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NTNU
Norwegian University of
Science and Technology

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Doctoral thesis

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Thesis for the Degree of
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Preface

> —*If I have seen further, it is by standing on the shoulders of giants.*
>
> Sir Isaac Newton (1676)

I am thankful for the opportunity to become deeply immersed in the fascinating world of biology, it has been challenging, rewarding and periodically exhausting. Several people deserve my thanks. First, my supervisor Bernt-Erik Sæther and co-supervisors Thor Harald Ringsby and Henrik Jensen for continued support, inspiration and knowledge. Steinar Engen, for statistical knowledge and advice. The rest of my co-authors, Hallvard Haanes, Knut H. Røed, Erling J. Solberg, Ingerid J. Hagen, Bernt Rønning, Henrik Pärn and Håkon Holand, for discussions and constructive comments.

The work of this thesis build on the effort of several people in study systems spanning two decades. They deserve many thanks for the dedication and careful collection of high quality data. I would also like to thank all the local people at the islands along the coast of Helgeland for the hospitality and friendliness experienced during all my fieldwork, it has been unprecedented.

During the days in the office, out in the field and in the lab, I have been lucky to be surrounded by a lot of great colleagues and friends. Thanks for the most welcomed distractions and good laughs, and thanks for the helpful, interesting and inspiring talks and discussions. Special thanks go to all my good colleagues in both the house sparrow and moose project. I have enjoyed working with you all.

At last I want to thank my friends, parents and family, your presence and support means a lot to me. Most of all I want to thank my dearest Eva Sofie for being loving, caring and supportive, and our two sons, William and Sebastian, for bringing so much joy into our lives. You three are most important of all.

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Trondheim
November 2015

Thomas Kvalnes

Contents

Papers I-IV

Summary

In age-structured populations, subject to environmental and demographic stochasticity, the response to selection on fitness-related traits will be a complex result of selection at different life stages. Understanding how selection at different stages of the life history interact to determine the total selection differential is important to enable predictions of evolutionary change. This thesis contributes to this end by showing how current methods for estimating selection can be extended using a demographic framework. Then reproductive values and the stable age distribution can be used to account for the effects of age-structure and estimate selection.

The individual reproductive value is the relevant measure of fitness in age-structured populations with no density regulation. This measure of fitness is defined as an individuals contribution to the total reproductive value of the population next year. Then the total selection on a trait was shown to be a weighted sum of age-specific selection gradients with weights equal to the stable age distribution. This enabled the estimation of temporal mean selection and fluctuation selection using maximum likelihood methods. The R package *lmf* was developed to implement these methods in statistical analyses.

In the Robertson-Price equation, the total change in a mean trait over a time step is separated into two additive components. The first is the covariance of trait and relative fitness (i.e. the selection differential). The second, an expectation which describe how offspring differ from their parents (a transmission term). A generalization of the Robertson-Price equation for a weighted mean was derived. The correct selection differential was obtained by using reproductive values as weights. For any other choice of weights, estimated selection differentials contained *transient quasi-selection* due to fluctuations in the age-distribution and variation in the mean trait between age classes.

Harvesting has repeatedly been shown to be non-random with respect to age in wild populations. For instance, due to a preference for old individuals which also are large. In a harvested moose population, an extension of the generalized Robertson-Price equation for multiple traits was applied to investigate harvest-induced selection. Hunters were shown to induce selection for later birth dates and smaller calf body mass. This may have detrimental effects on the population in the long run, as early birth date and high calf body mass are generally associated with high fecundity in moose.

An artificial selection experiment successfully perturbed body size in a population of house sparrows from their natural mean. This induced large age-specific variation in mean phenotypes and fluctuations in the age distribution. Using the R package *lmf*, natural selection was shown to oppose the artificial selection, indicating the presence of an optimal phenotype. While offspring of artificially selected parents produced less recruits than individuals with unselected parents, there was also some indications that this effect was most pronounced in the first age class.

The results in this thesis emphasize the advantages of using methods which allows for handling fluctuations in age distribution and variation in mean phenotypes between age classes when analysing selection in wild populations. Ignoring age-structure may seriously affect inferences of natural selection.

List of papers

I Engen, S., B.-E. Sæther, **T. Kvalnes**, H. Jensen. 2012. Estimating fluctuating selection in age-structured populations. Journal of Evolutionary Biology 25:1487-1499.[1]

II Engen, S. **T. Kvalnes**, B.-E. Sæther. 2014. Estimating phenotypic selection in age-structured populations by removing transient fluctuations. Evolution 68:2509-2523.[2]

III **Kvalnes, T.**, B.-E. Sæther, H. Haanes, K.H. Røed, S. Engen, E.J. Solberg. 2015. Harvest-induced phenotypic selection in an island moose *Alces alces* population. Evolution. *Revision welcomed.*[3]

IV **Kvalnes, T.**, T.H. Ringsby, H. Jensen, I.J. Hagen, B. Rønning, H. Pärn, H. Holand, S. Engen, B.-E. Sæther. 2015. Artificial selection on body size in a wild passerine bird: presence of an optimal phenotype. Evolution. *Submitted.*[4]

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[1] SE and BES initiated the project. SE developed the model with contributions from TK. TK programmed the R package *lmf* available through *The Comprehensive R Archive Network* (CRAN) for fitting models, handled data and performed the analyses. SE and BES wrote the paper with contributions and comments from TK and HJ.

[2] SE and BES initiated the project. SE developed the model. TK handled the data and performed the empirical analyses. BES and SE wrote the paper with contributions and comments from TK.

[3] BES and EJS initiated the project. TK handled the data, perfomed the analyses and wrote the paper. HH and KHR genotyped individuals and performed the parenthood analyses. SE contributed to the analyses. All authors contributed with comments to the manuscript.

[4] T.H.R., H.J. and B.-E.S. came up with the idea and study design. T.K. handled the data, performed the analyses and wrote the paper. H.J., I.J.H., B.R. and T.K. did the parentage analyses. S.E. advised the statistical analyses. All authors except S.E. performed fieldwork for the study. All authors contributed with comments and edits when writing up the manuscript.

Introduction

Natural selection is an important cause of evolution in heritable traits (Darwin, 1859; Fisher, 1930; Haldane, 1932; Charlesworth et al., 1982; Endler, 1986; Schluter, 2000). Selection on quantitative traits in contemporary natural populations has been investigated in a wide range of species (Kingsolver et al., 2001; Kingsolver and Diamond, 2011). Directional selection may often be quite strong (Hereford et al., 2004), differ in strength between fitness components (Kingsolver et al., 2001; Hereford et al., 2004), and display temporal fluctuations (Siepielski et al., 2009, 2011; Bell, 2010; Morrissey et al., 2012). In the fossil record, many macroevolutionary patterns may be explained by a few periods of rapid evolution followed by long periods of stabilizing selection around a optimum with small fluctuations (Estes and Arnold, 2007; Uyeda et al., 2011).

Adaptive evolutionary changes has been reported repeatedly in wild populations (Endler, 1980; Grant and Grant, 1995; Losos et al., 1997; Calsbeek and Cox, 2010; Hendry and Kinnison, 1999; Schluter, 2000). The key role of selection in adaptive evolution is easily appreciated from the Lande equation, $\mathbf{R} = \mathbf{G}\boldsymbol{\beta}$ (Lande, 1979). Where directional selection on a suite of traits $\boldsymbol{\beta}$ translates into adaptive responses $\mathbf{R}$ through the $\mathbf{G}$-matrix. The $\mathbf{G}$-matrix contain additive genetic (co)variances for all traits under selection (Lande, 1979, 1982).

Reznick and Ghalambor (2001) reviewed which population ecological conditions that generally seems to promote adaptive changes. Novel environmental biotic or abiotic elements are a common denominator which may be classified into two categories (Reznick and Ghalambor, 2001): (1) new environments due to colonization and (2) heterogeneous environments and metapopulation structure. As an example of the former process, Losos et al. (1997) made an experimental introduction of brown anole *Anolis sagrei* lizards to several new islands from a nearby source population. The lizards adapted morphologically to the new islands, with the magnitude of divergence predicted by the difference in vegetation from the source. Another example is the adaptive radiation in Darwin's finches following the colonization of the Galapagos islands by a common ancestor native to Central or South-America (Schluter, 2000; Sato et al., 2001). The present 14 species has diverged in beak morphology in accordance with the availability of food niches (Lack, 1947; Grant, 1999; Schluter, 2000). Adaptations to novel food sources is likely to have sparked speciation in their ancetor species (Lack, 1947; Schluter, 2000).

The second category defined by Reznick and Ghalambor (2001) are related to abrupt changes in the biotic or abiotic environment of a population, which result in a perturbed fitness landscape. For instance, populations of guppies *Poecilia reticulata* living in low predation habitats with vividly coloured males has been shown to evolve more dull males when introduced to high predation habitats (Endler, 1980). In a population of medium ground finch *Geospiza fortis* (one of the Darwin's finches), droughts has been found to cause major changes to their food supply (mainly seeds) during dry seasons. Each of two droughts which has been reported, resulted in viability selection and evolutionary responses towards larger or smaller beaks, depending on which type of food were most abundant during and after the droughts (Grant and Grant, 1995). Anthropogenic sources of selection also fall into this category of conditions which are often found to promote evolutionary changes (Law, 2007; Proaktor et al., 2007; Allendorf and Hard, 2009; Darimont et al., 2009; Engen et al., 2014). For instance, in bighorn sheep *Ovis canadensis* male horn size is a sexually selected trait used in male competition for matings (Coltman et al., 2002). Following more than 30 years of selective trophy hunting for large horns, Coltman et al. (2003) found that males had evolved smaller horns and body size. In commercially exploited fish populations, earlier maturation and smaller age-specific size has both been attributed to intensive selective fishing for large fish (Law, 2000).

Evolution might be both predictable and unpredictable depending on the time span considered (Grant and Grant, 2002). In the short term, selection may result in predictable evolutionary responses (Lande, 1979). However, in the long term evolutionary changes will be affected by random genetic drift, changing environmental conditions, changes in the genetic architecture and other processes, which might not have been predicted in advance (Lande, 1976, 1979; Uyeda et al., 2011). Fitness is a central concept to determine the relative performance of individuals. Individual fitness is usually defined from individual records of survival and production of offspring (Sæther and Engen, 2015). Both of these are affected by environmental and demographic stochasticity (Lande et al., 2003). Environmental stochasticity affects all individuals in a population equally and is caused by random environmental variation between time steps (e.g. years) (Engen et al., 1998; Lande et al., 2003). On the contrary, demographic stochasticity affects each individual independently and is caused by random demographic variation between individuals at a given time (Engen et al., 1998; Lande et al., 2003). It follows that demographic stochasticity will have the largest effect on evolutionary and population dynamics in small population, while the effects of demographic stochasticity in large populations will average to zero (Lande et al., 2003). Engen and Sæther (2014) showed how the two stochastic components generate fluctuating selection and genetic drift and affects the evolutionary changes in a population.

Phenotypic selection differentials may be estimated empirically by the covariance of traits and relative fitness, as defined in the Robertson-Price equation (Robertson, 1966;

Price, 1970, 1972; Frank, 1997, 2012; Gardner, 2008). Selection estimated this way includes both the direct selection on a trait and any indirect selection due to selection on correlated traits. If all traits correlated with a focal trait under selection is included, multiple regression may be applied to separate out the direct selection on a trait (Lande and Arnold, 1983). A key advantage of the Lande-Arnold method (1983) for estimating selection gradients, is the ease with which it might be applied to empirical data from natural populations. That is, the statistical method used in the estimation process, multiple regression, is readily available using any general statistical software. However, these methods are based on several simplifying assumptions, including no overlapping generations.

In age-structured populations, an individuals contribution to future generations is determined by its survival and production of offspring during several life stages (Lande, 1982; Brommer et al., 2004). For instance, the number of successfully fledged offspring has been found to increase and then decline with age in female red-billed choughs *Pyrrhocorax pyrrhocorax* (Reid et al., 2003). Under natural conditions, environmental and demographic stochasticity will generate fluctuations in these vital rates, with fluctuations in the age distribution of the population as a result (Lande et al., 2003; Engen et al., 2005, 2007). Furthermore, fluctuating selection and genetic drift may cause significant age-specific variation in fitness-related traits such that the response to selection will be a complex result of selection at different life stages (Coulson et al., 2006; Coulson and Tuljapurkar, 2008). Ignoring age-structure, for instance by using lifetime reproductive success and assuming a stable age-distribution (Grafen, 1988; Sæther and Engen, 2015), may seriously affect inferences of natural selection.

An intriguing thought would be to derive a type of individual weights which had the property of removing the effects of age-structure in populations with overlapping generations (Price and Smith, 1972; Lande, 1982). Such a weighting would have to remove the effects of age from individual differences in vital rates and phenotypes, while maintaining all other causes of individual variation. This weighting would then leave populations with overlapping generations to be treated similarly as populations with non-overlapping generations (e.g. Sæther et al., 1998). Thus, selection and evolutionary responses could be estimated using standard theory on the evolution of quantitative traits (Lande, 1979, 1982; Lande and Arnold, 1983). The reproductive value was introduced by Fisher (1930) to have such properties. In models with age-structured populations, Engen et al. (2009) investigated the evolution of allele frequencies and (Engen et al., 2011) the evolution in a plastic quantitative trait. A general conclusion from these papers was, that weighting by the reproductive value generally removed the effect of age-structure on the evolutionary dynamics of the populations. Engen et al. (2011) suggested that their results could be used to construct methods for the estimation of selection from samples of individuals with known age over a series of years.

Aim

The aim of this thesis was to expand the current knowledge on natural selection and adaptive evolution in populations with overlapping generations (age-structure) in fluctuating environments. Specifically, the thesis address some key assumptions of the Lande and Arnold (1983) method for estimating selection. Namely that the investigated population has obtained a stable age distribution, is not subject to stochastic fluctuations in the fitness function and has no demographic stochasticity in the vital rates (infinite population size). The following research objectives were addressed using simulations and long-term data sets on wild populations of house sparrow *Passer domesticus* and moose *Alces alces.*

1. Explore and contribute to novel demographic approaches for estimating selection (Paper I and II)
2. Illustrate the effects of fluctuations in age-structure on estimates of selection and evolutionary responses (Papers II)
3. Investigate selection and evolutionary response resulting from a known agent of selection in an age-structured population (Papers III)
4. Estimate the evolutionary responses to artificial selection in the wild and explore its evolutionary consequences (Papers IV)

General methods

The study of evolutionary processes in long-lived animals can greatly benefit from the use of high quality long-term data sets with phenotypes and fitness monitored on an individual basis (Clutton-Brock and Sheldon, 2010). In the following, I first describe the house sparrow (paper I, II and IV) and moose (paper III) study systems used in this thesis, then introduce matrix population models, the stable age distribution and reproductive value which are central concepts in the papers. The study systems are all located on the four islands Hestmannøy ($66°33'\text{N}, 12°50'\text{E}$), Aldra ($66°25'\text{N}, 13°04'\text{E}$), Vega ($65°40'\text{N}, 11°55'\text{E}$) and Leka ($65°06'\text{N}, 11°38'\text{E}$) in northern and mid-Norway as shown in the map in Figure 1.

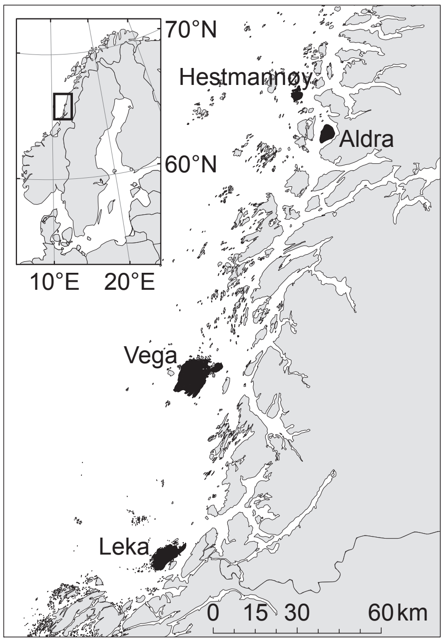

Figure 1: Map of the house sparrow and moose study islands (in black). House sparrows are studied on all four islands, while moose are studied at Vega.

The house sparrow study system

The house sparrow is a small passerine bird in the family Passeridae (Fig. 2). It is closely associated with human settlements and agriculture, and has a near worldwide distribution due to natural dispersals from its native range (most of Eurasia) and several deliberate introductions by humans (Anderson, 2006). The species is sexually dimorphic, where males differs from females by a more brightly coloured plumage and slightly larger size (Anderson, 2006).

Figure 2: A male house sparrow marked with a unique combination of three plastic colour rings and a numbered metal ring. Photo: Thomas Kvalnes.

House sparrows inhabit several islands with human settlements along the coast of northern and mid-Norway. The populations at Hestmannøy (paper IV) and Aldra (paper I and II) are part of a archipelago with 18 surrounding islands which has been monitored on an individual basis since 1992 until present (for a map over these islands see Pärn et al., 2012). Further south, the individuals in the populations at Leka and Vega has been followed since 2001 and was subject to an artificial selection experiment in the years 2002-2005 (paper IV). All four islands has large agricultural areas and farms where the sparrows live and breed. They build their nests in and around barns and cattle sheds, or in a few nest boxes which has been provided (Ringsby et al., 1998).

A very high proportion of individuals in these populations were marked with a unique combination of three plastic colour rings and a numbered metal ring from the Ringing Centre at Museum Stavanger. Individuals were captured by hand as nestlings, following thorough searches for active nests, or captured using mist nets. At Hestmannøy and

Aldra, individuals were captured and observed during the breeding season from May until mid-August and for a period during the autumn. Individuals on Leka and Vega were mainly captured or observed during approximately two weeks of intensive fieldwork in each population during February-March. All individuals were measures for tarsus length (± 0.01 mm) and body mass (± 0.1 g), and full grown individuals were further measured for wing length (± 1 mm), bill length (± 0.01 mm) and bill depth (± 0.01 mm). Nestlings were set up to be measured at the age of 11 days. However, due to logistical reasons measurements were allowed to be made at ages 8-13 days. Hence, all nestling measurements (paper I and II) had to be standardised to a 10-day-old measure prior to analyses using quadratic regression (Ringsby et al., 1998). Using blood samples from all marked individuals, genetic pedigrees were constructed for all four populations (for details see Jensen et al., 2004, 2008; Billing et al., 2012; Rønning et al., 2015).

The moose study system

The moose is an even-toed ungulate in the family Cervidae (Fig. 3), in which it is the largest extant species (Bubenik, 2007). It is found in the boreal forests of the northern hemisphere where it has a broad circumpolar distribution (Karns, 2007). Males are considerably larger than females and grow antlers which they shed annually following the end of the rut (i.e. mating season) (Solberg and Sæther, 1994).

Figure 3: A four year old female moose marked with a numbered ear tag and tracking collar. Photo: Kari Bjørneraas.

On the island Vega (paper III, see Fig. 1) the population of moose has a history which has been tracked back to one male and two female yearling immigrants which founded the population in 1985 (Sæther et al., 2007; Haanes et al., 2013). Several immigrants to the population has been recorded since and a few moose has emigrated (Sæther et al., 2007; Herfindal et al., 2014). The island has an area of 119 km^2 that is dominated by agricultural areas, marsh and moor land, and areas of deciduous and coniferous forest (Solberg et al., 2008). The population has been monitored at an individual level in the period from 1992 until present. Each winter (January-March) all new calves (and immigrants) has been individually marked by ear tags and tracking collars (VHS/GPS), ensuring that $> 90\%$ of individuals has been marked at all times during the study (Solberg et al., 2007, 2010). All captured individuals has been measured for calf body mass (± 2 kg). Birth date (± 1 day) was recorded by tracking pregnant females in May-June (the calving season) until the presence, number and age of calves were confirmed (Sæther et al., 2003). Annually since 1989, the population has been subject to harvesting (throughout October) by local moose hunters (Sæther et al., 2003). This has kept the winter population size around 25 to 43 individuals annually (Solberg et al., 2007). Using tissue samples from harvested and marked individuals, a genetic pedigree had been constructed with a total of 499 individuals born in the period 1984-2012 (Haanes et al., 2013).

Matrix population models

Both house sparrows and moose can live for several years and reproduce repeatedly during their lifetime (Anderson, 2006; Van Ballenberghe and Ballard, 2007). In fluctuating environments the population dynamics of age-structured populations can be described using matrix population models with stochastic projection matrix $\mathbf{L}_t$, where t denotes time (Caswell, 2001; Lande et al., 2003; Engen et al., 2005). Here it is only dealt with one of the sexes in the population, assuming that the other sex is not limiting the population growth rate (Leslie, 1948). Assuming a density independent population with age classes $x = (1, 2, ..., k)$ and population vector $\mathbf{n}_t$ in year t, the population vector in year $t + 1$ is given by $\mathbf{L}_t\mathbf{n}_t = \mathbf{n}_{t+1}$ or,

$$\begin{bmatrix} F_0 & F_1 & F_2 & \cdots & F_k \\ S_0 & 0 & \cdots & \cdots & 0 \\ 0 & S_1 & 0 & \cdots & \vdots \\ \vdots & \cdots & \ddots & \cdots & \vdots \\ 0 & \cdots & 0 & S_{k-1} & 0 \end{bmatrix}_t \begin{bmatrix} n_0 \\ n_1 \\ n_2 \\ \vdots \\ n_k \end{bmatrix}_t = \begin{bmatrix} n_0 \\ n_1 \\ n_2 \\ \vdots \\ n_k \end{bmatrix}_{t+1}$$

Where $\mathbf{L}_t$ is the square projection matrix in year t known as the Leslie matrix where all elements are zero, except age-specific fecundities (F_x) in the first row and survivals (S_x) in the subdiagonal (Leslie, 1945, 1948; Caswell, 2001; Engen et al., 2005). More generally, for a stage-structured population the projection matrix is known as the Lefkovitch matrix, which may have additional non-zero elements (Lefkovitch, 1965; Caswell, 2001). For instance, all individuals above a given age may be collected in a final stage such that the element $L_{k,k}$ gives the probability for surviving and staying in this stage. Taking the expectation $\mathrm{E}\mathbf{L}_t = \mathbf{l}$, the elements of $\mathbf{l}$ may be estimated as the mean age-specific fecundities and survivals across individuals and years (Engen et al., 2005, 2009). The dominant eigenvalue of $\mathbf{l}$ is then the deterministic multiplicative growth rate λ in the average environment (Caswell, 2001; Lande et al., 2003). Furthermore, the stable age distribution ($\mathbf{u}$) and age-specific reproductive value ($\mathbf{v}$) are given by the corresponding left and right eigenvectors of $\mathbf{l}$, provided that these are scaled such that $\Sigma u_x = 1$ and $\Sigma u_x v_x = 1$ (Caswell, 2001; Lande et al., 2003). The reproductive value v_x of a female of age x is her expected contribution to the future growth of the population. Furthermore, the sum $\mathbf{v}\mathbf{n}_t$ equals the total reproductive value of the population V_t in year t (Fisher, 1930; Lande et al., 2003; Engen et al., 2007).

In a population without age-structure (i.e. where reproduction and survival is independent of age), the contribution of an individual i to next years breeding population is simply $W = B_i + J_j$, where B is the number of offspring and J is 1 if the individual survived and 0 if it dies (Engen et al., 1998; Sæther et al., 1998). Now, weighting by the reproductive value, Engen et al. (2009) defined the individual reproductive value as an individuals contribution to the total reproductive value of the population next year. For an individual i this is simply calculated as,

$$W_i = B_i v_1 + J_i v_{x+1}. \tag{1}$$

Where B and J are as defined above and v is the age-specific reproductive value (Engen et al., 2009). This is a relevant measure of absolute individual fitness for studying natural selection in density independent age-structured populations.

Main results and discussion

We use the concept of reproductive value (Fisher, 1930) to develop a method for estimating selection in density independent age-structured populations in the two first papers (paper I and II). Bridging the gap between theory and practice is essential if novel statistical methods are to be used in applications to empirical data. Hence, one of the objectives in paper I was to make the framework we developed for estimating selection easily available to the scientific community. The result was the program *lmf*, an add-on package available for use in the statistical software R (R Core Team, 2015). Several of the methods made available through this package is equally applicable in analyses using the method developed in Paper II. Both papers utilize properties of reproductive values to estimate the total selection on traits.

In paper I it is shown that the individual reproductive value (eqn. 1) can be used as dependent variable (fitness) in multiple regression models to estimate selection on a set of traits (covariates). First, reproductive values ($\mathbf{v}$) and the stable age distribution ($\mathbf{u}$) has to be estimated using the expected projection matrix ($\mathbf{l}$). This matrix can be populated by the mean age-specific fecundities and survivals across years (Engen et al., 2009). Then, if the traits are centred by their mean across years, selection on a set of traits can be estimated within age-classes and years. The annual estimates of selection from this model are weighted means of the age-specific estimates, with the stable age distribution ($\mathbf{u}$) as weights. Temporal mean selection gradients and estimates of fluctuating selection can be estimated using maximum likelihood methods. Estimates of demographic and environmental variance is also calculated in this framework. Uncertainty in the estimated parameters and hypothesis testing can be performed using parametric or non-parametric bootstrapping. Here the uncertainty due to demographic variance may be accounted for. All of these methods are implemented in the R package *lmf*.

Selection was estimated using data on house sparrows in the population at Aldra (see Fig. 1). There was a non-significant temporal trend for negative selection on body mass and positive selection on tarsus length. There was no fluctuating selection, but large temporal variation in the estimated selection gradients due to a large demographic variance in this population, compared to previous estimates in short-lived birds (Sæther et al., 2004). Large demographic variance will in general limit our ability to detect significant selection unless sample sizes are large or selection is very strong (Engen and

Sæther, 2014). Accordingly, estimates of selection in natural population may often be associated with large uncertainties (Morrissey et al., 2012). In the discussion of paper I the developed method is discussed with reference to the classical methods by Lande and Arnold (1983) for estimating selection.

The Robertson-Price equation (Robertson, 1966; Price, 1970, 1972) is an exact accounting of the change in phenotype in a finite population during a time step. However, it has a clear interpretation only in populations without age-structure (see Price, 1972). In paper II, a generalization of the Robertson-Price equation for the change in a weighted mean $\Delta\tilde{\mathbf{z}}$ is derived as,

$$\Delta\tilde{\mathbf{z}} = \tilde{\text{cov}}(\Lambda_{rel}, \boldsymbol{\xi}) + \tilde{\text{E}}(\Lambda_{rel}, \overline{\Delta\boldsymbol{\xi}}). \tag{2}$$

Where Λ_{rel} is the vector of individual relative fitness, $\boldsymbol{\xi}$ is the individual phenotype vector, $\overline{\Delta\boldsymbol{\xi}}$ is the difference between the phenotype of a parents and the mean of its offspring. Tilde $\sim$ over the covariance and expectation, indicate that individuals are weighted in the calculations. The selection differential (covariance term) in equation 2 can be separated into two additive covariance terms, one which is actual selection and another named *transient quasi-selection*. This latter term was shown to contain changes in the mean phenotype due to transient changes in the age-distribution and differences in mean phenotype between age classes. It may appear like selection but has no long-term evolutionary significance. Thus, it is a false selection differential. Using age-specific reproductive values as weights in equation 2 was shown to resolve this issue. Then the relative fitness will be defined through the individual reproductive value (eqn. 1) and the *transient quasi-selection* get an expectation of zero. The *transient quasi-selection* was shown to induce temporal fluctuations in the arithmetic mean phenotype of the population. The reproductive value weighted mean phenotype does not fluctuate, however, predicted responses to selection will only be obtained when all individuals under selection has left the population (died).

Re-analysing selection on body mass and tarsus length in the house sparrow population at Aldra (see Fig. 1) made the consequences of ignoring age-structure clear. The absolute values of *transient quasi-selection* were often larger than the actual selection on these traits. Hence, analyses ignoring fluctuations in age-structure and transient differences in mean phenotype between the age classes would mainly estimate false fluctuations in selection. In the discussion of paper II the weighted Robertson-Price equation is discussed with reference to earlier analyses of evolution in age-structured population. Often a stable age-distribution and constant environment is assumed by using lifetime reproductive success as a measure of fitness (Grafen, 1988).

In paper III and IV, the methods from the first two papers were applied to study selection in populations subject to known agents of selection. Either harvesting (paper

III) or experimentally induced artificial selection (paper IV). We first note that the Lande and Arnold (1983) method for estimating selection is a multivariate generalization of the covariance term in the original Robertson-Price equation (Robertson, 1966; Price, 1970, 1972). Hence, the weighted Robertson-Price equation (paper II) may also be extended to the multivariate case, estimating selection as a vector of weighted partial regression coefficients. We defined three measures of fitness when analysing harvest-induced selection in moose (paper III), total fitness (eqn. 1), viability fitness (last additive component in eqn. 1) and fecundity fitness (first additive component in eqn. 1). In this population there was only a small fraction of individuals that died from natural causes, most were harvested at some point. The high harvest pressure was found to depend on age, as has been demonstrated in a previous study of Norwegian moose (Solberg et al., 2000).

Harvest-induced and natural selection on calf body mass and birth date were analysed. There was negative fecundity selection on birth date in both female and male moose, indicating that early birth is associated with individual qualities that enhance reproductive success (Rödel et al., 2009; Plard et al., 2015). However, due to large non-selective harvesting, there was no total selection in females. On the contrary, in males there was total selection for later birth date due to a large proportion of early born males being harvested. There was no selection on calf body mass in male moose. However, in females there was harvest-induced selection for smaller females. This was due to larger females losing a higher proportion of calves to hunters than smaller females. Twin mothers was found have a higher probability of losing a calf to hunters than mothers with a single calf. Hence, as large females having a higher twinning rate than smaller females early in life (Solberg et al., 2008), this could partly explain the selection for smaller calf body mass. The heritability of calf body mass and birth date were estimated and used to predict responses to selection. Birth date was found to delay over the years in accordance with predictions. Hence, the current harvest regime may have detrimental effects on the population in the long-run by perturbing birth dates from their natural mean. Another evident effect of harvesting was related to the increased demographic variance in individual reproductive values. Despite fecundity selection for earlier births in females, the increased mortality through non-selective harvesting made it impossible to detect any significant total selection. Accordingly, selection differentials estimated in natural populations will generally contain components due to environmental and demographic stochasticity (Engen and Sæther, 2014).

The artificial selection experiment in paper IV was analysed using the *lmf* package. Tarsus length was the target of artificial selection over four consecutive years (2002-2005). Variation in this trait has earlier been associated with early life survival (Ringsby et al., 1998) and lifespan (Jensen et al., 2004) in house sparrows. In general, tarsus length is considered as a proxy for structural body size in passerine birds (Rising and Somers, 1989; Senar and Pascual, 1997). Hence, selection on this trait was expected to affect individual body size in general due to genetic correlations between traits (Hansen and Houle, 2004, 2008). Each year before the breeding season, approximately 60 % of individuals on two islands were selected against. Either because they had longer or shorter tarsi than the chosen cut-off (mean ± 0.3 SD). These populations are referred to as *low* (selected for short tarsus) and *high* (selected for long tarsus).

In both populations tarsus length responded as expected in this heritable trait (Jensen et al., 2003, 2008; Teplitsky et al., 2014). Additionally, wing lengths displayed a small significant correlated response. This was in accordance with previously found positive additive genetic covariance between wing and tarsus length (Jensen et al., 2003, 2008). A side effects of the strong artificial selection, was a high demographic variance (range $\sigma_d^2 = [0.91, 1.18]$) during the years of artificial selection, compared to the four years (2006-2009) after stopping artificial selection (range $\sigma_d^2 = [0.67, 0.86]$; see also Sæther et al., 2004). Separating individuals by their selective ancestry, individuals were defined as *unselected* (with no artificially selected parents) or *selected* (both parents artificially selected), or some combination of these two categories. Selected individuals produced significantly less recruits (offspring that survived until age 1) than unselected individuals in both experimental populations. However, this effect was present only among individuals of age 1 in the *low* population, where individuals were selected for small size. There was no difference in survival between selected and unselected individuals.

In accordance with the above results, directional selection was generally opposing the artificial selection during the first four years (2002-2005). However, due to the large demographic variance and non-selective mortality in the populations, the selection gradients were only significant in males of the *low* population. When artificial selection was stopped, the mean tarsus length generally approached the pre-experimental means. Partly this was due to the opposing fecundity selection. However, this was also an effect of mating between unselected and selected individuals and natural mortality among artificially selected parents. The results indicated the presence of an intermediate phenotype, maintained by selection towards an optimal value affected by environmental variation (Blows and Brooks, 2003; Lande, 2007; Engen et al., 2011).

Future prospects

There are currently several methods for inferences of natural selection in wild populations (see Morrissey et al., 2012; Morrissey and Sakrejda, 2013; Morrissey, 2014; Stinchcombe et al., 2014, and references therein). The methods developed in paper I and II characterise selection in a demographic framework, which provides a natural connection to common population dynamic parameters (Lande, 1982; Sæther et al., 1996; van Tienderen, 2000; Coulson et al., 2003; Lande et al., 2003).

van Tienderen (2000) clarified the the relationship between demographic and evolutionary dynamics, allowing mean-scaled selection gradients to be interpreted as elasticities. Elasticities quantify the direct effect of a trait on the population growth rate (van Tienderen, 2000; Coulson et al., 2003). Hence, they may be used to identify which traits has the highest impact on the viability of a species, which is of importance in conservation and population management (Benton and Grant, 1999). However, care must be taken as mean-scaling is only meaningful for traits on a ratio or log-interval scale, where there is an absolute zero point such that the mean is not arbitrary (e.g. tarsus length; Hansen and Houle, 2008). Thus, birth date or body condition which are used in papers III and IV cannot be mean-scaled.

Currently, only traits which can be considered fixed throughout an individuals life can be analysed using the demographic approaches in paper I and II. Hence, analysing plastic traits, such as individual variation in phenology (Charmantier et al., 2008), would require a more complex approach with more parameters (Lande, 2009; Chevin et al., 2010, 2015; Engen et al., 2011). The number of parameters needed is likely to be a challenge with respect to the uncertainty in the estimates (Chevin et al., 2015).

Density regulation of the population size is an important feature of many natural population. Thus, density-dependent selection is an area of research which needs attention in future theoretical and empirical work. While density-dependent selection has been explored in populations without age-structure (Lande, 2009; Engen et al., 2013), including age-structure would be a difficult challenge. Lande et al. (2006) provide an definition of the reproductive value in density-dependent populations. However, density dependence is likely to introduce complex interactions between age classes which needs to be handled correctly.

The effects of environmental and demographic stochasticity on the population and evolutionary dynamics of natural age-structured populations complicates interpretations of selection and evolutionary responses. Future studies should explore the possibility of integrating demographic frameworks and selection analyses to gain novel insights into both fields.

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Paper I

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Estimating fluctuating selection in age-structured populations

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Abstract

In age-structured populations, viability and fecundity selection of varying strength may occur in different age classes. On the basis of an original idea by Fisher of weighting individuals by their reproductive value, we show that the combined effect of selection on traits at different ages acts through the individual reproductive value defined as the stochastic contribution of an individual to the total reproductive value of the population the following year. The selection differential is a weighted sum of age-specific differentials that are the covariances between the phenotype and the age-specific relative fitness defined by the individual reproductive value. This enables estimation of weak selection on a multivariate quantitative character in populations with no density regulation by combinations of age-specific linear regressions of individual reproductive values on the traits. Demographic stochasticity produces random variation in fitness components in finite samples of individuals and affects the statistical inference of the temporal average directional selection as well as the magnitude of fluctuating selection. Uncertainties in parameter estimates and test power depend strongly on the demographic stochasticity. Large demographic variance results in large uncertainties in yearly estimates of selection that complicates detection of significant fluctuating selection. The method is illustrated by an analysis of age-specific selection in house sparrows on a fitness-related two-dimensional morphological trait, tarsus length and body mass of fledglings.

