivities

The sensitivity of population dynamics to climate change was assessed using computer simulations of the stochastic population model (Eqs. 1 and 2) in R (R Development Core Team 2007). We determined the sensitivity of the median time to extinction, because the stochastic population growth rate in a density-regulated population is density dependent itself and therefore less suitable for sensitivity analyses. Median time to extinction was defined as the number of "years" it took for 50% of 300 000 simulated populations to go extinct. As we are dealing with fecundity and survival rates that are approximately lognormally and logit-normally distributed, respectively, it is more convenient to study their effects on the log and logit scales, respectively (e.g., $x_i = \log[F_{\mathrm{H}}]$ or $x_i = \mathrm{logit}[S_1]$). We can decompose the effect of climate change in winter temperature (w) on the median time to extinction (T) into an effect due to changes in the expectation (E) of w and an effect due to the change in the standard deviation (σ) of w:

$$dT = \frac{\partial T}{\partial E(w)} dE(w) + \frac{\partial T}{\partial \sigma_w} d\sigma_w. \qquad (3)$$

Eq. 3 allows a quantitative comparison of the impact of a X°C change in $E(w)$ on T relative to the impact of a similar X°C change in σ_w on T (is $|\partial T/\partial E(w)| >$ or $< |\partial T/\partial \sigma_w|$?). Eq. 3 can be further decomposed into how climate effects on each vital rate x_i contribute to the overall effect on dT:

$$dT = \left(\sum_{x_i} \frac{\partial T}{\partial E(x_i)} \frac{\partial E(x_i)}{\partial E(w)} \right) dE(w) + \left(\sum_{x_i} \frac{\partial T}{\partial \sigma_{x_i}} \frac{\partial \sigma_{x_i}}{\partial \sigma_w} \right) d\sigma_w. \qquad (4)$$

Eq. 4 thereby permits a quantitative comparison of the relative contribution of climate-dependent fecundity and survival to extinction dynamics (e.g., by comparing the $|\partial T/\partial E(x_i) \times \partial E(x_i)/\partial E(w)|$ of fecundity vs. survival rates). Sensitivities were estimated numerically using small perturbations (<1%) of the variables of interest in the population model.

Results

Climatic and density effects on vital rates

All vital rates across the life cycle were directly or indirectly associated with winter temperature, with temperature explaining 32–46% of the total environmental variance in each vital rate (Fig. 3). Survival rates of all stage classes were strongly positively associated with winter temperature (Fig. 3A–D; see the Appendix for parameter estimates). The effect of winter temperature on survival was strongest for juvenile age classes (see slopes in Fig. 3A, B vs. Fig. 3C, D). Winter temperature also explained 42–73% of the positive environmental covariances between stage-dependent survival rates (Appendix). Other environmental variables (e.g., food abundances, North Atlantic Oscillation index, summer temperature) did not explain any additional environmental variance in any of the stage-dependent survival rates, nor did we find any evidence for density-dependent survival (DIC increased >1 when including these covariates).

Movement probabilities between stages, specifically breeding dispersal from low- to high-quality breeding habitat (M_{LH}) and recruitment into the breeding population (M_{NL} and M_{NH}) were strongly dependent on the number of breeding vacancies per competitor. The number of vacancies in high-quality habitat per surviving competitor in low-quality habitat was a good predictor of M_{LH} (Fig. 3E). Similarly, the number of remaining vacancies in high-quality habitat per surviving nonbreeder was a good predictor of M_{NH} (Fig. 3F; similar results for M_{NL}). These results suggest that the climatic effects on recruitment and breeding dispersal are density dependent themselves, as these movement probabilities are determined by the product of the size of stage classes and climate-dependent survival rates (Fig. 3E, F).

Fecundity was indirectly dependent on winter temperature, by being positively correlated with ragworm abundance (Fig. 3G, H), oystercatchers' main food source during chick feeding (Bunskoeke et al. 1996). Cold winter temperatures promote egg production of ragworms (Lawrence and Soame 2004), and as expected the annual ragworm abundance was strongly negatively related to winter temperature in our study area (inset of Fig. 3I; $R^2 = 0.38$). Consequently, both F_{H} and F_{L} were indirectly negatively associated with winter temperature (Fig. 3I, J; see Appendix for parameter estimates). Fecundity was also negatively associated with flooding events during the breeding season (Fig. 3G, H), as these floods flushed away many nests. However, as there is currently no evidence that these flooding events will become systematically more or less frequent, we modeled flooding effects in the population model as a separate random (residual) environmental process that does not change systematically over time (see Appendix). Other environmental variables (e.g., summer temperature, precipitation, other food sources) did not explain any additional environmental variance in fecundity rates, nor did we find any evidence for density-dependent fecundity (DIC increased >1 when including these covariates). The fecundity of breeders in high- and low-quality habitat exhibit strong positive environmental covariance ($\sigma_{F_{\mathrm{H}}, F_{\mathrm{L}}} = 0.49 \pm 0.21$ [estimate ± SE]). However, this covariance disappeared after accounting for effects of food and floodings on

