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

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Abstract

Empirical evidence strongly indicates 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 population of moose, *Alces alces*. 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 body mass as calf in females. During the study period, birth date was delayed by 0.81 days per year for both sexes, while no significant changes occurred in calf body mass. Quantitative genetic analyses indicated that both traits harboured significant additive genetic variance. These results show that selective harvesting can induce strong selection which oppose natural selection. This may cause evolution of less favourable phenotypes that become maladaptive once harvesting ceases.

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Introduction

Adaptive evolution on ecological time scales (microevolution) is strongly influenced by the standing level of additive genetic variance 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 might 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; Pigeon et al., 2016). 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

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decrease in body weight and horn size over time (see also Pigeon et al., 2016). 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, body mass as a calf 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

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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. An individuals own 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). Individual 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). Timing of births 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 actively select on other cues of individual quality affected by individual differences in 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 were collected on the island of Vega in northern Norway ($65°40'$N, $11°55'$E, see map in Solberg et al., 2008). 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 mainland in 1985, with an additional 24 immigrants recorded between 1986 and 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 calves and adults are known to have died from causes other than hunting (Figs 1 and 2) (see also 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, calf body mass was recorded with an accuracy of $\pm$ 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 $\times$ 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 ($\pm$ 1

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day, 1st 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. 1 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. 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

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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 1.1.12 (Bates et al., 2014) with R version 3.2.5 (R Core Team, 2014).

Phenotypic selection analyses

We estimated selection on individual calf body mass and birth date, keeping these traits fixed throughout an individuals life. Hence, calf body mass is an individuals own body mass measured as calf and birth date is the date on which an individual was born. The selection analyses were restricted to the years 2000-2011 and included 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.

Selection was analysed in males and females separately using the demographic framework developed by Engen et al. (2009, 2011, 2012, 2014a) to account for age structure. Hence, for each sex, the data were structured with pre-breeding census (Caswell, 2001) for survival and fecundity (Fig. 1). 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. 1). Emigrants were treated as dead individuals. In this framework, fecundity includes both the number of calves produced and their survival until 8-9 months of age (Fig. 2). There are potential issues with assigning offspring viability to their parents fitness (e.g. Wolf and Wade, 2001; Hadfield, 2012, 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.

In the demographic framework, unbiased estimates of selection are achieved by weight-

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ing components of individual fitness and trait values by age-specific reproductive values

from the mean population projection matrix (Caswell, 2001; Engen et al., 2012, 2014a).

Hence, 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 scaled to $\sum_x u_x = 1$ and $\sum_x u_x v_x = 1$ are the stable

age distribution and reproductive values (Table 1 and Fig. 1; Caswell, 2001; Engen et al.,

2009, 2012).

Within each sex, the annual individual fitness of an individual i in age class 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,

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

where J_i is a dichotomous indicator of survival (0/1), B_i is the number of recruits pro-

duced and the v's are the sex- and age-specific reproductive values. The $B's$ were always

divided by 2 to account for the contribution from each sex. This definition of annual

individual fitness was used to estimate the total selection on a trait. We also estimated

viability and fecundity selection separately by using the first and second part of equation

1 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 almost

no natural mortality in this population (Fig. 2). However, to investigate the effects of

harvest on fecundity, we repeated the fecundity selection analyses while ignoring harvest

mortality among recruits (s_x^h in Fig. 1) 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 using the annual weighted mean fitness (Engen et al.,

2014a).

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To separate direct from indirect selection, we estimated selection gradients across years as a set of weighted partial regression coefficients (weights v_x) of relative fitness on trait values (Lande and Arnold, 1983; Engen et al., 2012, 2014a). 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). Directional ($\beta_{\sigma 1}$), correlational ($\gamma_{\sigma 12}$) and quadratic ($\gamma_{\sigma 11}$) selection gradients were estimated. 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 were doubled from the least squares estimates (Stinchcombe et al., 2008). *Post hoc* tests adding the individual inbreeding coefficient, *f*, to the models 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 expresses the vector ($\mathbf{y}$) of measurements on the individuals own 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

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Z_a a} + \mathbf{Z_m m} + \mathbf{e}, \tag{2}$$