Introduction

Following the seminal paper by Lande & Arnold (1983), strength of selection on quantitative characters has been estimated for a large number of species covering a wide range of taxa (Endler, 1986; Kingsolver *et al.*, 2001; Bell, 2008; Siepielski *et al.*, 2009). These studies have provided important insights into selective processes acting in natural populations and identified several general patterns (Kinnison & Hendry, 2001; Merilä *et al.*, 2001; Knapczyk & Conner, 2007; Bell, 2008, 2010; Kruuk *et al.*, 2008). For instance, selection may show large temporal variation among years both in direction, strength and form (Siepielski *et al.*, 2009, 2011; Morrissey & Hadfield, 2012). Furthermore, selection on life history traits may be stronger than selection on morphological traits (Hereford *et al.*, 2004; Kingsolver *et al.*, 2001).

Although Lande & Arnold's (1983) method greatly improved our understanding of selection as a process, this approach is still based on several simplifying assumptions that may influence the interpretation of the results. One of these is that the effects of age-structure are ignored. In most vertebrate species, significant age-specific variation has been found in several fitness-related traits (Sæther, 1990; Forslund & Pärt, 1995; Gaillard *et al.*, 2000). Thus, the response to selection will be a complex result of temporal variation in selection on fitness-related traits acting at different stages of the life history. Accordingly, several studies of different species have shown large age-specific differences in the pattern and strength of selection (McCleery *et al.*, 2004;

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Charmantier *et al.*, 2006a,b). This seriously complicates the interpretation of the evolutionary consequences of these selective processes because there is no single selection differential in age-structured populations.

Fisher (1930) preceded the derivation of his fundamental theorem of natural selection by a discussion of deterministic age-structured dynamics in continuous time, defining the Malthusian parameter r as the asymptotic growth rate on the log scale. He showed that the population will approach a stable age distribution and then grow asymptotically linear on the log scale with rate r. The value of r for a hypothetical population of identical individuals then serves as a measure of fitness for these individuals. To deal with populations that have not yet reached the stable age distribution, Fisher introduced the reproductive value. Each age has a reproductive value, and the population has a total reproductive value V that is the sum of the reproductive values of all individuals. Fisher then showed that V grows exactly exponential with rate r even if the population deviates from its stable age distribution. We have previously extended this approach to model selection acting on a single allele in an age-structured diploid population (Engen *et al.*, 2009a) as well as to describe fluctuating stabilizing and directional age-specific selection on a single quantitative trait constant with age in a variable environment (Engen *et al.*, 2011). In the latter case, assuming weak selection and fitness components with Gaussian shape, the response turned out to be a first-order autoregressive model with temporally correlated noise, characterized by simple weighted means of age-specific selection parameters defined separately for each vital rate.

Previously, analyses of evolutionary responses to selection in age-structured populations have been based on the net reproductive rate (Lande, 1982; Charlesworth, 1994) or the specific population growth rate at a single point of time (Coulson & Tuljapurkar, 2008) as a measure of fitness. The approach of Engen *et al.* (2011) based on reproductive value represents an important advance because it allows partitioning selection acting on a quantitative trait into age-specific components that can be estimated from a sample of individuals in the population. Another advantage of using the reproductive value can be illustrated by the effects of fluctuating environments on selection in natural populations with overlapping generations. For instance, a large number of studies have recently examined how fluctuations and trends in climate are likely to induce changes in the distribution of the phenotypes of fitness-related characters in natural populations (e.g. Gienapp *et al.*, 2006; Ozgul *et al.*, 2009, 2010). Following Engen *et al.* (2011), one effect of changes in the environment may be that the phenotype with the largest contribution to future generations may differ among years. As a consequence, the fitness contributions of two individuals with the same phenotype and life history, but born in different years will then differ. In addition, the strength of selection may also differ among years and age classes, which makes it difficult to compare contributions from individuals based on measurement of fitness components estimated at a single point of time (Wilson *et al.*, 2006).

Another stochastic effect affecting the dynamics of populations is random differences among individuals in vital rates within a year, known as demographic stochasticity (Lande *et al.*, 2003). Such random individual variation in fitness contributions has stronger effects on the dynamics of small populations (Lande *et al.*, 2003). However, it will affect estimates of directional and fluctuating selection even in an infinite population because estimates of selection inevitably must be based on finite samples of individual survival and reproduction. Thus, estimates will be strongly affected by demographic stochasticity, which in turn influences estimates of fluctuating selection caused by variation in the environment. Such sampling variation caused by demographic stochasticity must also be accounted for when estimating uncertainties in the strength of directional selection.

Here, we will develop methods for estimating weak directional as well as fluctuating selection based on individual data on age, fecundity, survival and fitness-related quantitative characters fixed at birth. Our statistical approach applies Fisher's (1930) concept of the total reproductive value as well as the concept of individual reproductive value introduced by Engen *et al.* (2009b). Selection in an age-structured population then acts through individual reproductive values. This leads to the correct combination of all age-specific components of selection within and among years that determines the evolutionary response to selection (Engen *et al.*, 2011). Having first estimated the mean projection matrix through time, individual reproductive values can be computed for all individuals of known age for which the survival and number of recruits produced are known. These estimates can then be used as dependent variables in age-specific regression models with measured phenotypes of the individuals as independent covariates, leading to estimates of directional and fluctuating selection.

Model

Age-structured populations in a stochastic environment without density regulation can be described by stochastic projection matrices with expected elements that are independent of the present population size (Caswell, 2001; Engen *et al.*, 2005). If the population vector a given year is $\boldsymbol{n} = (n_1, n_2, \ldots, n_c)'$, where the superscript $'$ denotes matrix transposition, the expected population vector in the next year is $\boldsymbol{ln}$, where $\boldsymbol{l}$ is a square matrix with non-negative elements describing transitions between stages. In an age-structured model, the nonzero elements are those in the first line representing mean fecundities of the different age classes 1, 2, …, *c*, defined as the mean number of offspring surviving to the next census, and the subdiagonal elements being survival probabilities. More generally, for stage-structured populations, the matrix may have other nonzero elements (Caswell, 2001).

Following Engen *et al.* (2011), we consider selection on a vector of phenotypes $\boldsymbol{z} = (z_1, z_2, \ldots, z_k)$ that determines the expected elements $l_{ij} = l_{ij}(\boldsymbol{z})$, assuming that the phenotype $\boldsymbol{z}$ does not change with age. We assume weak selection, that is, variation in $\boldsymbol{z}$ among individuals only induces small variation in the elements $l_{ij}(\boldsymbol{z})$ so that its dominant eigenvalue can be approximated by a linear function. If there is a temporal additive effect on the phenotype generated by fluctuations in the environment, we assume that this is the same for all individuals regardless the value of $\boldsymbol{z}$. Although this term will affect the stochastic growth rate of the population, it will not influence either selection or genetic drift, so this temporal component is ignored in the following. For simplicity of notation, we assume that $\boldsymbol{z}$ is centred by subtraction of its mean value across years so that the population mean is the zero vector.

Let $\lambda(\mathbf{0})$ be the real dominant eigenvalue of the mean matrix $\boldsymbol{l}(\mathbf{0})$ with right and left eigenvectors $\boldsymbol{u}$ and $\boldsymbol{v}$ defined by $\boldsymbol{l}(\mathbf{0})\boldsymbol{u} = \lambda(\mathbf{0})\boldsymbol{u}$ and $\boldsymbol{v}\boldsymbol{l}(\mathbf{0}) = \lambda(\mathbf{0})\boldsymbol{v}$. Provided that the eigenvectors are scaled so that $\sum u_i = 1$ and $\sum v_i u_i = 1$, $\boldsymbol{u}$ is the stable age distribution and $\boldsymbol{v}$ the vector of reproductive values associated with the projection matrix $\boldsymbol{l}(\mathbf{0})$. The eigenvalue $\lambda(\mathbf{0})$ represents the deterministic multiplicative growth rate of a pure population of individuals with $\boldsymbol{z} = \mathbf{0}$. Assuming that $\boldsymbol{z} \neq \mathbf{0}$ causes small changes in the expected elements $l_{ij}(\boldsymbol{z})$, we may apply the first-order approximation to the growth rate of a pure population with phenotype $\boldsymbol{z}$, giving

$$\lambda(\boldsymbol{z}) = \lambda(\mathbf{0}) + \sum_{ij} \frac{\partial \lambda(\mathbf{0})}{\partial l_{ij}(\mathbf{0})} [l_{ij}(\boldsymbol{z}) - l_{ij}(\mathbf{0})],$$

where the derivatives are evaluated at the population mean $\boldsymbol{z} = \mathbf{0}$. Using the fact that $\partial\lambda / \partial l_{ij} = v_i u_j$ (Charlesworth, 1994; Caswell, 2001), and by the definition of the eigenvectors $\sum_{ij} v_i u_j l_{ij}(\mathbf{0}) = \lambda(\mathbf{0})$, we find to the first order of approximation that

$$\lambda(\boldsymbol{z}) = \sum_{ij} v_i u_j l_{ij}(\boldsymbol{z}). \tag{1}$$

The stochastic projection matrix operating a given year is composed by individual contributions to the population the next year (Lande *et al.*, 2003). These contributions are dependent on survival of the individual itself as well as the production of offspring surviving to the next year. In the simple age-structured model, an individual of age *j* contributes with its number of offspring B_j to the first age class and adds one to age class *j*+1 if it survives. Engen *et al.* (2009b) defined the individual reproductive value as the contribution from the individual to the total reproductive value of the population the next year (Fisher, 1930), that is

$$W_j(\boldsymbol{z}) = v_1 B_j + v_{j+1} I_j. \tag{2}$$

Here $v_{j+1} = v_j$ and $I_j = 1$ if the individual survives and otherwise zero, and the $\boldsymbol{z}$ in $W_j(\boldsymbol{z})$ indicates that its distribution depends on the phenotype. The individual reproductive value $W_j(\boldsymbol{z})$ has expectation $v_1 l_{1j}(\boldsymbol{z}) + v_{j+1} l_{j+1,j}(\boldsymbol{z}) = \sum_i v_i l_{ij}(\boldsymbol{z})$. The relation $\mathrm{E}W_j(\boldsymbol{z}) = \sum v_i l_{ij}(\boldsymbol{z})$ is easily seen to be valid for any stage-structured model. From eqn (1), it follows that, to the first order of approximation, the deterministic growth rate of a hypothetical pure population of individuals with phenotype $\boldsymbol{z}$ can be expressed by the expected individual reproductive values for the different age classes,

$$\lambda(\boldsymbol{z}) = \sum_{j=1}^{c} u_j \mathrm{E} W_j(\boldsymbol{z}). \tag{3}$$

Now, because the $W_j(\boldsymbol{z})$ are stochastic quantities that can be recorded when samples of individuals with known age, survival and reproduction are available (Engen *et al.*, 2009b, 2010), eqn (3) is a fundamental equation for studying weak selection of the phenotype $\boldsymbol{z}$ in a stage-structured model using linear regression models with individual reproductive values $W_j(\boldsymbol{z})$ as dependent variables and individual phenotype as covariates. The eigenvectors, $\boldsymbol{u}$ and $\boldsymbol{v}$, must first be estimated by estimating the mean projection matrix $\bar{\boldsymbol{l}}(\bar{\boldsymbol{z}}) = \boldsymbol{l}(\mathbf{0})$ from temporal mean values of observed vital rates. An advantage of this approach is that it is based on reproductive values $W_j(\boldsymbol{z})$ from samples of individuals over a period of time and does not require observations of individuals throughout their whole life to record their lifetime reproductive rate. Another important advantage is that possible correlations between individual survival and reproduction are accounted for by introducing the single independent variable $W_j(\boldsymbol{z})$. Such correlations may be positive due to large stochastic fluctuation in the environment, or negative due to a trade-off in resource allocation between survival and reproduction (Engen *et al.*, 2011). These correlations will confound analyses based on separate use of individual fecundity and survival as measure of fitness (Wilson & Nussey, 2010).

To develop methods for estimation and testing as well as allowing correct interpretation of variances and uncertainties, it is necessary to include the stochastic properties of the individual reproductive values, as introduced by Engen *et al.* (2009b). Writing $\boldsymbol{\varepsilon}_t$ for the vector of environmental variables at time *t* affecting the vital rates, the age-specific demographic variance components for a constant $\boldsymbol{z}$ are defined as $\sigma^2_{dj} = \mathrm{E}\mathrm{var}(W_j \mid \boldsymbol{\varepsilon}_t) = \mathrm{E}\sigma^2_{djt}$, where the conditional variance is the variance among individuals within a year, and the expectation is the temporal expectation representing the mean value of $\sigma^2_{djt} = \mathrm{var}(W_j \mid \boldsymbol{\varepsilon}_t)$ through time. Similarly, the environmental covariance components are defined as $\tau_{eij} =$

$\mathrm{cov}[\mathrm{E}(W_i \,|\, \boldsymbol{\varepsilon}_t), \mathrm{E}(W_j \,|\, \boldsymbol{\varepsilon}_t)]$. The total demographic and environmental variance for the population is then $\sigma_d^2 = \sum_j u_j \sigma_{dj}^2$ and $\sigma_e^2 = \sum_{ij} u_i u_j \tau_{eij}$. These variances may in general depend weakly on the phenotype, but under our assumption of weak selection, they can be approximated by their values evaluated at $\boldsymbol{z} = \boldsymbol{0}$. The demographic and environmental variance defines the between year variance in the total reproductive value V of the population by

$$\mathrm{var}(V + \Delta V \,|\, V) = \sigma_d^2 V + \sigma_e^2 V^2.$$

Furthermore, the process V will have approximately white noise (Engen *et al.*, 2007a). The total population size N will fluctuate around its total reproductive value V with a return time at the order of a few generations. Hence, N will show transient fluctuation, whereas V serves as a filter removing these fluctuations. Furthermore, it is V that contains the information about future population sizes (Fisher, 1930), and thus, the process V rather than N should be used for predictions.

Fitness and selection differentials

Let z be some component of the phenotype vector $\boldsymbol{z}$. In populations with no age-structure, the selection differential is given by the covariance between phenotype and individual relative fitness (Lande, 1982; Coulson & Tuljapurkar, 2008; Morrissey *et al.*, 2010). In a constant environment, this also holds for the present model with weak selection, giving the selection differential $S = \mathrm{cov}[z, \lambda(\boldsymbol{z})/\bar{\lambda}] = \mathrm{cov}[z, \bar{\lambda}^{-1} \sum_{ij} v_i u_j l_{ij}(\boldsymbol{z})]$. Here $\bar{\lambda}$ is the mean fitness in the population, that is, the growth rate defined by the mean projection matrix. Because we measure growth and fitness using reproductive value weighting, all age classes have the same absolute fitness $\bar{\lambda}$ in this model because the total reproductive value of any subpopulation always grows exactly exponentially with the same growth rate as the whole population (Fisher, 1930), which is the dominant eigenvalue. From eqn (3), it now follows that $S = \sum_j u_j \mathrm{cov}[z, \bar{\lambda}^{-1} \mathrm{E}W_j(\boldsymbol{z})]$. In a fluctuating environment, the expected individual reproductive values and the growth rate may be time dependent, giving the selection differential at time t on the form

$$S_t = \sum_j u_j \mathrm{cov}_j[z, \bar{\lambda}^{-1} \mathrm{E}W_{jt}(\boldsymbol{z})].$$

Here the subscript j in cov_j is added to emphasize that this is the covariance for individuals of age j, whereas subscript t indicates that mean survivals and fecundities may fluctuate through time.

To express results in terms of age-specific fitnesses and selection differentials, we consider the subpopulation of individuals of age j at time t. Weighted by their reproductive value, individuals in this age class with phenotype $\boldsymbol{z}$ have multiplicative growth rate $\lambda_{jt}(\boldsymbol{z}) = [p_{jt}(\boldsymbol{z}) v_{j+1} + f_{jt}(\boldsymbol{z}) v_1]/v_j = \mathrm{E}W_{jt}(\boldsymbol{z})/v_j$ and relative age-specific fitness $\lambda_{jt}(\boldsymbol{z})/\bar{\lambda}_t = \mathrm{E}W_{jt}(\boldsymbol{z})/(\bar{\lambda}_t v_j)$. Here $p_{jt}(\boldsymbol{z})$ is the probability of survival $l_{j+1,j}(\boldsymbol{z})$ at time t, whereas $f_{jt}(\boldsymbol{z})$ is the mean fecundity $l_{1j}(\boldsymbol{z})$. From this, the selection differential produced by age class j is the covariance between phenotype and relative fitness, that is,

$$S_{jt} = \mathrm{cov}_j[z, \mathrm{E}W_{jt}(\boldsymbol{z})/(\bar{\lambda}_t v_j)],$$

and it follows that

$$S_t = \bar{\lambda}_t^{-1} \sum_j u_j \mathrm{cov}_j[z, \mathrm{E}W_{jt}(\boldsymbol{z})] = \sum_j u_j v_j S_{jt}.$$

Hence, the total selection differential is the weighted mean of the age-specific differentials with weight equal to the Fisherian stable age distribution $u_j v_j$, as defined by Engen *et al.* (2011).

Although this expression can be used to estimate selection differentials, the statistical inference is complicated by the presence of demographic stochasticity in the observed individual reproductive values $W_j(\boldsymbol{z})$ combined with small temporal fluctuations in $\mathrm{E}W_{jt}(\boldsymbol{z})$ and weak relationship between fitness and phenotypes.

If the relative fitness of individuals could be observed, the covariances could be estimated by random sampling. Notice then that estimation of age-specific covariances only would require random sampling of individuals within age classes, whereas estimation of the overall unconditional covariance must be based on random samples from the whole population, which is usually quite difficult to achieve in age-structured populations. This emphasizes the importance of the above decomposition of the overall covariance into age-specific components.

Response to selection in the linear model

Below we present the statistical analysis for linear models with fluctuating selection given by

$$\mathrm{E}W_{jt}(\boldsymbol{z}) = \alpha_{j0t} + \alpha_{j1t} z_1 + \cdots + \alpha_{jkt} z_k.$$

The mean fitness of all individuals with phenotype $\boldsymbol{z}$ (including all age classes) at time t is then the expectation of the individual reproductive values

$$\lambda_t(\boldsymbol{z}) = \sum_{j=1}^{c} u_j \mathrm{E}W_{jt}(\boldsymbol{z}) = \alpha_{0t} + \alpha_{1t} z_1 + \cdots + \alpha_{kt} z_k, \tag{4}$$

where $\alpha_{mt} = \sum_{j=1}^{c} u_j \alpha_{jmt}$. From this, we see that the vector of selection differentials is

$$\boldsymbol{S}_t = \boldsymbol{P}_t \boldsymbol{\beta}_t,$$

where $\boldsymbol{P}_t$ is the phenotypic $(k \times k)$ covariance matrix at time t and $\boldsymbol{\beta}_t$ is the vector with components $\beta_{mt} = \bar{\lambda}_t^{-1} \alpha_{mt}$ defined for $m = 1, 2, \ldots, k$. According to standard theory of evolution of quantitative characters (Lande, 1979, 1982), the response vector is then

$$\boldsymbol{R}_t = \boldsymbol{G}_t \boldsymbol{\beta}_t = \boldsymbol{G}_t \boldsymbol{P}_t^{-1} \boldsymbol{S}_t,$$

where $\boldsymbol{G}_t$ is the additive genetic covariance matrix.

Estimation

We consider individual reproductive values $W_{jt}(\boldsymbol{z})$ of individuals of age j with vital rates observed at time t at environmental conditions $\boldsymbol{\varepsilon}_t$, which are independently identically distributed given time and environments. We assume that the expected individual reproductive values are linear functions of the phenotypes $z_1, z_2, \ldots, z_k$ leading to eqn (4) with $p = k + 1$ unknown regression coefficients that in general depend on the environment $\boldsymbol{\varepsilon}_t$. The expectation refers to demographic stochastic variation among individuals in survival and reproduction at time t and is conditioned on $\boldsymbol{\varepsilon}_t$ (Engen *et al.*, 1998). Write n_{jt} for the number of observations of individual reproductive value and phenotype for age j at time t. By fixing age and time, the model then becomes a standard linear regression $\mathrm{E}\boldsymbol{W} = \boldsymbol{z\alpha}$, where $\boldsymbol{W}$ is the vector of observed individual reproductive values and $\boldsymbol{z}$ is the $n \times p$ matrix with the individual phenotype vectors $\boldsymbol{z} = (z_0, z_1, z_2, \ldots, z_k)$ as rows, where $\boldsymbol{z}$ has now been redefined by including the component z_0 which is one by definition. Under weak selection, the expectations $\mathrm{E}W(\boldsymbol{z})$ change little with $\boldsymbol{z}$, and therefore, small changes in the variance are a reasonable assumption and therefore can be approximated by a constant. The temporal distribution of this conditional variance $\mathrm{var}(W \mid \boldsymbol{z}, \boldsymbol{\varepsilon}_t) = \sigma^2_{djt}$ generated by temporal fluctuations in the environment $\boldsymbol{\varepsilon}_t$ then has a mean which is the age-specific components of the demographic variance $\sigma^2_{dj} = \mathrm{E}\mathrm{var}(W \mid \boldsymbol{z}, \boldsymbol{\varepsilon}_t)$, and the total demographic variance $\sigma^2_d = \sum_j u_j \sigma^2_{dj}$ (Engen *et al.*, 2009b). The least squares estimate of the regression coefficients in this model are $\hat{\boldsymbol{\alpha}} = (\boldsymbol{z}'\boldsymbol{z})^{-1}\boldsymbol{z}'\boldsymbol{W}$, whereas the variance estimate $\hat{\sigma}^2_{djt}$ is the residual sum of square divided by $n - p$. The covariance matrix for $\hat{\boldsymbol{\alpha}}_{jt}$ with (kl)-elements $\mathrm{cov}(\hat{\alpha}_{jkt}, \hat{\alpha}_{jlt})$ is estimated by $(\boldsymbol{z}'\boldsymbol{z})^{-1}\hat{\sigma}^2_{djt}$. Performing this estimation for age class j at times $t = 1, 2, \ldots, \tau$, the age-specific demographic variance is finally estimated by the relevant weighted mean over years as $\hat{\sigma}^2_{dj} = (N_j - p\tau)^{-1}\sum_t (n_{jt} - p)\hat{\sigma}^2_{djt}$, where $N_j = \sum_t n_{jt}$ is the total number of observations of individuals of age j. Although there may be temporal fluctuations in the σ^2_{djt}, these are likely to be small compared with the standard deviations of their sampling distributions. Hence, assuming that the variances are the same each year, we obtain improved estimators for the yearly covariance matrices for $\hat{\boldsymbol{\alpha}}_{jt}$ given above as $\hat{\boldsymbol{A}}_{jt} = (\boldsymbol{z}'\boldsymbol{z})^{-1}\hat{\sigma}^2_{dj}$, where $\boldsymbol{z}$ is the matrix of independent variables at time t.

The parameters determining the response to selection at time t are accordingly the weighted means α_{mt} estimated as $\hat{\alpha}_{mt} = \sum_j u_j \hat{\alpha}_{jmt}$ divided by $\bar{\lambda}_t$. The sampling variance of $\hat{\alpha}_{jmt}$ is only demographic because the α_{jmt} are defined conditional on the environment. Hence, for two different age classes $i \neq j$, $\hat{\alpha}_{imt}$ and $\hat{\alpha}_{jmt}$ have independent sampling distributions and the (lm)-element of the autocorrelation matrix $\boldsymbol{A}_t$ for $\hat{\boldsymbol{\alpha}}_t = (\hat{\alpha}_{0t}, \hat{\alpha}_{1t}, \ldots, \hat{\alpha}_{kt})$ is accordingly

$$A_t(lm) = \mathrm{cov}(\hat{\alpha}_{lt}, \hat{\alpha}_{mt}) = \sum u_j^2 \mathrm{cov}(\hat{\alpha}_{jlt}, \hat{\alpha}_{jmt}) = \sum_j u_j^2 A_{jt}(lm),$$

where (lm) denotes the (lm)-element of the matrices.

Under fluctuating selection, we assume that the vectors $\boldsymbol{\alpha}_t$ fluctuate among years with temporal covariance matrix $\boldsymbol{M}$ and no temporal autocorrelation. Including this temporal variation, the covariance matrix for the yearly estimates are $\boldsymbol{A}_t + \boldsymbol{M}$. In Appendix A, we show how to estimate $\boldsymbol{M}$ and the temporal mean coefficients $\boldsymbol{\alpha} = \mathrm{E}\boldsymbol{\alpha}_t$, assuming initially that the yearly estimates $\boldsymbol{\alpha}_t$ are multinormally distributed. However, this approximation is not crucial because it is only used to construct the estimators and the properties of all estimates are finally checked by resampling methods.

On the other hand, to find yearly estimates of $\boldsymbol{\alpha}_t$ corrected for sampling errors, we will have to use the normal approximation. The estimator can then be based on the conditional mean $\mathrm{E}(\boldsymbol{\alpha}_t \mid \hat{\boldsymbol{\alpha}}_t)$, known as the best linear predictor, which takes the form

$$\mathrm{E}(\boldsymbol{\alpha}_t \mid \hat{\boldsymbol{\alpha}}_t) = \boldsymbol{\alpha} + \boldsymbol{M}(\boldsymbol{A}_t + \boldsymbol{M})^{-1}(\hat{\boldsymbol{\alpha}}_t - \boldsymbol{\alpha}).$$

Finally, an estimator for $\boldsymbol{\alpha}_t$ is obtained replacing $\boldsymbol{\alpha}$ by the estimate $\hat{\boldsymbol{\alpha}}$ in this expression.

Environmental variance

Using the general expression for the environmental variance and the expression for $\lambda_t(\boldsymbol{z})$, we find that the environmental variance for a hypothetic population with phenotype $\boldsymbol{z}$ is

$$\sigma_e^2(\boldsymbol{z}) = \sum_{ij} u_i u_j \mathrm{cov}[\mathrm{E}W_{it}(\boldsymbol{z}), \mathrm{E}W_{jt}(\boldsymbol{z})] = \mathrm{var}[\lambda_t(\boldsymbol{z})],$$

giving using eqn (4),

$$\sigma_e^2(\boldsymbol{z}) = \sum_{ij} z_i z_j \mathrm{cov}(\alpha_{it}, \alpha_{jt}).$$

If the phenotypes are centred to fluctuate around zero with moderate variances, the major contribution to the environmental variance comes from the intercepts (the term proportional to $z_0^2 = 1$), and the total environmental variance σ_e^2 in the populations is therefore approximately $\mathrm{var}(\alpha_{0t})$.

Uncertainties and testing

Bootstrapping

To find approximations for uncertainties or for testing hypotheses resampling is required because the sampling distributions of the estimators are non-normal due to the fact that the dependent variables in the regressions (individual reproductive values) have discrete distributions very different from normal. First, we need to explore the uncertainties introduced by the demographic variances used to define the elements of the covariance matrices $\boldsymbol{A}_{jt}$ which in turn determine the uncertainty in $\boldsymbol{A}_t$. The estimates of the demographic variance σ^2_{djt} are all sum of squares of residuals in the regression divided by $n_{jt} - p$ so that $(n_{jt} - p)\hat{\sigma}^2_{djt}$ is a sum of n_{jt} squared residuals. Consequently, $(N_j - p\tau)\hat{\sigma}^2_{dj}$ is a sum of N_j squared residuals. Although the residuals are not independent due to the linear relations defining the estimated coefficients, the squared residuals are very weakly correlated and thus can be considered as approximately independent. Consequently, writing $\sum_{i=1}^{N_j} e_i^2$ for the total sum of squared residuals, the variance of this sum can be estimated by

$$\mathrm{var}(\sum e_i^2) \approx \frac{N_j^2}{N_j - 1}[\bar{e^4} - (\bar{e^2})^2],$$

where the bar defines mean values. This expression divided by $(N_j - p\tau)^2$ provides an estimate of the variance of $\hat{\sigma}^2_{dj}$. Accordingly, in each resampling of estimates, we may include the uncertainty in the estimation of $\boldsymbol{A}_t$ by choosing bootstrap replicates of the σ^2_{dj} defining this matrix as independent normal variables with means $\hat{\sigma}^2_{dj}$ and the above variance. A complete bootstrap replication including the temporal variation in the regression coefficients is then obtained by parametric bootstrapping of the $\boldsymbol{\alpha}_t$ using the overall estimated mean and covariance matrices $\boldsymbol{A}_t + \boldsymbol{M}$ for the yearly estimates. Standard bootstrapping by resampling among the $\boldsymbol{\alpha}_t$ with replacement can alternatively be performed provided that τ is large enough to avoid bias. From these simulations, we can compute confidence intervals and sampling variance and covariances for any of the parameters we estimate.

Statistical inference under the assumption of no fluctuating selection

It follows from the derivation in Appendix A that the estimate of $\boldsymbol{\alpha}$ under the assumption of no fluctuating selection ($\boldsymbol{M} = \boldsymbol{0}$) is

$$\hat{\boldsymbol{\alpha}}(\boldsymbol{0}) = (\sum \boldsymbol{A}_t^{-1})^{-1} \sum_t \boldsymbol{A}_t^{-1} \hat{\boldsymbol{\alpha}}_t \tag{5}$$

with covariance matrix $(\sum \boldsymbol{A}_t^{-1})^{-1}$. The (co)variances will usually be rather accurate because they are based on a large number of regressions. Accordingly, testing the hypothesis of no selection under the assumption of no fluctuating selection can be performed by simply using the normal approximation for $\hat{\boldsymbol{\alpha}}(\boldsymbol{0})$ considering the covariance matrix as known equal to the estimated one.

Statistical inference assuming fluctuating selection

An interesting null hypothesis is that there is directional but no fluctuating selection, that is $\boldsymbol{M} = \boldsymbol{0}$. We then first perform estimation of $\boldsymbol{\alpha}$ by eqn (5). Under the null hypothesis, the covariance matrix for $\hat{\boldsymbol{\alpha}}_t$ is $\boldsymbol{A}_t$ which we have estimated as $\hat{\boldsymbol{A}}_t$. Hence, we can simulate replicates of $\hat{\boldsymbol{\alpha}}_t$ for $t = 1, 2, \ldots, \tau$ using the overall estimated mean and assuming that the vectors of estimated regression coefficients are multinormally distributed. From each resampling of τ regression vectors, we then estimate $\boldsymbol{M}$ obtaining a multivariate bootstrap distribution of the temporal covariance matrix for the regression vector under the null hypothesis which can be compared to the estimates found from the real data.

An example: selection on the morphology of house sparrows

As a methodological example, we analyse selection on two fitness-related morphological traits of house sparrows *Passer domesticus* living at the small island of Aldra off the coast of northern Norway (66°24′N, 13°05′E). This population, located within a larger metapopulation (Jensen *et al.*, 2007; Pärn *et al.*, 2009, 2012), was founded by four individuals (one female and three males) in 1998. Afterwards the population increased rapidly to reach a maximum breeding population size of 26 pairs in 2005 (Billing *et al.*, 2012). During the period 1998–2008, all juvenile and adult individuals on the island have been banded with a numbered aluminium ring and three coloured plastic rings for individual identification and measured for morphological traits. The birds live in close association with human settlements and during the breeding season, nests were localized and visited repeatedly until hatching. Number of eggs and fledglings were recorded for each nest. Hatching date was determined either directly or based on a subjective estimate of nestling age at the first visit after hatching. Several morphological traits of fledgelings were measured and standardized to a 10-day-old measure by regression techniques (see Ringsby *et al.*, 1998), including tarsus length to the nearest 0.1 mm by a sliding caliper and body mass to the nearest 0.1 g by a Pesola spring balance (see Ringsby *et al.*, 1998 and Jensen *et al.*, 2008 for further details). A fledgling was considered to have recruited to the breeding population if it was recorded during the breeding season the following year. House sparrows in this area reach reproductive age the year after hatching. The number of female recruits produced was determined by genetic parenthood analyses as described in Billing *et al.* (2012). Emigrants to surrounding islands are rare (Tufto *et al.*, 2005) and were considered as dead individuals.

Previous studies have shown that both the body mass and tarsus length at fledging are related to the probability of first-year survival of house sparrows in this study area (Ringsby *et al.*, 1998, 2002) and therefore represent two quantitative characters fixed at an early stage of life which are related to individual differences in fitness. To illustrate our approach, we here analyse how differences in these two morphological traits affect variation among 65 female fledglings from the cohorts 1999–2008 in their contribution to the total reproductive value of the population.

We use two age classes, birds in their first year of life and birds older than 1 year. Surviving individuals in age

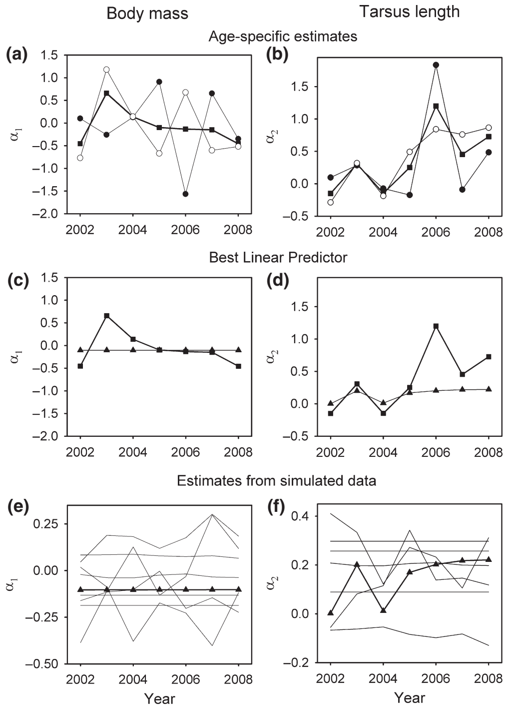

Fig. 1 Age-specific annual variation in selection on body mass and tarsus length of fledgling house sparrows. (a, b) Annual estimates of directional selection coefficients α_j affected by sampling error and fluctuating selection (squares and thick lines) decomposed into age-specific components for 1 year old (solid circles and thin line) and adult (2 years or older) birds (open circles and thin line). (c, d) Estimates of temporal mean coefficients α_j corrected for sampling error (triangles) using a best linear predictor approach (see p. 15). (e, f) Realizations of temporal variation in mean directional selection coefficient α_j using best linear predictor obtained by parametric bootstrapping of the temporal covariance matrix of the regression vector (thin lines), compared to the bias-corrected estimates (triangles).

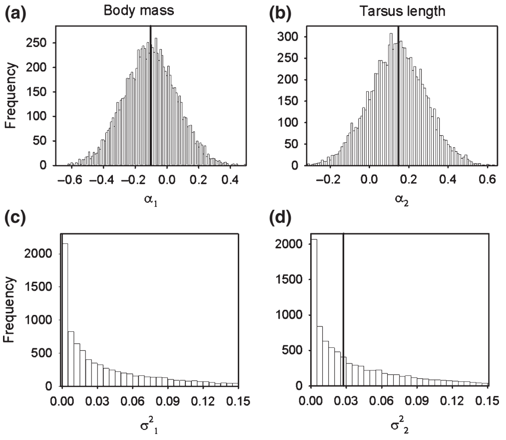

Fig. 2 Bootstrap replicates of the estimates of selection coefficients α_j (a, b) and temporal variance due to fluctuating selection σ_j^2 (c, d) on body mass ($j = 1$) and tarsus length ($j = 2$) of fledgling house sparrows. The solid vertical lines show the estimates of α_j and σ_j^2. Only estimates of $\sigma_j^2 > 0.00001$ were included in the distribution, which yielded 87.1 % and 87.4 % of the bootstrap replicates for body mass and tarsus length, respectively.

class 2 remain in this age class. Morphological measurements of each bird were standardized as deviations from the overall mean across years. Over the whole study period, there was no significant directional selection on either body mass (Fig. 1a, $\hat{\alpha}_1 = -0.103$, two-tailed: $P = 0.36$, $n = 104$) or tarsus length (Fig. 1b, $\hat{\alpha}_2 = 0.146$, two-tailed: $P = 0.28$, $n = 104$) of fledgling house sparrows based on resampling under the null hypothesis of no fluctuating selection. Although there was large annual variation in the $\hat{\alpha}_i$ (Fig. 1a, b), there was still no significant fluctuating selection ($P > 0.3$). As expected from the large demographic variance in this population ($\hat{\sigma}_d^2 = 0.493$) as well as in other house sparrow populations in this area (Engen *et al.*, 2007b), the uncertainty in the estimates of the directional selection α_j (Figs 1c–f and 2a,b) and the fluctuation selection σ_j (Fig. 2c,d) are large. This is illustrated by the large reduction in the selection coefficients after accounting for the uncertainties in the estimates of directional selection (Fig. 1c,d) Accordingly, several of the realizations obtained by parametric bootstrapping of the model show no temporal variation in the α_j corresponding to $\sigma_j^2 = \mathrm{var}(\alpha_{jt}) = 0$ (Fig. 1e,f). The power of detecting significant selection coefficients was strongly influenced by the demographic variance (Fig. 3).