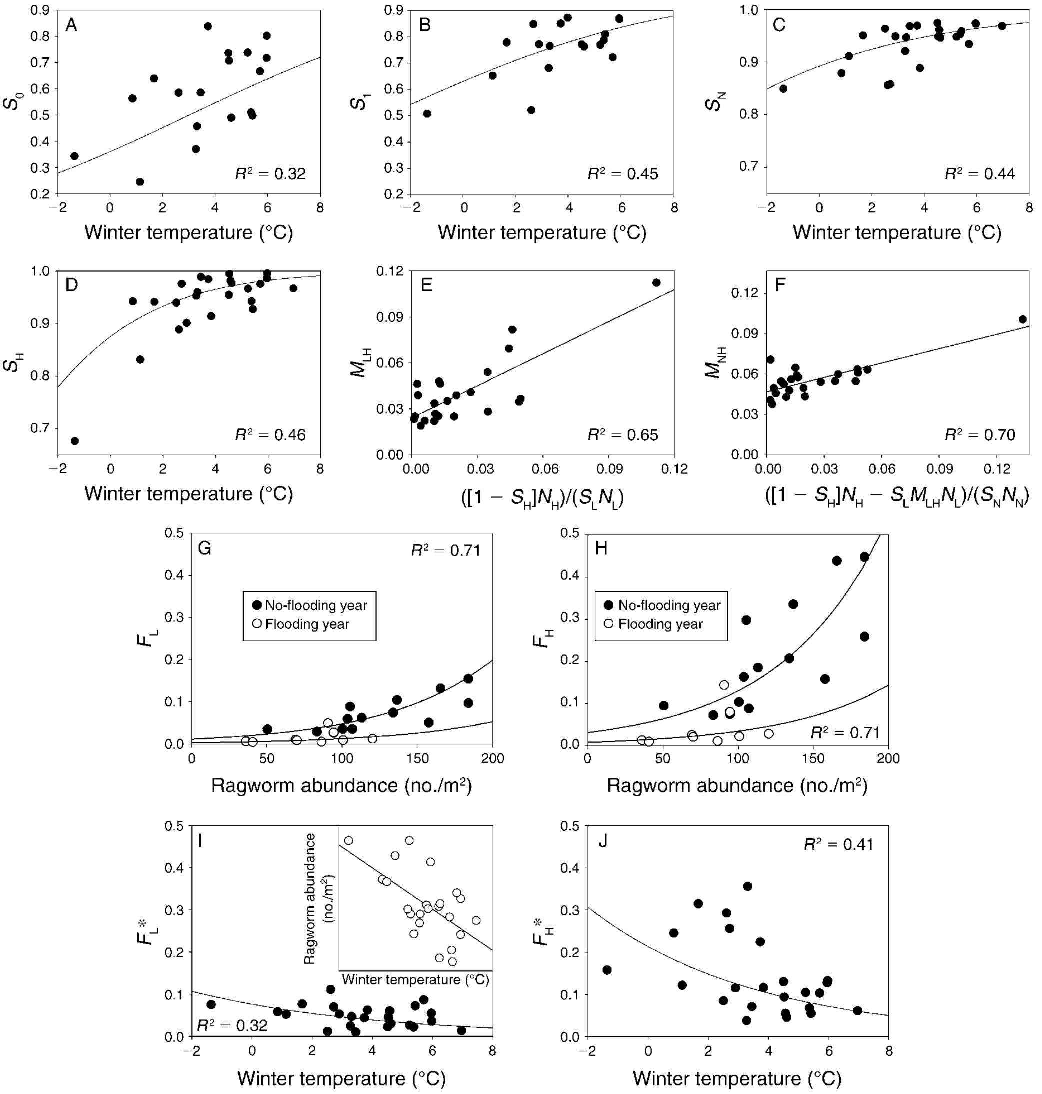

FIG. 3. Relationships of annual survival (S), movement (M), and fecundity (F) rates to winter temperature, competitor density, and other environmental variables (1983–2007). The competitor density term on the x-axis in panels (E) and (F) is explained in *Methods*. In panels (I) and (J), F_L^* and F_H^* are adjusted for flooding effects and for the dependency between ragworm abundance and winter temperature; see panels (G) and (H) and the subpanel within (I). All regression equations and parameter estimates with standard errors are given in the Appendix, including those not presented in this figure (S_2, S_L, and M_{NL}). Six states are distinguished: 0, fledged offspring; 1, one-year-old juveniles; 2, two-year-old juveniles; N, adult nonbreeders; L, breeders in low-quality habitat; H, breeders in high-quality habitat.

fecundity (σ_{F_H, F_L} = 0.02 ± 0.08), which is consistent with the observation that breeders in high- and low-quality habitat are both affected by the same food stocks and flooding events.

Climate effects on population dynamics

Different realizations of the stochastic population model can give quite dissimilar trajectories (Fig. 4A), and prediction intervals for time to extinction were wide (Fig. 4B). Under current environmental conditions this population is likely to go extinct, but the estimated median time to extinction for this strongly declining population (~5% annually from 1983 to 2007) was estimated to be still rather long at 413 years (Fig. 4B). The duration to extinction is typically long, because simulated populations can fluctuate for centuries at