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 envi-

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ronment effects. **X** is a design matrix relating fixed predictors to each individual, each **Z** is a design matrix relating random predictors to each individual, and **e** is a vector of residuals (Lynch and Walsh, 1998; Kruuk, 2004). Hence, in this model the total phenotypic variance (σ_P^2) was partitioned into three additive components such that $\sigma_P^2 = \sigma_A^2 + \sigma_M^2 + \sigma_R^2$, where each component is the estimated variance for the corresponding vector in equation 2. 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 2.22.1 (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 non-informative improper prior was used for the variance components by specifying V = 0 and nu = -2. 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 period 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 genet-

ics. 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 ($\chi^2 = 25.40$, $df = 1$, $P < 0.001$), but there was no sexual difference in birth date ($\chi^2 = 0.66$, $df = 1$, $P = 0.418$, Table 2). In both sexes calf body mass decreased with later 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 significant directional change in calf body mass across years ($b = 0.25 \pm 0.30$, $\chi^2 = 0.73$, $df = 1$, $P = 0.394$), whereas birth dates delayed with a rate of 0.81 ± 0.20 days per year ($\chi^2 = 15.47$, $df = 1$, $P < 0.001$). The annual delay was similar in both sexes ($\chi^2 = 1.52$, $df = 1$, $P = 0.218$) and did not deviate from linearity ($\chi^2 = 0.47$, $df = 1$, $P = 0.493$).

Phenotypic selection

For females, there was significant negative directional selection on calf body mass (Fig. 3A, Table 3A, CI = [-0.16, 0.00]), but no significant directional selection on birth date (Fig. 3B, Table 3A, CI = [-0.10, 0.04]). When considering only survival (see Fig. 2), the estimates of directional viability selection were non-significant for calf body mass (Fig. 3C, Table 3A, CI = [-0.14, 0.02]) and birth date (Fig. 3D, Table 3A, CI = [-0.04, 0.11]). In contrast, there was evidence for directional fecundity selection towards lighter calf body mass (Fig. 3E, Table 3A, CI = [-0.52, 0.01]) and earlier birth date (Fig. 3F, Table 3A, CI = [-0.56, -0.13]). Hence, small and early born females produced more recruits. However, the confidence interval for the directional fecundity selection on calf body mass marginally crossed zero.

Re-analysing fecundity selection while excluding the effect of harvesting (see Figs 1 and 2), i.e. adding harvested calves to fecundity fitness, indicated no significant directional selection on calf body mass before the hunting season (Table 3A, CI = [-0.20, 0.05]). Hence, the variation in the number of calves born and their natural mortality were not the causes of selection on female calf body mass. The estimates of directional

fecundity selection with and without the effect of harvesting have confidence intervals which greatly overlap. Still, when adding the negative effect induced by hunters on fitness there was significant directional selection for smaller females (Table 3A). In contrast, the negative fecundity selection on birth date was unaffected by removing the effect of harvesting (Table 3A). In no cases were there any significant estimates of correlational or quadratic selection (Table 3A).

In males, there was significant positive directional selection for later birth date (Fig. 3B, Table 3B, CI = [0.00, 0.35]). The estimated directional selection on calf body mass was also positive, however, the confidence interval crossed zero (Fig. 3A, Table 3B, CI = [-0.02, 0.28]). In accordance with the estimated total selction, there was significant directional viability selection for later birth date (Fig. 3D, Table 3B, CI = [0.11, 0.49]). Almost all deaths were harvest-induced (see Fig. 2) and males born early in the season were more likely to be shot. The mean difference in birth date between killed and surviving individuals within years was 9 days. The estimated directional viability selection on calf body mass had a confidence interval which crossed zero (Fig. 3C, Table 3B, CI = [-0.03, 0.32]). In the analyses of fecundity selection in males there was found significant negative directional selection for earlier birth date (Fig. 3F, Table 3B, CI = [-0.86, -0.09]). Early born males had a higher reproductive success, hence, fecundity and viability selection on birth date acted in opposite directions. There was not any significant fecundity selection on calf body mass in males (Fig. 3E, Table 3B, CI = [-0.44, 0.29]). Re-analysing fecundity selection for males while excluding the effect of harvesting on recruit production (see Figs 1 and 2), did not indicate any harvest-induced fecundity selection. No significant estimates of correlational or quadratic selection were found (Table 3B).