Discussion

In the simple case of purely directional selection and characters not varying with age, we here provide methods using the concept of individual reproductive value for estimation and testing fluctuating and directional selection on multiple quantitative characters in age-structured populations. Components of selection are estimated by simple regression models for each age class within years. These are combined using results from the theoretical analysis by Engen *et al.* (2011) to provide estimates of how selection in all age classes jointly within a year affects the total selection on the trait, which in turn determine the evolutionary response to selection. Our analyses are based on the concept of individual reproductive value, that is the contribution of an individual to the total reproductive value of the population the next year, which varies in a stochastic way among individuals within as well as among years, thus deter-

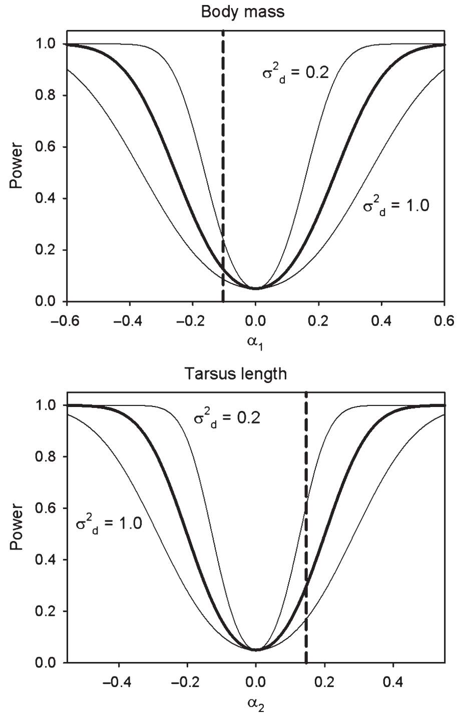

Fig. 3 The power function for two-sided tests for α_j differing from zero, for body mass ($j = 1$) and tarsus length ($j = 2$) of fledgling house sparrows. The significance level is chosen as 0.05. Power functions are shown for the estimated value of the demographic variance, $\sigma_d^2 = 0.49$ (solid line), as well as for $\sigma_d^2 = 1.0$ and 0.2 (thin lines). The vertical dashed lines show the estimates of α_j.

mining the demographic and environmental variance of the population (Engen *et al.*, 2009b). In agreement with Fisher (1930), we show that selection acts through this quantity rather than the unweighted contribution to the next generation measured in number of individuals as generally used in classical theory.

The present method provides an extension of the approach by Lande & Arnold (1983) in four important ways. First, we can estimate age-specific components of selection resulting from selection on viability or fecundity, or both (Fig. 1). Lifetime production of offspring has generally been considered an appropriate measure of fitness in age-structured populations, treating the population as one with new discrete generations at time steps T (Lande, 1982; Charlesworth, 1994). Several studies of vertebrate age-structured populations have used this measure of fitness (e.g. Gustafsson, 1986; Merilä & Sheldon, 2000; Brommer *et al.*, 2004; McCleery *et al.*, 2004; Jensen *et al.*, 2008). However, this approach makes it difficult to handle correctly the variability in survival and fecundity among age classes and deviations from a stable age distribution (Grafen, 1988). Here we use the result obtained by Fisher (1930), who showed that the total reproductive value always grows exactly exponentially with growth rate equal to the Malthusian parameter, regardless of the actual age distribution. Thus, the problem of age-structure in relation to Fihers's fundamental theorem of natural selection could be overcome simply by weighting individuals by their reproductive value rather than just counting them in calculations of allele frequencies (Engen *et al.*, 2009a). In this way, all age classes could be treated jointly and selection considered at each time step as in the case of no age-structure. We extend this approach to estimate parameters describing selection from samples of individuals of different ages that can be included in stochastic models of evolutionary processes in age-structured populations (Engen *et al.*, 2010, 2011).

Second, we estimate the temporal covariance matrix for the vectors of selection coefficients $\boldsymbol{\alpha}_t$, which can be used for statistical inference on fluctuating selection based on bootstrap methods developed for this purpose. In contrast to Lande & Arnold (1983), selection episodes do not need to be independent.

Third, available evidence suggests that estimates of selection coefficients in natural populations often are uncertain (Morrissey & Hadfield, 2012). The uncertainty in the estimates of temporal variation in selection may be large (Fig. 2c,d), making it difficult to detect significant variation among years in selection (Fig. 1c,d). Thus, our approach provides estimates of uncertainties as well as bias corrections based on bootstrapping. Our analyses illustrate the importance of considering uncertainties when deriving conclusions from analyses of selection based on samples of individuals (Mitchell-Olds & Shaw, 1987). Our results indicate that large sample sizes in terms of number of individuals and long time series are required to obtain sufficient power in tests for directional and fluctuating selection. Accordingly, Morrissey & Hadfield (2012) argued that much of the evidence for fluctuating selection in natural populations (e.g. Siepielski *et al.*, 2009) in fact could be explained by uncertainties in the estimates of the selection coefficients.

Fourth, our method takes into account demographic stochasticity which induces random variation in realized fitness components among individuals in a sample. Such individual differences in demography produce uncertainty that can erroneously be interpreted as directional and fluctuating selection. In particular, actual temporal fluctuations in the coefficients may become invisible due to the stochastic sampling noise in the estimates. The possibility of detecting statistically significant fluctuating selection is therefore small when demographic variance is large, unless extremely large data sets are available or temporal variation in selection is large. Figure 3 illustrates how the power of tests for selection, under the assumption of no fluctuating selection, strongly depends on the demographic variance.

We have proposed using resampling to find uncertainties in estimates, confidence limits and p-values in statistical tests. This implies resampling from different empirical distributions of individual reproductive values defined by eqn (2). The demographic noise in these quantities generated by correlated noise in survival and reproduction is an essential component of the stochasticity leading to uncertainties in yearly estimates as well as estimates of parameters describing fluctuating selection. Alternatively, the statistical analysis of the model can be carried out using MCMC methods, but this may be rather difficult to implement because the distribution of individual reproductive values rarely follows any well-known class of distributions that can be parameterized. One possibility may be that all probabilities describing these distributions are considered as unknown parameters with some parameterized temporal fluctuations and that relevant prior distributions are defined for all these parameters.

Because our approach is based on standard linear regressions, it can also be used to study models where the effect of phenotypes is nonlinear, such as for example second degree polynomials with a maximum, representing stabilizing selection (Mitchell-Olds & Shaw, 1987). However, when the function is linear in the phenotypes, as in our example, plasticity (Lande, 2009) will not have any effect on the estimated selection coefficients, whereas for a second degree polynomial, plasticity will affect the coefficients (Engen *et al.*, 2011). Thus, if plasticity occurs, a more complex approach including more parameters is necessary, which will further increase the uncertainty in the parameter estimates.

The present theory is based on the important simplification that the characters are constant through life although fitness may fluctuate through time. Fisher's (1930) weighting of individuals by their reproductive values ensures that the mean fitness does not change with age because the total reproductive value of any subpopulation has the same expected exponential growth as the whole population. The fitness of a given type z, however, will in general differ among ages. Hence, selection also differs at different ages. We have expressed this by defining age-specific selection differentials with temporal fluctuations, S_{jt}, as covariances between the phenotype and relative age-specific fitness (Engen *et al.*, 2011), analogous to models with no age-structure (e.g. Lande, 1976, 1979). The selection differential for the total population is then the sum of these differentials weighted by the Fisherian stable age distribution, that is $S_t = \sum u_j v_j S_{jt}$. This decomposition allows us to perform estimation for each age class separately based on age-specific vital rates and then to combine these estimates to provide a total selection differential determining the overall response to selection through time (Engen *et al.*, 2011).

Several approaches have recently appeared estimating selection and evolution of quantitative traits in natural populations using modifications of Price's (1970, 1972) equation. Basically, this involves separating the total change in a character into two components (Gardner, 2008). One component is the change that can be ascribed to selection, described by covariance between individual phenotypic values and relative fitness. The remaining term describes to what extent offspring differ from their parents, either due to genetic causes or changes in the environment. This avoids the problem of unaccounted effects of selection on unmeasured traits (Morrissey *et al.*, 2010) and allows analyses of selection on characters that change throughout the life of an individual taking the deterministic components of temporal phenotypic changes into account (Coulson & Tuljapurkar, 2008; Ellner *et al.*, 2011). In practice, these components are estimated relying heavily on retrospective analyses on the covariance between variation in the character and relative fitness (Coulson & Tuljapurkar, 2008; Ozgul *et al.*, 2009, 2010; Coulson *et al.*, 2010; Ellner *et al.*, 2011). Because many mechanisms affect the degree of parent–offspring similarity, prediction of future evolutionary changes may become difficult. In contrast, our approach is extended to age-structured populations within a similar general theoretical framework as previously developed for evolution of quantitative characters in unstructured populations (Lande, 1976, 1979, 1982).

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Appendix A: Estimation of fluctuating selection

We now model fluctuating selection by assuming that the vectors $\boldsymbol{\alpha}_t$ at τ different times are identically independently distributed among years with mean $\boldsymbol{\alpha}$ and covariance matrix $\boldsymbol{M}$. The vectors $\hat{\boldsymbol{\alpha}}_t$ are then also independent with the same mean $\boldsymbol{\alpha}$ but covariance matrices $\boldsymbol{A}_t + \boldsymbol{M}$ differing among years due to different number of individuals sampled. One will often have a large number of individual observations for each age class so that $\boldsymbol{A}_t$ may be considered as known equal to $\hat{\boldsymbol{A}}_t$ in the construction of an estimation method for ($\boldsymbol{\alpha}$, $\boldsymbol{M}$). Finally, the properties of the estimation method derived by this assumption, including the effects of the sampling distributions of the $\boldsymbol{A}_t$, can be investigated by stochastic simulations.

Because the regression coefficients are linear combinations of observations of the dependent variable with a large number of terms, rather efficient estimates are obtained by the maximum likelihood method based on the assumption that the $\boldsymbol{\alpha}_t$ have a multivariate normal distribution. Because the estimators are not exactly normal, this does not lead to the maximum likelihood estimators, but is still likely to give estimators with high precision relative to what is possible with demographic noise in survival and fecundity. Ignoring the trivial constant, the log likelihood multiplied by 2 based on the yearly estimates $\hat{\boldsymbol{\alpha}}_t$ is then

$$2\ln L(\boldsymbol{\alpha},\boldsymbol{M}) = -\sum_{t=1}^{\tau}\left[\ln|\boldsymbol{A}_t+\boldsymbol{M}| + (\hat{\boldsymbol{\alpha}}_t-\boldsymbol{\alpha})'(\boldsymbol{A}_t+\boldsymbol{M})^{-1}(\hat{\boldsymbol{\alpha}}_t-\boldsymbol{\alpha})\right],$$

where $|\boldsymbol{A}_t + \boldsymbol{M}|$ is the determinant of $\boldsymbol{A}_t + \boldsymbol{M}$. Here we may reduce the number of dimensions in the numerical maximization of the likelihood by first substituting $\boldsymbol{\alpha}$ by the vector $\boldsymbol{\alpha}(\boldsymbol{M})$ maximizing log likelihood for a given value of $\boldsymbol{M}$, or equivalently minimizing $\sum_{t=1}^{\tau}(\hat{\boldsymbol{\alpha}}_t-\boldsymbol{\alpha})'(\boldsymbol{A}_t+\boldsymbol{M})(\hat{\boldsymbol{\alpha}}_t-\boldsymbol{\alpha})$. The solution to this problem is

$$\hat{\boldsymbol{\alpha}}(\boldsymbol{M}) = \left[\sum_t(\boldsymbol{A}_t+\boldsymbol{M})^{-1}\right]^{-1}\sum_t(\boldsymbol{A}_t+\boldsymbol{M})^{-1}\hat{\boldsymbol{\alpha}}_t.$$

Inserting this for $\boldsymbol{\alpha}$ in the expression for log likelihood gives an expression $2\ln L(\boldsymbol{M})$ to be maximized numerically with respect to $\boldsymbol{M}$.

It is preferable to write the symmetric covariance matrix using the Cholesky decomposition (Ripley, 1987) $\boldsymbol{M} = \boldsymbol{D}\boldsymbol{D}'$, where $\boldsymbol{D}$ is a lower triangular matrix with positive diagonal elements. Then $\boldsymbol{M}$ is positive definite for any choice of elements of $\boldsymbol{D}$, and there is an equivalence between $\boldsymbol{D}$ and $\boldsymbol{M}$. For a given $\boldsymbol{D}$ the elements of $\boldsymbol{M}$ are given by $\boldsymbol{M} = \boldsymbol{D}\boldsymbol{D}'$, whereas the elements of $\boldsymbol{D}$ for a given $\boldsymbol{M}$ can be computed recursively as shown in Appendix B.

Now, we use the $p(p + 1)/2$ elements in $\boldsymbol{D}$ as variables determining $2\ln L$, which for any values of d_{ij} corresponds to a positive definite matrix $\boldsymbol{M}$. Hence, maximization can be carried out numerically by some procedure maximizing functions of a given number of variables with no constraints on the elements. If the maximization procedure chooses a negative diagonal element d_{ii}, we simply replace it by the corresponding positive number $|d_{ii}|$.

Using the same Cholesky decomposition writing $\boldsymbol{A}_t + \boldsymbol{M} = \boldsymbol{C}\boldsymbol{C}'$ where $\boldsymbol{C}$ is lower triangular, we also obtain a very simple expression for the log of the determinant occurring in the likelihood function,

$$\ln|\boldsymbol{A}_t+\boldsymbol{M}| = 2\sum_{i=1}^{p}\ln c_{ii},$$

where c_{ii} are the diagonal elements of $\boldsymbol{C}$ at time t.

Appendix B: The Cholesky decomposition

To find the elements of the lower triangular matrix $\boldsymbol{D}$ by the elements m_{ij} of the symmetric covariance matrix $\boldsymbol{M}$, we first observe that $d_{11} = m_{11}^{1/2}$, $d_{21} = m_{21}/d_{11}$ and $d_{22} = (m_{22} - d_{21}^2)^{1/2}$. If $p > 2$ we go on recursively for $i = 3, 4 \ldots, p$ first computing $d_{i1} = m_{i1}/d_{11}$ and then for $j = 2, 3, \ldots, i-1$,

$$d_{ij} = \left(m_{ij} - \sum_{k=1}^{j-1} d_{ik}d_{jk}\right) / d_{jj}$$

and finally

$$d_{ii} = \left(m_{ii} - \sum_{k=1}^{i-1} d_{ik}^2\right)^{1/2}.$$

Appendix C: A worked example with the R package lmf

In this appendix, we first go through the estimation procedures in the paper step-by-step, then we work through the methodological example with selection on the morphology of house sparrows and provide R codes using the R package lmf.

Here are the procedures, step-by-step, to estimate selection with the approach described in the paper:

(a) We begin by calculating the mean projection matrix ($\boldsymbol{l}(\mathbf{0})$) and accompanying stable age distribution ($\mathbf{u}$), reproductive values ($\mathbf{v}$) and the deterministic multiplicative growth rate (λ).
  - $\boldsymbol{l}(\mathbf{0})$: The projection matrix with mean age-specific fecundities (f_j) across years in the first row and mean age-specific survival probabilities (p_j) across years on the subdiagonal. The survival probability for the final age class (p_c) enters as the l_{cc} element of the matrix.
  - $\mathbf{u}$: The stable age distribution is calculated as the right eigenvector of $\boldsymbol{l}(\mathbf{0})$ scaled so that $\sum u_i = 1$.
  - $\mathbf{v}$: The reproductive values are calculated as the left eigenvector of $\boldsymbol{l}(\mathbf{0})$ scaled so that $\sum v_i u_i = 1$.
  - λ: The deterministic multiplicative growth rate is calculated as the dominant eigenvalue of $\boldsymbol{l}(\mathbf{0})$.

(b) The next step is to calculate the individual reproductive values ($W_{jt}(z)$) for each individual in our data set.
  - $W_{jt}(z)$: The individual reproductive values are given by $W_j(z) = v_1 B_j + v_{j+1} I_j$, that is the sum of the number of offspring contributed by an individual of age j to the first age class (B_j) weighted by the reproductive value of the first age class (v_1) and the survival of the individual to the next reproductive event (I_j) weighted by the reproductive value for the following age class (v_{j+1}).

(c) Then we are in position to estimate the yearly age-specific selection components ($\boldsymbol{\alpha}_{jt}$), covariance matrices ($\boldsymbol{A}_{jt}$), demographic variances (σ_{djt}^2) and individual residual values (e_i) by standard least square regression of $W_j(z)$ (fitness) on the individual phenotypes (z).
  - $\boldsymbol{\alpha}_{jt}$: The yearly age-specific selection components are the parameters from the linear regressions.
  - $\boldsymbol{A}_{jt}$: The yearly age-specific covariance matrices contain the variance for each estimated selection component on the diagonal and the covariance between the selection components on the off-diagonal elements.
  - σ_{djt}^2: The yearly age-specific demographic variances are estimated as the residual standard errors from the linear regressions.

(d) We now have what we need to calculate the yearly selection components ($\boldsymbol{\alpha}_t$). They are obtained by the sum of $\boldsymbol{\alpha}_{jt}$ within years weighted by $\mathbf{u}$, the stable age distribution.

(e) Furthermore, the age-specific demographic variances (σ_{dj}^2) can be calculated as the mean σ_{djt}^2 within each age class weighted by the degrees of freedom for each linear regression.

(f) With σ_{dj}^2 and $\boldsymbol{\alpha}_t$ at hand, the total demographic variance (σ_d^2) can be calculated as the sum of σ_{dj}^2 weighted by $\mathbf{u}$, and the environmental variance (σ_e^2) can be estimated as the variance of α_{0t}, the first element of the $\boldsymbol{\alpha}_t$ for all years (This corresponds to the intercepts of the yearly linear regressions).

(g) To account for uncertainty in the estimation of σ_{djt}^2 which affect our estimate of $\boldsymbol{A}_{jt}$, we assume that the variances are the same each year and improve the estimated $\boldsymbol{A}_{jt}$ by scaling with σ_{dj}^2 (and not σ_{djt}^2 which give the standard covariance matrix for any regression).

(h) The variances of σ_{dj}^2, which are needed when resampling estimates of selection, can be estimated using the residuals (e_i) from the least square regressions and the sample size for each age class (N_j) when applying the equation given under Bootstrapping in the Uncertainties and testing section.

(i) At this point, we can obtain the yearly covariance matrices ($\boldsymbol{A}_t$). These are calculated as the sum of $\boldsymbol{A}_{jt}$ within years weighted by $\mathbf{u}$, the stable age distribution.

(j) Finally, we are in position to estimate the temporal selection components. Under fluctuating selection, the temporal covariance matrix ($\boldsymbol{M}$) and the temporal mean selection components ($\boldsymbol{\alpha}$) given $\boldsymbol{\alpha}_t$ can be estimated through a numerical maximization of twice the log likelihood function ($2\ln L(\boldsymbol{\alpha}, \boldsymbol{M})$). Using the analytical solution for $\boldsymbol{\alpha}$ given $\boldsymbol{M}$, the log likelihood function can be maximized with respect to $\boldsymbol{M}$, after replacing $\boldsymbol{M}$ by the lower triangular matrix of its Cholesky decomposition. Thus, assuring that the solution for $\boldsymbol{M}$ remains positive definite.

- $\boldsymbol{M}$: The temporal covariance matrix provides the temporal variance (σ_j^2) across all years for each estimated selection component on the diagonal and the temporal covariance across all years between the selection components on the off-diagonal elements.
- $\boldsymbol{\alpha}$: The estimated mean selection components across all years.

(k) If we assume that there is no fluctuating selection $\boldsymbol{M} = \boldsymbol{0}$ the mean selection components $\boldsymbol{\alpha}(\boldsymbol{M})$ can be estimated by inserting $\boldsymbol{M} = \boldsymbol{0}$ into the analytical solution for $\boldsymbol{\alpha}$ (see eqn 5), and the corresponding covariance matrix is found by $(\sum \boldsymbol{A}_t^{-1})^{-1}$.

(l) Confidence intervals and statistical inference on the estimates of selection can be performed by parametric bootstrapping accounting for demographic variance as described in the Uncertainties and testing section of the main text.

We have made all the procedures above available through the R package lmf. Now we will use this package and provide the R codes to work through the methodological example in the main text to show how the procedures above are implemented in the statistical software R. The data set (sparrowdata) is available with the distribution of the R package.

After loading the data set into R, we first fit the desired model to estimate selection acting on the fledgling mass and tarsus length of house sparrows and view the output from the model (outputs are not printed in the appendix). All the steps from (a) through (k) are performed as we fit the model.

```
> model <- lmf(formula = cbind(recruits,
  survival) ~ weight + tars, age = age,
  year = year, data = sparrowdata)
> print(model)
```

Next we look at the summary of the fitted model to see the estimated projection matrix, variance components, temporal mean selection components and temporal covariance matrix.

```
> summary(model)
```

To extract the yearly or the yearly and age-specific estimates, we can specify an additional argument to `summary()` as shown below.

```
> summary(model, what.level = 'year')
> summary(model, what.level = 'age')
```

Now, as mentioned in step (l), confidence intervals for the estimated parameters can be estimated through parametric bootstrapping using the function `boot.lmf()`. Using this function, we specify the number of bootstraps (`nboot`), whether we want to include uncertainty in the parameters due to demographic variance (`sig.dj`), what parameters to bootstrap (`what`) and whether we want to perform a parametric or ordinary bootstrap (`asim`).

```
> bootmodel <- boot.lmf(object = model,
  nboot = 10000, sig.dj = TRUE, what =
  'all', asim = 'parametric')
```

A summary of the bootstrapped parameters is available with the `summary()` function that also have the optional argument `ret.bootstraps` to return the bootstraps that have been generated.

```
> summary(bootmodel)
> bootstraps <- summary(bootmodel,
  ret.bootstraps = TRUE)
```

Additional insight into the distribution of the bootstrapped parameters can be gained by density plots that are available using the function `plot()`. The optional `what` argument can be used to plot density plots for subsets of the parameters.

```
> plot(mod.boot, what = 'all')
> plot(mod.boot, what = 'projection')
> plot(mod.boot, what = 'alpha')
```

Now the confidence intervals can be generated using the function `ci.boot.lmf()` as shown below.

```
> ci.boot.lmf(bootmodel)
```

The final step that remains is testing of hypotheses. The p-values provided in the summary of the model are only to be considered as suggestive, and tests of hypotheses should be performed by bootstrapping. The `boot.lmf()` function has additional arguments to this end. By specifying the expected parameter values under the null hypothesis (`H0exp`) and the conditions, we want to test hypotheses under (`H0con`) the bootstrap function resamples parameter estimates under the null hypothesis and compares with the estimates from the data. Again, results of the bootstrap are available through the `summary()` function.

```
> hypmodel <- boot.lmf(object = model,
  nboot = 10000, what = 'all',
  asim = 'parametric', sig.dj = TRUE,
  H0exp = list(a = rep(0, 3), M = matrix(rep
  (0, 9), ncol = 3)),
  H0con = c('fs', 'nfs', 'ds'))
> summary(hypmodel)
```

Additional information for all functions can be obtained via the reference manual distributed with the R package.

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Paper II

ORIGINAL ARTICLE

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ESTIMATING PHENOTYPIC SELECTION IN AGE-STRUCTURED POPULATIONS BY REMOVING TRANSIENT FLUCTUATIONS

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An extension of the selection differential in the Robertson–Price equation for the mean phenotype in an age-structured population is provided. Temporal changes in the mean phenotype caused by transient fluctuations in the age-distribution and variation in mean phenotype among age classes, which can mistakenly be interpreted as selection, will disappear if reproductive value weighting is applied. Changes in any weighted mean phenotype in an age-structured population may be decomposed into between- and within-age class components. Using reproductive value weighting the between-age class component becomes pure noise, generated by previous genetic drift or fluctuating selection. This component, which we call transient quasi-selection, can therefore be omitted when estimating age-specific selection on fecundity or viability within age classes. The final response can be computed at the time of selection, but can not be observed until lifetime reproduction is realized unless the heritability is one. The generality of these results is illustrated further by our derivation of the selection differential for the continuous time age-structured model with general age-dependent weights. A simple simulation example as well as estimation of selection components in a house sparrow population illustrates the applicability of the theory to analyze selection on the mean phenotype in fluctuating age-structured populations.

KEY WORDS: **Age structure, demographic stochasticity, phenotypic evolution, quantitative genetics, reproductive value, reproductive value weighting, Robertson-Price equation.**

Natural selection occurs when there are consistent differences in fitness among phenotypes. This process causing change $\Delta\bar{z}$ during a time step in mean phenotype $\bar{z}$ in a finite population of N individuals was expressed by Price (1972) as

$$\Delta\bar{z} = \mathrm{cov}(w, z) + \mathrm{E}(w\overline{\Delta z}), \qquad (1)$$

where w is the relative individual fitness. The covariance and expectation in equation (1), the Robertson–Price equation, should be interpreted as the empirical ones, that is, $N^{-1}\sum w_i(z_i - \bar{z})$ and $N^{-1}\sum w_i\overline{\Delta z_i}$, respectively. Here individuals are numbered by subscript i so that $\overline{\Delta z_i}$ is the mean difference between the phenotype z_i of individual i and that of its offspring, whereas w_i is its relative individual fitness. The first term of equation (1) is the selection differential $\boldsymbol{S}$, the covariance formula first derived by Robertson (1966), whereas the second is the transmission term (Frank 1997, 2012; Gardner 2008).

Although the Robertson–Price equation is exact, its interpretation in studies of selection in natural populations is complicated by the fact that an individual's contribution to future generations is determined by its production of offspring at different life stages (Brommer et al. 2004; Moorad 2013, 2014; Sæther et al. 2013). Many empirical studies of selection have therefore focused on detecting selection in particular parts of the life

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cycle of individuals, such as juvenile survival, adult survival, and adult fecundity (Kingsolver et al. 2001; Kingsolver and Pfenning 2007; Bell 2008). This approach ignores that different components of selection may be dependent (Lande 1982) and does not consider how they interact to produce the total selection acting on the population. This interaction depends on how selection on different fitness-components affects the total contribution of an individual to future generations as well as how selection acts at different life-history stages (Charmantier et al. 2006; Morrissey et al. 2012; Moorad 2013), influencing the total selection differential (Lande 1982; Jensen et al. 2008; Engen et al. 2011; Moorad 2013, 2014).

Our understanding of selection acting on populations with complex life histories was advanced by Hamilton's (1966) and Charlesworth's (1994) analyses of deterministic age-structured models. Based on the sensitivity of the population growth rate to changes in fecundity or survival at a given age, they were able to explain general life-history patterns such as declines in age-specific fitness. An important extension of this approach was provided by Lande (1982), who, using a model in continuous time and assuming a stable age distribution as well as weak selection, derived a gradient formula for the evolution of the population mean of multivariate correlated characters in an age-structured population in a constant environment, taking into account selection operating at all stages in the life cycle. Another approach was provided by Tuljapurkar (1982), who analyzed how temporal variation in the environment affected evolution of basic life-history characteristics by deriving an approximation to the long-run growth rate of an age-structured population subject to environmental stochasticity. For instance, Orzack and Tuljapurkar (1989) showed that increasing variability in juvenile survival favored the evolution of an iteroparous life cycle. An important generalization that appears from these analyses is that the strength of selection depends on the age of action (Charlesworth 2000).

Usually selection is studied by giving all individuals the same weight, as for example by studying the response to unweighted mean phenotype or allele frequency. However, in structured populations the fitness of identical individuals may be different at different life-history stages. Then, a useful approach in theoretical models of selection is to compensate for these differences by weighting individuals differently according to their state (Leturque and Rousset 2002; Rousset and Ronce 2004), as first proposed by Fisher (1930). Engen et al. (2011) used Fisher's concept of reproductive value to study weak selection on a quantitative character with plasticity at early ontogenetic stages remaining constant throughout an individual's life. They found that the expected evolutionary response to fluctuating age-specific selection caused by temporal environmental fluctuations both in fecundity and survival is strongly dependent on age-specific selective weights, which are related to the stable distribution of reproductive values among age classes. The power of using reproductive value weighting of allele frequencies to smooth out effects of fluctuating age structure has been investigated by Crow (1979) and Engen et al. (2009a). Here we extend these approaches by decomposing the change in mean phenotype into age-specific components of viability and fecundity selection. We show that there will be a component that possibly has nonzero mean and complicating transient fluctuations, caused by deterministic as well as stochastically generated differences in mean phenotypes and individual fitnesses among age classes. This component, which is present even if all phenotypes have the same expected vital rates within age classes, has no long-term evolutionary impact and should therefore not be included in the selection differential. We show how this component can be excluded from the selection differential using the reproductive value weighted mean.

Our approach provides an age-dependent extension of the stochastic Robertson–Price equation of Engen and Sæther (2014), who decomposed the selection differential $\boldsymbol{S}$ into expectation through time as well as components due to demographic and environmental stochasticity. Their approach enabled partitioning of the variation in the selection differential due to genetic drift caused by demographic stochasticity (Rice 2008) and fluctuating selection caused by environmental variability (Lande 2007).

The main novel insight given by this article is obtained by studying mechanisms generating changes in mean phenotypes that may appear to be selection, but are mainly just effects of mean phenotypes varying among age classes due to previous selection events or genetic drift, and are accordingly not affected by vital rates dependent on the phenotypes. We do this by structuring the article as follows: We first discuss temporal changes in different weighted mean phenotypes in neutral deterministic and stochastic age-structured models, including the overall mean and reproductive value weighted mean as well as mean of newborns or adults, and show how Fisher's concept of reproductive value appears to be extremely useful in filtering out transient fluctuations. Turning to nontrivial situations in which individuals with different phenotypes have different life histories, we derive an extension of the Robertson–Price equation for weighted means and show that with reproductive value weighting one may define an individual fitness measure that is independent of age, providing an equation almost identical to the classical Price equation. For the discrete time model, we propose estimation methods under age-biased sampling and show in Appendix B how uncertainty under sampling, or genetic drift in case of a fully censused population, is related to the demographic variance of the age-structured population (Engen et al. 2005a). We further show how the selection differential can be partitioned into two additive components, $\boldsymbol{S}_{between}$ generated by stochastic fluctuations in individual fitnesses and variation in mean phenotypes among age classes caused by previous drift and selection events, and $\boldsymbol{S}_{within}$ caused by viability and fecundity selection operating within age classes. To link our findings to the work of Fisher (1930) and Lande (1982), we also consider selection on weighted means in continuous time models and show that the covariance formula of Lande (1982) is valid even for strong selection in populations not in their stable age distribution (Appendix A), provided the use of reproductive value weighting. We demonstrate the applicability of our results by a simple numerical example showing the effects of a single selection event acting in one age class. Finally, we include an empirical illustration of our approach, estimating phenotypic selection in a small population of house sparrows *Passer domesticus* (Engen et al. 2012).

Neutral Models

DETERMINISTIC THEORY

Let individuals have phenotypes $\boldsymbol{z} = (z_1, z_2, \ldots, z_p)^T$ of p different traits that by definition are constant throughout their lifetime (see Table 1 for summary of parameters used). Furthermore, let $\bar{\boldsymbol{z}}_x$ be the mean phenotype of individuals in age class x. The model is neutral in the sense that the vital rates of individuals do not depend on their phenotype, so that there is no selection. The population vector next year is given by premultiplication with the projection matrix $\boldsymbol{L}$, that is, $\boldsymbol{n} + \Delta\boldsymbol{n} = \boldsymbol{L}\boldsymbol{n}$. In a standard Leslie model, the projection matrix has zero elements except for the fecundities in the first line and the survivals at the subdiagonal. More generally, the model may be a stage-structured one and also have some other nonzero elements (Lefkovitch 1965; Vindenes et al. 2008).

The reproductive value is defined for each age class in an age-structured population without density regulation, in which the population vector next year is given by premultiplication with a projection matrix (Leslie 1945, 1948; Lefkovitch 1965; Caswell 2001). Regardless of initial population size and age distribution, such a population will approach a stable age distribution and exponential growth with constant multiplicative rate λ that is the real dominant eigenvalue of the projection matrix. Comparing two realizations of such processes with N_0 individuals at time $t = 0$, where all individuals have age x and y, respectively, the population sizes at time t accordingly tend to, say $N_0 c_x \lambda^t$ and $N_0 c_y \lambda^t$. Here the constants c_x and c_y express the size of the contributions that the two age classes give to future populations. Fisher defined reproductive values using a continuous time model, but the concept is more easily understood using discrete time. The reproductive values of age classes x and y, v_x and v_y, are then the constants c_x and c_y scaled in some appropriate way, that is, $v_x/v_y = c_x/c_y$. These reproductive values and the stable age distribution turn out to be the left and right eigenvectors given by $\boldsymbol{L}\boldsymbol{u} = \lambda\boldsymbol{u}$ and $\boldsymbol{v}\boldsymbol{L} = \lambda\boldsymbol{v}$ (Charlesworth 1994; Caswell 2001). Writing $\boldsymbol{n} = (n_1, n_2, \ldots, n_k)^T$ for the population vector, where ^{T} denotes matrix transposition, the most appropriate scaling is defined so that the sum of the reproductive values of all individuals, $\sum_x n_x v_x$, equals the total population size $N = \sum_x n_x$ when the population has reached its stable age distribution (Engen et al. 2009b), implying that $\boldsymbol{v}\boldsymbol{u} = \sum_x v_x u_x = 1$, where $\boldsymbol{u} = (u_1, u_2, \ldots, u_k)^T$ is the stable age distribution.

Now, for some specified component of the trait vector, consider the vector $\boldsymbol{a} = (a_1, a_2, ..., a_k)^T$ with elements $a_x = n_x \bar{z}_x$. Hence, a_x is the sum of phenotypes for this trait over all individuals in age class x. The main idea of using Fisher's reproductive value weighting is easily demonstrated by a simple haploid model in which individuals exactly transmit their phenotype to their offspring. Then the dynamics of $\boldsymbol{a}$ is given exactly by the same matrix multiplication as for $\boldsymbol{n}$, $\boldsymbol{a} + \Delta\boldsymbol{a} = \boldsymbol{L}\boldsymbol{a}$. For example, the n_x individuals in age class x produce $n_x L_{1x}$ individuals with mean phenotype $\bar{z}_x$ in the first class next year, so that a_x generates a corresponding term $n_x \bar{z}_x L_{1x} = a_x L_{1x}$ the next year.