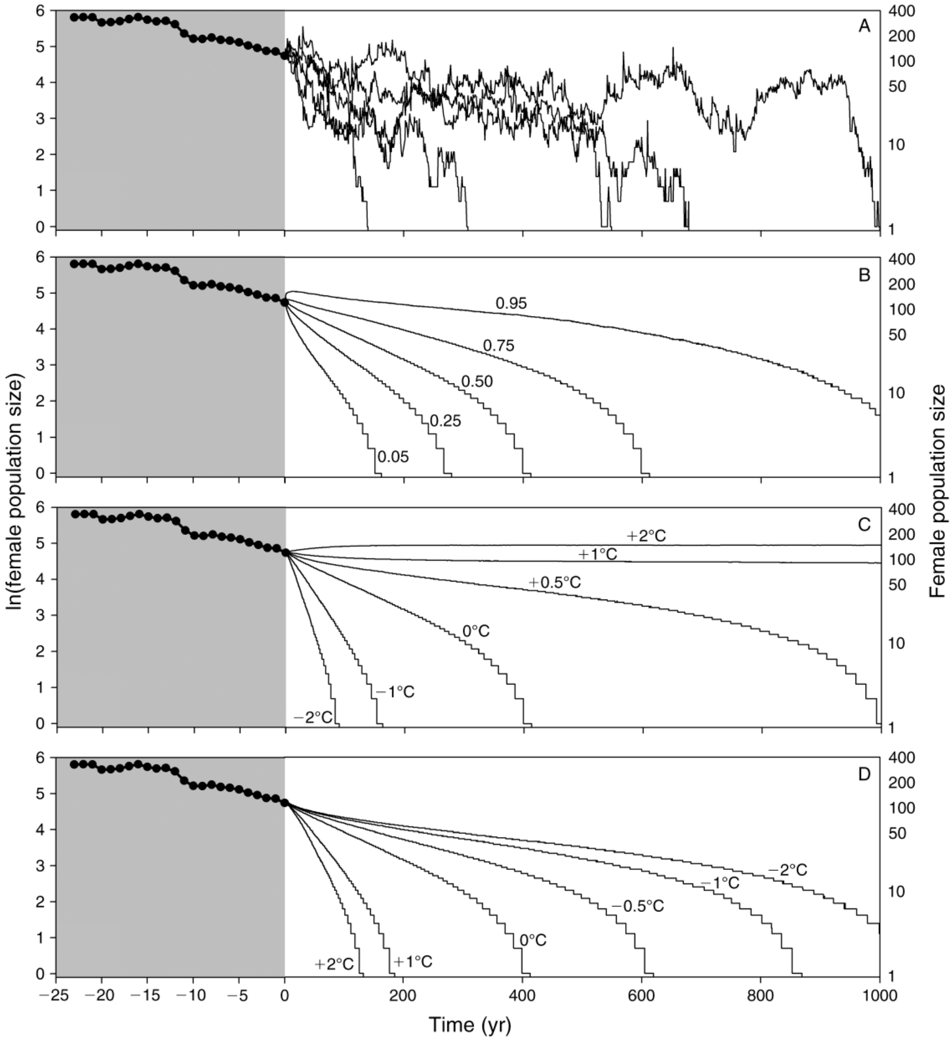

FIG. 4. Historical (gray panels) and projected (white panels) changes in population numbers for scenarios of changing winter temperature (w). (A) Time plots of five randomly selected realizations of a stochastic population model with no changes in the mean and SD of winter temperature. (B) Time plots of 5th, 25th, 50th, 75th, and 95th percentiles of the population size of 300 000 simulated populations of a stochastic population model with no changes in the mean and standard deviation of winter temperature. (C) The 50th percentile of population size for scenarios with changes in the expectation of winter temperature, $E(w)$, while keeping the standard deviation of winter temperature, σ_w, constant. (D) The 50th percentile of population size for scenarios with changes in σ_w, while keeping $E(w)$ constant. The point in time at which the 50th percentile reaches a population size of zero is defined as the median time to extinction, T. Note the logarithmic y-axes; the timescale on the x-axis differs between the gray and white panels (year 2007 set to time = 0).

intermediate population sizes (Fig. 4A). At intermediate population sizes all low-quality habitat is abandoned and only high-quality habitat is occupied ($N_{\mathrm{pop}} < N_{\mathrm{H(max)}}$), which increases the per capita productivity (as $F_{\mathrm{H}} > F_{\mathrm{L}}$) of this declining population to the point at which the population growth is close to zero. The final process of extinction can occur relatively abruptly (Fig. 4A), with growth rate becoming strongly negative again ($\sim$6% per year) at low population size ($N_{\mathrm{pop}} < 20$) due to demographic stochasticity.

A rise in mean winter temperature, $E(w)$, increased median time to extinction, T, substantially; using small perturbations we estimated $\partial T/\partial E(w) = 543$, meaning that an increase in $E(w)$ of 0.1°C leads to an increase in T of $\sim$54 years. Increasing the standard deviation of winter temperature σ_w led to a decrease in T and we estimated $\partial T/\partial\sigma_w = -364$, meaning that an increase in σ_w of 0.1 decreases T by roughly 36 years. Thus, a 0.1°C change in mean temperature is predicted to alter persistence time by 1.5 times (=54/36), as many years as would a 0.1°C change in the standard deviation in temperature, suggesting that the dynamics of oystercatchers are intrinsically more sensitive to changes in the mean than in the variability of this climatic variable ($|\partial T/\partial E(w)| > |\partial T/\partial\sigma_w|$). In addition, as climate models (van der Hurk et al. 2006) predict 10-fold larger changes in $E(w)$ than in σ_w until the year 2100 ($dE(w) = +1.5$°C to $+4.4$°C; $d\sigma_w = -0.1$°C to -0.3°C; Fig. 2A, B), the predicted effect of $|\partial T/\partial E(w) \times dE(w)|$ on T is expected to overwhelm the effect of $|\partial T/\partial\sigma_w \times d\sigma_w|$ on T even more strongly (see Eq. 3). Fortunately for oystercatchers, changes in the mean and variability of winter temperature both are expected to improve population viability, as future climate scenarios predict that $E(w)$ will increase but σ_w will decrease.

The sensitivities reported above deal only with small changes in $E(w)$; large changes in $E(w)$ are predicted to result in strongly nonlinear responses of T (Fig. 4C). If $E(w)$ increases by 1°C or more (as projected by all climate models; Fig. 2A) then $T \to \infty$, and populations typically fluctuate stochastically around a certain carrying capacity (Fig. 4C). Thus, an increase in $E(w)$ of ~1°C is expected to shift the population dynamics from almost certain extinction toward stationary fluctuations around a mean population size. Contrastingly, even a 1°C decrease in σ_w (which is much more than projected by all climate models; Fig. 2B), seems to have relatively little impact on T (Fig. 4D), again suggesting that oystercatcher population dynamics are more sensitive to changes in mean winter temperature than in variability of winter temperature.

Population impact of climate change decomposed per vital rate

In total the cumulative effect of changes in $E(w)$ through each vital rate was estimated to be positive, namely,

$$\sum_{x_i} \frac{\partial T}{\partial x_i}\frac{\partial x_i}{\partial E(w)} = 569$$

(see Table 1). Considering the finite number of simulations, this estimate is close to our earlier direct estimate of $\partial T/\partial E(w) = 543$, illustrating the consistency of our decomposition approach. Future climate change that increases $E(w)$ has a negative impact on T through its effects on stage-dependent fecundity rates, but has a positive impact on T through its effects on stage-dependent survival rates (Table 1). The cumulative sensitivity of T to effects of $E(w)$ on all survival rates was three times as large in magnitude, i.e.,

$$\sum_{x_i=\text{logit}(s_i)} \frac{\partial T}{\partial x_i}\frac{\partial x_i}{\partial E(w)} = 835$$

than the cumulative sensitivity of T to effects of $E(w)$ on all fecundity rates, i.e.,

$$\sum_{x_i=\log(f_i)} \frac{\partial T}{\partial x_i}\frac{\partial x_i}{\partial E(w)} = -276$$

showing that the effects on this population's time to extinction by the climate mean are largely mediated by mean temperature effects on survival. The stage-specific vital rates that had by far the largest positive and negative contributions to the overall effect of $E(w)$ on T were both vital rates of breeders in high-quality habitat (namely S_H and F_H; Table 1). The reason S_H and F_H contributed more strongly to the overall effect of $E(w)$ on T than other vital rates was because T is very sensitive to changes in S_H and F_H; S_H and F_H are not more sensitive to changes in $E(w)$ than other vital rates (Table 1).

The cumulative effect of changes in σ_w through all vital rates was estimated to be negative, namely,

$$\sum_{x_i} \frac{\partial T}{\partial\sigma_{x_i}}\frac{\partial\sigma_{x_i}}{\partial\sigma_w} = -316$$

(close to the direct estimate of $\partial T/\partial\sigma_w = -364$). Future climate change that increases σ_w positively impacts T through its effects on stage-specific fecundity rates, while it negatively impacts T through its effects on stage-specific survival rates (Table 1). The cumulative sensitivity of T to effects of σ_w on all survival rates was three times as large in magnitude, i.e.,

$$\sum_{x_i=\text{logit}(s_i)} \frac{\partial T}{\partial\sigma_{x_i}}\frac{\partial\sigma_{x_i}}{\partial\sigma_w} = -497$$

than the cumulative sensitivity of T to effects of σ_w on all fecundity rates, i.e.,

$$\sum_{x_i=\log(f_i)} \frac{\partial T}{\partial\sigma_{x_i}}\frac{\partial\sigma_{x_i}}{\partial\sigma_w} = 181$$

showing that climate variability effects on this population's time to extinction are largely mediated by temperature variability effects on survival. The vital rates that had the strongest positive and negative contributions to the overall effect of σ_w on T were the same vital rates that were the main contributors to the overall effect of $E(w)$ on T (namely S_H and F_H; Table 1).