The total reproductive value of the population is $V = \sum v_x n_x = \boldsymbol{v}\boldsymbol{n}$, and let us write $Y = \sum v_x a_x = \boldsymbol{v}\boldsymbol{a}$ for the corresponding quantity defined for the vector $\boldsymbol{a}$ using some specified trait. An important property of reproductive values is that V has exactly exponential growth with multiplicative rate λ regardless of the age distribution, that is, $V + \Delta V = \lambda V$, and as functions of time, $V_t = V_0 \lambda^t$ (Fisher 1927, 1930; Lande et al. 2003; Engen et al. 2009b; Sæther et al. 2013). Because $\boldsymbol{n}$ and $\boldsymbol{a}$ follow exactly the same matrix model, the quantity Y has the same property as V, $Y_t = Y_0 \lambda^t$, and the same formula holds for any component of the phenotype vector.

For a specified trait, the mean phenotype in the total population is $\bar{z} = \sum \bar{z}_x n_x / \sum n_x$ whereas the reproductive weighted mean is $\tilde{z} = \sum \bar{z}_x v_x n_x / \sum v_x n_x = Y/V$. Because Y and V both grow exactly exponentially with the same multiplicative rate, it appears that $\tilde{z}$ is constant through time. The unweighted mean $\bar{z}$ or the mean of newborns or some defined class of adults will, on the other hand, in general undergo transient fluctuations before they finally reach the value $\tilde{z}$ as demonstrated in the upper panel of Figure 1. Hence, a neutral population with mean phenotypes varying among age classes tends to undergo transient fluctuations in the unweighted mean of any component of $\bar{z}$, which finally reaches its reproductive value weighted mean $\tilde{z}$ that remains constant through time. These changes in mean phenotype that we shall call *transient quasi-selection* are not just an effect of deviations from the stable age distribution of individuals among age classes, but depend also strongly on how the mean phenotype varies among age classes. Such variation may be due to previous genetic drift or migration in neutral populations with no selection, or in addition caused by fluctuating selection if selection operates in a fluctuating environment. Although transient quasi-selection has been discussed in the literature (Crow 1979;

Table 1. Definition of mathematical symbols used in the text.

Mathematical Symbol	Description
Model in discrete time	
$z = (z_1, z_2, \ldots, z_{\mathbf{p}})^T$	Phenotypic vector
$\bar{z}$	Mean phenotype
ξ_i	Phenotype of individual i when numbering individuals
$\overline{\Delta z}$ and $\overline{\Delta \xi_i}$	Mean deviation between phenotype of parent and offspring
$\boldsymbol{S} = \boldsymbol{S}_{within} + \boldsymbol{S}_{between}$	Selection differential decomposed into components describing selection within and between-age classes
$\mathbf{L} = \bar{\mathbf{L}} + \varepsilon$	Leslie matrix as mean $\bar{\boldsymbol{L}}$ plus noise ε with $\mathrm{E}\varepsilon = 0$
λ	Real dominant eigenvalue of $\boldsymbol{L}$
$u = (u_1, u_2, \ldots u_k)^T$	Stable age distribution, right eigenvector given by $\boldsymbol{Lu} = \lambda\mathbf{u}$ and scaled by $\sum u_i = 1$
$v = (v_1, v_2, \ldots v_k)$	Reproductive values, left eigenvector given by $\boldsymbol{vL} = \lambda\boldsymbol{v}$ and scaled by $\sum v_i u_i = 1$
J_i and B_i	Indicator variable of survival and number of offspring for individual i
$W_i = J_i v_{x+1} + B_i v_1$	Individual reproductive value for individual i with age x
$n = (n_1, n_2, \ldots, n_k)^{\mathrm{T}}$	Population vector
$N = \sum n_x$	Total population size
$a = (a_1, a_2, \ldots, a_k)^T$	$a_x = n_x \bar{z}_x$, where $\bar{z}_x$ is the mean of some phenotype component over individuals with age x
$V = \sum n_x v_x$	Total reproductive value of the population
$Y = \sum a_x v_x$	Total reproductive value referring to $\boldsymbol{a}$
v_i	Reproductive value of individual i when numbering individuals
$\bar{z} = \sum_i \xi_i v_i / V = \sum_x \bar{z}_x n_x v_x / V$	Reproductive value weighted mean phenotype
$\Lambda_i = W_i / v_i =$ with $\mathrm{E}\Lambda_i = \lambda$	Fitness of individual i
Model in continuous time	
$n_x(z), N(z) = \int n_x(z) dx$	Density of individuals with age x and phenotype z and total density of individuals with phenotype z
$b_x(z)$, $\mu_x(z)$ and $v_x(\mathrm{z})$	Birth and death rate, and reproductive value of individuals with age x and phenotype z
$V(z) \int n_x(z) v_x(z) dx$	Total reproductive value of individuals with phenotype z
$V = \int V(z) dz$	Total reproductive value of the population
$\bar{z} = \int z V(z)/V dz$	Reproductive value weighted mean

Engen et al. 2009a) and the power of reproductive value weighting is well known, the generating mechanisms through variation in phenotypes among age classes, in addition to deviation from the stable age distribution, have not been emphasized. Here we discuss this in some detail, also considering relevant estimation procedures in discrete time.

STOCHASTIC THEORY

In a fluctuating environment, the vital rates will fluctuate among years so that the projection matrix $\boldsymbol{L}$ is stochastic (Cohen 1979; Tuljapurkar 1982; Caswell 2001; Lande et al. 2003). Assuming a large population size so that demographic stochastic effects can be ignored, writing $\bar{\boldsymbol{L}}$ for the expected matrix, $\boldsymbol{L} = \bar{\boldsymbol{L}} + \boldsymbol{\varepsilon}$ and defining λ, $\boldsymbol{u}$, $\boldsymbol{v}$ by $\bar{\boldsymbol{L}}$, we have

$$V + \Delta V = \boldsymbol{v}(\boldsymbol{n} + \Delta \boldsymbol{n}) = \boldsymbol{v}\boldsymbol{L}\boldsymbol{n} = \boldsymbol{v}(\bar{\boldsymbol{L}} + \boldsymbol{\varepsilon})\boldsymbol{n}$$

and using the definition of $\boldsymbol{v}$, we find $V + \Delta V = \lambda V + \boldsymbol{v\varepsilon n}$. For small stochastic fluctuations, we may approximate the $\boldsymbol{n}$ in the noise term by its value at the stable age distribution (Engen et al. 2009b), which is $N\boldsymbol{u} = V\boldsymbol{u}$, giving $V + \Delta V = \lambda V(1 + \lambda^{-1}\boldsymbol{v\varepsilon u})$. Because the dynamics of $\boldsymbol{a}$ is given by the same stochastic projection matrix, we also have to have the same order of approximation that $Y + \Delta Y = \lambda Y(1 + \lambda^{-1}\boldsymbol{v\varepsilon u})$ so that $(Y + \Delta Y)/(V + \Delta V) = Y/V$. In other words, to this order of approximation $\bar{z} = Y/V$ is constant for each trait even under stochastic fluctuations. Some illustrating numerical examples are shown in the middle and lower panel of Figure 1.

Selection

DISCRETE TIME

The above discussion suggests that a useful approach for age-structured populations is to study selection on the mean phenotype weighted by reproductive values to smooth out fluctuations in the mean value due only to fluctuations in the age distribution and variation in $\bar{z}_x$ among age classes. For a population with varying phenotypes the vital rates of different types may define different projection matrices, and hence different stable age

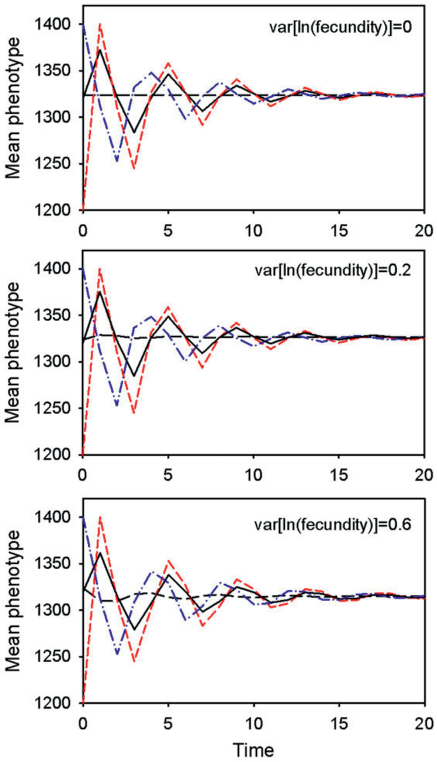

Figure 1. The variation in the mean phenotype $\bar{z}$ (solid black line) and in the reproductive value weighted mean phenotype $\tilde{z}$ (dashed black line) over a period of 20 years for an age-structured population with five age classes for three different levels of variance in fecundity. The red line shows the mean $\bar{z}_1$ for newborns, whereas the blue line is the mean $\bar{z}_{adults}$ of adults defined as individuals of age 3 and older. The initial population has 2000 individuals in each age class with $\bar{z}_1 = \bar{z}_2 = 1200$, $\bar{z}_3 = 1300$, $\bar{z}_4 = 1400$ and $\bar{z}_5 = 1500$. In the upper panel the model is deterministic. The elements of the projection matrix are zero except for the survivals $L_{21} = 0.3$, $L_{32} = 0.6$, $L_{43} = 0.9$, $L_{54} = 0.9$; and fecundities $L_{11} = L_{12} = 0$, $L_{13} = 2$, $L_{14} = 3$, and $L_{15} = 2$. These parameters yield $\lambda = 1.033$, stable age distribution $u = (0.577, 0.167, 0.097, 0.085, 0.074)^T$, and reproductive values $v = (0.442, 1.523, 2.623, 2.029, 0.856)$. In the medium and lower panels all fecundities are multiplied by a common stochastic log-normally distributed factor $e^{\tau u - \tau^2/2}$, where u is a standard normal variate. The expected value of this factor is 1. The variance τ^2 of log fecundities is 0.2 in the medium panel and 0.6 in the lower.

distributions and reproductive values. In the following derivation we use the reproductive values derived from the mean projection matrix as weights. The selection equation that we derive, however, in general gives the correct change in mean phenotype for any choice of weights, but it is still recommended to use the reproductive values from the mean matrix as those weights. They are likely to smooth out most of the nonselective transient fluctuations in mean phenotype due only to stochastic fluctuations in age structure. However, nowhere in the derivation do we use any particular properties of the reproductive values. It is also important to notice that if all weights are chosen equal to one, our result is equivalent to the standard Robertson–Price equation.

To find the appropriate generalization of the Robertson–Price equation for a generally weighted mean, we now number the N individuals in the population at a given time by index i rather than numbering the age classes, writing $\boldsymbol{\xi}_i$ and ν_i for the phenotype vector and weight of individual i. However, each individual in an age class has the same weight. Hence, $\nu_i = v_x$ if individual i has age x and the weights are the reproductive values, but in general the v_x may represent any weighting of age classes. The weighted mean is $\tilde{z} = \sum_i \boldsymbol{\xi}_i \nu_i / \sum_i \nu_i$, whereas the unweighted arithmetic mean corresponding to equal weights is $\bar{z} = \sum \boldsymbol{\xi}_i / N$. The concept of individual reproductive value was introduced by Engen et al. (2009b) as an individual's realized contribution to the total reproductive value next year. For a stochastic Leslie model this is, for an individual in age class x, $W_i = J_i v_{x+1} + B_i v_1$ where J_i is an indicator of the survival of individual i and B_i is its number of offspring (Engen et al. 2009b). The quantities W_i may similarly be defined for any chosen weights different from reproductive values. Then, in general, W_i is the individual's contribution to the sum of weights $V = \sum \nu_i$ the next year.

Now, starting with a population with sum of weights over all individuals $V = \sum \nu_i$ and $\boldsymbol{Y} = \sum \nu_i \boldsymbol{\xi}_i$, the values the next year are $V + \Delta V = \sum W_i$ and $\boldsymbol{Y} + \Delta \boldsymbol{Y} = \sum W_i (\boldsymbol{\xi}_i + \overline{\Delta \boldsymbol{\xi}_i})$, where $\boldsymbol{\xi}_i + \overline{\Delta \boldsymbol{\xi}_i}$ is the mean value of the the offspring of individual i, including this individual itself if it survives. Hence $\overline{\Delta \boldsymbol{\xi}_i}$ is the difference between the mean phenotype of the offspring of individual i and its own phenotype. The value of the weighted mean next year is

$$\tilde{z} + \Delta \tilde{z} = \sum W_i (\boldsymbol{\xi}_i + \overline{\Delta \boldsymbol{\xi}_i}) / \sum W_i .$$

Subtracting the initial value $\tilde{z} = \sum \nu_i \boldsymbol{\xi}_i / \sum \nu_i$ yields the change in weighted mean as

$$\Delta \tilde{z} = \frac{\sum W_i (\boldsymbol{\xi}_i - \tilde{z})}{\sum W_i} + \frac{\sum W_i \overline{\Delta \boldsymbol{\xi}_i}}{\sum W_i}, \tag{2}$$

where the first and second term are the selection differential and the transmission bias, respectively, exactly as in the original Robertson–Price equation. This is the simplest equation to use for estimating the selection differential from a sample as described in the section on estimation.

If there is no heritability and the weights are exactly the reproductive values then $\mathrm{E}(W_i)/\nu_i = \lambda$ for all individuals regardless of their age. Hence, $\Lambda_i = W_i/\nu_i$ is the individual fitness with mean λ not changing with age. Engen et al. (2011)

showed that this also in general is the relevant individual fitness measure under weak selection. To see the relation of equation (2) to the original Robertson–Price equation, we use this definition of Λ_i and alternatively write equation (2) with weights chosen as reproductive values as

$$\Delta\tilde{z} = \frac{\sum \Lambda_i \nu_i(\boldsymbol{\xi}_i - \tilde{z})}{\sum \Lambda_i \nu_i} + \frac{\sum \Lambda_i \nu_i \overline{\Delta\boldsymbol{\xi}_i}}{\sum \Lambda_i \nu_i}.$$

Using tilde ˜ to indicate that mean values and sum of cross products are weighted by reproductive values we obtain, dividing numerators and denominators by $\sum \nu_i$, an equation with exactly the same form as the Robertson–Price equation

$$\Delta\tilde{z} = \tilde{\mathrm{cov}}(\Lambda_{rel}, \boldsymbol{\xi}) + \tilde{\mathrm{E}}(\Lambda_{rel}\overline{\Delta\boldsymbol{\xi}}), \tag{3}$$

where $\tilde{E}$ and $\tilde{\mathrm{cov}}$ are sums over all individuals weighted by their reproductive values and $\Lambda_{rel} = \Lambda/\tilde{\Lambda}$ is the relative individual fitness. Plugging in unit weights $\nu_i = 1$ in equation (3) yields exactly the standard Robertson–Price equation.

For a discussion of estimation under age-biased sampling and evaluation of the random genetic drift, see Appendix B, equations (B1)–(B3).

Decomposition of the Selection Differential

Estimation of selection differentials can be done for single fitness components using Robertson's (1966) covariance formula. In the present model the viability components are $\boldsymbol{S}_{Jx} = \mathrm{cov}_x(J/\bar{J}_x, \boldsymbol{\xi})$, where subscript x in cov_x indicates that the covariance sum is taken over the n_x individuals in age class x, whereas $\bar{J}_x$ is the mean survival of these individuals. Similarly, we define the fecundity components as $\boldsymbol{S}_{Bx} = \mathrm{cov}_x(B/\bar{B}_x, \boldsymbol{\xi})$. Writing $\sum W_i = \sum n_x \bar{W}_x = N \sum \hat{u}_x \bar{W}_x$ where $\hat{u}_x = n_x/N$, and $\sum W_i(\boldsymbol{\xi}_i - \tilde{z}) = N \sum \hat{u}_x \overline{W(\boldsymbol{\xi} - \tilde{z})}_x$, where $\overline{W(\boldsymbol{\xi} - \tilde{z})}_x$ is the mean of $W(\boldsymbol{\xi} - \tilde{z})$ over the n_x individuals observed in age class x, the selection differential in equation (2) is $\boldsymbol{S} = \sum \hat{u}_x \overline{W(\boldsymbol{\xi} - \tilde{z})}_x / \sum \hat{u}_x \bar{W}_x$. Using the decomposition

$$\overline{W(\boldsymbol{\xi} - \tilde{z})}_x = \bar{W}_x(\bar{z}_x - \tilde{z}) + \overline{W(\boldsymbol{\xi} - \bar{z}_x)}_x$$

then yields a decomposition of the selection differential into two additive terms, $\boldsymbol{S} = \boldsymbol{S}_{between} + \boldsymbol{S}_{within}$, where $\boldsymbol{S}_{between} = (z^* - \tilde{z})$, with $z^* = \sum_x \hat{u}_x \bar{W}_x \bar{z}_x / \sum_x \hat{u}_x \bar{W}_x$ whereas the reproductive value weighted mean for any choice of weights can be computed as $\tilde{z} = \sum v_x \hat{u}_x \bar{z}_x / \sum \hat{u}_x v_x$. Notice that z^* is the mean phenotype obtained when weighting age class x by $\hat{u}_x \bar{W}_x$. The within-age class component can be written as a weighted sum of age-specific viability and fecundity selection differentials,

$$\boldsymbol{S}_{within} = \sum_x \hat{u}_x(\bar{J}_x v_{x+1} \boldsymbol{S}_{Jx} + \bar{B}_x v_1 \boldsymbol{S}_{Bx}) / \sum_x \hat{u}_x \bar{W}_x. \tag{4}$$

If there is no selection, then $\mathrm{E}(\boldsymbol{S}_{within}) = \boldsymbol{0}$ so that an eventual nonzero expectation of the total selection differential, such as illustrated by the transient fluctuations shown in Figure 1, must come from $\mathrm{E}(\boldsymbol{S}_{between}) \neq \boldsymbol{0}$.

For a large population the mean value of the $W_i = J_i v_{x+1} + B_i v_1$ over individuals of age x is $\bar{W}_x = L_{x+1,x} v_{x+1} + L_{1,x} v_1$. Accordingly, the "false" selection due to differences between age classes, which we call transient quasi-selection, is

$$\boldsymbol{S}_{between} = (z^* - \tilde{z}) = \frac{\sum(L_{x+1,x} v_{x+1} + L_{1,x} v_1)\hat{u}_x(\bar{z}_x - \tilde{z})}{\sum(L_{x+1,x} v_{x+1} + L_{1,x} v_1)\hat{u}_x}. \tag{5}$$

Choosing reproductive value weighting, we have $L_{x+1,x} v_{x+1} + L_{1,x} v_1 = \lambda v_x$ so that $\boldsymbol{S}_{between}$ is zero for any values of the age-specific mean phenotypes $\bar{z}_x$. In a finite population $L_{x+1,x}$ and $L_{1,x}$ should be replaced by $\bar{J}_x$ and $\bar{B}_x$, respectively. Stochasticity may then lead to significant differences between $\bar{W}_x$ and its theoretical expectation so that some age classes on average may have individuals with mean individual fitnesses much larger or smaller than expected. In addition to compensating for differences in the $\bar{z}_x$ due to stochasticity or previous selection events, reproductive value weighting ensures that $\boldsymbol{S}_{between}$ in a finite population is a pure noise term with zero expectation not generating future transient fluctuations. This term can actually be omitted when estimating selection by computing selection differentials separately for all age classes and adopt the weighting defined by equation (4).

Examples of Other Choices of Weights

SIMPLE ARITHMETIC MEAN

We can compare the selection differentials obtained from equations (4) and (5) for the weighted and unweighted means simply by plugging in $v_x = 1$ for all age classes. Then $W = J + B$, $\mathrm{E}(\bar{W}_x) = L_{x+1,x} + L_{1,x}$ and $\tilde{z} = \bar{z}$. Inserting this in the expression for $\boldsymbol{S}$ still gives $\mathrm{E}(\boldsymbol{S}_{within}) = 0$ when there is no selection, whereas the value of $\boldsymbol{S}_{between}$ conditioned on the age-specific phenotypes in a large population is

$$\boldsymbol{S}_{between} = \frac{\sum(L_{x+1,x} + L_{1,x})\hat{u}_x(\bar{z}_x - \bar{z})}{\sum(L_{x+1,x} + L_{1,x})\hat{u}_x}, \tag{6}$$

which is no longer zero. Hence we will on average find a nonzero selection differential for the arithmetic mean phenotype even if there is no selection at all, in agreement with the transient fluctuations in the differentials for the mean phenotypes shown in Figure 1, only due to differences in mean vital rates and mean phenotypes among age classes. For a general projection matrix $\boldsymbol{L}$, the term $L_{x+1,x} + L_{1,x}$ in equation (6) should be replaced by $\sum_j L_{j,x}$.

MEAN PHENOTYPE OF NEWBORNS

Another interesting choice of weights is $v_1 = 1$ and $v_x = 0$ for $x > 1$. Then $\bar{W}_x = \bar{B}_x$ and $\tilde{z} = \bar{z}_1$, that is, $\tilde{z}$ is the mean phenotype of newborns. Assuming a large population and inserting this in equation (5) then yields

$$\boldsymbol{S}_{between} = \sum \hat{u}_x(\bar{z}_x - \bar{z}_1)L_{1,x} / \sum \hat{u}_x L_{1,x}. \tag{7}$$

As in equation (6) the age effect is partly generated by differences in the $\bar{z}_x$ produced by viability selection on different stages in the life cycle, and will also be affected by differences in the $\bar{z}_x$ caused by drift or other nonselective mechanisms. Selection within years occurs only as fecundity selection by the fecundity terms of equation (4) with only v_1 different from zero. Viability selection within age classes does not appear in equation (4) but may produce differences in the $\bar{z}_x$ and thus affect $\boldsymbol{S}_{between}$.

MEAN ADULT PHENOTYPE

Defining the adult class as all individuals of age larger than y by choosing $v_x = 1$ for $x > y$ and zero for $x \leq y$ so that $\tilde{z}$ is the mean phenotype of adults in a large population yields

$$\boldsymbol{S}_{between} = \frac{\sum_{x=y}^{k} \hat{u}_x L_{x+1,x}(\bar{z}_x - \tilde{z})}{\sum_{x=y}^{k} \hat{u}_x L_{x+1,x}}, \tag{8}$$

where $\tilde{z} = \sum_{x=y+1}^{k} \hat{u}_x \bar{z}_x / \sum_{x=y+1}^{k} \hat{u}_x$, now is the mean phenotype of adults. Notice that the sum in the numerator is taken over the adults as well as the last age class before the adult stage. Hence $\boldsymbol{S}_{between}$ is strongly affected by the differences in the $\bar{z}_x$ among adult age classes as well the class before the adult stage.

Numerical Illustration

As a clarification of the concepts, it may be illustrating to consider a population that at first is stable with no selection and then affected by a selection event in one age class a single year. This is illustrated in Figure 2 using a model with five age classes in which reproduction starts at age 3. The single year selection event is chosen to be viability selection on the first age class, using survivals $L_{21}(z) = 0.3 + \beta(z - \bar{z}_1)$, where $\beta = 0$ except for this single year with $\beta = 0.04$. Assuming that the phenotypic variance is 900, this yields a selection differential $S_{J1} = 0.04 \times 900 = 36$ in the year of selection whereas all other age-specific differentials for viability and fecundity are zero. For a haploid model with heritability $h^2 = 1$ (Fig. 2, right panels) and a large population in stable age distribution (which is not disturbed by this event because the mean survival is not affected by selection), this yields a selection differential and response to the reproductive value weighted mean according to equation (4) as $S = u_1 v_2 L_{21} S_{J1} = 9.18$. Figure 2 illustrates the changes this event makes in the reproductive value weighted mean $\tilde{z}$, the arithmetic mean $\bar{z}$, and the mean of newborns and adults of age 3–5. The reproductive value weighted mean makes a single change and thereafter remains constant (the black solid line and the red line coincides in Fig. 2). The other weighted mean values show different types of transient fluctuations. These fluctuations occurring together with nonzero differentials $S_{between}$ are generated by transient fluctuations among age classes with different mean vital rates. Hence, for weights different from the reproductive values the selection differential observed in the year of selection does not coincide with the final response. For example, the differential for the arithmetic mean is 6.02 whereas the final response is 9.18.

With heritability smaller than one, the picture is more complicated. In Figure 2 (left panels) we have assumed that the heritability is 0.5 for all age classes so that only one half of the selection differential in an age class is transmitted to their offspring. According to the present theory, the selection differential 9.18 for the reproductive value weighted mean yields the response of 4.59. However, due to the age structure, transmissions to offspring are partly delayed until reproduction occur so that the final reproductive value weighted mean is not reached until the cohort under selection stops producing offspring, which is four years after the selection event in this model (see Fig. 2). More specifically, viability selection has a direct effect on the mean (or weighted mean) phenotype equal to the actual selection component corresponding to unit heritability, but at later transmission to its offspring the selection component is multiplied by the heritability. Accordingly, the immediate effect of viability selection is larger than the actual response, as seen in Figure 2 (middle left panel).

An Example: House Sparrows at an Island in Northern Norway

To illustrate practical application of this theory, we analyze selection on two morphological traits of house sparrows living on an island in northern Norway. Two morphological traits of fledglings (tarsus length and body mass) were measured in this population at the Island of Aldra during the period 2002–2007. A large proportion of all individuals in this population was individually recognizable by the use of an individually numbered metal ring and a unique set of color rings, which enabled estimation of survival and age-specific reproductive rates. These data were previously used by Engen et al. (2012) to estimate fluctuating selection by the use of age-specific linear regression of individual reproductive values on the traits. Here, we extend this approach to account for transient fluctuations in selection due to variation in age structure. Our analyses include only the female segment of the population, using two age classes, juveniles (first calendar year) and adults (second or more calendar years). We assume postreproduction census (Caswell 2001), assuming that all

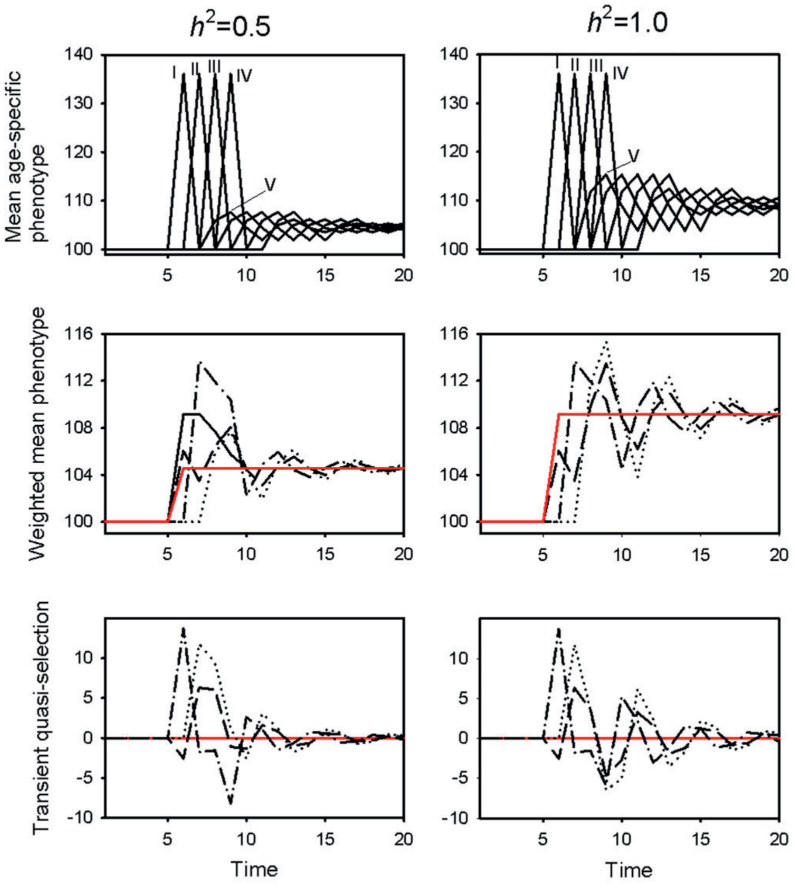

Figure 2. The same Leslie model and parameters as in Figure 1 with a single selection event between year 5 and 6 and no selection the other years. Selection only affects the survival of individuals in the first age class modeled as $L_{21}(z) = 0.3 + \beta(z - \bar{z})$ with $\beta = 0$ except for the year of selection when $\beta = 0.04$. The phenotypic variance is 900 so that the viability selection differential the year of selection is $S_{J1} = 0.04 \times 900 = 36$. Effects of this single selection event are shown for heritability $h^2 = 0.5$ (left panels) and $h^2 = 1$ (right panels). The upper panels show the age-specific mean values $\bar{z}_x$ for the five age classes (indicated by Roman numerals). The middle panel shows the four different weighted mean phenotypes, reproductive weighted mean (solid line), arithmetic mean $\bar{z}$ (medium dashed line), mean of newborns (dotted line), and mean of adults of age $x \geq 3$ (dashed and dotted line). The red lines are the values obtained using the response $h^2 S_{within}$, where S_{within} is given by equation (4) with reproductive value weighting. In the middle right panel, the solid black line coincides with the red line and is not seen. This line coincides with the reproductive weighted mean for $h^2 = 1$. The lower panel shows the transient quasi-selection $S_{between}$ for the same four weighted means, with a zero red line for reproductive value weighting.

individuals recorded during the breeding season (May–August) also were alive just after the end of breeding. Thus, the survival of an individual in year t was 1 if it was recorded during the breeding season in year $t+1$ (or later) and 0 if not. The fecundity rate in year t was determined by the number of juveniles captured by mist-netting after fledging in year $t+1$. For further details about the study area and field procedures, see Billing et al. (2012) and Engen et al. (2012).

Analyses of selection in both morphological characters revealed that the different weightings used on the mean character produced somewhat different temporal variation in the selection differentials within age classes (Fig. 3). The differentials for reproductive value weighting will most exactly predict the future effects of each selection event. Differences in estimated selection between different weightings are most clearly seen in the between-age classes selection components. This component is close to zero

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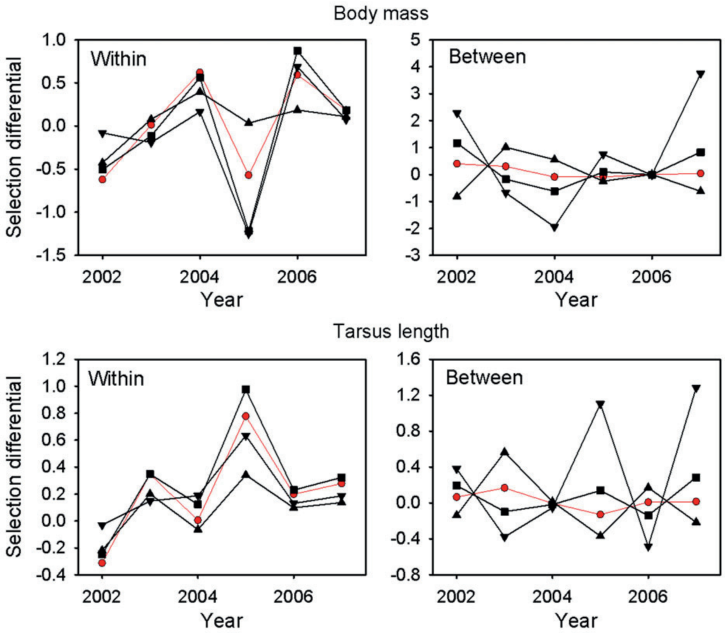

Figure 3. **Selection differential within- and between-age classes for two morphological characters (body mass and tarsus length) of fledglings in a house sparrow population in northern Norway. The selection differential is calculated for the reproductive weighted mean (red solid line and circles), arithmetic mean (squares), mean of newborns (downward triangles), and mean of adults (upward triangles).**

with less temporal variation by reproductive value weighting than for the other weighted means. Accordingly, using the Price equation and ignoring age structure by giving all individuals, the same weight will mainly produce transient quasi-selection.

Continuous Time

In Appendix A, we show some related results using continuous time as Fisher (1930) did originally. Writing $n_x(z)$ for the density of individuals with age x and phenotype z, $v_x(z)$ for their reproductive value expressed by the birth rates $b_x(z)$ and death rates $\mu_x(z)$ (equation A1), $V(z) = \int n_x(z)v_x(z)dx$ for the total reproductive value of individuals of age x, and $V = \int V(z)dz$ for the total reproductive value of the population, the reproductive value weighted mean is $\tilde{z} = \int zV_x(z)/V dx dz$ where $V_x(z) = n_x(z)v_x(z)$. As in the discrete time case we may replace the reproductive values by any other weights. It is shown that the selection differential for $\tilde{z}$ using general weighting then is

$$\boldsymbol{S} = \mathrm{cov}[z, r_x(z)], \tag{9}$$

where the covariance refers to then joint distribution of x and z defined as $V_x(z)/V$ and $r_x(z)$ is an age- and phenotype-specific growth rate given by

$$r_x(z) = [-\mu_x(z)v_x(z) + dv_x(z)/dx + b_x(z)v_0(z)]/v_x(z). \tag{10}$$

Using reproductive value weighting Fisher's equation for reproductive values (equation A2, Fisher 1930) implies that $r_x(z) = r(z)$ does not depend on age. Then the selection differential is

$$\boldsymbol{S} = \mathrm{cov}[z, r(z)], \tag{11}$$

where the covariance refer to the distribution $V(z)/V$ of z. This is then equivalent to the result of Lande (1982) if the population is in its stable age distribution so that $V(z)/V = N(z)/N$, where $N(z) = \int n_x(z)dx$ and $N = \int N(z)dz$.

It is not possible to decompose the selection as we have done in the discrete case because it can be at most a single individual with age and phenotype exactly equal to x and z, so that covariances such as $\boldsymbol{S}_{Bx}$ in the discrete time model can not be estimated. However, if the population is not in its stable age distribution due to drift and previous selection events, we explain in Appendix A why there must be a transient quasi-selection also in this model when the weights are not the reproductive values. More details are given in Appendix A.

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Discussion

Most analyses of evolution in age-structured populations, following Hamilton (1966), rely heavily on sensitivity analyses, which measure the effects on the population growth rate of small perturbations of age-specific demographic traits (Charlesworth 1994; Caswell 2001). Such fitness sensitivities (Charlesworth and Charlesworth 2010) can be used to explore the consequences of trade-offs between components of the life history (Schaffer 1974; Roff 1992; Caswell 1978, 1996) or the influence of environmental fluctuations at different life-history stages (Tuljapurkar et al. 2003; Morris and Doak 2004). Our approach using the reproductive value weighting proposed by Fisher (1930) provides an important extension of these models because it combines different components of fitness into a single measure of individual fitness that accounts for fluctuations in age structure and variation in mean phenotype among age classes. In contrast, other measures of fitness in age-structured populations (e.g., Hamilton 1966; Charlesworth 1994; McGraw and Caswell 1996; Brommer et al. 2004; Moorad 2014) assume a stable age-distribution and no among-cohort phenotypic variation.

We have showed that effects of demographic stochasticity and fluctuations in the age distribution, causing variation in phenotypic mean among age classes, may have significant influence on observed selection at a given time. In a stochastic environment, or in relatively small populations in which the effects of demographic noise and genetic drift are significant (Lande 1976), these two factors will always complicate the analysis of age-dependent selection. First, there will be stochastic fluctuations in the age distribution with fractions of individuals in given age classes possibly deviating much from that given by the stable age distribution defined by the mean Leslie matrix (Caswell 2001). Second, selection and drift induce differences in mean phenotypes among age classes that tend to be further increased by sampling (Appendix B; Engen et al. 2012). Although our Figure 1 is based on a simple haploid model with constant projection matrix, it illustrates how the two complicating factors given above will affect evolution. Theoretically, only the reproductive value weighted mean will remain constant when there is no selection in the sense that no vital rates depend on phenotype. The arithmetic mean, as well as the mean phenotype of newborns or adults, however, will undergo transient fluctuations that may be large, which are our selection components $\boldsymbol{S}_{between}$. Simple statistical analyses of evolution in mean values other than the reproductive value weighted mean are therefore likely to produce significant transient quasi-selection between years demonstrated in our numerical illustration, which may look like strong stabilizing selection over time even when selection in reality is absent. This may influence analyses of selection in age-structured populations, in which one often uses lifetime reproductive success as a measure of fitness (e.g., Brommer et al. 2004; Charmantier et al. 2006), which requires a stable age distribution (Grafen 1988). Our simulations (Fig. 2) and analyses of selection in house sparrows (Fig. 3) reveal that transient fluctuations resulting in biased estimates of selection within an age class can be reduced by using reproductive value weighting. However, if selection is measured in this way and the response is correctly calculated as the product of the selection differential and the heritability, this response is still delayed until lifetime reproduction is realized unless the heritability is one, and is therefore not observable at the time of selection as illustrated in Figure 2 (left middle panel). The power of applying reproductive values in analyses of selection was emphasized by Fisher (1930), who invented the concept, and further illustrated by Crow (1979). Rather strangely, Fisher did not give any details about this other than saying that allele frequencies should be based on this weighting. He did not even state that the basic mean quantitative character in his fundamental theorem of natural selection, the mean Malthusian parameter, should be weighted in the same way as pointed out by Crow (1979), probably because he considered this to be a trivial consequence of weighting allele frequencies.

Lande (1982) developed a theory for the evolution of a multivariate phenotype in an age-structured population in continuous time assuming weak selection and stable age distribution, showing that the selection gradient is given by the sensitivity of λ to the phenotype (see also Charlesworth 1993 and Moorad 2014). Lande (1982) derived the selection differential cov$[r(z), z]$ as an approximation, referring to the actual distribution $N(z)/N$ of z in the population using the mean phenotype of newborns. This is in agreement with our results because $V(z)/V = N(z)/N$ under the stable age distribution, and the assumption of weak selection ensures that the selection differential is approximately the same for all weighted means of phenotypes, in particular the mean of newborns. However, our equation (9) is exact and assumes neither weak selection nor stable age distribution. Charlesworth (1993), also studying the mean phenotype of newborns, showed that the result of Lande (1982) holds under deviations from the stable age distribution, still assuming weak selection. Furthermore, Moorad (2013, 2014) used (assuming a stable age distribution) Fisher's (1930) expression for the reproductive value at birth, $w = \sum_x \bar{\lambda}^{-x} l_x b_x$, with l_x as defined in Appendix A, as a measure of relative fitness, where $\bar{\lambda}$ is the multiplicative growth rate of the total population given by the Euler equation $\sum_x \bar{\lambda}^{-x} \bar{l}_x \bar{b}_x = 1$. Here $l_x b_x$ refers to individuals whereas $\bar{l}_x \bar{b}_x$ are the population mean values. However, this is a limited application of Fisher's concept of reproductive value because it is used only for one age class, whereas Fisher's main idea was to use its variation among age classes to compare their contributions to future populations. For weak selection, writing $l_x b_x = \bar{l}_x \bar{b}_x + d(l_x b_x)$, where $d(l_x b_x)$

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represents infinitesimal variation in vital rates among individuals, the above definition yields exactly $w = (\lambda/\bar{\lambda})^T$, where T is the generation time and λ is the solution of $\sum_x \lambda^{-x} l_x b_x = 1$. Hence, the use of the relative fitness measure w is equivalent to using $(\lambda/\bar{\lambda})^T$, which again is equivalent to using $\lambda/\bar{\lambda}$, as shown by Moorad (2013). Thus, Moorad (2013) uses the Euler equation to express the traditional relative fitness as the growth rate of individuals with given vital rates relative to the growth rate of the population.

A further extension of multivariate selection in age-structured populations was provided by Coulson and Tuljapurkar (2008) and Coulson et al. (2010), showing that the demographic impact of changes in the distribution of phenotypes affects the long-term population growth rate and hence selection acting on the mean phenotype in the population. This approach has also been used to evaluate long-term changes in fitness-related characters as a response to environmental variation (e.g., Ozgul et al. 2009, 2010). This application of the Robertson–Price equation decomposes the selection on mean phenotype into all of its components and makes it possible to measure them. However, analysis of interactions of different stochastic components through time, as provided by our decomposition, and separating actual selection from nonselective stochastic fluctuations and effects of previous selection events is not possible with their approach.

Lande (1982) derived his covariance formula for the selection differential of mean of newborns, assuming stable age distribution and weak selection. Under those assumptions the selection differential will be approximately the same for all weighted means, provided that there are no stochastic fluctuations in mean phenotypes among age classes generated by genetic drift, fluctuating selection and/or migration. In particular the selection differential for the reproductive value weighted mean used in our equation (11) will also be given by this covariance. Hence, transient quasi-selection is removed by the simplifying assumptions made in the modeling, provided that there are no stochastic fluctuations in mean phenotypes among age classes. However, when the population deviates from its stable age distribution the exact general formula for any type of weights is given by equation (9) regardless how mean phenotypes vary with age, which is a much more complex result because it involves the joint distribution of age and phenotype among individuals. The intention of Fisher (1930) by proposing the use of reproductive value weighting was probably the simplicity obtained when going from general weights as in equation (9), such as the simple arithmetic mean, to the reproductive value weighted mean used in equation (11), giving the exact selection differential for $\bar{z}$ with no assumption of stable age distribution. It also introduces a problem not considered by Fisher: the weight of an individual should be the reproductive value computed from the vital rates of that phenotype. Hence, it is a complex thing to compute unless we have fitted models expressing how the rates depend on phenotype. The general result for reproductive value weighting expressed by equation (9) does not give a decomposition of $\boldsymbol{S}$ into real selection and noise with no impact on the future as for the decomposition into $\boldsymbol{S}_{between}$ and $\boldsymbol{S}_{within}$ that we have given in discrete time. But we can still see from equation (A3) in Appendix A for the arithmetic mean that if b_x and μ_x are constants not depending on z, one could still observe transient quasi-selection due to covariation between z and $b_x - \mu_x$ generated by previous stochastic fluctuations in mean phenotype among age classes.

As a simplified illustration of reproductive value weighting, in addition to our numerical example, we may consider a population with two age classes in which individuals in the last class do not reproduce at all, but still may survive to remain in the same class and show large viability dependence on phenotype. In addition, assume that there is no selection at all among reproducing individuals in the first class. In this model, the first and second class have reproductive values one and zero, respectively. Ignoring age structure and measuring the selection differential for the overall mean during one time step will then result in observed selection due to the viability selection in the last class. However, there will be no evolution in this population, providing a biased record of selection in this population similar to those demonstrated in Figure 1. On the contrary, by using reproductive value weighting we consider only the first class of reproducing individuals that represent the total reproductive value of the population. Within this class, we will correctly observe that there is no selection.

Another illustration of the concepts and decomposition is provided by only considering the newborns or some particular age groups defined as adults. There are still two components of selection. In the case of newborns $\boldsymbol{S}_{within}$ is generated by pure fecundity selection wheeas $\boldsymbol{S}_{between}$ is affected by viability selection previous years generating differences in $\bar{z}_x$ among age classes. For the adult stage it is the opposite. Then the $\boldsymbol{S}_{within}$ is generated by pure viability selection, which means that all fecundity selection only acts through the differences in the $\bar{z}_x$ it may previously have caused.

Our analysis is constructed for traits that do not change with age. Many traits, such as body size, change with age and can only be analyzed appropriately by our approach by replacing them by sets of traits chosen as parameters in individual growth curves not changing with age. Measurement of such traits require special regression techniques as considered, for example, by Schaeffer (2004) and Kirkpatrick (2009).

To summarize, we have provided an age-structured extension of the stochastic Robertson–Price equation for weighted means of phenotypes that can be used to analyze age-dependent selection. We do this by using the idea originally proposed by Fisher (1930) that the mean value of the character should be calculated

[redacted]

using reproductive value weighting. We show that selection in general can be decomposed into components due to individual differences between and within age classes. Using reproductive value weighting, the between-age class component due to previous stochastic effects or selection events becomes pure noise with no effect on the future. This component, which we call transient quasi-selection, should therefore be omitted in the estimation of selection. For other mean values, in particular the arithmetic mean phenotype and mean phenotype of newborns, this component will have nonzero mean and show complicated transient fluctuations that could wrongly be interpreted as selection.

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DATA ARCHIVING

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Appendix A: Continuous Time

The use of reproductive values in evolution was introduced by Fisher (1930) in the second chapter of his book, preceding the derivation of his fundamental theorem of natural selection. Fisher considered the Malthusian parameter m as a quantitative character of an individual, and showed, using a continuous time model, that under very general assumptions the temporal change in mean Malthusian parameter $d\bar{m}/dt$ equals exactly the additive genetic variance of m when the time unit is the mean generation time. To call this a *fundamental* theorem he argued that it was also correct for an age-structured population, provided that population mean values were defined in a specified way. Fisher only expressed this in words with reference to allele frequencies p and q and the following comment to his theorem: *The rigor of the demonstration requires that the terms employed should be used strictly as defined; the ease of its interpretation may be increased by appropriate conventions of measurement. For example, the ratio p:q should strictly be evaluated at any instant by enumeration, not necessarily of the census population, but of all individuals having reproductive value, weighted according to the reproductive value of each.*

We see that Fisher mentioned gene frequencies as *an example* of quantities that should be evaluated by weighting the individuals in the population by their reproductive value. So, if some gene frequency of individuals of age x is q_x and their reproductive value is v_x, then the appropriate gene frequency in the population is the weighted mean $\int q_x v_x p_x dx / \int v_x p_x dx$, where p_x is the distribution of x among individuals in the population (Engen et al. 2009a). He did not state explicitly that the mean value of any quantitative character, in particular the Malthusian parameter that he studied, should be evaluated in the same way, but it follows from the weighting of frequencies that the mean value in the theorem should also be interpreted as the weighted mean

$$\bar{m} = \int \bar{m}_x v_x p_x dx / \int v_x p_x dx,$$

where $\bar{m}_x$ is the mean Malthusian parameter for individuals of age x. That Fisher actually meant that the mean fitness in his fundamental theorem of natural selection should be interpreted in this way was pointed out by Crow (1979). In other words, it is the temporal change in this mean value that equals the additive genetic variance in m. Probably, Fisher also meant that the computation of the additive genetic variance in the case of an age-structured population, which is not necessarily in its stable age distribution also should be based on the same weighting (see Crow 1979, 2002).

Several authors have analyzed selection in continuous time, assuming that the population is in its stable age distribution (Lande 1982 and references therein). For a model of this type to be realistic, we must assume large population size, writing $n_x dx$ for

[redacted]

the number of individuals with age in $(x, x+dx)$, first defining all variables for a model with no phenotypic variation. The age distribution is accordingly $p_x = n_x/N$, where $N = \int n_x dx$ is the total population size. Individuals of age x has death rate μ_x and birth rate b_x. The probability of surviving from age 0 to x is then according to general survival theory (Cox and Oakes 1994)

$$l_x = \exp\left[-\int_0^x \mu_y dy\right].$$

Fisher (1930) showed that the total population size $N = \int_0^\infty n_x dx$ approaches exponential growth with rate r given by the unique real solution of the Euler equation

$$\int_0^\infty e^{-rx} l_x b_x dx = 1,$$

while the age distribution converges to the stable age distribution

$$u_x = \frac{l_x e^{-rx}}{\int_0^\infty l_y e^{-ry} dy}.$$

Further, the reproductive value v_x defined relative to the value v_0 at birth is

$$v_x/v_0 = \frac{e^{rx}}{l_x}\int_x^\infty e^{-ry} l_y b_y dy. \tag{A1}$$

Defining the total reproductive value of the population as $V = \int v_x n_x dx$, Fisher showed that, regardless of the age distribution n_x, the total reproductive value will grow exactly exponential with rate r, that is, $dV/dt = rV$. This was his reason for introducing the reproductive value and proposing that individuals should not simply be counted to define the total population, but they should be weighted by their reproductive value so that V rather than N should be used as a measure of total population size. He was unclear with respect to choice of value of v_0 in his book (Fisher 1930), but in an earlier article (Fisher 1927) he argued that the reproductive values should be scaled so that $V = N$ when the population is at its stable age distribution, implying that the scaling of the reproductive values should be chosen so that $\int u_x v_x dx = 1$. During the derivation Fisher (1930) also showed that the reproductive values obey the equation

$$-\mu_x v_x + dv_x/dx + b_x v_0 = r v_x. \tag{A2}$$

Now, as in the discrete case, let the weighted mean phenotype $\tilde{z}$ be the mean obtained by weighting the individuals by their reproductive value defined by the phenotype specific model using functions $n_x(z)$, $N(z)$, $\mu_x(z)$, $b_x(z)$, which then determine $r(z)$ and $u_x(z)$ as well as the reproductive values $v_x(z)$ obeying equation (A1) for a given z. We also specify the total subpopulation of individuals with phenotype z as $V(z) = \int n_x(z) v_x(z) dx = \int V_x(z) dx$, where $V_x(z) = n_x(z) v_x(z)$. We emphasize that we are not assuming that the population (or subpopulations with given z) is at its stable age distribution. Again, we first consider the $v_x(z)$ as general weights not necessarily equal to the reproductive values and V as the corresponding total population size based on these weights. Then, weighting each individual by its weight $v_x(z)$, the weighted mean phenotype is

$$\tilde{z} = \frac{\int z n_x(z) v_x(z) dx dz}{\int n_x(z) v_x(z) dx dz} = \int z V_x(z)/V dx dz.$$

Then, we consider the age and phenotype component $V_x(z)$ of $V(z)$. The contribution to $V(z)$ from this component when time dt has elapsed and surviving individuals of age x has reached age $x + dx$, where $dx = dt$, is then

$$n_x(z)[1 - \mu_x(z)dt]v_{x+dx}(z) + b_x(z)v_0(z)dt,$$

which can be written as $V_x(z)[1 + r_x(z)dt]$ so that $dV_x(z)/dt = r_x(z)V_x(z)$, where

$$r_x(z) = [-\mu_x(z)v_x(z) + dv_x(z)/dx + b_x(z)v_0(z)]/v_x(z),$$

is the exponential growth rate of the component $V_x(z)$, meaning that $V_x(z)$ contributes with $V_x(z)\exp[r_x(z)dt]$ to the total expected sum of weights $V(z)$ after time dt. Hence $r_x(z)$ is the fitness of individuals (x, z) with our specified choice of weights. Now, writing $\tilde{z}$ as $\boldsymbol{T}/V$, where $\boldsymbol{T} = \int z V_x(z) dx dz$ and $V = \int V_x(z) dx dz$, and taking the time derivative of $\tilde{z}$ using $d\boldsymbol{T}/dt = \int z V_x(z) r_x(z) dx dz$ and $dV/dt = \int V_x(z) r_x(z) dx dz$, we find that the vector of selection differentials for the weighted mean $\tilde{z}$, $(V d\boldsymbol{T}/dt - \boldsymbol{T} dV/dt)/V^2$, is

$$\tilde{\boldsymbol{S}} = \mathrm{cov}[z, r_x(z)], \tag{A3}$$

where the covariance refers to the joint distribution $V_x(z)/V$ of (x, z).

Consider first the case of simple arithmetic mean corresponding to choosing $v_x(z) = 1$, giving $r_x(z) = b_x(z) - \mu_x(z)$, which is the age-specific net reproductive rate expressing net production per individual, or logarithmic growth rate $d \ln n_x(z)/dt$. Writing $\bar{r}(z) = \mathrm{E}_x[r_x(z)]$, the selection differential may alternatively be written as

$$\mathrm{cov}[z, \bar{r}(z)] = \mathrm{cov}[z, \bar{b}(z) - \bar{\mu}(z)], \tag{A4}$$

where $\bar{b}(z)$ and $\bar{\mu}(z)$ are the average birth- and death-rates of individuals with phenotype z in the population which has not necessarily reached its stable age distribution, and the covariance refers to the actual distribution $N(z)/N$ of z in the population at any time.

The problems occurring by using equation (A4) for the arithmetic mean phenotype is easiest illustrated by again considering the neutral model with birth- and death-rates not depending on z. Then, if some mechanisms has made z vary among age classes, the mean values $\bar{b}(z)$ and $\bar{\mu}(z)$ will still vary with z because the conditional distribution of x given z varies with z. Hence, there will be a 'selection' differential according to equation (A4), which then must be the transient quasi-selection because there is no phenotypic variation in vital rates.

The strength and purpose of adopting Fisher's reproductive value weighting for populations that deviate from the stable age distribution and have any variation in phenotype among age classes now follow immediately from Fisher's equation (A2) using the reproductive values as weights, showing that the fitnesses $r_x(z)$ then no longer are functions of the age x but equals $r(z)$ defined by the model parameters valid for phenotype z. Then, in the former example of no selection $r(z)$ is constant because it is only the age distribution that varies among phenotypes whereas the age-specific vital rates are constant, and the growth rate using Fisher's reproductive value is the same for any age distribution. Using Fisher's reproductive value weighting exactly as he suggested, gives in general a unique fitness measure $r(z)$ for each phenotype as a continuous analogue to our age-independent fitness measure $\Lambda_i = W_i/\nu_i$ in the discrete time model with finite population size as defined by Engen et al. (2012). The selection differential for the reproductive value weighted mean takes the form

$$\tilde{\boldsymbol{S}} = \mathrm{cov}[z, r(z)] \tag{A5}$$

with no age variable x, so that the covariance refer simply to the distribution of $V(z)/V$ of z among individuals. In the neutral model with vital rates not varying with phenotype this covariance is zero so that there is no transient quasi-selection. However, in general this equation is still rather complex, remembering that we actually have weighted each individual by its reproductive value determined by its phenotype, so that individuals of the same age with different phenotypes may even have different weights. Thus, the use of this equation requires that one has enough data to estimate rates as functions of z. Otherwise, the most natural approach is to use the reproductive values calculated from the mean rates across all phenotypes. Under weak selection such an approximation would be accurate even when the population is not in its stable age distribution.

Appendix B: Genetic Drift and Estimation Uncertainty

Provided that a random sample is available an estimate of the selection differential is obtained using equation (2) as if the observed values were those of the total population. If the sampling is biased with respect to age classes, however, the age distribution $\hat{\boldsymbol{u}}$ should be replaced by the stable age distribution for the population computed from an estimate of the mean projection matrix based on observations through time.

To analyze the drift component of the selection term, we write the within-age class component of the selection differential as

$$\boldsymbol{S}_{within} = \bar{W}^{-1}\sum_x \hat{u}_x n_x^{-1}\sum_{i=1}^{n_x} W_{xi}(\boldsymbol{\xi}_{xi} - \bar{z}_x),$$

where i denotes the numbering of individuals within age classes. The last sum can now be written as a covariance

$$\mathrm{cov}_x(W, \boldsymbol{\xi}) = n_x^{-1}\sum_{i=1}^{n_x}(W_{xi} - \bar{W}_x)(\boldsymbol{\xi}_{xi} - \bar{z}_x),$$

so that $\boldsymbol{S}_{within} = \bar{W}^{-1}\sum_x u_x \mathrm{cov}_x(W, \boldsymbol{\xi})$. In a simple model without age structure Engen and Sæther (2014) decomposed the covariance between individual fitness W and phenotype $\boldsymbol{\xi}$ into its expected value and a demographic and environmental component. Ignoring environmental fluctuations the genetic drift term in the case of a full census, or sampling covariance matrix for $\mathrm{cov}_x(W, \boldsymbol{\xi})$ in case of sampling, is

$$\boldsymbol{C}_{dx} = n_x^{-1}\mathrm{E}[\sigma_{dx}^2(\boldsymbol{\xi})(\boldsymbol{\xi} - \bar{z}_x)(\boldsymbol{\xi} - \bar{z}_x)^T], \tag{B1}$$

where $\sigma_{dx}^2(\boldsymbol{\xi})$ is the (demographic) variance of individual fitness W for individuals with phenotype $\boldsymbol{\xi}$ and age x, and E here denotes the actual mean value over the individuals of age x as in the Robertson-Price equation (see Engen and Sæther (2014) for details). If follows that the covariance matrix for $\boldsymbol{S}_{within}$ is

$$\boldsymbol{C}_{d,within} = \lambda^{-2}\sum_x \hat{u}_x^2 \boldsymbol{C}_{dx}. \tag{B2}$$

If $\sigma_{dx}^2(\boldsymbol{\xi})$ depends weakly on the phenotype $\boldsymbol{\xi}$ we may replace it by its mean σ_{dx}^2. Furthermore, if the phenotypic covariance matrix vary little among age classes we may replace it by an average covariance matrix $\boldsymbol{P}$. Finally, approximating $\hat{u}_x$ by the stable age distribution we obtain a result with the same form as that of Lande (1976),

$$\boldsymbol{C}_{d,between} \approx \lambda^{-2}\sigma_d^2\boldsymbol{P}/N = \lambda^{-2}\boldsymbol{P}/N_e, \tag{B3}$$

where σ_d^2 is the demographic variance for the population process defined as the average of the σ_{dx}^2 weighted by the stable age distribution (Engen et al. 2009b). For a complete census $N_e = N/\sigma_d^2$ is the effective population size (Engen et al. 2005b), whereas for a sample we may call it the effective sample size determining the uncertainty in the estimated selection differentials including the effect of the genetic drift.

Paper III

Harvest-induced phenotypic selection in an island moose *Alces alces* population

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Abstract

Empirical evidence strongly indicate that human exploitation has frequently led to rapid evolutionary changes in wild populations, yet the mechanisms involved are often poorly understood. Here we applied a recently developed demographic framework for analysing selection to data from a 20-year study of a wild moose *Alces alces* population. In this population, a genetic pedigree has been established all the way back to founders. We demonstrate harvest-induced directional selection for delayed birth dates in males and reduced calf body mass in females. During the study period, birth date advanced by 0.76 days per year for both sexes, while no significant changes occurred in calf body mass. The recorded changes in birth date were in the same direction as predicted using standard quantitative genetic theory. These results show that selective harvesting can induce strong selection, which may cause phenotypic evolution in directions not favoured under natural selection.

Introduction

Adaptive evolution on ecological time scales (microevolution) is strongly influenced by the standing level of additive genetic variation and selection expressed as the covariance of phenotype and fitness (Price, 1972; Lande, 1979). In exploited populations, the natural direction of evolutionary changes may be substantially affected by the phenotypic characteristics of harvested individuals and the increased mortality added by harvesting (Sæther et al., 2001; Law, 2007; Proaktor et al., 2007; Allendorf and Hard, 2009; Darimont et al., 2009; Engen et al., 2014b). Sustainable harvest strategies should consequently include considerations of how harvest selection interfere with natural selection and how this in turn will affect phenotypic evolution (Dunlop et al., 2009; Hutchings, 2009; Hendry et al., 2011; Kuparinen and Hutchings, 2012; Laugen et al., 2014).

In many heavily exploited mammalian populations, harvest may be the largest source of mortality (e.g. Solberg et al., 2000; Stubsjøen et al., 2000; reviewed in Collins and Kays, 2011). As harvesting is often non-random with respect to individual characteristics, this mortality will have the potential for shifting the distribution of phenotypes (Law, 2000; Allendorf and Hard, 2009; Mysterud, 2011; Garcia et al., 2012). Such harvest-induced selection may occur through several mechanisms (Mysterud, 2011). For instance, the use of harvest equipment that select some types of individuals more than others (e.g. size selective fishing nets, Law, 2000; Carlson et al., 2007; Enberg et al., 2012; Kuparinen and Merilä, 2007; Kendall et al., 2009), or hunters that are choosy due to individual variation in harvesting value or attractiveness (e.g. trophy-hunting in ungulates, Coltman et al., 2003; Hedrick, 2011). In addition, there could be individual differences in vulnerability or exposure to hunters (e.g. bold vs less conspicuous behaviour, Ciuti et al., 2012). Several traits affected by harvesting may be heritable (Law, 2000; Kruuk and Hadfield, 2007; Allendorf et al., 2008; Carlson and Seamons, 2008; Sasaki et al., 2009). Thus, there is a growing body of empirical evidence on how harvest-induced selection may cause rapid evolutionary changes (Olsen et al., 2004; Garel et al., 2007; Law, 2007; Allendorf and Hard, 2009; Darimont et al., 2009; Sharpe and Hendry, 2009). In bighorn sheep *Ovis canadensis*, Coltman et al. (2003) found that trophy hunting had induced a decrease in body weight and horn size over time. In wild boar *Sus scrofa scrofa*, Gamelon et al. (2011) showed that birth date had advanced in response to harvest selection for early maturation. Also Sasaki et al. (2009) found that harvested populations of Japanese Mamushi Snake *Gloydius blomhoffii* were smaller, matured earlier and displayed stronger anti-predator behaviour than unharvested populations.

The strength and form of selection resulting from harvest-induced and natural causes of mortality and fecundity, and which age classes are more strongly affected, are important determinants for the outcome of selective harvest (Carlson et al., 2007; Edeline et al., 2007; Proaktor et al., 2007; Mysterud, 2011; Olsen and Moland, 2011; Engen et al., 2012, 2014b). In age-structured populations, the contribution of an individual to future generations (reproductive value) depends on age-specific transitions among different phenotypic categories affecting their fecundity and survival (Caughley, 1966; Caswell, 2001; Coulson et al., 2010; Sæther et al., 2013). For instance, natural mortality rates in large ungulates are typically low for prime aged adults, and higher for young and old individuals (Gaillard et al., 1998; Loison et al., 1999). Exploited populations will have harvest mortality interfering with natural mortality, changing the distribution of reproductive values by affecting age classes differently (Langvatn and Loison, 1999; Solberg et al., 2000; Engen et al., 2014b). Thus, the total selection imposed through harvest and natural mortality will be a complex function of annual age-specific covariances of traits and fitness, which best can be understood in a demographic framework (Lande, 1982; van Tienderen, 2000; Coulson et al., 2003, 2006, 2010; Engen et al., 2011, 2012, 2014a; Morrissey et al., 2012). This allows fitness to be defined through both fecundity and survival, and describes how selection at different stages of the life cycle affects both ecological and evolutionary dynamics (Wilson and Nussey, 2010; Engen et al., 2009, 2012, 2014a).

In this paper we investigated selective and evolutionary effects of harvesting on two fitness-related traits in ungulates, calf body mass and birth date (see also Coulson et al., 2003). We used data from a population of radio-collared moose in northern Norway, where most individuals have been followed in detail with life histories monitored from birth (Sæther et al., 2003, 2004, 2007; Solberg et al., 2007, 2010; Haanes et al., 2013). This enabled us to partition out the effects of harvest from other environmental factors that affect individual phenotype and fitness. Both traits investigated are closely associated with individual fitness. Calf body mass can explain a large proportion of individual variation in recruitment (Wilson et al., 2005b; Grøtan et al., 2009; Milner et al., 2013), age at maturity (Sæther and Haagenrud, 1983, 1985; Sæther and Heim, 1993; Sæther et al., 1996; Sand, 1996) and early life fecundity (Sæther and Haagenrud, 1985; Schwartz and Hundertmark, 1993; Sand, 1996) in moose as well as in other ungulates (Gaillard et al., 2000b). Furthermore, calf body mass is positively correlated with adult body mass at all age classes in our population (Solberg et al., 2008). Birth date is considered a key trait influencing early growth and recruitment in several species of ungulates (Festa-Bianchet, 1988; Coulson et al., 2003; Wilson et al., 2005b; Solberg et al., 2007; Plard et al., 2015), which timing has profound population dynamic effects under seasonal variation in resource abundance (Albon and Langvatn, 1992; Sæther and Heim, 1993; Clutton-Brock and Coulson, 2002; Solberg et al., 2007; Plard et al., 2014). If the individual phenotypic variation in these traits causes some individuals to be more attractive or susceptible to hunters, harvest may be an important selective force driving phenotypic changes in this population. For instance, hunters may target individuals with large calf body mass for high yield, preferably shoot barren females (with on average low calf body mass) to avoid shooting calves or females with calves, or may act selective on other cues of individual quality associated with individual birth date. Our objectives were to (1) reveal whether there were temporal trends in the two traits while controlling for other confounding factors, (2) estimate phenotypic selection across years separating between harvest-induced and natural selection, (3) estimate the additive genetic variation for each trait and (4) predict evolutionary responses under the current harvest regime.

Material and methods

Study system and data collection

The data was collected on the island of Vega in northern Norway ($65°40'\text{N}, 11°55'\text{E}$, Fig. 1). The island has an area of 119 km^2, of which approximately 80 km^2 are preferred moose habitat, and had a human population of 1250-1500 during the study (Solberg et al., 2008, 2010). The moose population was founded by one male and two female yearlings immigrating from the main land in 1985, with additional 24 immigrants recorded until 2011. Starting in 1989, annual hunting has been allowed throughout October, with a break around peak ovulation (Garel et al., 2009). During the first four years hunting intensity was low (2-4 individuals annually), but increased since 1993 (Sæther et al., 2003), keeping the population at winter densities of 25 to 43 individuals annually (Solberg et al., 2007). With this regime, less than 5% of individuals are known to have died from causes other than hunting (Solberg et al., 2007). Thus, we assume that density dependence has a minor influence on the dynamics of this population.

During 1992 and 1993 all individuals in the population were radio collared for the first time. In January-March every year until present (except 2003 and 2008), this procedure was repeated to mark all new calves (born in May-June) which survived the annual hunting. At the same time, calves were weighed to the nearest kilogram (± 2 kg) by use of an analogue or digital scale installed on a helicopter. At this stage, calves were 8-9 months of age and follow their mothers closely for another 2-4 months. No data are available on live body mass of calves at earlier ages. Calf body mass was standardised by simple linear regression as there was significant weight loss by date during the period of fieldwork ($b = -0.166$, $t = -1.85$, $P = 0.067$), which was similar for both sexes (*sex* × *date interaction*: $t = -0.23$, $P = 0.818$). The adjusted calf body mass (z) was estimated by $z = z' - bd$, where d equals date of measurement relative to 15th of February and b is the slope of calf body mass (z') on date of measurement. Pregnant females were approached during May-July at 3-5 days intervals until calving, when birth date (± 1 day, 1th of January = day 1) was determined for all calves based on calf size, behaviour, and the condition of the mother (Sæther et al., 2003). In total over the years 1992-2011, there were 181 individuals phenotyped for calf body mass, birth date or both (see Table 2). The high intensity of fieldwork combined with relative small area and open landscape of the study site, ensured that >90% of individuals were radio collared at all times during the study and could have survival determined with a high degree of certainty (Stubsjøen et al., 2000; Solberg et al., 2007, 2010). Furthermore, with tissue samples from all marked and hunted individuals, a genetic pedigree with a total of 499 individuals born in the period 1984-2012 was constructed (for details see Haanes et al., 2013). This enabled the number of offspring to be determined genetically for both sexes. The diagram in Fig. 2 indicates the chronological order of events during a time step and relevant demographic parameters monitored.

Temporal phenotypic trends

We tested for temporal trends across the years 1992-2011 in calf body mass and birth date by constructing linear mixed effects models with year as a continuous effect and mother identity as random effect to account for non-independence of siblings. Previous investigations in this population has found the age of the mother, twin status (1 = twin, 0 = singleton) and degree of inbreeding, f, to account for some of the phenotypic variance in calf body mass and birth date (Solberg et al., 2007; Haanes et al., 2013). Thus, we included them as covariates in our models. In addition, the trait not included as the response was a covariate in the models to account for phenotypic correlations (see *Results*). With these models a significant year effect was taken as evidence for a temporal trend. However, we also fitted a quadratic effect of year in our models to test whether any trends found displayed an effect-reduction over time, as predicted if caused by manipulations of sex ratio and age structure that were made in the early years (Sæther et al., 2003). All adult males were shot after the rut in 1994 and a high off-take of males in all age classes followed in 1996, which kept the sex ratio strongly biased towards females until 1999 (Sæther et al., 2003, 2004). Statistical significance was assessed by likelihood ratio tests, in which twice the difference in log likelihood between two nested models (fitted by maximum likelihood), is χ^2-distributed with degrees of freedom (df) equal to $df_1 - df_2$. Model assumptions were checked graphically using diagnostic plots. Estimates are provided with standard errors in the text. All analyses were performed using the R package *lme4*, version 1.1.7 (Bates et al., 2014) with R version 3.1.1 (R Core Team, 2014).

Phenotypic selection analyses

The selection analyses were restricted to the years 2000-2011, analysing males and females separately and including only individuals with both traits of interest. Thus, we avoided the period of sex ratio and age structure manipulations, and ensured that phenotypes (as calf) were available within most age classes. The age-structured Robertson-Price equation, developed by Engen et al. (2014a), was applied to estimate selection. This approach divides the total evolutionary change in a weighted character $\Delta\tilde{\mathbf{z}}$ during a time step into two additive components, a selection differential and a transmission term

$$\Delta\tilde{\mathbf{z}} = \tilde{\mathrm{cov}}(\Lambda_{rel}, \mathbf{z}) + \tilde{\mathrm{E}}(\Lambda_{rel}, \overline{\Delta\mathbf{z}}), \tag{1}$$

where Λ_{rel} is relative fitness, $\mathbf{z}$ is the individual phenotype, $\overline{\Delta\mathbf{z}}$ is the mean difference between the phenotype of an individual and the phenotype of its offspring (including itself if it survives) and tilde indicated weighting of mean values and sums of cross products by age-specific weights. Thus, this represents a generalization of the Robertson-Price equation for a general weighted mean, where unit weights reduce the equation to the original one derived by Price (1970, 1972) and Robertson (1966). It immediately follows that in the multivariate case we can apply the results from Lande and Arnold (1983) and express selection gradients as a set of weighted partial regression coefficients of relative fitness on the traits (Morrissey et al., 2012; Morrissey and Hadfield, 2012; Morrissey, 2014). Unbiased estimates of selection in age-structured populations are achieved by incorporating the analyses in a demographic framework (Fig. 2; Engen et al., 2009, 2011, 2014a), choosing weights as the age-specific reproductive values from the mean population projection matrix (Caswell, 2001; Engen et al., 2012, 2014a).

We had our data structured separately for females and males with pre-breeding census

(Caswell, 2001) for survival and fecundity (Fig. 2). Calves (aged 8-9 months) constituted the first age class and the oldest individuals were collected in age class 11 (females) and 7 (males), as only 4 females and 3 males survived these age classes. An individual was recorded as surviving from year t to $t + 1$ if recorded in year $t + 1$, and had fecundity equal to half the number of calves produced in year t which were alive in year $t + 1$ (i.e. recruits, see Fig. 2). Emigrants were treated as dead individuals. Thus, in this demographic framework for analysing selection, fecundity includes both the number of calves produced and their survival until approx. 10 months of age (Fig. 3). There are potential issues with assigning offspring viability to their parents fitness (e.g. Wolf and Wade, 2001, and references therin). However, the viability of calves are largely dependent on characteristics of the female. Moose calves are weaned at approx. 6 months of age, and follow their mothers closely until just before the next calving season.

For each sex, the mean age-specific fecundity and survival were estimated across the years 2000-2012 to populate the sex-specific projection matrix, $\mathbf{l}$. The real dominant eigenvalue of $\mathbf{l}$ is the multiplicative growth rate (λ) of the population. The corresponding right ($\mathbf{u}$) and left ($\mathbf{v}$) eigen vectors were scaled to $\sum_x u_x = 1$ and $\sum_x u_x v_x = 1$ to estimate the stable age distribution and reproductive values (Table 1 and Fig. 2; Caswell, 2001; Engen et al., 2009, 2012). Within each sex, the annual individual fitness of an individual i of age x was defined as $\Lambda_i = W_i/v_x$, where v_x is the sex- and age-specific reproductive value and W_i is the individual reproductive value (Engen et al., 2009). W_i estimate the individual contribution to the total reproductive value of the population next year (Engen et al., 2009, 2014a) and is defined by,

$$W_i = J_i v_{x+1} + B_i v_1/2, \tag{2}$$

where J_i is a dichotomous indicator of survival (0/1), B_i is the number of recruits produced and the v*'s* are the sex- and age-specific reproductive values. The $B's$ are always divided by 2 to account for the contribution from each sex. Within each sex, both traits were centred by the annual weighted mean and scaled by the global weighted standard deviation (SD-scaled) of the centred traits (see Table 2). In addition to total selection, we also estimated viability and fecundity selection separately by using the first and second part of equation 2 as measures of viability (W_{si}) and fecundity (W_{fi}) fitness (Engen et al., 2011). Any selection that is detected on survival is by definition harvest-induced, as there are essentially no natural mortality in this population (Fig. 3). However, to investigate the effects of harvest on fecundity, we repeated the fecundity selection analyses while ignoring harvest mortality among calves (s_x^h in Fig. 2) in fecundity fitness. That is, using $f_x = m_x s_1^{n1} s_1^{n2}$ for fecundity in projection matrices and adding the number of harvested calves to the number of recruits (B_i) produced by an individual i in the selection analyses. In each case, relative fitness was defined by the annual weighted mean fitness (Engen et al., 2014a).