DISCUSSION

We have quantified how climate affects the major vital rates over a structured life cycle of a long-lived species and determined the sensitivity of population dynamics to changes in the mean and variability of these vital rates. This demographic approach allowed us to investigate how climatic effects on each demographic rate give rise to changes in the population dynamics. We now discuss the implications of our results for some important unresolved questions in our field.

Table 1. Sensitivities of median time to extinction, T, to changes in expectation and standard deviation of winter temperature, $E(w)$ and σ_w, respectively, decomposed for each vital rate x_i (see Eq. 4) for a declining Eurasian Oystercatcher (*Haematopus ostralegus*) population on the Dutch island of Schiermonnikoog.

x_i	$\partial T/\partial E(x_i)$	$\partial E(x_i)/\partial E(w)$	$(\partial T/\partial E(x_i))(\partial E(x_i)/\partial E(w))$	$\partial T/\partial \sigma_{x_i}$	$\partial \sigma_{x_i}/\partial \sigma_w$	$(\partial T/\partial \sigma_{x_i})(\partial \sigma_{x_i}/\partial \sigma_w)$
$\log f_{\text{L}}$	28	−0.182	−5	41	0.182	8
$\log f_{\text{H}}$	1602	−0.169	−271	1024	0.169	173
Sum of fecundity			−276			181
logit s_0	559	0.190	106	−76	0.190	−14
logit s_1	380	0.182	69	−39	0.182	−7
logit s_2	60	0.200	12	−50	0.200	−10
logit s_{N}	4	0.195	1	−49	0.195	−10
logit s_{L}	79	0.235	18	−34	0.235	−8
logit s_{H}	1827	0.344	629	−1301	0.344	−448
Sum of survival			835			−497
Sum of all			559			−316

Notes: Sensitivities of stage-dependent fecundities, f_i, and survival, s_i, are on the log or logit scale, respectively (see *Methods*). Environmental conditions during the study period were $E(w) = 3.7°\text{C}$ and $\sigma_w = 1.7°\text{C}$, resulting in $T = 413$ years.

Impact of changes in climatic mean vs. variability

Global climate change not only results in changes in the mean of climatic variables, but also in their variance (Easterling et al. 2001), which has been shown to affect population dynamics (e.g., Drake 2005, Altwegg et al. 2006, Boyce et al. 2006). So far no study directly compared the relative importance of changes in mean and variance of climatic variables on population dynamics via their effect on each vital rate across the life cycle using empirical data. Eq. 4 shows there can be various mechanisms by which changes in the climatic mean or variability can affect time to extinction, i.e., multiple terms can cause

$$\sum_{x_i} \frac{\partial T}{\partial E(x_i)} \frac{\partial E(x_i)}{\partial E(w)} dE(w) \neq \sum_{x_i} \frac{\partial T}{\partial \sigma_{x_i}} \frac{\partial \sigma_{x_i}}{\partial \sigma_w} d\sigma_w.$$

In our study two mechanisms were important: (1) time to extinction was more sensitive to changes in the mean than in the standard deviation of most vital rates, i.e.,

$$\left| \frac{\partial T}{\partial E(x_i)} \right| > \left| \frac{\partial T}{\partial \sigma_{x_i}} \right|$$

(see Table 1) and (2) climate models predicted much larger changes in the mean than in the standard deviation of temperature ($|dE(w)| > |d\sigma_w|$; Fig. 2). Since in most animal and plant species the sensitivity of population dynamics to standard deviations of vital rates is much lower than the sensitivity to mean vital rates (Haridas and Tuljapurkar 2005, Morris et al. 2008), we would expect changes in climatic means to have often a stronger impact on population dynamics than changes in climatic variability (as long as climatic variability does not cause the catastrophic death of the entire population and projected changes in climatic variability are not much larger than those for climatic means). Potentially, our conclusion might thus hold for a wide variety of life histories.

The environmental canalization hypothesis suggests that the vital rates to which population growth is most sensitive in terms of changes in their mean values might also be the vital rates most resilient to environmental variation (Pfister 1998, Sæther and Bakke 2000, Gaillard and Yoccoz 2003). In long-lived species such as the oystercatcher, population growth is more sensitive to changes in the mean of adult than of juvenile survival (van de Pol et al. 2006). In line with the environmental canalization hypothesis we found that juvenile survival was more variable in time and more sensitive to winter temperature than adult survival (Fig. 3A, B vs. Fig. 3C, D). However, although juvenile survival was very sensitive to temperature variability, this variability barely affected the extinction dynamics (Table 1). In contrast, while adult survival of breeders in high-quality habitat was less sensitive to winter temperature variability, this low variability strongly affected the extinction dynamics (Table 1). Thus, although the vital rates to which population growth is most sensitive in terms of changes in their mean values might be more resilient to environmental variation, this does not mean that effects of climate change via such canalized vital rates are not important for population dynamics.

Does increased climatic variability reduce population viability?

Although classical stochastic population theory suggests that environmental variability reduces population viability (Lewontin and Cohen 1969, Lande and Orzack 1988), recent work suggests that increased climatic variability can sometimes also improve population viability, depending on the exact relationship between vital rates and climatic variables (Drake 2005, Boyce et al. 2006, Morris et al. 2008). In oystercatchers, fecundity rates have a decreasing convex relationship with winter temperature (Fig. 3I, J) and consequently increasing variance in winter temperature is expected to increase mean fecundity and, thereby, persistence time (due to Jensen's inequality; Caughley 1987, Ruel and Ayres 1999, Boyce et al. 2006). Conversely, due to the increasing concave relationship between survival and winter temperature (Fig. 3B–D), increased variability in winter temperature is expected to decrease mean survival and thereby persistence time (Table 1). Thus, the key element in understanding the impact of climatic variability on vital rates is to be able to explain why some relationships between vital rates and climatic variables are convex and others concave.