Selection gradients were estimated across years using multiple regression models (Lande and Arnold, 1983). Directional ($\beta_{\sigma 1}$), correlated ($\gamma_{\sigma 12}$) and quadratic ($\gamma_{\sigma 11}$) selection were estimated keeping both traits in the models to separate direct from indirect selection. Uncertainties in the estimates were assessed by resampling with replacement for 10000 bootstrap replicates (Mitchell-Olds and Shaw, 1987). Standard errors and confidence intervals (CI) were estimated as the standard deviations and adjusted bootstrap percentile intervals of the bootstrap replications. Quadratic selection gradients and standard errors are doubled from the least squares estimates (Stinchcombe et al., 2008). In addition, to ensure robustness of conclusions and fully evaluate the statistical evidence for estimated selection gradients, weighted generalized linear models with a compound Poisson-gamma error structure and log link function were fitted (R package *cplm*, version 0.7.2, Zhang, 2013; see also Mitchell-Olds and Shaw, 1987; Lecomte et al., 2013). Thirteen a priori plausible models relating the traits to fitness were constructed and compared using AICc (Burnham and Anderson, 2002). The most complex model fitted included both quadratic effects and the interaction between the main terms in the model. Main terms were always kept in the model when quadratic terms were present. With this approach, models with ΔAICc < 2 are considered to have very high support in the data. *Post hoc* tests adding the individual inbreeding coefficient, *f*, to all models with ΔAICc < 2, revealed no inflation of estimated selection gradients due to heterogeneity among individuals in *f*

(Kvalnes et al. unpublished results; see Willis, 1996). Standard errors of weighted means were estimated by the ratio variance approximation as recommended by Gatz and Smith (1995).

Quantitative genetics analyses

Pruning the pedigree to only the phenotyped individuals and connecting pedigree links, we ended up with an informative pedigree of 210 individuals born in the period 1992-2011. This pedigree information was utilized in univariate animal models (Lynch and Walsh, 1998; Kruuk, 2004). This is a form of mixed model which express the vector ($\mathbf{y}$) of individual measurements of calf body mass or birth date in terms of their additive genetic effects and other random and fixed effects. Pooling the sexes and mean-scaling the traits across years (see Table 2), we constructed models of the following structure

$$\mathbf{y} = \mathbf{X}\mathbf{b} + \mathbf{Z_a}\mathbf{a} + \mathbf{Z_m}\mathbf{m} + \mathbf{e}, \tag{3}$$

where $\mathbf{b}$ is a parameter vector with the fixed effects of sex and the individual inbreeding coefficient, $\mathbf{a}$ is a vector of additive genetic effects and $\mathbf{m}$ is a vector of maternal environment effects. $\mathbf{X}$ is a design matrix relating fixed predictors to each individual, each $\mathbf{Z}$ is a design matrix relating random predictors to each individual, and $\mathbf{e}$ is a vector of residuals (Lynch and Walsh, 1998; Kruuk, 2004). Hence, in this model the total phenotypic variance (σ^2_P) was partitioned into three additive components such that $\sigma^2_P = \sigma^2_A + \sigma^2_M + \sigma^2_R$, where each component is the estimated variance for the corresponding vector in equation 3. Individual f-values were included to avoid inflated additive genetic effects due to correlations among close relatives (Reid and Keller, 2010; Haanes et al., 2013), while sex was included to have estimates of heritability on the same scale as the estimated selection gradients (Wilson, 2008).

The models were fitted using Bayesian methods implemented in MCMCglmm version 2.21 (Hadfield, 2010) with Gaussian distribution and identity link function. Priors for the fixed effects were the normal distribution with zero mean and large variance (10^{10}), while a flat improper prior specified by V = 0 and nu = -2 was used for the variance components. Care was taken to ensure good mixing of the chains and that specified priors did not have exaggerated influence on posterior distributions by graphical examinations of different priors. In the analyses, runs with a burn-in of 10 000 and a thinning interval of 200 ensured low autocorrelation (generally < 0.1) for a total of 10 000 independent random samples from the stationary posterior distribution. The deviance information criterion (DIC) was calculated (Spiegelhalter et al., 2002) to determine the statistical support for variance components by comparing the full model with reduced models where the component of interest was left out. Unscaled variance components (σ^2) were reported in the results by back-transforming with the square of the mean across years (Table 2), accompanied by variance-scaled estimates to obtain the narrow sense heritability ($h^2 = \sigma_A^2/\sigma_P^2$). All estimates are reported as the posterior mode and 95 % credibility intervals from the full model.

Predicting responses to selection

We separated direct and indirect selection on calf body mass and birth date in the selection analyses, but were limited by sample size to univariate analyses of quantitative genetics. Hence, to predict responses to selection we obtained the vector of unscaled selection differentials by $\mathbf{S} = \mathbf{P}\boldsymbol{\beta_\sigma} \circ \boldsymbol{\sigma}^{-1}$, where $\mathbf{P}$ is the weighted phenotypic (co)variance matrix, $\boldsymbol{\beta_\sigma}$ is the vector of estimated SD-scaled selection gradients, $\boldsymbol{\sigma}$ the vector of weighted phenotypic standard deviations and $\circ$ denotes element-wise multiplication (Lande and Arnold, 1983). Then the predicted response (R) in the weighted mean of each trait follows from the breeders equation $R = h^2 S$, where h^2 is the narrow sense heritability of a trait (Lush, 1937).

Propagation of uncertainty is important to assess the uncertainty in predicted evolutionary responses (de Villemereuil et al., 2013). We obtained the empirical distributions of R by resampling with replacement for 10000 iterations from the estimated distributions of the parameters in the breeders equation. The predicted responses to selection are presented with 95 % percentile confidence intervals.

Results

Temporal phenotypic trends

Males were heavier than than females (χ^2 = 21.13, *df* = 1, P < 0.001), but there was no sexual difference in birth date (χ^2 = 0.83, *df* = 1, P = 0.361, Table 2). In both sexes calf body mass decreased with increasing birth date (males: r_p = -0.456, $t = -4.522$, *df* = 78, P < 0.001, females: r_p = -0.220, $t = -1.864$, *df* = 68, P = 0.067). Accounting for the differences between sexes, we found no overall directional change in calf body mass across years (χ^2 = 2.72, *df* = 1, P = 0.099), whereas birth dates increased with a rate of 0.76 ± 0.20 days per year (χ^2 = 13.24, *df* = 1, P < 0.001). The annual increase was similar in both sexes (χ^2 = 1.52, *df* = 1, P = 0.218) and did not deviate from linearity (χ^2 = 0.72, *df* = 1, P = 0.218).

Phenotypic selection

For females, there was weak evidence for negative directional selection on calf body mass (Fig. 4A, Tables 3A and 5A, CI = [-0.16, 0.00]), but no evidence for directional selection on birth date (Fig. 4B, Tables 3A and 5A). When considering only survival (see Fig. 3), both traits were present among the models with ΔAICc < 2 (Table 3B). However, the confidence intervals of the directional viability selection, which were negative for calf body mass (Fig. 4C, Table 5A, CI = [-0.14, 0.02]) and positive for birth date (Fig. 4D, Table 5A, CI = [-0.04, 0.11]), were wide enough to include zero. In contrast, there was clear evidence for negative directional fecundity selection on calf body mass (Fig. 4E, Tables 3C and 5A) and birth date (Fig. 4F, Tables 3C and 5A). However, the confidence interval for the directional fecundity selection on calf body mass marginally included zero (CI = [-0.52, 0.01]).

Re-analysing fecundity selection while excluding the effect of harvesting (see Figs 2 and 3), i.e. including harvested calves in fecundity fitness, indicated no directional selection on calf body mass before the hunting season (Tables 3D and 5A). Hence, the directional selection for smaller calf body mass found after the hunting season was harvest-induced. In contrast, the negative fecundity selection on birth date was unaffected by harvesting (Tables 3D and 5A). In no cases were there any evidence of correlated or quadratic selection (Tables 3 and 5A).

In males, there was weak evidence for positive directional selection for delayed birth date (Table 4A), as this effect was present in four out of six models with ΔAICc < 2 and had a confidence interval that barely touched zero (Fig. 4B, Table 5B, CI = [0.00, 0.35]). A positive directional selection on calf body mass was also present in two of these models (Table 4A), although, the confidence interval included zero (Fig. 4A, Table 5B, CI = [-0.02, 0.28]). The separate analysis of survival (almost all deaths are harvest-induced, see Fig. 3), indicated clear evidence for positive directional viability selection for later birth date (Table 4B). Males born early in the season were more likely to be shot (Fig. 4D, Table 5B). The mean difference in birth date between killed and surviving individuals within years was 9 days. While the highest ranked model also included a quadratic selection gradient on birth date (Table 4B), the confidence interval was very wide and included zero (Table 5B, CI = [-0.36, 0.27]). Similarly, we found two of the models with ΔAICc < 2 to include positive directional selection on calf body mass (Table 4B), but the confidence interval included zero (Fig. 4C, Table 5B, CI = [-0.03, 0.32]). Contrary to the estimated viability selection, the analyses of fecundity selection in males provided clear evidence for a negative directional selection for earlier birth date (Fig. 4F, Tables 4C and 5B). Hence, early born males had higher reproductive success. Again, the confidence interval for the quadratic selection gradient included zero (Tables 4C and 5B, CI = [-0.57, 0.24]). There was no evidence for fecundity selection on calf body mass in males (Table 4C). Re-analysing fecundity selection for males while excluding the effect of harvesting on recruit production (see Figs 2 and 3), did not render this result (Tables 4D and 5B). There were no further evidence of correlated or quadratic selection (Tables 4 and 5B).

Predictions of phenotypic evolution

There was high support for an additive genetic component in calf body mass and birth date (Table 6). In addition, there was high support for a maternal environment effect in both traits as judged by DIC (Table 6). The heritability of calf body mass was 18.4 %, a little larger than the heritability of birth date. Maternal environment effects contributed to more than 50 % of the phenotypic variation in birth date (Table 6B), while calf body mass had a much smaller maternal variance component (Table 6A). Estimates for fixed effects were b_f = -0.14 (CI = [-0.32, 0.04]) and b_{sex} = 0.07 (CI = [0.04, 0.10]) for calf body mass, and b_f = -0.01 (CI = [-0.11, 0.09]) and b_{sex} = 0.00 (CI = [-0.02, 0.01]) for birth date.

Using the total selection differentials, which include direct and indirect selection on traits, we estimated the response to selection on calf body mass as -0.22 (CI = [-0.85, 0.01]) kg/year in females and 0.12 (CI = [-0.62, 1.12]) kg/year in males, and on birth date as -0.02 (CI = [-0.25, 0.13]) days/year in females and 0.12 (CI = [-0.06, 0.65]) days/year in males. Although there are considerable uncertainties in these estimates, the predicted response for birth date in males was in the same direction as the observed change in birth date among calves.

Discussion

The body mass of female ungulates is often closely associated with individual variation in several fitness components (Hewison, 1996; Sand, 1996; Sæther et al., 1996; Sæther, 1997; Tveraa et al., 2003; Grøtan et al., 2009). For instance, fertility rates increased with body mass in female caribou *Rangifer tarandus* (Pachkowski et al., 2013) and muskox *Ovibos moschatus* (White et al., 1997), while Gaillard et al. (2000a) found the life span to increase with higher body mass in female roe deer *Capreolus capreolus* and bighorn sheep. In moose, females with high body mass as calves and adults are more likely to ovulate and produce twins early in life (Sæther and Haagenrud, 1983, 1985; Schwartz and Hundertmark, 1993; Sæther et al., 1996; Solberg et al., 2008; Garel et al., 2009). Hence, the negative directional selection we found on female calf body mass was not expected through an effect on fecundity *per se* (Fig. 4, Table 5A). Accordingly, the analyses indicated that it was caused by harvest-induced fecundity selection with no phenotypic selection through mortality. Large females lost a higher proportion of calves to hunting than small ones (see Table 5A). The probability of losing a calf was 60±7 % for females with one calf and 76±5 % for females with two. Consequently, prime-aged females producing twins lost in 6 out of 10 age classes a higher proportion of calves due to harvesting than mothers with only a single calf. Hence, either hunters prefer to shoot a calf from females with twins or females with twins are more likely to be spotted by hunters. However, twin mothers would still have a higher probability to raise at least one calf than mothers with only one calf. Thus, the increased risk of losing a calf for twin mothers could not be the only cause of the negative selection on calf body mass. There has to be an additional increased risk of losing a calf for females that themselves were heavy as calf. This could be mediated by a preference among hunters to harvest large calves, as produced by large females (see Table 6), or calf body mass could be correlated with traits that affect the susceptibility to hunting (Law, 2000; Sasaki et al., 2009; Mysterud, 2011; Ciuti et al., 2012; but see Moe et al., 2009). Whatever mechanism, the increased risk of losing a calf among twin mothers or females with large calf body mass in general, will modify any selection for increased fecundity among heavy females and may explain the negative harvest-induced selection on female calf body mass (Fig. 4, Table 5A).

Our results indicated no selection on calf body mass of males in our population (Fig. 4, Table 5B). Thus, hunters were non-selective in their harvest of yearlings and adults with respect to calf body mass, and males with large calf body mass did not have larger reproductive success than males with smaller calf body mass. These results seems surprising as only a small proportion of males are often found to mate with most of the females in polygamous ungulates (Clutton-Brock, 1982; Mysterud et al., 2002) and body mass is usually seen as an important trait explaining variation among males in mating success (Stewart et al., 2000). Furthermore, Solberg et al. (2008) found that calf body mass generally predicts adult body mass well in our population. However, male moose grow for a long period and do not reach their asymptotic body mass until old ages (Solberg and Sæther, 1994; Solberg et al., 2004). In small and isolated populations under high harvest pressure, demographic stochasticity will be large and few males will reach the size at which they might compete successfully for females (Langvatn and Loison, 1999; Solberg et al., 2000; Stewart et al., 2000; Darimont et al., 2009; Engen et al., 2014b). Hence, individuals that enter older age classes might not be those that were large as calves, indicating that age is a major determinant of reproductive success (see Table 1; Sæther et al., 2003; Coulson et al., 2010; Sæther et al., 2013). This also imply that hunters can appear to be selective with respect to body mass across age classes, but that this selective harvest may not have any direct evolutionary effect on body mass if the mechanism is a preference for old individuals that are large (Solberg et al., 2000; Ericsson and Wallin, 2001; Mysterud, 2011). Indeed, from Table 1 we see that survival rates, which are almost exclusively determined by harvest mortality (see Fig. 3), are at its lowest among yearling and prime aged (above age 5) males. The oldest male in our population was 11 years old at harvest, and only 3 males got older than 7 years.

For herbivores in seasonal environments, getting the timing right with respect to the advance of spring vegetation is important to achieve optimal foraging conditions for lactating females and their calves (Klein, 1965; Albon and Langvatn, 1992; Mysterud et al., 2001; Solberg et al., 2007). Being born too early or late may increase calf mortality due to low amounts of available high quality food and have negative developmental consequences which lasts into adulthood (Solberg et al., 2004, 2008; Rödel et al., 2009). Accordingly, Schmidt et al. (2001) found antler size in red deer *Cervus elaphus* to be negatively related to birth date and Plard et al. (2015) found higher probability of recruitment and larger adult body mass for early-born roe deer. In our study, we found significant negative fecundity selection on birth date in both sexes (Fig. 4, Table 5). Thus, supporting the idea that early-born individuals possess qualities which increase their reproductive performance (Rödel et al., 2009; Plard et al., 2015; but see Wilson et al., 2005a). However, the response to fecundity selection depends on its interaction with survival (Coulson et al., 2003, 2006; Wilson and Nussey, 2010). In our study, we found strong opposing harvest-induced viability selection on birth date in males (Fig. 4, Table 5B), where early-born males were shot more frequently than late-born males. There are two not mutually exclusive hypotheses for such a pattern. Phenotypic variation in birth date could make some individuals (1) more attractive (hunter preference) or (2) more susceptible to hunters (Law, 2000; Coltman et al., 2003; Carlson et al., 2007; Allendorf and Hard, 2009; Sasaki et al., 2009; Ciuti et al., 2012). As adult moose generally are solitary and the population is subject to high hunting pressure during a relatively short hunting season, the possibility for hunters to be choosy might be restricted (Solberg et al., 2000; Mysterud, 2011). However, at present we are not able to rule out this possibility from the susceptibility hypothesis, where early-born males are more frequently shot due to increased exposure. Possible mechanisms by which the latter could occur, include variation in rates and pattern of movement or size of home range and habitat use in relation to distribution of hunters, and variation in other behaviour traits (e.g. shyness) during the rutting season that affect susceptibility (Law, 2000; Sasaki et al., 2009; Mysterud, 2011; Ciuti et al., 2012). In either case, the harvest-induced viability selection caused the total selection in males in favour of later births. This contrasts with females, where harvest mortality was non-selective with respect to birth date and confounded negative fecundity selection by increased demographic stochasticity (Table 5). Probably hunters have less opportunities to selectively shoot females than males, because they expose themselves less often to hunters (Solberg et al., 2010; Ericsson and Wallin, 2001) and are followed by one or more calves (see also Table 1 and Fig. 3). Previous studies has suggested that hunters preferably shoot females without calves, and if they are to shot females with calves the calves have to be shot first, thus, allowing females to escape (Solberg et al., 1999, 2000; Ericsson, 2001).

We found unequivocal evidence for additive genetic variance in both traits in this study (Table 6). The heritability estimated for birth date and calf body mass were of the same order as previously recorded in reindeer (both traits, Muuttoranta et al., 2013), bighorn sheep (parturition date, Feder et al., 2008), soay sheep *Ovis aries* (both traits, Wilson et al., 2005a) and red deer (body mass, Kruuk and Hadfield, 2007). Our sample sizes of less than 170 individuals (see Table 2) limited the quantitative genetic analyses to univariate models (Kruuk, 2004; de Villemereuil et al., 2013). Hence, the unmeasured additive genetic covariance could have limited the additive genetic variation in each trait that was available for unconstrained phenotypic evolution (Hansen and Houle, 2008; Morrissey et al., 2010). Indeed, a negative genetic covariance between birth mass and date has earlier been found for instance in reindeer (Muuttoranta et al., 2013), while a positive genetic covariance has been found in soay sheep (Wilson et al., 2005a). Although we were not able to estimate genetic covariances in this study, we found a negative phenotypic covariance between calf body mass and birth date, which could indicate the presence of a negative genetic covariance (see Table 2; Cheverud, 1988). Thus, the evolutionary response to negative directional selection on female calf body mass could be constrained by any negative directional fecundity selection on birth date (see Table 5). In addition, the final response to selection on a suite of traits within each sex will generally also depend on intersexual genetic covariances which may limit the possibility of increased sexual dimorphism (e.g. Jensen et al., 2008; Gosden et al., 2012).

Both traits in this study are to some degree likely to be maternally determined. Accordingly, approximately 50 % of the variance in birth date and 20 % of the variance in calf body mass were attributed to maternal environmental effects (Table 6). The maternal environment effects estimated in these models contains an environmental source of phenotypic variation, but also parts of this variation is likely to have a genetic origin (Mousseau and Fox, 1998). Such maternal genetic effects represent a heritable component of phenotypic variation, inherited through maternal inheritance, which contribute to the rate and direction of evolutionary changes in a trait (Kirkpatrick and Lande, 1989; Lande and Kirkpatrick, 1990). However, estimating maternal genetic effects are not a trivial matter and requires extensive sample sizes in a well connected pedigree (Kruuk and Hadfield, 2007; Wilson et al., 2010). When not directly estimated these effects will mostly be concealed within maternal environment effects (e.g. Wilson et al., 2005a; Kruuk and Hadfield, 2007; Wilson et al., 2010). Antagonistic selection through mothers and offspring on calf body mass or birth date could act to constrain evolutionary changes (Kirkpatrick and Lande, 1989). Thus, while we find directional selection on both calf body mass and birth date from the perspective of the offspring (i.e. an individuals own trait values), there could also be selection on these traits through their maternal analogues, offspring body mass and parturition date (the trait values of an individuals offspring; e.g. Wilson et al., 2005b; Janzen and Warner, 2009).

We predicted a negative response in calf body mass in females and a positive response in birth date in males over the years (see *Results*). Although, confidence intervals of predicted responses marginally included zero in both cases, the prediction for birth date was in the same direction as the observed significant change towards later births at a rate of 0.76 days per year. The lack of a observed response to selection on calf body mass could be related to the unaccounted effects of genetic covariances or maternal selection discussed above. However, other explanations for a lack of response cannot for certain be left out. For instance, selection on a unmeasured genetically correlated trait could constrain the evolutionary response, or the response could be masked by environmental effects which are not accounted for (reviewed in Merilä et al., 2001). In our population with such a long life expectancy, estimated responses will only be observable if consistent in direction over several years (Engen et al., 2014a). At any time, the population will consist of reproducing individuals in different age classes which has been exposed to potentially fluctuating selection pressures over their life span (Engen et al., 2012). The full response to selection will in such populations only be observable when all individuals under selection in the population has stopped reproducing (i.e. achieved lifetime reproduction; Engen et al., 2011, 2014a). Indeed, there has been a change of -0.61 kg/year in the weighted calf body mass of all females in the population, which could translate into changes among calves with time. In birth date, we are already able to record phenotypic evolution in the predicted direction of harvest-induced viability selection.

Demographic and evolutionary consequences of harvesting has been investigated in several populations, however, thus far only as separate processes (Law, 2000; Solberg et al., 2000). The demographic framework which we utilize here enable us to investigate harvest-induced selection and phenotypic evolution while keeping track of the relationships to demographic parameters such as population growth rate and the age structure of the population (Engen et al., 2009, 2011, 2012, 2014a; Morrissey et al., 2012; Sæther and Engen, 2015). Thus, the general implications of our results can more readily be related to demography of the population and be available for developing better harvest strategies over short and long time scales (Dunlop et al., 2009). In this study we demonstrate how harvesting can result in phenotypic selection through non-random hunting of calves from females which differ in fecundity rates and calf body mass (Fig. 4A, Table 5A). Thus, in species with extended parental care, sustainable harvest strategies should not only consider the phenotypic distribution of harvested individuals, but also that of parents when harvesting their young (Fig. 3; see also Solberg et al., 2000). However, our measure of fitness consists of both fecundity (production and early survival of calves) and own survival (Engen et al., 2014a). We clearly demonstrate how non-selective harvesting might effectively mask any natural selection occurring (e.g. fecundity selection on birth date in females) by introducing additional demographic stochasticity through mortality (Engen and Sæther, 2014; Sæther and Engen, 2015). Under the high hunting pressures which many exploited populations experience, this effect will be considerable (Solberg et al., 2000; Stubsjøen et al., 2000; Darimont et al., 2009; Collins and Kays, 2011).

In conclusion, we here demonstrate how selective harvest led to directional selection in a population of ungulates, and show how this may lead to evolutionary changes on an ecological time-scale. Even though several previous studies have demonstrated selective harvest, this has only rarely been manifested into harvest-induced directional selection due to a lack of knowledge on fitness and phenotypic distributions in most harvested populations (Mysterud, 2011). We emphasise the importance of considering and including the potential for harvest-induced selection through both viability and fecundity to develop sustainable harvest strategies. Even under non-selective harvest the increased demographic stochasticity due to harvesting might affect the evolutionary potential of the population by diminishing the strength of natural selection (Sæther and Engen, 2015).

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Tables

Table 1: Age-specific fecundity (f_x) and survival (s_{x+1}) (mean±SE), and stable age distribution (u_x), reproductive value (v_x) and number of individuals (n_x) for female (A) and male (B) moose on the island of Vega in northern Norway over the years 2000-2012. The stable age distribution and reproductive values for each sex result from the sex-specific projection matrix, $\mathbf{l}$, populated by the age-specific vital rates in the table. Individuals of each sex in the final age class (k), stay in this age class with survival $s_{k+1} = s_k$. The life cycle of moose in this population is shown in Fig. 2.

Age (x)	Fecundity (f_x)	Survival (s_{x+1})	u_x	v_x	n_x
(A) Females					
1	0	0.62±0.06	0.20	0.91	61
2	0.19±0.05	0.94±0.04	0.12	1.47	36
3	0.23±0.06	0.91±0.05	0.12	1.38	35
4	0.32±0.07	0.81±0.07	0.10	1.30	31
5	0.32±0.07	1.00±0.00	0.08	1.26	25
6	0.22±0.07	0.88±0.07	0.08	0.98	25
7	0.26±0.07	0.90±0.07	0.07	0.89	21
8	0.33±0.09	0.89±0.08	0.07	0.73	18
9	0.28±0.08	0.88±0.09	0.06	0.48	16
10	0.21±0.09	0.64±0.13	0.05	0.26	14
11	0.08±0.08	0.33±0.21	0.05	0.11	6
(B) Males					
1	0	0.43±0.06	0.33	0.53	69
2	0.05±0.03	0.74±0.08	0.15	1.19	31
3	0.30±0.16	0.91±0.06	0.11	1.51	22
4	0.22±0.07	0.89±0.08	0.11	1.43	18
5	0.88±0.26	0.94±0.06	0.10	1.42	16
6	0.84±0.23	0.56±0.13	0.09	0.97	16
7	0.75±0.25	0.50±0.19	0.11	0.86	8

Table 2: Mean±SE, variance, covariance and number of individuals (n) with calf body mass (kg) and birth date (A) across individuals born in the years 1992-2011 and (B) across years (repeated individuals) in the years 2000-2011 for moose at the island of Vega in northern Norway. Estimates in (B) are weighted using age-specific reproductive values (see Table 1), and the (co)variances are estimated after centering by weighted means within years. Birth date is measured as day of the year (1th of January = day 1). In (A) 70 females and 80 males were measured for both traits. Individuals with missing trait values were excluded in (B).

	Females				Males			
	Mean±SE	Var	Cov	n	Mean±SE	Var	Cov	n
(A) Across individuals								
Calf body mass	179±2	342		76	192±2	450		89
Birth date	152±1	97	-35	79	151±1	96	-92	87
(B) Across years 2000-2011								
Weighted calf body mass	177±1	250		188	189±3	759		105
Weighted birth date	152±1	97	-24	188	157±1	96	-174	105

Table 3: AICc ranking of generalized linear models estimating the relationship between calf body mass (M) and birth date (BD) and four measures of relative fitness in female moose over the years 2000-2011 at the island of Vega in northern Norway. The measures of relative fitness are (A) total fitness, (B) viability fitness and (C, D) fecundity fitness. In the analyses of fecundity excluding harvest mortality among calves, the number of recruits in the analyses were replaced by the number of potential recruits by including calves shot during the atumn hunt in measures of individual fecundity fitness. AICc for the top ranked models were (A) 319.14, (B) 319.26, (C) 780.64 and (D) 534.88. See the main text for further details.

Rank	Models	K	ΔAICc	AICc weight
(A) Total				
1	M	1	0.00	0.26
2	Intercept	0	0.62	0.19
3	$M + BD$	2	1.75	0.11
4	$M + M^2$	1	1.98	0.10
5	BD	1	2.55	0.07
6	$BD + BD^2 + M$	2	2.91	0.06
(B) Viability				
1	Intercept	0	0.00	0.21
2	M	1	0.14	0.19
3	BD	1	1.28	0.11
4	$M + BD$	2	1.73	0.09
5	$M + M^2$	1	1.82	0.08
6	$BD + BD^2$	1	1.90	0.08
(C) Fecundity				
1	$M + BD$	2	0.00	0.21
2	$M + M^2 + BD$	2	0.42	0.17
3	$BD + BD^2 + M$	2	0.93	0.13
4	BD	1	1.76	0.09
5	$M + M^2 + BD + BD^2$	2	1.90	0.08
6	$M + BD + M : BD$	2	2.00	0.08
(D) Fecundity (excl. harvest)				
1	BD	1	0.00	0.34
2	$M + BD$	2	1.37	0.17
3	$BD + BD^2$	1	1.77	0.14
4	$M + M^2 + BD$	2	2.96	0.08
5	$M + BD + M : BD$	2	3.04	0.08
6	$BD + BD^2 + M$	2	3.12	0.07

Table 4: AICc ranking of generalized linear models estimating the relationship between calf body mass (M) and birth date (BD) and four measures of relative fitness in male moose over the years 2000-2011 at the island of Vega in northern Norway. The measures of relative fitness are (A) total fitness, (B) viability fitness and (C, D) fecundity fitness. In the analyses of fecundity excluding harvest mortality among calves, the number of recruits in the analyses were replaced by the number of potential recruits by including calves shot during the atumn hunt in measures of individual fecundity fitness. AICc for the top ranked models were (A) 238.85, (B) 258.13, (C) 411.36 and (D) 390.17. See the main text for further details.

Rank	Models	K	ΔAICc	AICc weight
(A) Total				
1	Intercept	0	0.00	0.17
2	$BD + BD^2$	1	0.06	0.17
3	BD	1	0.75	0.12
4	$M + BD$	2	0.92	0.11
5	$BD + BD^2 + M$	2	1.05	0.10
6	M	1	1.94	0.07
(B) Viability				
1	$BD + BD^2$	1	0.00	0.21
2	BD	1	0.30	0.18
3	$M + BD$	2	1.11	0.12
4	$BD + BD^2 + M$	2	1.37	0.11
5	Intercept	0	1.45	0.10
6	$M + BD + M : BD$	2	2.57	0.06
(C) Fecundity				
1	BD	1	0.00	0.30
2	$BD + BD^2$	1	0.96	0.19
3	$M + BD$	2	2.00	0.11
4	$BD + BD^2 + M$	2	2.68	0.08
5	Intercept	0	3.25	0.06
6	$BD + BD^2 + M + M : BD$	2	3.84	0.04
(D) Fecundity (excl. harvest)				
1	BD	1	0.00	0.24
2	$BD + BD^2$	1	0.03	0.24
3	$M + BD$	2	2.01	0.09
4	$BD + BD^2 + M$	2	2.10	0.08
5	M	1	2.50	0.07
6	$BD + BD^2 + M + M : BD$	2	2.92	0.06

Table 5: SD-scaled directional ($\beta_{\sigma i}$), quadratic ($\gamma_{\sigma ii}$) and correlated ($\gamma_{\sigma ij}$) selection gradients for calf body mass and birth date in female (A) and male (B) moose at the island of Vega in northern Norway during the years 2000-2011. Selection gradients are presented as estimate±SE from multiple regressions where traits were centered by the annual weighted mean and scaled by the weighted standard deviation in the centered traits. Estimates in bold are significanly different from zero. Selection gradients are estimated using total fitness (the combinations of survival and fecundity according to equation 2), viability fitness and two measures of fecundity fitness. In the analyses with fecundity fitness excluding harvest mortality among calves, the number of recruits were replaced by the number of potential recruits by including calves shot during the atumn hunt in the measures of individual fecundity fitness. Hence, fecundity (excl. harvest) is the fecundity selection which would have been if there had been no hunting. Weighted means and variances for the traits are given in Table 2, with further details of the procedures in the text.

	Calf body mass		Birth date		Calf b. m. × Birth date
	$\beta_{\sigma 1}$	$\gamma_{\sigma 11}$	$\beta_{\sigma 2}$	$\gamma_{\sigma 22}$	$\gamma_{\sigma 12}$
(A) Females					
Total	**-0.08±0.04**	0.08±0.07	-0.03±0.04	0.03±0.11	0.03±0.05
Viability	-0.06±0.04	0.10±0.07	0.03±0.04	-0.02±0.10	0.03±0.05
Fecundity	**-0.25±0.14**	-0.05±0.23	**-0.33±0.11**	0.31±0.27	0.07±0.13
Fecundity (excl. harvest)	-0.07±0.07	0.16±0.13	**-0.28±0.07**	0.13±0.14	-0.04±0.05
(B) Males					
Total	0.14±0.08	-0.04±0.08	**0.18±0.09**	-0.15±0.13	0.05±0.08
Viability	0.16±0.09	-0.05±0.10	**0.30±0.10**	-0.17±0.14	0.08±0.09
Fecundity	-0.08±0.19	-0.02±0.23	**-0.42±0.20**	-0.12±0.20	-0.05±0.19
Fecundity (excl. harvest)	0.05±0.22	0.18±0.25	**-0.32±0.18**	-0.23±0.21	-0.05±0.09

Table 6: Variance components from the quantitative genetic analyses of (A) calf body mass (kg) and (B) birth date (days since 1th of January) among moose born in the years 1991-2011 at the island of Vega in northern Norway. Estimates are posterior modes with 95 % highest posterior density intervals. $\sigma_P^2 = \sigma_A^2 + \sigma_M^2 + \sigma_R^2$, where each component is indicated by its first letter. Means and variances for the traits are given in Table 2, with further details of the procedures in the text.

	σ^2	σ^2/σ_P^2	ΔDIC
(A) Calf body mass			
animal	75.0 (0.3-242.4)	0.184 (0.001-0.593)	13.94
maternal	80.1 (5.1-193.8)	0.196 (0.012-0.474)	13.39
residual	253.5 (162.0-359.5)	0.621 (0.397-0.880)	
(B) Birth date			
animal	16.0 (0.1-59.5)	0.137 (0.001-0.509)	31.63
maternal	66.5 (32.1-130.2)	0.569 (0.274-1.114)	68.67
residual	34.4 (14.4-51.4)	0.294 (0.123-0.440)	

Figure legends

Figure 1: Map of the moose study area, the island Vega ($65^\circ 40'\mathrm{N}, 11^\circ 55'\mathrm{E}$, in black), off the coast of northern Norway.

Figure 2: Diagram showing the life cycle of moose (for one sex) at the island of Vega in northern Norway during one time step (*t* to *t+1*). For each age class x = (1, 2,..,k), N_x = the number of individuals, m_x is the average number of offspring produced divided by 2, s^{n1}_{x+1} and s^{n2}_{x+1} are the annual natural probabilities of survival before and after harvest and s_{x+1h} = the probability of surviving the annual hunting season (*Harvest*). Using pre-breeding census, the grey rectangle indicate the part of the life cycle which are part of the census at time t. Individuals enter out data at age 1 (c. 9 months), and are prior to this included in their parents fecundity. Calves are weaned at the age of approx. 6 months, follow their mother closely at the time of census and are not rejected until just before the calving season (*Calving*). The corresponding sex specific projection matrix **l** (see Table 1) has fecundities, $f_x = m_x s^{n1}_{1,x} s^{h}_{1,x} s^{n2}_{1,x}$ for all x, in the first row and survivals, $s_{x+1} = s^{n1}_{x+1} s^{h}_{x+1} s^{n2}_{x+1} = N_{x+1}/N_x$ for $x < k$, in the subdiagonal. For $x = k$ we have survival $s_{k+1} = s_k$ in the lower left corner element of **l**, because individuals in the final age class stay in this age class until death.

Figure 3: The mean annual probability of survival and for calves, and (adult and yearling) female and male moose over the years 2000-2011 on the island of Vega in northern Norway. The mean survival probabilities following two sources of mortality are shown, natural ($\overline{s^{n1}}$, e.g. diseases and accidents) and harvest($\overline{s^{h}}$), with the mean total survival $\overline{s}$ as their product (see Fig. 2 and Table 1). The mean annual natural probabilities of survival after harvest ($\overline{s^{n2}}$ in Fig. 2), were 1 in all cases. The dotted line indicate that survival probabilities of calves, which follow their mothers closely for a whole year, are included in the fecundity of their parents.

Figure 4: Directional selection gradients (SD-scaled) on calf body mass (A, C, E) and birth date (B, D, F) for female (solid circles and lines) and male (open circles and dashed

lines) moose during the years 2000-2011 at the island of Vega in northern Norway. Three different measures of relative fitness, total fitness (A, B), viability fitness (C, D) and fecundity fitness (E, F), where used to estimate selection gradients. Age-specific directional selection gradients (circles and lines) are from simple linear regressions. Estimated selection gradients of the population (horizontal lines) are coloured black when significant. Weighted means and (co)variances for the traits are given in Table 2. Further details are given in the text and in Table 5.

Figures

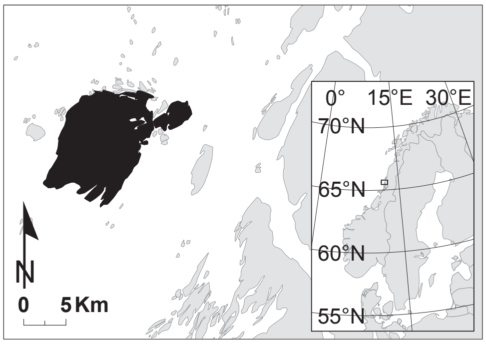
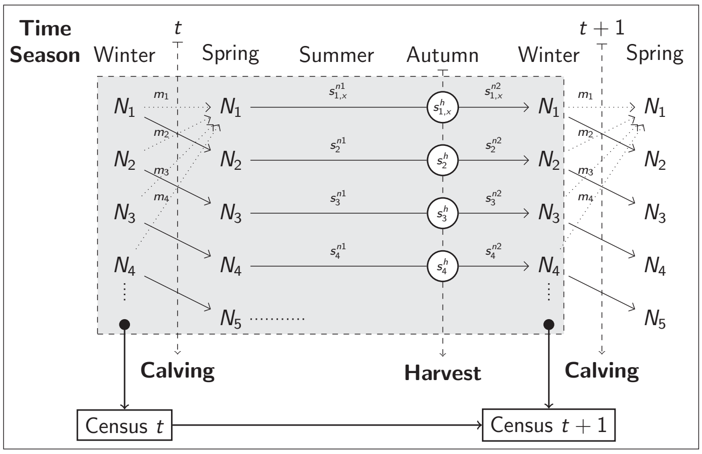


Figure 1


Time
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s^{n2}_{1,x}
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Census t + 1

Figure 2

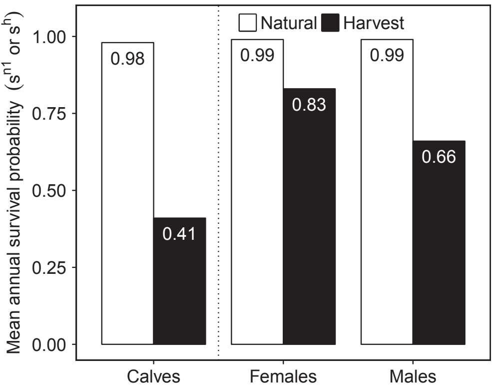
Mean annual survival probability $(\overline{s^{n}}$ or $\overline{s^{h}})$
1.00
0.75
0.50
0.25
0.00
Natural
Harvest
0.98
0.41
0.99
0.83
0.99
0.66
Calves
Females
Males

Figure 3

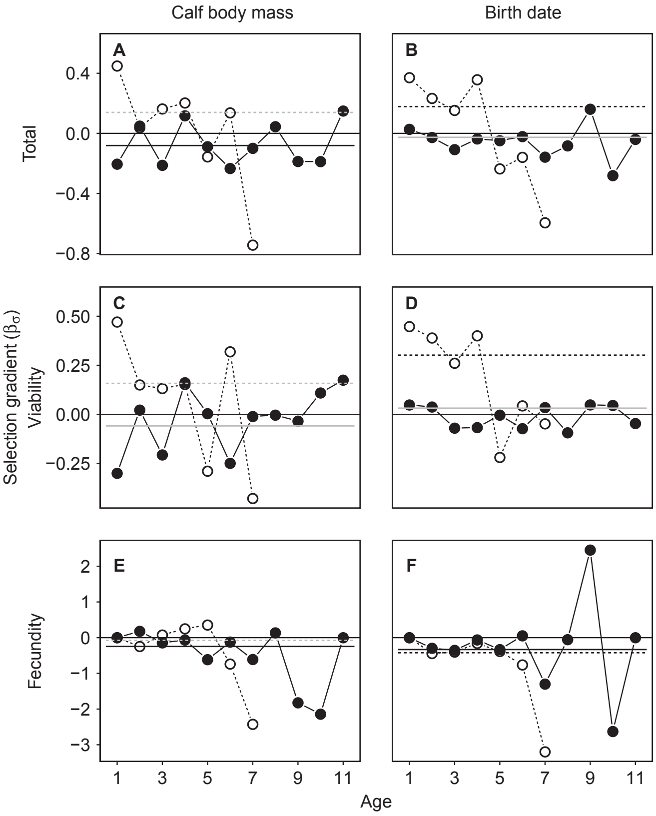
Calf body mass
Birth date
Total
Selection gradient (βσ)
Viability
Fecundity
A
B
C
D
E
F
0.4
0.0
−0.4
−0.8
0.50
0.25
0.00
−0.25
2
1
0
−1
−2
−3
1
3
5
7
9
11
Age

Figure 4

Paper IV

Artificial selection on body size in a wild passerine bird: presence of an optimal phenotype

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Abstract

Selection is of profound importance for how fast organisms adapt to changing environmental conditions, yet few studies have manipulated selection wild vertebrates. Here we perform an artificial selection experiment for long (*high*) and short (*low*) tarsus length in two wild island populations of house sparrow. We examine the response during four years of strong artificial selection, and during four additional years after stopping artificial selection. Tarsus length of offspring of artificially selected parents increased with 0.6 % annually in the *high* population, and decreased with 0.5 % in the *low* population. These individuals also had a significantly reduced fitness due to lower production of recruits, whereas there was no effect on survival. This resulted in weak opposing natural selection on tarsus length through fecundity during years of manipulation. When the artificial selection was stopped, tarsus length gradually returned towards pre-experimental means. This was due to opposing fecundity selection, mating among selected and unselected individuals (gene flow), and natural mortality among artificially selected parents. The results strongly indicates the presence of an intermediate phenotype, maintained by stabilizing and fluctuating selection for an optimal value subject to environmental variation.

Introduction

Wild populations are subject to natural selection, enabling them to adapt to their environment (Darwin, 1859; Endler, 1986). Such adaptive evolution may result in rapid phenotypic changes under major perturbations of the fitness landscape (Endler, 1980; Grant and Grant, 1995; Losos et al., 1997; Reznick et al., 1997; Hendry and Kinnison, 1999; Reznick and Ghalambor, 2001; Darimont et al., 2009; Calsbeek and Cox, 2010). Understanding how and when selective processes drive phenotypic changes in wild populations has been a long standing goal of evolutionary biology (Hendry and Kinnison, 1999; Kingsolver et al., 2001, 2012; Kinnison and Hendry, 2001; Sheldon et al., 2003; Estes and Arnold, 2007; Bell, 2008, 2010, 2013; Kingsolver and Diamond, 2011; Haller and Hendry, 2014; Sæther and Engen, 2015). However, a frequently reported discrepancy between expected response and observed rates of phenotypic changes in heritable traits under directional selection, elucidates the presence of deficiencies in our current knowledge of evolutionary dynamics in the wild (Merilä et al., 2001; Postma et al., 2007; Morrissey and Hadfield, 2012; Siepielski et al., 2009, 2013; Haller and Hendry, 2014).

The evolutionary response to selection on correlated traits, $\mathbf{R}$, can be expressed by $\mathbf{R} = \mathbf{G}\boldsymbol{\beta}$ (Lande, 1979), the Lande equation. This simple quantitative genetic model, where $\mathbf{G}$ is the additive genetic variance-covariance matrix and $\boldsymbol{\beta}$ the vector of selection gradients, has been instrumental in shaping our knowledge of adaptive evolution. The model has a large body of empirical support in animal breeding and laboratory experiments (Hill and Caballero, 1992; Falconer and Mackay, 1996; Lynch and Walsh, 1998; Brakefield, 2003; Conner, 2003). For instance, when artificial selection has been applied to explore quantitative genetic constraints (e.g. Beldade et al., 2002; Tigreros and Lewis, 2011; Bolstad et al., 2015) and predictions about rates of adaptive phenotypic evolution (e.g. Lendvai and Levin, 2003; Teuschl et al., 2007). However, the leap from laboratory to wild populations has proved to be a big one. Temporal environmental changes may mask evolutionary responses (Merilä et al., 2001), gene flow between populations under differing selective regimes may limit responses (Hendry et al., 2001) and genetic drift has an increasing influence on evolutionary dynamics with decreasing population size (Engen and Sæther, 2014). In addition, unfavourable environments may decrease the heritability in a trait (Charmantier and Garant, 2005), and selection on unmeasured correlated characters (Lande and Arnold, 1983) and a 'misidentified target of selection' (Price et al., 1988) could result in lack of evolutionary responses (see Merilä et al., 2001, for an extended discussion on causes of stasis). In populations with overlapping generations, individual contributions to the growth of the population depends on age-specific components of fecundity and survival (e.g. Reid et al., 2003). Hence, fluctuations in the age distribution and temporal variation in genetic drift and selection, are additional sources of phenotypic changes in age-structured populations (Lande, 1982; Coulson et al., 2003, 2006; Coulson and Tuljapurkar, 2008; Morrissey et al., 2012; Engen et al., 2009, 2011, 2012, 2014).

Detailed knowledge of the causes of observed variation in phenotype or fitness in unmanipulated wild populations is rare (Endler, 1986; Grafen, 1988; Kingsolver et al., 2001; Morrissey et al., 2010; Kingsolver and Diamond, 2011). Available evidence from the fossil record and contemporary populations suggest that stabilizing selection towards an optimum is a likely explanation for phenotypic traits displaying stasis over time (Charlesworth et al., 1982; Merilä et al., 2001; Estes and Arnold, 2007; Uyeda et al., 2011; Haller and Hendry, 2014; but see Hansen and Houle, 2004, 2008; McGuigan et al., 2011). Once populations has adapted to a fitness peak, the observable variation in phenotype and fitness may be limited, decreasing our ability to make inferences of the underlying fitness landscape (Schluter, 1988; Kingsolver et al., 2001; Kingsolver and Diamond, 2011; Kingsolver et al., 2012; Haller and Hendry, 2014). In fluctuating environments the optimal phenotype may vary, which causes temporal variation in individual fitness and fluctuating selection (Bell, 2010; Chevin and Haller, 2014). However, estimates of fluctuating selection are strongly dependent on demographic stochasticity in finite populations (Lande et al., 2003; Engen et al., 2012). Thus, large sample sizes and long time series of individual phenotype and fitness may be needed to obtain the statistical power to detect directional and fluctuating selection.

Selection experiments in the wild, have a large potential to reveal novel insights into adaptive evolutionary dynamics, by manipulating the natural observed link between phenotypes and environmental factors (Arnold, 1983; Wade and Kalisz, 1990; Merilä et al., 2001; Conner, 2003; Brakefield, 2003; Reznick and Ghalambor, 2005; Bell, 2008, 2010; Merilä and Hendry, 2014). There are two basic approaches to manipulate selection in the wild, (1) indirectly by manipulating biotic or abiotic environmental factors or (2) directly by imposing artificial selection. Both approaches have their advantages, the first offers control over the causal agents of selection, while the second offers control over the strength of selection applied and expected evolutionary responses. Examples of the former include Losos et al. (1997, 2001) which introduced brown anole *Anolis sagrei* lizards to islands with vegetation diverging from their native habitat. The lizards adapted morphologically to the new conditions, in accordance with knowledge of the evolutionary diversification throughout their natural geographical range. In the same species, Calsbeek and Cox (2010) found that experimentally increased population density induced directional selection for increased body size, with no effect on directional selection from manipulating the presence of predators. In guppies *Poecilia reticulata*, translocating populations from high to low predation environments induced strong selection for later maturation (Reznick et al., 1997) and resulted in males with more conspicuous and diverse colour patterns (Endler, 1980).

In contrast, there has been very few artificial selection experiments in the wild. Over ten years, Flux and Flux (1982) artificially selected for large clutch size in starlings *Sturnus vulgaris*. The response was evident when comparing selected to unselected individuals, but due to high levels of gene flow there was only a small response in the population as a whole. In a more elaborate experiment, Postma et al. (2007) selected great tits *Parus major* over 8 years for clutch size in opposite directions in each of two subpopulations. Despite strong artificial selection, they found no clear evidence of evolutionary change in mean clutch size at the phenotypic level. Large environmentally induced variation in clutch size among years was believed to mask the response.

In this study, artificial selection on tarsus length was applied in two wild populations of house sparrow *Passer domesticus*. The main objectives were to investigate the response to selection and the contribution of phenotype to variation in individual fitness. Tarsus length was selected in opposite directions in two island populations in four subsequent years. Then the artificial selection was stopped and the populations were monitored for another four years. An unmanipulated control population was monitored over the same period. The target of selection, tarsus length, is a heritable trait commonly used as a proxy for structural body size in passerine birds (Jensen et al., 2003, 2008; Rising and Somers, 1989; Senar and Pascual, 1997). The following four objectives were addressed. First, the rates of direct and correlated responses to artificial selection were investigated. Second, variation in individual fitness were compared among individuals with different selective ancestry. Third, directional selection (after artificial selection) and the separate contributions of survival and fecundity components were estimated. Finally, after the period with strong artificial selection, phenotypic trajectories were investigated and changes in the proportion of individuals with different selective ancestry was explored.

Material and methods

Study system

The study was conducted using data from three island populations of house sparrow in northern Norway. The islands, Hestmannøy ($66°33'\mathrm{N}, 12°50'\mathrm{E}$), Vega ($65°40'\mathrm{N}, 11°55'\mathrm{E}$) and Leka ($65°06'\mathrm{N}, 11°38'\mathrm{E}$), are located along a north-south gradient, separated by 97 and 54 km of ocean and small islands along the coastline (see map in Hagen et al., 2013). Thus, the geographical distance and the sedentary nature of the house sparrow ensured virtually no migration between the study populations (Altwegg et al., 2000; Tufto et al., 2005). Almost all individuals in the populations inhabited dairy farms and human settlements, where they bred in holes and cavities from May until mid-August (Ringsby et al., 1998).

In the years 2001-2009 almost all individuals were captured and marked with a unique combination of a numbered metal leg ring from the Ringing Centre at Museum Stavanger and three plastic colour leg rings. The Hestmannøy population had been followed since 1993 (further details in Ringsby et al., 1998, 2002; Sæther et al., 1999; Jensen et al., 2008), but in this study we used data from same period as Leka and Vega. Individuals were either followed from nestling stage or when captured in mist nets during summer (May-August), autumn (late September-October) (all populations) or winter (February-March) (Leka and Vega). Over 90 % (Hestmannøy) and $\sim$ 90 % (Leka and Vega) of the winter population were marked at all times during the study. In addition to the captures, observations of colour banded birds contributed to high re-sighting rates. At first capture, a small blood sample (25 μL) was collected, which enabled the construction of a genetic pedigree for each population. Parentage analyses were performed in Cervus 3.0 software with 90 % confidence for parentage assigned (Marshall et al., 1998; Kalinowski et al., 2007), based on genotyping putative parents and offspring for 14 microsatellite markers (Jensen et al., 2004, 2008; Rønning et al., 2015).

The data was organized with pre-breeding census and two age classes were used: 1 year old (recruits) and 2+ years old. House sparrows go through a complete post-juvenile and post-breeding moult. Hence, during autumn all individuals have the same appearance. Ageing was based on marking of nestlings or juveniles. Because the proportion of marked individuals were high before the breeding season, we assumed that full-grown unmarked individuals were born in the most recent breeding season. Individuals which we were unable to age were excluded from the analyses in the year they were marked. In addition, we excluded a few individuals with missing traits (see below) and all individuals from one farm at each experimental island, where we did not have access until the final three years of the study. Annual individual survival was recorded as 1 if an individual was re-sighted in the next census (otherwise 0). Emigrants where treated as dead individuals. For each individual the annual number of recruits, i.e. offspring which survived to the next year, was estimated by summing over the pedigree.

Morphological measurements

Full-grown individuals were measured for tarsus length (± 0.01 mm), body mass (± 0.1 g), wing length (± 1 mm), bill length (± 0.01 mm) and bill depth (± 0.01 mm). The measurements were performed by several different fieldworkers. After an initial period of training, each fieldworker measured approximately 30 individuals together with T.H.R or, in some cases, another experienced fieldworker. Then all linear measurements were adjusted according to T.H.R. by adding mean differences when found significant ($P < 0.05$) using paired t-tests. All traits, except tarsus length, display seasonal variation (Anderson, 2006). Hence, only measurements from the main sampling periods were used in the analyses, i.e. summer for the Hestmannøy population and winter for the Leka and Vega populations. Furthermore, within-individual age effects were investigated for body mass, wing length, bill length and bill depth using an extended data set over the years 1993-2012 at Hestmannøy and 2001-2012 at Leka and Vega. Due to the difference in sampling season, Hestmannøy was analysed separately. Traits were age-standardised by fitting a linear mixed effects model with age and age^2 as explanatory variables, random intercepts with year, cohort and individual identity, and an individual random slope to separate out any between-individual variation (Bates et al., 2014; Schielzeth and Forstmeier, 2009).

The significance of each age variable was tested by likelihood ratio tests of nested models (for details see *Data analysis*). All traits with significant age effects were adjusted to age 1, using predicted values from the model, before individual means were calculated.

Body mass scale with body size, measured as tarsus length, through an allometric relationship $bodymass = b \times bodysize^k$, where k is the allometric exponent (Huxley, 1932). This relationship was linearised for each sex and population separately by log transformation. Residuals from the log-log linear regressions were used as measures of individual body condition in subsequent analyses (Schulte-Hostedde et al., 2005).

Experimental procedure

Each winter of the four years 2002-2005, opposing artificial selection on tarsus length was imposed in the Leka and Vega populations. During the experimental manipulations $\sim$ 90 % of individuals in each population were captured and kept in a large aviary (abandoned cow barn) with *ad libitum* access to food (sunflower seeds, grain feed for cattle, oats and slices of bread), water and perching branches. Then, all individuals with tarsi longer (Leka) or shorter (Vega) than the limit of mean ± 0.3 SD were returned to their origins, while the remaining individuals were translocated to populations located at least 70 km from the islands (see also Skjelseth et al., 2007). On average, 56.4 % (Leka) and 62.8 % (Vega) of all captured individuals were removed at each annually episode of artificial selection, such that the artificially selected individuals constituted approximately 78 % of the breeding populations. The whole procedure took between one and two weeks. The artificial selection resulted in large selection differentials on tarsus length and correlated selection on other phenotypic traits as well (Fig. 1). In the subsequent four years (2006-2009) on Leka and Vega, the same fieldwork procedure was followed, except that all individuals were returned to their origin. The Hestmannøy population was used as an unmanipulated control, where individuals were returned directly to the place of capture after banding and measurements. Henceforth, these populations are referred to as *high* (selected for large body size), *low* (selected for small body size) and *control*. All individuals in the *high* and *low* populations were assigned a selection category: Selected, unselected, indirectly selected or intermediate. The assignment of selection category was based on whether their parents had been artificially selected or were lineal descendants of artificially selected ancestors (Table 1). When no genetic parent could be detected, this parent was assumed not to have been artificially selected, as our genetic parenthood analyses had a very high probability of assigning a parent to an individual if the parent had been sampled. In the analyses of variation in individual fitness between selection categories, individuals classified as indirectly selected were excluded as they were few and present mostly in the last few years of the study (i.e. when artificial selection was stopped).

Data analysis

Population differences and phenotypic change

Overall sexual dimorphism and population differences in body size in 2002, before the onset of the experiment, were explored using a multivariate analysis of variance (MANOVA). *Post hoc* tests for each phenotypic trait were performed by separate analyses of variance (ANOVA). Tukey HSD were used to identify which populations that displayed significant phenotypic differences.

The the phenotypic changes following artificial selection was analysed in two ways for each population. First, we estimated the response to artificial selection as the annual change in phenotypic traits of age 1 individuals. To account for local environmental effects in the observed phenotypic changes, the annual means (across sexes) of age 1 unselected individuals were subtracted and the differences for each trait used as response variable in the analyses. Second, we estimated the annual changes in the phenotypic traits across all individuals after stopping artificial selection (years 2006-2009). In both cases, annual change in each trait was estimated by linear regressions with year as a covariate while accounting for any differences between the sexes and testing for sex-specific differences in the response by fitting a year-sex interaction. All traits measured correlated positively with tarsus length (Table 2). Hence, to investigate if each trait changed more than expected from the trait to body size relationship, tarsus length was included as an explanatory variable in the models. Alternative models were tested using a F-test with $p_2 - p_1$ and $n - p_2$ degrees of freedom, where p_i is the number of parameters in model i and n is the sample size.

Variation in individual fitness

The difference in survival and production of recruits among the selection categories (see Table 1) in the years 2003-2009 were analysed using mixed effects logistic and Poisson regression fitted in the R package *lme4* (Bates et al., 2014). In order to investigate the environmental effect on each of the two dependent variables, a year effect (slope) with only unselected individuals was estimated. Any significant environmental effect was accounted for in subsequent analyses by fitting it as a covariate with known effect (offset). In addition, a random intercept associated with individual identity was estimated, age and sex were included to account for differences in survival and fecundity between ages and sexes, and two-way interactions to estimate age- and sex-specific differences among selection categories were included. The significance of the terms of interest were tested using likelihood ratio tests of pairs of nested models, where twice the difference in log-likelihood is χ^2-distributed with $df_1 - df_2$ degrees of freedom.

Analyses of directional selection

Analyses of directional selection were performed for each sex and population separately, and structured into two periods, (1) year 2002-2005 (with only individuals present after artificial selection) and (2) year 2006-2009. The demographic framework in the R package *lmf* was applied (Engen et al., 2012) to analyse selection. The annual absolute fitness of an individual i in age class x is defined by the individual reproductive value (Engen et al., 2009),

$$W_i = J_i v_{x+1} + B_i v_1 / 2. \tag{1}$$

Where J_i is 1 if the individual survives (otherwise 0), B_i is the number of recruits produced and v_{x+1} and v_1 are age-specific reproductive values (Engen et al., 2009; Sæther and

Engen, 2015). Defining fitness this way enables correct estimation of the individual contributions to next years total reproductive value and accounts for correlations between survival and reproduction (Engen et al., 2011, 2012; Metcalf and Pavard, 2007; Wilson and Nussey, 2010). However, additional insights into the selective processes could be obtained by examining different fitness components separately. This was achieved by defining viability (W_{si}) and fecundity (W_{fi}) fitness as the first and second additive component in equation 1 (Engen et al., 2011).

The sex-specific expected projection matrix ($\mathbf{l}$) was estimated separately for each population (Caswell, 2001). With two age classes, 1 year old and 2+ years old, $\mathbf{l}$ has age-specific fecundities in the first row and age-specific survivals in the bottom row. Age-specific fecundities and survivals for each sex and population, were estimated as means across the study period (Engen et al., 2011). Then the age-specific reproductive values ($\mathbf{v}$), stable age distribution ($\mathbf{u}$) and deterministic growth rate (λ) were estimated as the scaled left and right eigenvector, and the dominant eigenvalue of $\mathbf{l}$ (Caswell, 2001). Eigenvectors were scaled according to $\Sigma u_x = 1$ and $\Sigma v_x u_x = 1$ (Engen et al., 2009).

All traits were centred by the global mean across years prior to analyses. Then selection gradients were estimated for each year and age class separately, using multiple regressions of absolute fitness on the trait values (Lande and Arnold, 1983). Annual selection gradients were given as the weighted average of age-specific gradients with weights $\mathbf{u}$. Then temporal mean selection gradients (assuming no fluctuating selection) were obtained following the methods outlined by Engen et al. (2012). Directional (total) selection, viability selection and fecundity selection were estimated. The statistical significance of temporal mean selection gradients were assessed using a multinormal bootstrap procedure for 10000 bootstrap replicates (Engen et al., 2012). 95 % percentile confidence intervals were calculated from the estimated sample distributions. Selection gradients ($\boldsymbol{\alpha}$) were obtained using absolute fitness. Thus, standardised SD-scaled selection gradients, $\boldsymbol{\beta_\sigma}$, were given as $\boldsymbol{\beta_\sigma} = \lambda^{-1}\boldsymbol{\alpha} \circ \boldsymbol{\sigma}$, where $\boldsymbol{\sigma}$ is the vector of trait standard deviations (averaged over years) and $\circ$ denotes element-wise multiplication. Analyses were performed using the statistical software R version 3.1.1 (R Core Team, 2014).

Results

To explore the effects of artificial selection on body size, the phenotypic variation before the experimental manipulations in 2002 is described and the response to artificial selection is estimated. Then variation in individual fitness, annual survival and fecundity, in each population is explored. First, contrasting individuals of different selective ancestry (see Table 1). Then, estimating directional selection (excluding artificial selection). Finally, phenotypic variation after the period of strong artificial selection is investigated.

In 2002, before the onset of artificial selection, males were larger than females ($F_{5,347}$ = 47.91, $P < 0.001$) with no variation in sexual dimorphism across populations ($F_{10,692}$ = 0.63, $P = 0.792$, Table 3). Males had longer tarsi and wings (both $P < 0.01$), but did not differ significantly from females in body condition, bill length or bill depth (all $P > 0.05$). The three populations differed in all traits before the experiment (MANOVA: $F_{10,696} = 20.67$, $P < 0.001$, ANOVAs: all $P < 0.001$, Table 3). Tarsus length was shorter in the *low* population than in the *high* (mean difference = −0.27, $P = 0.004$) and *control* (mean difference = −0.44, $P < 0.001$) population. The *high* and *control* populations did not differ significantly (mean difference = −0.18, $P = 0.275$).

Direct and correlated response to selection

Both sexes responded to artificial selection based on changes in phenotypes among age 1 selected individuals. Tarsus length increased by 0.6 % and decreased by 0.5 % per year in the *high* and *low* populations relative to the pre-experimental means in 2002 (Table 4, Fig. 2B and D). The response to selection did not differ between females and males (*High*: $b_{year \times sex}$ = -0.04±0.05, $F_{1,249}$ = 0.79, P = 0.374, *Low*: $b_{year \times sex}$ = -0.04±0.07, $F_{1,243}$ = 0.37, P = 0.546). There was no significant annual change in tarsus length of intermediate offspring (one selected parent) (*High*: b_{year} = 0.03±0.02, $F_{1,393}$ = 3.11, P = 0.078, *Low*: b_{year} = 0.02±0.01, $F_{1,556}$ = 2.33, P = 0.127). However, pooling sexes and years, intermediate and unselected individuals differed significantly in tarsus length in the expected directions (*High*: mean difference = 0.13, t = 3.22, df = 395, P = 0.001, *Low*: mean difference = −0.06, t = −1.7, df = 558, P = 0.045). There was no significant difference in tarsus length between indirectly selected and unselected individuals across years and sexes (*High*: mean difference = -0.17, $t = -1.29$, df = 29, $P = 0.897$, *Low*: mean difference = -0.01, $t = -0.05$, df = 36, $P = 0.482$).

Wing length showed a significant correlated response to artificial selection among selected offspring in both the *high* and *low* population (Table 4). However, including tarsus length in the model, there was no changes above that accounted for by the phenotypic correlation with tarsus length (*High*: b_{year} = 0.02±0.05, $F_{1,249}$ = 0.2, P = 0.653, *Low*: b_{year} = -0.10±0.07, $F_{1,243}$ = 2.16, P = 0.143). In addition, body condition increased significantly in both sexes of selected offspring in the *high* population (Table 4). Bill length showed an annual increase in females but a decrease in males in the *low* population (Table 4). This was independent of changes in tarsus length ($b_{year \times sex}$ = -0.09±0.04, $F_{1,242}$ = 4.62, P = 0.033). In the *control* population, there was no temporal changes in tarsus length, but some minor annual increases in wing length and bill depth (Table 4).

Directional selection and variation in individual fitness

Among unselected individuals, there was no significant trend during the years 2003-2009 in the recruit production in the *high* population (b_{year} = -0.04±0.04, χ^2 = 1.10, df = 1, P = 0.293), but a slight decrease in the *low* population (b_{year} = -0.14±0.04, χ^2 = 11.73, df = 1, P = 0.001). The survival rates did not show any significant temporal trend across years in unselected individuals in either population (*High*: b_{year} = -0.11±0.09, χ^2 = 1.66, df = 1, P = 0.197, *Low*: b_{year} = -0.08±0.07, χ^2 = 1.44, df = 1, P = 0.231).

Selected and intermediate individuals produced significantly fewer recruits than unselected individuals in the *high* population (χ^2 = 6.74, df = 2, P = 0.034, Table 5A). In the *low* population a similar pattern was evident among age 1 individuals (*selection status* × *age*: χ^2 = 19.20, df = 2, $P < 0.001$, Table 5B), where selected individuals of both sexes and intermediate males produced fewer recruits than unselected individuals (*selection status* × *sex*: χ^2 = 7.14, df = 2, P = 0.028, Table 5B). There were no significant differences among selection categories in survival (*High*: χ^2 = 0.31, df = 2, P = 0.857, *Low*: χ^2 = 1.02, df = 2, P = 0.600).

In the period 2002-2005, there was significant directional selection on tarsus length towards the pre-experimental phenotypic means in males of the *low* population (Fig. 3B). While both viability and fecundity selection gradients were positive, only the latter was significant (Fig. 3B). Thus, the production of recruits increased with tarsus length in males in the *low* population. A similar, but non-significant, directional selection pressure was also observed in females in the *low* population, where larger females produced more recruits (Fig. 3A). No estimates of directional selection were significant in the *high* population (Fig. 3A and B). However, the trend was in favour of directional selection towards pre-experimental phenotypic means due to a higher production of recruits among individuals with small tarsus length in both sexes (Fig. 3A and B). Other traits were generally not under directional selection in this period. However, males with large body condition had higher rates of survival in both experimental populations (Fig. 3D). There was no significant directional selection on phenotypic traits in the *control* population (Fig. 3).

During the four years after the artificial selection experiment (2006-2009), there was no longer any detectable directional selection towards pre-experimental phenotypic means (Fig. 4). Instead, there was positive directional selection for larger tarsus length in males in the *high* population (Fig. 4B). This was due to higher production of recruits among individuals with large tarsus length (Fig. 4B). There was no further significant directional selection on tarsus length or any other trait in the *high* and *low* populations (Fig. 4). However, there was significant positive directional selection on wing length in males in the *control* population, as individuals with long wings had higher probability of survival and produced more recruits (Fig. 4F). Also, males with large bill depths had higher probability of survival in this population (Fig. 4J).

The demographic variance (σ_d^2) was generally larger in the *high* and *low* populations during the period of artificial selection than in the subsequent period (Table 6). On average across the populations, the variance in recruit production decreased by 34.0 % and the variance in survival decreased by 4.3 % in the period after the artificial selection ended. Hence, the disturbance caused by removing individuals from the populations increased the demographic variation in recruit production, but only during the manipulated breeding seasons. The environmental variance (σ_e^2) was high and variable in both experimental populations (Table 6).

In the years 2006-2009, the proportion of selected and indirectly selected individuals recruiting into the experimental populations rapidly decreased, while the proportion of intermediate individuals increased (Table 7). The proportion of unselected individuals fell from 2006 to 2007, then increased in both populations (Table 7). Accordingly, when artificial selection was stopped, mean tarsus lengths gradually returned towards pre-experimental means in females of the *high* population (*year* × *sex*: $F_{1,445} = 7.01$, $P = 0.008$, Females: b_{year} = -0.13±0.04, Males: b_{year} = 0.03±0.04) and in both sexes of the *low* population (Both sexes: b_{year} = 0.14±0.03, $F_{1,570} = 23.05$, $P < 0.001$). This is also shown in Figures 2A and C.

Discussion

Strong directional artificial selection were exerted on tarsus length (Fig. 1), a heritable trait (Jensen et al., 2003, 2008), in two wild house sparrow populations. Tarsus length changed in the expected direction in both populations, with correlated responses observed in wing lengths (Fig. 2 and Table 4). The production of recruits was found to be lower in selected individuals (Table 5). However, the reduction was age-dependent in the *low* population (Table 5). This resulted in directional selection towards the pre-experimental means in both populations (Fig. 3), but selection gradients were only significant in males of the *low* population (Fig. 3B). Furthermore, when stopping the strong artificial selection, directional selection decreased towards zero in the *low* population and in females of the *high* population (Fig. 4). Males in the *high* population were in this period subject to positive directional selection for larger tarsus length (Fig. 4B). Fecundity selection in the opposite direction of artificial selection, mating among selected and unselected individuals, and natural mortality resulted in a gradual return towards pre-experimental means in all but males of the *high* population (Fig. 2 and Table 7).

Artificial selection experiments in wild populations remain rare despite the high potential for novel insights to evolutionary dynamics they may provide (Wade and Kalisz, 1990; Merilä et al., 2001; Conner, 2003; Brakefield, 2003; Bell, 2008, 2010; Merilä and Hendry, 2014). To our knowledge, only two artificial selection experiments have been performed in wild vertebrate populations (but see also Semlitsch and Wilbur, 1989), both on clutch size in birds (Flux and Flux, 1982; Postma et al., 2007). Tarsus length in selected individuals responded to our artificial selection, as expected given the significant estimates of additive genetic variance from earlier quantitative genetic studies in house sparrows (Jensen et al., 2003, 2008) and other species of birds (e.g. Alatalo and Lundberg, 1986; Merilä, 1997; Charmantier et al., 2004; Åkesson et al., 2008). However, the mating of unselected and artificially selected parents produced intermediate individuals in which mean trait values were only marginally different from unselected individuals (see *Results*). A corresponding process in unmanipulated populations would be gene flow under spatially varying selection. This has repeatedly been suggested as a possible constraint on the phenotypic response under directional selection on heritable traits (e.g. Slatkin, 1973; Storfer and Sih, 1998; Hendry et al., 2001; Postma and van Noordwijk, 2005; Postma et al., 2007). In a recent review, Siepielski et al. (2013) found the strength of directional selection to vary spatially in magnitudes comparable to earlier reported temporally fluctuating selection (Siepielski et al., 2009; Morrissey and Hadfield, 2012). Holand et al. (2011) investigated spatial variation in genetic differentiation of quantitative traits between 14 house sparrow populations (including the three populations in this study). They found that spatially varying directional selection was the most likely explanation for population differences in some traits (not tarsus length; see also Jensen et al., 2013). Hence, the identification of spatially varying patterns of selection and evolutionary responses in wild unmanipulated populations hinge on our ability to discriminate individuals of different origin. Failing to do so could be an important cause of mismatch between expected and observed phenotypic responses to selection.