It is possible that species' life histories can be used to make general predictions about the impact of climatic variability on vital rates. In species with low reproductive output most individuals typically do not produce any young at all in an average year. Thus, in such species fecundity cannot get much worse in bad years, whereas it can get much better in good years, resulting in a convex relationship between fecundity and climatic variables (Boyce et al. 2006). Similar arguments can be used to propose that the relationship between survival and climatic variables is typically concave for long-lived species, as survival is already so high that in good years it cannot get much better, while in bad years it can get much worse. Conversely, this hypothesis suggests that for short-lived species with low juvenile or adult survival ($<50\%$) the relationship between survival and climatic variables might be convex and increasing climatic variability might actually increase these survival rates and thereby population viability. Our results on the Eurasian Oystercatcher, a species at the extreme of the low-productivity and longevity spectrum of life histories (Sæther and Bakke 2000), are well in line with these predictions on how life history might affect the impact of climatic variability on vital rates and population viability.

Decomposing climate effects per vital rate

Determining the critical periods affecting population dynamics is a first step in predicting the consequences of climate change on population fluctuations (Hallett et al. 2004, Sæther et al. 2004). Many studies have shown that climate affects the population dynamics through an effect on either fecundity during the breeding season or on the number of individuals that survive the nonbreeding season. In avian species, the dynamics of precocial birds seem to be especially strongly dependent upon climate during the breeding season, while the population fluctuations of altricial birds covary strongest with climatic variables during the nonbreeding season (Sæther et al. 2004). At first sight our results on semi-precocial oystercatchers seem to suggest both pathways are important, as climatic effects on both fecundity and survival affected population dynamics (Fig. 3, Table 1). However, the effect of climate on fecundity was not caused by (summer) climate during the breeding season, but was due to an indirect effect of winter temperature on the dynamics of oystercatchers' main prey species. Consequently, both fecundity and survival were affected by the same climatic variable during the nonbreeding winter season (albeit in opposing ways). Thus, when finding that population fluctuations are most strongly associated with climatic variables during the nonbreeding season, this does not necessarily imply that this climatic variable only affects demography via survival during this season. In addition, it may be problematic to generalize across populations, as Sæther et al. (2007) and Grøtan et al. (2008) have shown that there is often large interpopulation variation in the critical season during which the strongest climate-induced influences on the population dynamics arise.

The spatial heterogeneity in habitat quality and the resulting stage structure and density dependence in vital rates strongly affect the extinction dynamics. As density decreases, first surplus nonbreeders will disappear and subsequently low-quality habitat will not be reoccupied, resulting in an increase of the per capita productivity with declining density (the "buffer effect"; Kluijver and Tinbergen 1953). Consequently, in our simulations the population typically fluctuated for long periods around an intermediate population size at which only high-quality territories are occupied ($N_{\mathrm{pop}} < 60$ $(=N_{H(\max)})$; Fig. 4A) with a realized growth rate close to zero. Only when by chance populations became small (<20 individuals) was the population growth further reduced due to demographic stochasticity, and typically extinction followed quickly (a stochastic Allee effect; Lande 1998; see Fig. 4A). An important consequence of this buffer effect is that the sensitivity of time to extinction was highest for vital rates associated with breeding in high-quality habitat (Table 1). Thus, although survival and fecundity in low-quality habitat were both affected by winter temperature (Fig. 3I, Appendix), this had little impact on population viability (Table 1). The huge variation in sensitivities among stage classes highlights the importance of investigating the impact of climate change on vital rates across the entire life cycle before making strong inferences about the population consequences. Furthermore, it underlines the critical role of density regulatory mechanisms in determining the population impacts of climate effects on vital rates.

Contribution of climate change to population change

Even small increases in mean winter temperature were expected to improve the population viability in our population model substantially. Due to nonlinearity in the dynamics we expect that somewhat larger increases of ~1°C will have a disproportional larger effect, and our results suggest that such warming could potentially save this population from extinction (Fig. 4C). However, predicting long-term consequences of climate change remains a problematic task, as climate models predict large changes in temperatures (+1.5 to +4.4°C). These large temperature rises mean that the domain of winter temperatures will shift to a range of which we still have little knowledge regarding the manner in which vital rates react to such temperatures. In addition, other aspects of the climate might also change in the future. It is still unclear how intra-annual climatic variability might change in the future (e.g., will cold spells become more or less common?) and how this will affect vital rates (Hallet et al. 2004). Also, the predicted positive effect of rising winter temperatures might be counteracted by negative effects of flooding events (Fig. 3G, H), which seem to have become more frequent recently (van de Pol 2006). Finally, individuals might adapt to climate change (Visser 2008); for example, oystercatchers might shift to alternative food sources that are less sensitive to increased winter temperature. Although we are still a long way from accurately predicting long-term consequences of the large climatic changes many populations are facing nowadays, we hope this study illustrates that by decomposing the effects of small changes in climatic variables on vital rates and population dynamics we can gain important insight into the mechanisms determining how populations will respond to climate change. Disturbingly, the duration and level of detail of field data required to gain these insights is typically unavailable for the species for which these insights are actually most needed (i.e., those of conservation concern).

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APPENDIX

Estimates of model parameters used in the stochastic population model (*Ecological Archives* E091-085-A1).

Ecological Archives **E091-085-A1**

Martijn van de Pol, Yngvild Vindenes, Bernt-Erik Sæther, Steinar Engen, Bruno J. Ens, Kees Oosterbeek, and Joost M. Tinbergen. 2010. Effects of climate change and variability on population dynamics in a long-lived shorebird. *Ecology* 91:1192–1204.

Appendix A: Estimates of model parameters used in stochastic population model.

General modeling approach

By assuming that the fecundity in state *k* of individual *i* in year *j* is $F_{kij} \sim Poisson(f_{k\,ij})$ and survival is $S_{kij} \sim Binomial(s_{k\,ij})$, the temporal variation in fecundity and survival was decomposed into components due to demographic variation, climatic and other environmental variables, density effects and residual unexplained environmental (co)variation using the following statistical model:

$$\begin{bmatrix} \log f_{L\,ij} \\ \log f_{H\,ij} \\ \text{logit } s_{o\,ij} \\ \text{logit } s_{1ij} \\ \text{logit } s_{2ij} \\ \text{logit } s_{N\,ij} \\ \text{logit } s_{L\,ij} \\ \text{logit } s_{H\,ij} \end{bmatrix} = \begin{bmatrix} \beta_{f_L 0} \\ \beta_{f_H 0} \\ \beta_{s_0 0} \\ \beta_{s_1 0} \\ \beta_{s_2 0} \\ \beta_{s_N 0} \\ \beta_{s_L 0} \\ \beta_{s_H 0} \end{bmatrix} + \begin{bmatrix} \underline{\beta_{f_L Z}} \\ \underline{\beta_{f_H Z}} \\ \underline{\beta_{s_0 Z}} \\ \underline{\beta_{s_1 Z}} \\ \underline{\beta_{s_2 Z}} \\ \underline{\beta_{s_N Z}} \\ \underline{\beta_{s_L Z}} \\ \underline{\beta_{s_H Z}} \end{bmatrix} \underline{Z_j} + \begin{bmatrix} \underline{\beta_{f_L N}} \\ \underline{\beta_{f_H N}} \\ \underline{\beta_{s_0 N}} \\ \underline{\beta_{s_1 N}} \\ \underline{\beta_{s_2 N}} \\ \underline{\beta_{s_N N}} \\ \underline{\beta_{s_L N}} \\ \underline{\beta_{s_H N}} \end{bmatrix} \underline{N_j} + \begin{bmatrix} \underline{\beta_{f_L ZN}} \\ \underline{\beta_{f_H ZN}} \\ \underline{\beta_{s_0 ZN}} \\ \underline{\beta_{s_1 ZN}} \\ \underline{\beta_{s_2 ZN}} \\ \underline{\beta_{s_N ZN}} \\ \underline{\beta_{s_L ZN}} \\ \underline{\beta_{s_H ZN}} \end{bmatrix} \underline{Z_j N_j} + \begin{bmatrix} u_{f_L 0 j} \\ u_{f_H 0 j} \\ u_{s_0 0 j} \\ u_{s_N 0 j} \\ u_{s_N 0 j} \\ u_{s_N 0 j} \\ u_{s_L 0 j} \\ u_{s_H 0 j} \end{bmatrix},$$

where $\underline{Z_j}$ is a column vector of climatic and other environmental variables (e.g., winter temperature, food) and $\underline{N_j}$ is a column vector of conspecifics densities (e.g., N_{pop}, N_L) observed during the study period. The beta's ($\beta_{f_k 0}$, $\beta_{s_k 0}$, and row vectors $\underline{\beta_{f_k Z}}$, $\underline{\beta_{s_k N}}$, etc.) are constants estimated by the statistical model. We specifically considered interactions between climate and density effects ($\underline{Z_j N_j}$). In addition, we estimated the residual environmental process variance and covariance in demographic rates that was not explained by $\underline{Z_j}$ or $\underline{N_j}$, by including random intercepts (u_{0j}) that vary between years.

Due to data limitations we were forced to constrain $u_{s_1 0j} = u_{s_2 0j} = u_{s_N 0j}$. Based on preliminary data exploration it seemed reasonable to assume that $u_{f_k 0j}$ and $u_{s_k 0j}$ can be approximated by a multivariate normal distribution (MVN) with mean zero and a between-year variance-covariance matrix *Ω_u:*

$$\begin{bmatrix} u_{f_L 0j} \\ u_{f_H 0j} \\ u_{s_0 0j} \\ u_{s_N 0j} \\ u_{s_L 0j} \\ u_{s_H 0j} \end{bmatrix} \sim MVN(0,\Omega_u) : \Omega_u = \begin{bmatrix} \sigma^2_{u_{f_L 0}} & & & & & \\ \sigma_{u_{f_L 0 f_H 0}} & \sigma^2_{u_{f_H 0}} & & & & \\ \sigma_{u_{f_L 0 s_0 0}} & \sigma_{u_{f_H 0 s_0 0}} & \sigma^2_{u_{s_0 0}} & & & \\ \sigma_{u_{f_L 0 s_N 0}} & \sigma_{u_{f_H 0 s_N 0}} & \sigma_{u_{s_0 0 s_N 0}} & \sigma^2_{u_{s_N 0}} & & \\ \sigma_{u_{f_L 0 s_L 0}} & \sigma_{u_{f_H 0 s_L 0}} & \sigma_{u_{s_0 0 s_L 0}} & \sigma_{u_{s_N 0 s_L 0}} & \sigma^2_{u_{s_N 0}} & \\ \sigma_{u_{f_L 0 s_H 0}} & \sigma_{u_{f_H 0 s_H 0}} & \sigma_{u_{s_0 0 s_H 0}} & \sigma_{u_{s_N 0 s_H 0}} & \sigma_{u_{s_L 0 s_H 0}} & \sigma^2_{u_{s_H 0}} \end{bmatrix}$$

Note that we assume a multivariate normal distribution of (co)variances of vital rates on the transformed log and logit scale (with base *e*). Between-year covariances between fecundity and survival were based on fecundity in the breeding season and survival during the preceding period (and not survival during the following period).

Model without climatic, density and other environmental covariates

We first fitted a multivariate model that only included an intercept and a separate year random effect for each vital rate with a fully specified between-year variance covariance matrix. All parameter estimates are given with standard errors between parentheses. The model can be described by the following multivariate regression equation:

$$\begin{bmatrix} \log f_{L\,ij} \\ \log f_{H\,ij} \\ \operatorname{logit} s_{o\,ij} \\ \operatorname{logit} s_{1\,ij} \\ \operatorname{logit} s_{2\,ij} \\ \operatorname{logit} s_{N\,ij} \\ \operatorname{logit} s_{L\,ij} \\ \operatorname{logit} s_{H\,ij} \end{bmatrix} = \begin{bmatrix} -1.801(0.156) \\ -2.612(0.146) \\ 0.126(0.153) \\ 1.203(0.136) \\ 3.358(0.165) \\ 2.830(0.099) \\ 3.057(0.116) \\ 3.213(0.175) \end{bmatrix} + \begin{bmatrix} u_{f_L 0j} \\ u_{f_H 0j} \\ u_{s_0 0j} \\ u_{s_N 0j} \\ u_{s_N 0j} \\ u_{s_N 0j} \\ u_{s_L 0j} \\ u_{s_H 0j} \end{bmatrix}$$

with

$$\begin{bmatrix} u_{f_L 0j} \\ u_{f_H 0j} \\ u_{s_0 0j} \\ u_{s_N 0j} \\ u_{s_L 0j} \\ u_{s_H 0j} \end{bmatrix} \sim MVN(0,\Omega_u):\Omega_u = \begin{bmatrix} 1.210(0.349) & & & & & \\ 0.491(0.208) & 0.661(0.191) & & & & \\ 0.117(0.183) & 0.064(0.133) & 0.641(0.185) & & & \\ -0.215(0.140) & -0.120(0.101) & 0.275(0.112) & 0.351(0.101) & & \\ -0.167(0.161) & -0.179(0.122) & 0.379(0.138) & 0.310(0.106) & 0.491(0.142) & \\ -0.095(0.236) & 0.038(0.174) & 0.471(0.196) & 0.363(0.147) & 0.395(0.170) & 1.094(0.316) \end{bmatrix}$$

Note that in this model Ω_u describes the variance within vital rates and covariances between vital rates, which also includes (co)variation due to density dependence and climatic or environmental variables.