The direction and rate of evolutionary change in a heritable trait, depend on the strength of selection on the trait itself and selection on any other genetically covarying traits (Lande, 1979, 1980a, 1982; Hansen and Houle, 2004, 2008; McGuigan et al., 2011). In this study, a correlated response in wing length was observed in the same direction as the artificial selection on tarsus length (Fig. 1, Table 4). This is in accordance to our expectations, because positive additive genetic covariance between these two traits has earlier been documented in house sparrows (Jensen et al., 2003, 2008) (non-significant in males), as well as in quantitative genetics studies of other bird species (Teplitsky et al., 2014). In contrast, neither the two bill traits nor body condition changed in response to correlated selection in the two experimental populations. While all three traits harbour significant additive genetic variance in house sparrows, the additive genetic covariance between bill length and depth has opposite sign in males (negative) and females (positive) (Jensen et al., 2003, 2008). In addition, there are opposite signs on the additive genetic covariance between each bill trait and tarsus length which differs between sexes, and significant intersexual additive genetic covariance (Jensen et al., 2003, 2008). Thus, the G-matrix harbour additive genetic components with large potential for constraining the evolution of each trait separately both within and among sexes (Lande, 1980b; Gosden et al., 2012). Body condition was found to increase in the *high* population. However, this was not likely to be a response to artificial selection, as Jensen et al. (2003) found a negative additive genetic covariance with tarsus length and there was no change in the *low* population. The G-matrix of house sparrows published by (Jensen et al., 2003, 2008) were estimated using data from the *control* population in this study and a few other populations in its vicinity. The degree of spatial and temporal stability, and evolutionary changes in the G-matrix is yet to be explored in full (reviewed in Arnold et al., 2008). However, theoretical and empirical studies have shown that there are a number of circumstances under which the G-matrix vary spatially between populations and may evolve rapidly due to genetic drift or selection (Lande, 1980a; Roff, 2000; Steppan et al., 2002; Coltman et al., 2003; Arnold et al., 2008; Eroukhmanoff and Svensson, 2011; Björklund et al., 2013; Björklund and Gustafsson, 2015; Chevin, 2013). Hence, the most exact predictions of evolutionary responses to selection should be based on population-specific quantitative genetic matrices.

Replicated selection lines in artificial selection experiments are rare, despite their obvious advantages in, for instance, separating between selection and genetic drift as causes of phenotypic changes (Henderson, 1989, 1997; Konarzewski et al., 2005). Here, adding replicates would entail experiments on additional suitable populations of similar population size in congruent environmental conditions. Given the time and resources available, such an increased effort was infeasible in this study. In the wild, another important challenge in artificial selection experiments is that it requires capturing a large proportion of individuals to be subjected to selection. Then their offspring has to be monitored to obtain unbiased estimates of response to selection. Here, a morphological trait was subject to selection, such that all birds had to be kept in large aviaries for a short period. Our efforts to capture and include all individuals in the experiment were considerable. Despite this, sampling was incomplete and approximately 20 % of the breeding populations remained unselected each year, resulting in a mixture of selected, intermediate and unselected offspring to be captured at next census. Utilizing high quality genetic pedigrees for these populations, the offspring of artificially selected parents could be identified. Then unselected offspring were successfully used as a control, to account for phenotypic changes not due to the artificial selection and explore variation in individual fitness. This approach, which also was used in the artificial selection experiment by Flux and Flux (1982), enabled robust conclusions on the evolutionary dynamics in this study.

Immigrants into these populations could not be distinguished from unselected resident individuals. However, the experimental island populations are located distant to other known populations, and house sparrows are generally sedentary of nature with only a small proportion of individuals dispersing between populations separated by more than a few kilometres (Altwegg et al., 2000; Tufto et al., 2005; Anderson, 2006; Pärn et al., 2009, 2012). Furthermore, earlier investigations in house sparrows has found that immigrants are morphologically indistinguishable from residents (Altwegg et al., 2000), but that immigrant males has a lower production of recruits than resident males (Pärn et al., 2009, 2012). Hence, immigrants are likely to constitute a very small fraction of the unselected individuals, and to have morphological trait values randomly distributed around the average before artificial selection started (Table 2; see also Holand et al., 2011). As a consequence, this should not compromise the results of this study, but rather make the analyses conservative.

Natural selection shape the phenotypic distribution of a population by selecting against less fit individuals (Darwin, 1859; Endler, 1986). Given a partial genetic origin of phenotypic variation, the mean phenotype will evolve towards optimum phenotypes of high fitness (Lande, 1976, 1979; Kinnison and Hendry, 2001; Sæther and Engen, 2015). When the mean phenotype is stable over longer periods of time, a common observation in contemporary populations (Merilä et al., 2001) and in the fossil record (Estes and Arnold, 2007; Uyeda et al., 2011), stabilizing selection often seems a likely explanation (Charlesworth et al., 1982; Estes and Arnold, 2007; Uyeda et al., 2011; Chevin and Haller, 2014; Haller and Hendry, 2014; but see Hansen and Houle, 2004). At the same time, abundant stabilizing selection has been difficult to demonstrate empirically in contemporary populations (Kingsolver et al., 2001; Kingsolver and Diamond, 2011; but see Blows and Brooks, 2003). In this study, selected individuals with body size perturbed from their natural mean, produced fewer recruits than unselected individuals (Table 5). However, this result was age-depended in the *low* population (Table 5B). The reduction in fitness was evident in both directions from the pre-experimental means, which suggests that overall there is stabilizing selection on body size. Accordingly, directional fecundity selection on body size opposed the artificial selection in the first four years (Fig. 3), but was only significantly different from zero in males in the *low* population (Fig. 3B).

The detectability of a given strength of selection is generally strongly dependent on the magnitude of demographic stochasticity (Hersch and Phillips, 2004; Engen et al., 2012; Haller and Hendry, 2014). Here, the demographic stochasticity was found to be large during the years of artificial selection (Table 6) compared to previous estimates in house sparrows (Engen et al., 2007) and other small passerines (Sæther et al., 2004). This was mainly due to an increased demographic variation in recruit production (see *Results*), probably as a side effect breaking down the social structure in the populations by translocating individuals. Furthermore, environmental stochasticity was found to be higher in the experimental populations than the *control* population (Table 6; see also Sæther et al., 2004). Hence, there was large variation among years in mean individual fitness which could result from differences between years in the effect of translocating birds with additional effects from reductions in the population size. Generally, our results fit well with the idea that natural populations often are well adapted, with few individuals in the phenotypic space of very low fitness (Grafen, 1988; Schluter, 1988; Haller and Hendry, 2014). In such cases the detection of selection and the underlying fitness function might be difficult, and could be approached by experimental manipulations of the phenotype (Flux and Flux, 1982; Cresswell, 2000; Brakefield, 2003; Postma et al., 2007; Vignieri et al., 2010) or the ambient biotic or abiotic environmental conditions (Endler, 1980; Snaydon and Davies, 1982; Wade and Kalisz, 1990; Losos et al., 1997, 2001; Svensson and Sinervo, 2000; Calsbeek and Smith, 2007; Barrett et al., 2008; Calsbeek et al., 2009; Calsbeek and Cox, 2010; Logan et al., 2014).

The mean phenotype in populations with overlapping generations, is subject to transient changes due to fluctuations in the age distribution and earlier episodes of genetic drift and selection in different age classes (Caswell, 2001; Coulson et al., 2003, 2006; Coulson and Tuljapurkar, 2008; Engen et al., 2011, 2012, 2014). In this study the populations were found to gradually return towards their pre-experimental means when stopping the artificial selection. Three interacting mechanisms are believed to be involved in this process: directional fecundity selection opposing the artificial selection, natural mortality, and mating between selected and unselected individuals. While selected individuals produced fewer recruits than unselected individuals, they did not have lower survival (see *Results*). Still, there were almost no selected individuals in the population by the final year of this study due to natural mortality (Table 7). Mating between selected (or intermediate or indirectly selected) and unselected individuals further contributed to the phenotypic changes, where intermediate individuals increased in abundance and rapidly constituted the majority of the population (Table 6). The small inevitable gene flow from non-study populations, likely reinforced this process. Generally, the final evolutionary response to selection in age-structured populations is not observable at the time of selection. It will only be achieved when the individuals under selection no longer contribute directly to the next generation through own reproduction (i.e. reach life time reproductive success) and thereby no longer contributes to the population's mean phenotype (Engen et al., 2014). Here, by the time most selected individuals had left the population, the phenotypic footprint of our artificial selection was mostly lost.

Manipulating selection in the wild can yield novel insights into several evolutionary dynamic aspects of populations under natural conditions. We have demonstrated that strong directional selection on heritable traits produce evolutionary responses in accordance with well known quantitative genetic models. However, we also illustrate the potentially large impact of gene flow on the phenotypic trajectory of natural populations under temporally or spatially varying selection pressure. Phenotypically perturbing the populations from its natural mean had profound negative fitness consequences. Overall the results provided clear indications of an intermediate phenotype maintained by stabilizing and fluctuating selection for an optimum subject to environmental variation.

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Author Contributions

T.K. did the analyses and wrote the paper. T.H.R., H.J. and B.-E.S. came up with the idea and study design. H.J., I.J.H., B.R. and T.K. did the parentage analyses. S.E. advised the statistical analyses. All authors except S.E. performed fieldwork for the study. All authors contributed to the intellectual content through comments and edits when writing up the manuscript.

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Tables

Table 1: Individual selection category based on whether parents are artificially selected, or lineal descendants of artificially selected ancestors in two house sparrow populations in northern and mid-Norway. The populations were subject to artificial selection for long or short tarsus.

Selection category	Description
Selected	Both parents artificially selected
Unselected	No parent artificially selected
Indirectly selected	Both parents are lineal descendants of artificially selected ancestors
Intermediate	One parent artificially selected or lineal descendant of artificially selected ancestors

Table 2: Phenotypic correlation matrix across the years 2002-2009 for female (below diagonal) and male (above diagonal) house sparrows in three populations (A, B, C) in northern and mid-Norway. $^*P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

	Tarsus length	Body mass	Body condition	Wing length	Bill length	Bill depth
(A) *High*						
Tarsus length		0.474***	0.073	0.344***	0.272***	0.248***
Body mass	0.416***		0.912***	0.304***	0.247***	0.295***
Body condition	0.016	0.915***		0.183***	0.153***	0.221***
Wing length	0.285***	0.235***	0.133**		0.245***	0.180***
Bill length	0.225***	0.175***	0.096*	0.221***		0.292***
Bill depth	0.240***	0.356***	0.285***	0.218***	0.303***	
(B) *Low*						
Tarsus length		0.407***	0.025	0.332***	0.257***	0.199***
Body mass	0.305***		0.922***	0.242***	0.103**	0.225***
Body condition	0.003	0.952***		0.129***	0.005	0.166***
Wing length	0.291***	0.241***	0.160***		0.111**	0.148***
Bill length	0.291***	0.212***	0.131***	0.203***		0.312***
Bill depth	0.241***	0.259***	0.194***	0.169***	0.421***	
(C) *Control*						
Tarsus length		0.361***	-0.022	0.254***	0.400***	0.220***
Body mass	0.137*		0.924***	0.333***	0.201***	0.217***
Body condition	-0.028	0.983***		0.261***	0.057	0.138*
Wing length	0.246***	0.335***	0.310***		0.179**	0.192***
Bill length	0.264***	-0.065	-0.110	0.137*		0.239***
Bill depth	0.129*	0.057	0.037	0.221***	0.299***	

Table 3: Phenotypic mean±SE, variance and number of female and male individuals (n) in three popoulations (A, B, C) of house sparrows in northern and mid-Norway. The data are from 2002, before onset of artificial selection to increase or decrease tarsus length in the *high* and *low* population.

	Females		Males	
	Mean±SE	Variance	Mean±SE	Variance
(A) *High* (n = 65 and 75)				
Tarsus length	19.44±0.08	0.44	19.71±0.09	0.55
Body condition × 100	-0.94±0.61	0.24	-1.84±0.49	0.18
Wing length	77.5±0.2	2.3	80.5±0.2	2.5
Bill length	13.55±0.06	0.22	13.65±0.06	0.29
Bill depth	7.93±0.03	0.05	8.00±0.03	0.06
(B) *Low* (n = 80 and 82)				
Tarsus length	19.25±0.07	0.43	19.37±0.09	0.69
Body condition × 100	-3.24±0.57	0.26	-3.29±0.49	0.20
Wing length	78.9±0.2	4.0	81.2±0.2	2.6
Bill length	13.56±0.06	0.26	13.60±0.06	0.32
Bill depth	8.11±0.03	0.06	8.15±0.03	0.05
(C) *Control* (n = 25 and 28)				
Tarsus length	19.57±0.12	0.36	19.93±0.14	0.52
Body condition × 100	-0.39±0.96	0.23	-0.21±0.85	0.20
Wing length	78.3±0.3	2.0	81.4±0.3	2.2
Bill length	14.16±0.12	0.39	14.14±0.10	0.26
Bill depth	8.25±0.04	0.04	8.29±0.05	0.07

Table 4: Phenotypic change per year (slope) over the years 2002-2009 in both sexes of selected age 1 house sparrows in three populations in northern and mid-Norway. Changes were induced by artificial selection on tarsus length and the slopes are estimated relative to unselected age 1 individuals in each population. There was a significant difference between the slopes for bill length in females and males for the *low* population (female, male), otherwise the common slope is reported. $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

	Population		
	High	*Low*	*Control*
Tarsus length	0.12±0.02***	-0.10±0.03**	-0.01±0.02
Body condition × 100	0.43±0.16**	0.46±0.24	0.00±0.17
Wing length	0.09±0.05*	-0.16±0.07*	0.11±0.04*
Bill length	0.01±0.02	(0.05±0.03, -0.05±0.03)*	0.02±0.01
Bill depth	0.01±0.01	0.01±0.01	0.02±0.01*

Table 5: Differences in production of recruits among selection categories over the years 2003-2009 in two populations of house sparrow in northern and mid-Norway. The populations were subject to artificial selection for either long (A; *high*) or short (B; *low*) tarsus. Selection statuses (according to selective ancestry) were, unselected, intermediate and selected. Estimates are given relative to the unselected category, age 1, and females. Further details are given in the text.

		Confidence interval	
	Estimate	Lower	Upper
(A) *High*			
Intercept	-0.42	-0.69	-0.14
Selection status			
Intermediate	-0.29	-0.57	0.00
Selected	-0.40	-0.72	-0.09
Age			
2	0.41	0.22	0.61
Sex			
Male	-0.02	-0.26	0.21
(B) *Low*			
Intercept	-0.06	-0.37	0.26
Selection status			
Intermediate	0.05	-0.32	0.42
Selected	-0.60	-1.13	-0.07
Age			
2	-0.25	-0.58	0.08
Sex			
Male	0.23	-0.16	0.62
Sel.status × age			
Intermediate × 2	0.26	-0.17	0.68
Selected × 2	1.11	0.60	1.62
Sel.status × sex			
Intermediate × male	-0.65	-1.13	-0.16
Selected × male	-0.22	-0.87	0.42

Table 6: The demographic and environmental stochasticity in three populations (A, B, C) of house sparrow in northern and mid-Norway. The *high* and *low* populations were subject to opposing artificial selection on tarsus length in the years 2002-2005. Further details are given in the text.

	2002-05		2006-09	
	σ_d^2 (SD)	σ_e^2	σ_d^2 (SD)	σ_e^2
(A) *High*				
Female	1.02 (0.15)	0.04	0.70 (0.08)	0.15
Male	0.91 (0.10)	0.05	0.86 (0.11)	0.13
(B) *Low*				
Female	1.12 (0.15)	0.44	0.68 (0.06)	0.15
Male	1.18 (0.17)	0.07	0.67 (0.07)	0.07
(C) *Control*				
Female	0.72 (0.16)	0.08	0.64 (0.05)	0.02
Male	0.71 (0.09)	0.05	0.51 (0.04)	0.04

Table 7: The proportion of recruiting individuals (i.e. age 1) in each selection category over the years 2003-2009 in two populations of house sparrow in northern and mid-Norway. The populations were subject to artificial selection for either long (A, *high*) or short (B, *low*) tarsus in the years 2002-2005. The numbers presented are proportions calculated before artifical selection. Further details are given in the text.

	2003	2004	2005	2006	2007	2008	2009
(A) *High*							
Unselected	0.32	0.32	0.23	0.14	0.07	0.18	0.23
Intermediate	0.47	0.35	0.47	0.32	0.43	0.58	0.63
Indirectly selected	0.00	0.04	0.02	0.00	0.12	0.15	0.06
Selected	0.21	0.30	0.28	0.54	0.38	0.08	0.08
(B) *Low*							
Unselected	0.36	0.31	0.24	0.19	0.11	0.17	0.16
Intermediate	0.35	0.44	0.54	0.32	0.59	0.73	0.82
Indirectly selected	0.00	0.04	0.03	0.12	0.15	0.06	0.02
Selected	0.29	0.21	0.18	0.37	0.15	0.03	0.00

Figure legends

Figure 1: The temporal mean of SD-scaled directional selection gradients due to artificial selection over the four years 2002-2005 for female (**A**) and male (**B**) house sparrows on two islands in northern and mid-Norway. Tarsus length was the target of selection. In addition, the figure shows correlated selection on other traits. By translocating all individuals outside the limit of mean ± 0.3 SD to distant populations, one population was selected for long (*high*) and one for short (*low*) tarsus. Estimates are from simple linear regressions of relative fitness on the traits, with fitness defined as 1 if the individual stayed on the island (otherwise 0). All estimates were SD-scaled by the mean SD of each trait across the four year period.

Figure 2: Trajectories of tarsus length (annual mean ± SE) in three populations of house sparrow on three islands in northern and mid-Norway. (**A**, **C**) show the means across all individuals and (**B**, **D**) show only 1 year old individuals. Females (top row) and males (bottom row) are shown separately, and the grey points in (**A**, **C**) show means ± SE after artificial selection in the *high* and *low* population in year 2002-2005. Values in (**B**, **D**) show only offspring of artificially selected parents in the year 2003-2009, while all age 1 individuals are present in the pre-experimental means in 2002.

Figure 3: Temporal mean SD-scaled directional selection gradients over the period 2002-2005 for female (left) and male (right) house sparrows on each of three populations (*high*, *low* and *control*) in northern and mid-Norway. In this period the *low* and *high* populations were subject to artificial selection for long (*high*) or short (*low*) tarsus. *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

Figure 4: Temporal mean SD-scaled directional selection gradients over the period 2006-2009 for female (left) and male (right) house sparrows on each of three islands in northern and mid-Norway. The *low* and *high* populations had been subject to opposing artificial selection for long (*high*) or short (*low*) tarsus in the four previous years, but in this period all three populations were monitored without additional manipulations. *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

Figures

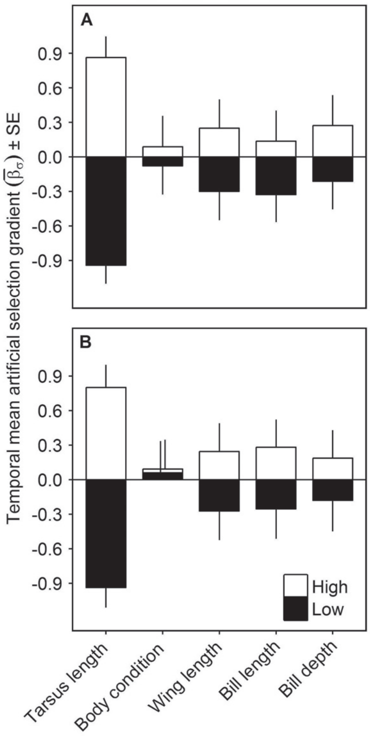

Figure 1

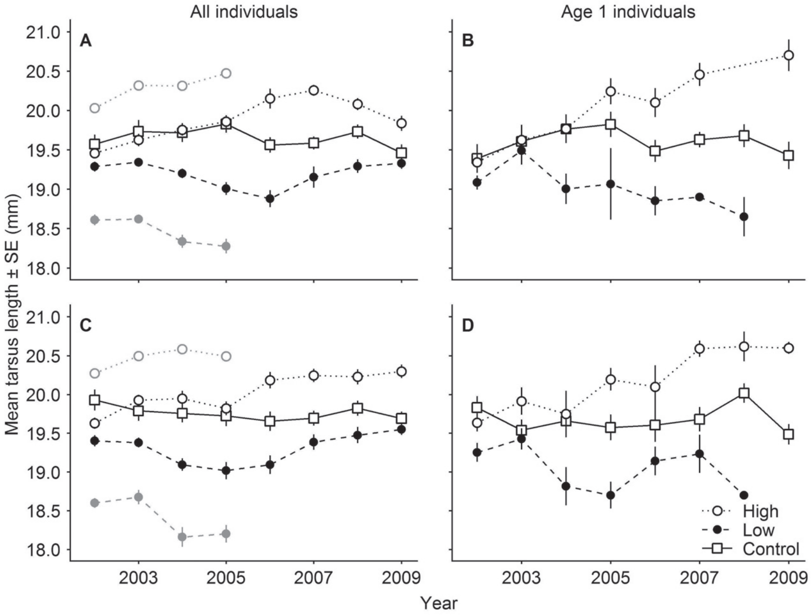
All individuals
Age 1 individuals
A
B
C
D
Mean tarsus length ± SE (mm)
21.0
20.5
20.0
19.5
19.0
18.5
18.0
2003
2005
2007
2009
Year
High
Low
Control

Figure 2

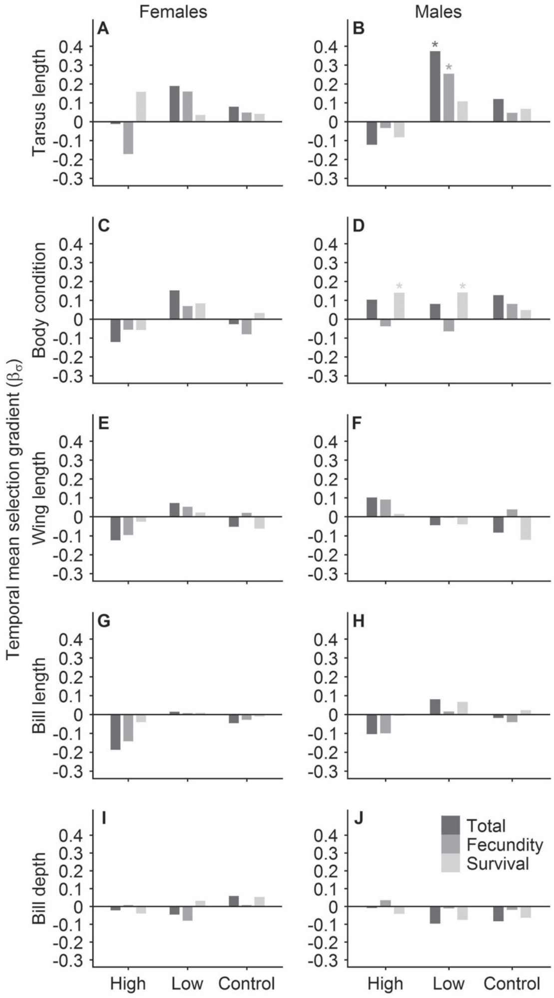
Females
Males
A
B
C
D
E
F
G
H
I
J
Temporal mean selection gradient (β_σ)
Tarsus length
Body condition
Wing length
Bill length
Bill depth
0.4
0.3
0.2
0.1
0
-0.1
-0.2
-0.3
*
*
*
*
High
Low
Control
Total
Fecundity
Survival

Figure 3

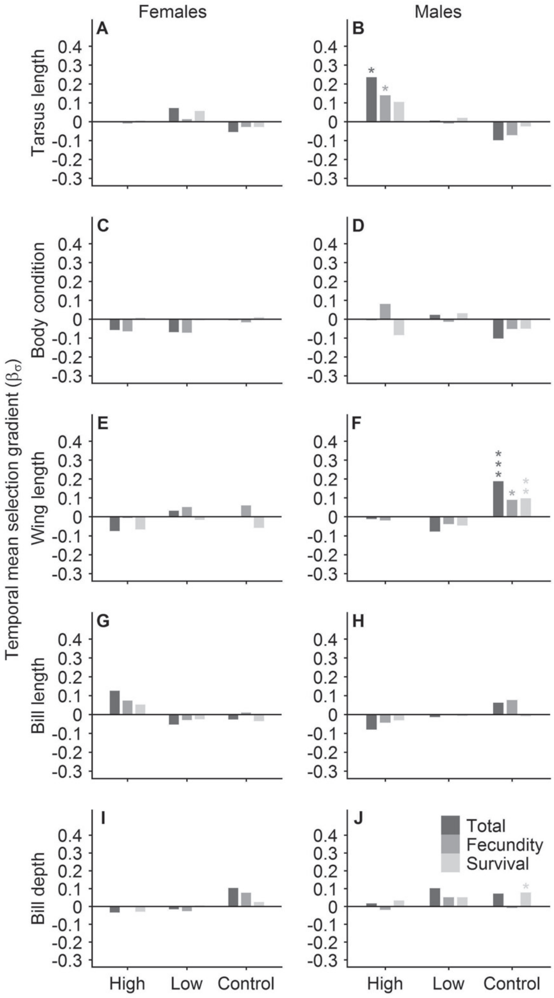
Females
Males
Temporal mean selection gradient (β_σ)
A
B
C
D
E
F
G
H
I
J
Tarsus length
Body condition
Wing length
Bill length
Bill depth
0.4
0.3
0.2
0.1
0
-0.1
-0.2
-0.3
Total
Fecundity
Survival
High
Low
Control
*
* * *

Figure 4

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 Zoology	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	Reflectometric studies of photomechanical adaptation in superposition eyes of arthropods
1991	Thyra Solem	Dr. scient Botany	Age, origin and development of blanket mires in Central Norway
1991	Odd Terje Sandlund	Dr. philos Zoology	The dynamics of habitat use in the salmonid genera *Coregonus* and *Salvelinus*: Ontogenic niche shifts and polymorphism

1991	Nina Jonsson	Dr. philos Zoology	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 Botany	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 Botany	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 Botany	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 Botany	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 Botany	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
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 Botany	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:
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 Zoology	Expressional and functional analyses of human, secretory phospholipase A2
2000	Ingrid Salvesen	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 Zoology	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 Biology	*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
2010	Yngvild Vindenes	ph.d Biology	Stochastic modeling of finite populations with individual heterogeneity in vital parameters
2010	Hans-Richard Brattbakk	ph.d Medical technology	The effect of macronutrient composition, insulin stimulation, and genetic variation on leukocyte gene expression and possible health benefits
2011	Geir Hysing Bolstad	ph.d Biology	Evolution of Signals: Genetic Architecture, Natural Selection and Adaptive Accuracy
2011	Karen de Jong	ph.d Biology	Operational sex ratio and reproductive behaviour in the two-spotted goby (*Gobiusculus flavescens*)
2011	Ann-Iren Kittang	ph.d Biology	*Arabidopsis thaliana* L. adaptation mechanisms to microgravity through the EMCS MULTIGEN-2 experiment on the ISS:– The science of space experiment integration and adaptation to simulated microgravity
2011	Aline Magdalena Lee	ph.d Biology	Stochastic modeling of mating systems and their effect on population dynamics and genetics
2011	Christopher Gravningen Sørmo	ph.d Biology	Rho GTPases in Plants: Structural analysis of ROP GTPases; genetic and functional studies of MIRO GTPases in Arabidopsis thaliana
2011	Grethe Robertsen	ph.d Biology	Relative performance of salmonid phenotypes across environments and competitive intensities
2011	Line-Kristin Larsen	ph.d Biology	Life-history trait dynamics in experimental populations of guppy (*Poecilia reticulata*): the role of breeding regime and captive environment
2011	Maxim A. K. Teichert	ph.d Biology	Regulation in Atlantic salmon (*Salmo salar*): The interaction between habitat and density
2011	Torunn Beate Hancke	ph.d Biology	Use of Pulse Amplitude Modulated (PAM) Fluorescence and Bio-optics for Assessing Microalgal Photosynthesis and Physiology
2011	Sajeda Begum	ph.d Biology	Brood Parasitism in Asian Cuckoos: Different Aspects of Interactions between Cuckoos and their Hosts in Bangladesh
2011	Kari J. K. Attramadal	ph.d Biology	Water treatment as an approach to increase microbial control in the culture of cold water marine larvae
2011	Camilla Kalvatn Egset	ph.d Biology	The Evolvability of Static Allometry: A Case Study
2011	AHM Raihan Sarker	ph.d Biology	Conflict over the conservation of the Asian elephant (*Elephas maximus*) in Bangladesh
2011	Gro Dehli Villanger	ph.d Biology	Effects of complex organohalogen contaminant mixtures on thyroid hormone homeostasis in selected arctic marine mammals
2011	Kari Bjørneraas	ph.d Biology	Spatiotemporal variation in resource utilisation by a large herbivore, the moose
2011	John Odden	ph.d Biology	The ecology of a conflict: Eurasian lynx depredation on domestic sheep
2011	Simen Pedersen	ph.d Biology	Effects of native and introduced cervids on small mammals and birds
2011	Mohsen Falahati-Anbaran	ph.d Biology	Evolutionary consequences of seed banks and seed dispersal in *Arabidopsis*

2012	Jakob Hønborg Hansen	ph.d Biology	Shift work in the offshore vessel fleet: circadian rhythms and cognitive performance
2012	Elin Noreen	ph.d Biology	Consequences of diet quality and age on life-history traits in a small passerine bird
2012	Irja Ida Ratikainen	ph.d Biology	Theoretical and empirical approaches to studying foraging decisions: the past and future of behavioural ecology
2012	Aleksander Handå	ph.d Biology	Cultivation of mussels (*Mytilus edulis):* Feed requirements, storage and integration with salmon (*Salmo salar*) farming
2012	Morten Kraabøl	ph.d Biology	Reproductive and migratory challenges inflicted on migrant brown trour (*Salmo trutta* L) in a heavily modified river
2012	Jisca Huisman	ph.d Biology	Gene flow and natural selection in Atlantic salmon
	Maria Bergvik	ph.d Biology	Lipid and astaxanthin contents and biochemical post-harvest stability in *Calanus finmarchicus*
2012	Bjarte Bye Løfaldli	ph.d Biology	Functional and morphological characterization of central olfactory neurons in the model insect *Heliothis virescens*.
2012	Karen Marie Hammer	ph.d Biology	Acid-base regulation and metabolite responses in shallow- and deep-living marine invertebrates during environmental hypercapnia
2012	Øystein Nordrum Wiggen	ph.d Biology	Optimal performance in the cold
2012	Robert Dominikus Fyumagwa	Dr. philos Biology	Anthropogenic and natural influence on disease prevalence at the human –livestock-wildlife interface in the Serengeti ecosystem, Tanzania
2012	Jenny Bytingsvik	ph.d Biology	Organohalogenated contaminants (OHCs) in polar bear mother-cub pairs from Svalbard, Norway. Maternal transfer, exposure assessment and thyroid hormone disruptive effects in polar bear cubs
2012	Christer Moe Rolandsen	ph.d Biology	The ecological significance of space use and movement patterns of moose in a variable environment
2012	Erlend Kjeldsberg Hovland	ph.d Biology	Bio-optics and Ecology in *Emiliania huxleyi* Blooms: Field and Remote Sensing Studies in Norwegian Waters
2012	Lise Cats Myhre	ph.d Biology	Effects of the social and physical environment on mating behaviour in a marine fish
2012	Tonje Aronsen	ph.d Biology	Demographic, environmental and evolutionary aspects of sexual selection
	Bin Liu	ph.d Biology	Molecular genetic investigation of cell separation and cell death regulation in *Arabidopsis thaliana*
2013	Jørgen Rosvold	ph.d Biology	Ungulates in a dynamic and increasingly human dominated landscape – A millennia-scale perspective
2013	Pankaj Barah	ph.d Biology	Integrated Systems Approaches to Study Plant Stress Responses
2013	Marit Linnerud	ph.d Biology	Patterns in spatial and temporal variation in population abundances of vertebrates
2013	Xinxin Wang	ph.d Biology	Integrated multi-trophic aquaculture driven by nutrient wastes released from Atlantic salmon (*Salmo salar*) farming
2013	Ingrid Ertshus Mathisen	ph.d Biology	Structure, dynamics, and regeneration capacity at the sub-arctic forest-tundra ecotone of northern Norway and Kola Peninsula, NW Russia
2013	Anders Foldvik	ph.d Biology	Spatial distributions and productivity in salmonid populations
2013	Anna Marie Holand	ph.d Biology	Statistical methods for estimating intra- and inter-population variation in genetic diversity
2013	Anna Solvang Båtnes	ph.d Biology	Light in the dark – the role of irradiance in the high Arctic marine ecosystem during polar night

2013	Sebastian Wacker	ph.d Biology	The dynamics of sexual selection: effects of OSR, density and resource competition in a fish
2013	Cecilie Miljeteig	ph.d Biology	Phototaxis in *Calanus finmarchicus* – light sensitivity and the influence of energy reserves and oil exposure
2013	Ane Kjersti Vie	ph.d Biology	Molecular and functional characterisation of the IDA family of signalling peptides in *Arabidopsis thaliana*
2013	Marianne Nymark	ph.d Biology	Light responses in the marine diatom *Phaeodactylum tricornutum*
2014	Jannik Schultner	ph.d Biology	Resource Allocation under Stress - Mechanisms and Strategies in a Long-Lived Bird
2014	Craig Ryan Jackson	ph.d Biology	Factors influencing African wild dog *(Lycaon pictus*) habitat selection and ranging behaviour: conservation and management implications
2014	Aravind Venkatesan	ph.d Biology	Application of Semantic Web Technology to establish knowledge management and discovery in the Life Sciences
2014	Kristin Collier Valle	ph.d Biology	Photoacclimation mechanisms and light responses in marine micro- and macroalgae
2014	Michael Puffer	ph.d Biology	Factors influencing African wild dog *(Lycaon pictus*) habitat selection and ranging behaviour: conservation and management implications
2014	Gundula S. Bartzke	ph.d Biology	Effects of power lines on moose *(Alces alces)* habitat selection, movements and feeding activity
2014	Eirin Marie Bjørkvoll	ph.d Biology	Life-history variation and stochastic population dynamics in vertebrates
2014	Håkon Holand	ph.d Biology	The parasite *Syngamus trachea* in a metapopulation of house sparrows
2014	Randi Magnus Sommerfelt	ph.d Biology	Molecular mechanisms of inflammation – a central role for cytosolic phospholiphase A2
2014	Espen Lie Dahl	ph.d Biology	Population demographics in white-tailed eagle at an on-shore wind farm area in coastal Norway
2014	Anders Øverby	ph.d Biology	Functional analysis of the action of plant isothiocyanates: cellular mechanisms and in vivo role in plants, and anticancer activity
2014	Kamal Prasad Acharya	ph.d Biology	Invasive species: Genetics, characteristics and trait variation along a latitudinal gradient.
2014	Ida Beathe Øverjordet	ph.d Biology	Element accumulation and oxidative stress variables in Arctic pelagic food chains: Calanus, little auks (alle alle) and black-legged kittiwakes (Rissa tridactyla)
2014	Kristin Møller Gabrielsen	ph.d Biology	Target tissue toxicity of the thyroid hormone system in two species of arctic mammals carrying high loads of organohalogen contaminants
2015	Gine Roll Skjervø	Dr. philos Biology	Testing behavioral ecology models with historical individual-based human demographic data from Norway
2015	Nils Erik Gustaf Forsberg	ph.d Biology	Spatial and Temporal Genetic Structure in Landrace Cereals
2015	Leila Alipanah	ph.d Biology	Integrated analyses of nitrogen and phosphorus deprivation in the diatoms *Phaeodactylum tricornutum* and *Seminavis robusta*
2015	Javad Najafi	ph.d Biology	Molecular investigation of signaling components in sugar sensing and defense in *Arabidopsis thaliana*
2015	Bjørnar Sporsheim	ph.d Biology	Quantitative confocal laser scanning microscopy: optimization of in vivo and in vitro analysis of intracellular transport
2015	Magni Olsen Kyrkjeeide	ph.d Biology	Genetic variation and structure in peatmosses (*Sphagnum*)

2015	Keshuai Li	ph.d Biology	Phospholipids in Atlantic cod (*Gadus morhua* L.) larvae rearing: Incorporation of DHA in live feed and larval phospholipids and the metabolic capabilities of larvae for the de novo synthesis
2015	Ingvild Fladvad Størdal	ph.d Biology	The role of the copepod *Calanus finmarchicus* in affecting the fate of marine oil spills