Model with climatic, density and other environmental covariates

Below we give the final model that included three climatic/environmental variables explaining a substantial amount of the temporal variation in vital rates (see Fig. 3 in the main text). Models that included various density and other environmental variables were not better supported by the data as determined by model selection procedures based on information theoretic criteria (all ΔDIC>1). The model can be described by the following multivariate regression equation:

$$\begin{bmatrix} \log f_{L\,ij} \\ \log f_{H\,ij} \\ \text{logit}\, s_{o\,ij} \\ \text{logit}\, s_{1\,ij} \\ \text{logit}\, s_{2\,ij} \\ \text{logit}\, s_{N\,ij} \\ \text{logit}\, s_{L\,ij} \\ \text{logit}\, s_{H\,ij} \end{bmatrix} = \begin{bmatrix} -1.821(0.156) \\ -2.712(0.146) \\ 0.126(0.153) \\ 1.203(0.136) \\ 3.358(0.165) \\ 2.830(0.099) \\ 3.057(0.116) \\ 3.213(0.175) \end{bmatrix} + \begin{bmatrix} 0 \\ 0 \\ 0.190(0.081) \\ 0.182(0.067) \\ 0.200(0.095) \\ 0.195(0.053) \\ 0.235(0.061) \\ 0.344(0.093) \end{bmatrix} (w - w^*) + \begin{bmatrix} 0.0142(0.0044) \\ 0.0132(0.0028) \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \end{bmatrix} (r - r^*) + \begin{bmatrix} -1.318(0.388) \\ -1.229(0.404) \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \end{bmatrix} (q - q^*) + \begin{bmatrix} u_{f_L 0 j} \\ u_{f_H 0 j} \\ u_{s_0 0 j} \\ u_{s_N 0 j} \\ u_{s_N 0 j} \\ u_{s_N 0 j} \\ u_{s_L 0 j} \\ u_{s_H 0 j} \end{bmatrix}$$

with three environmental variables winter temperature w (°C), ragworm abundance r (individuals/m^2*)* and flooding event q (0 or 1) included. These variables were standardized to mean 0 by subtracting the normalization constants w^*=3.67, r^*=107.2 and q^*=0.375 as determined over the study period 1983-2007. Ragworm abundance was subsequently modeled as a function of the variable winter temperature (Fig. 3I): $r = 153.04(15.0) - 12.8(3.6)w + e_{r_j}$.

Winter temperature was modeled as a random variable described by a transformed lognormal process $w \sim 10 - LogNormal(\mu - 10, \sigma)$, with μ and σ chosen such that $E(w) = 3.67(0.44)$ and $\sigma_w = 1.71(0.49)$ as in the study period 1983-2007 (see Fig. 2C). In this paper we focus on temperature effects (as this is the only variables for which we have evidence that it will change systematically in the future) and therefore residual ragworm process variance (e_{r_j}) and flooding events were modeled as random variables part of the residual environmental stochasticity:

$$\begin{bmatrix} \log f_{L\,ij} \\ \log f_{H\,ij} \\ \operatorname{logit} s_{o\,ij} \\ \operatorname{logit} s_{1ij} \\ \operatorname{logit} s_{2\,ij} \\ \operatorname{logit} s_{N\,ij} \\ \operatorname{logit} s_{L\,ij} \\ \operatorname{logit} s_{H\,ij} \end{bmatrix} = \begin{bmatrix} -1.821(0.156) \\ -2.712(0.146) \\ 0.126(0.153) \\ 1.203(0.136) \\ 3.358(0.165) \\ 2.830(0.099) \\ 3.057(0.116) \\ 3.213(0.175) \end{bmatrix} + \begin{bmatrix} -0.182(0.076) \\ -0.169(0.060) \\ 0.190(0.081) \\ 0.182(0.067) \\ 0.200(0.095) \\ 0.195(0.053) \\ 0.235(0.061) \\ 0.344(0.093) \end{bmatrix} + (w - w^*) + \begin{bmatrix} 0.0142(0.0044) \\ 0.0132(0.0028) \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \end{bmatrix} e_{r_j} + \begin{bmatrix} -1.318(0.388) \\ -1.229(0.404) \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \end{bmatrix} e_{q_j} + \begin{bmatrix} u_{f_L 0 j} \\ u_{f_H 0 j} \\ u_{s_0 0 j} \\ u_{s_N 0 j} \\ u_{s_N 0 j} \\ u_{s_N 0 j} \\ u_{s_L 0 j} \\ u_{s_H 0 j} \end{bmatrix}$$

with ragworm process variance $e_{r_j} \sim N(0, \sigma_{e_r}) : \sigma_{e_r} = 31.5(9.1)$, flooding variance

$e_{q\,j} \sim \left(Bin(\pi) - \pi\right) : \pi = 0.375(0.049)$ and residual environmental (co)variances:

$$\begin{bmatrix} u_{f_L 0 j} \\ u_{f_H 0 j} \\ u_{s_0 0 j} \\ u_{s_N 0 j} \\ u_{s_L 0 j} \\ u_{s_H 0 j} \end{bmatrix} \sim MVN(0, \Omega_u) : \Omega_u = \begin{bmatrix} 0.617(0.178) & & & & & \\ 0.021(0.088) & 0.300(0.087) & & & & \\ 0.114(0.117) & -0.114(0.083) & 0.513(0.148) & & & \\ -0.078(0.076) & -0.116(0.057) & 0.143(0.074) & 0.216(0.062) & & \\ 0.010(0.0087) & -0.163(0.069) & 0.221(0.091) & 0.147(0.060) & 0.295(0.085) & \\ -0.030(0.132) & -0.119(0.095) & 0.239(0.130) & 0.124(0.082) & 0.108(0.094) & 0.674(0.195) \end{bmatrix}$$

The contribution of variance component of environmental variable *Z* (or density variable *N*) to total process variance in vital rate x_i was calculated using the formula:

$$R^2_{Z,x_i} = \frac{\sigma^2_{u_{x_i 0}\,\text{model without Z}} - \sigma^2_{u_{x_i 0}\,\text{model with Z}}}{\sigma^2_{u_{x_i 0}\,\text{model without Z}}}$$

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

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

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

1991	Odd Terje Sandlund	Dr. philos Zoology	The dynamics of habitat use in the salmonid genera *Coregonus* and *Salvelinus*: Ontogenic niche shifts and polymorphism
1991	Nina Jonsson	Dr. philos	Aspects of migration and spawning in salmonids
1991	Atle Bones	Dr. scient Botany	Compartmentation and molecular properties of thioglucoside glucohydrolase (myrosinase)
1992	Torgrim Breiehagen	Dr. scient Zoology	Mating behaviour and evolutionary aspects of the breeding system of two bird species: the Temminck's stint and the Pied flycatcher
1992	Anne Kjersti Bakken	Dr. scient Botany	The influence of photoperiod on nitrate assimilation and nitrogen status in timothy (*Phleum pratense* L.)
1992	Tycho Anker-Nilssen	Dr. scient Zoology	Food supply as a determinant of reproduction and population development in Norwegian Puffins *Fratercula arctica*
1992	Bjørn Munro Jenssen	Dr. philos Zoology	Thermoregulation in aquatic birds in air and water: With special emphasis on the effects of crude oil, chemically treated oil and cleaning on the thermal balance of ducks
1992	Arne Vollan Aarset	Dr. philos Zoology	The ecophysiology of under-ice fauna: Osmotic regulation, low temperature tolerance and metabolism in polar crustaceans.
1993	Geir Slupphaug	Dr. scient Botany	Regulation and expression of uracil-DNA glycosylase and O^6-methylguanine-DNA methyltransferase in mammalian cells
1993	Tor Fredrik Næsje	Dr. scient Zoology	Habitat shifts in coregonids.
1993	Yngvar Asbjørn Olsen	Dr. scient Zoology	Cortisol dynamics in Atlantic salmon, *Salmo salar* L.: Basal and stressor-induced variations in plasma levels ans some secondary effects.
1993	Bård Pedersen	Dr. scient Botany	Theoretical studies of life history evolution in modular and clonal organisms
1993	Ole Petter Thangstad	Dr. scient Botany	Molecular studies of myrosinase in Brassicaceae
1993	Thrine L. M. Heggberget	Dr. scient Zoology	Reproductive strategy and feeding ecology of the Eurasian otter *Lutra lutra*.
1993	Kjetil Bevanger	Dr. scient. Zoology	Avian interactions with utility structures, a biological approach.
1993	Kåre Haugan	Dr. scient Bothany	Mutations in the replication control gene trfA of the broad host-range plasmid RK2
1994	Peder Fiske	Dr. scient. Zoology	Sexual selection in the lekking great snipe (*Gallinago media*): Male mating success and female behaviour at the lek
1994	Kjell Inge Reitan	Dr. scient Botany	Nutritional effects of algae in first-feeding of marine fish larvae
1994	Nils Røv	Dr. scient Zoology	Breeding distribution, population status and regulation of breeding numbers in the northeast-Atlantic Great Cormorant *Phalacrocorax carbo carbo*
1994	Annette-Susanne Hoepfner	Dr. scient Botany	Tissue culture techniques in propagation and breeding of Red Raspberry (*Rubus idaeus* L.)
1994	Inga Elise Bruteig	Dr. scient Bothany	Distribution, ecology and biomonitoring studies of epiphytic lichens on conifers
1994	Geir Johnsen	Dr. scient Botany	Light harvesting and utilization in marine phytoplankton: Species-specific and photoadaptive responses
1994	Morten Bakken	Dr. scient Zoology	Infanticidal behaviour and reproductive performance in relation to competition capacity among farmed silver fox vixens, *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
1997 Jon Arne Grøttum	Dr. scient. Zoology	Physiological effects of reduced water quality on fish in aquaculture
1997 Per Gustav Thingstad	Dr. scient. Zoology	Birds as indicators for studying natural and human-induced variations in the environment, with special emphasis on the suitability of the Pied Flycatcher
1997 Torgeir Nygård	Dr. scient Zoology	Temporal and spatial trends of pollutants in birds in Norway: Birds of prey and Willow Grouse used as Biomonitors

1997	Signe Nybø	Dr. scient. 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. 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 Zoology	Adaptive and incidental biological ice nucleators
1997	Arild Magne Landa	Dr. scient Zoology	Wolverines in Scandinavia: ecology, sheep depredation and conservation
1997	Kåre Magne Nielsen	Dr. scient Botany	An evolution of possible horizontal gene transfer from plants to sail bacteria by studies of natural transformation in *Acinetobacter calcoacetius*
1997	Jarle Tufto	Dr. scient Zoology	Gene flow and genetic drift in geographically structured populations: Ecological, population genetic, and statistical models
1997	Trygve Hesthagen	Dr. philos Zoology	Population responces of Arctic charr (*Salvelinus alpinus* (L.)) and brown trout (*Salmo trutta* L.) to acidification in Norwegian inland waters
1997	Trygve Sigholt	Dr. philos Zoology	Control of Parr-smolt transformation and seawater tolerance in farmed Atlantic Salmon (*Salmo salar*) Effects of photoperiod, temperature, gradual seawater acclimation, NaCl and betaine in the diet
1997	Jan Østnes	Dr. scient Zoology	Cold sensation in adult and neonate birds
1998	Seethaledsumy Visvalingam	Dr. scient Botany	Influence of environmental factors on myrosinases and myrosinase-binding proteins
1998	Thor Harald Ringsby	Dr. scient Zoology	Variation in space and time: The biology of a House sparrow metapopulation
1998	Erling Johan Solberg	Dr. scient. Zoology	Variation in population dynamics and life history in a Norwegian moose (*Alces alces*) population: consequences of harvesting in a variable environment
1998	Sigurd Mjøen Saastad	Dr. scient Botany	Species delimitation and phylogenetic relationships between the Sphagnum recurvum complex (Bryophyta): genetic variation and phenotypic plasticity
1998	Bjarte Mortensen	Dr. scient Botany	Metabolism of volatile organic chemicals (VOCs) in a head liver S9 vial equilibration system in vitro
1998	Gunnar Austrheim	Dr. scient Botany	Plant biodiversity and land use in subalpine grasslands. – A conservtaion biological approach
1998	Bente Gunnveig Berg	Dr. scient Zoology	Encoding of pheromone information in two related moth species
1999	Kristian Overskaug	Dr. scient Zoology	Behavioural and morphological characteristics in Northern Tawny Owls *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
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*
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
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
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