Predictions of phenotypic evolution

There was high support for an additive genetic component in calf body mass and birth date (Table 4). In addition, there was high support for a maternal environment effect in both traits as judged by DIC (Table 4). 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 4B), while calf body mass had a much smaller maternal variance component (Table 4A). 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 predicted 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. The uncertainty in the estimates of heritability were large, thus, the confidence intervals for these prediction are wide. Furthermore, these predictions do not account for any genetic correlations between traits within and between sexes.

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 lifespan 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). In this study, we found indications of harvest-induced directional selection for females with smaller body mass as calf (Fig. 3, Table 3A). This was induced by hunting of calves (Table 3A), which at this stage still follow their mothers closely and have yet to become independent individuals in the analyses. The confidence interval for the estimated directional fecundity selection on calf body mass was wide and marginally included zero. However, the estimate was outside the range defined by the confidence interval for fecundity selection when excluding harvest (see *Results*). Large females lost a higher proportion of calves to hunting than small ones (see Table 3A). 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 females 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, females with twins would still have a higher probability to raise at least one calf than females with only one calf. Thus, the increased risk of losing a calf for females with twins could not be the only cause of the negative selection on body mass as calf. 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 4), or body mass as calf could be correlated with traits that affect the susceptibility to hunting (Law, 2000;

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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 large females may explain the negative harvest-induced selection on female body mass as calf and will modify any natural fecundity selection (Fig. 3, Table 3A).

Our results indicated no selection on calf body mass in males in our population (Fig. 3, Table 3B). Thus, hunters were non-selective in their harvest of yearlings and adults with respect to their 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). 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). Large individual deviations from the predicted relationship between calf and adult body mass could reduce the power of detecting any selection on body mass. Alternatively, 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 implies 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. 2), are 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. The demographic approach used to estimate selection in this study correctly accounted for the dependency between age and fitness. Generally, estimates of selection will contain a component of false selection when age-structure is ignored. This is caused by transient changes in the age-distribution and differences in the mean phenotype between age classes (Engen et al., 2014a).

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. 3, Table 3). 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. 3, Table 3B), 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 3). 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. 2). Previous studies has suggested that hunters preferably shoot females without calves, and if they are to shoot females with calves the calves have to be shot first, thus, allowing females to escape (Solberg et al., 1999, 2000; Ericsson, 2001).

We found evidence for additive genetic variance in both traits in this study (Table 4). The heritability estimated for birth date and calf body mass were of the same order as previously recorded with similar analyses of 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, we used the univariate breeders equation to predict a negative response in calf body mass in females and a positive response in birth date in males over the years (see *Results*). These predictions ignore genetic covariances between traits within and between sexes (Morrissey et al., 2010) which certainly would have been important in shaping the observed change towards later births at a rate of 0.81 days per year and the lack of change in calf body mass. Generally, unmeasured additive genetic covariance between selected traits limit the additive genetic variation in each trait that is available for unconstrained phenotypic evolution (Hansen and Houle, 2008; Morrissey et al., 2010). In previous studies on un-

gulates, a negative genetic covariance between birth mass and date has 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). In this study, we found a negative phenotypic covariance between calf body mass (at 8-9 months of age) and birth date (Table 2; see also Solberg et al., 2008). A quantitative genetic analysis would be required to separate genetic effects from environmental effects due to higher foraging quality for early born individuals. However, the negative phenotypic covariance could be taken to indicate the presence of a negative genetic covariance (Cheverud, 1988). A strong negative genetic covariance would constrain the evolutionary response in traits selected in the same direction, while a positive genetic covariance would have the opposite effect (Lande, 1979). In this study, a negative genetic covariance between body mass as calf and birth date could constrain the evolutionary responses in females to negative directional selection on body mass as calf, while causing a response of delayed birth date (see Table 3). In males, a negative covariance would constrain evolutionary responses in both traits and if sufficiently strong could even cause predicted responses in the opposite direction of selection. However, the final response to selection on a suite of traits within each sex will generally also depend on intersexual genetic covariances (Lande, 1980; Gosden et al., 2012). The intersexual genetic covariance for each trait in this study seems likely to be positive and may even be quite strong. Hence, our inability to estimate all of these additive genetic components, could be an important cause of differences between predicted and observed phenotypic changes. However, other explanations for differences between observed and predicted phenotypic changes which are difficult to rule out should also be mentioned. For instance, selection on a unmeasured genetically correlated trait could constrain evolutionary responses and responses could be masked by environmental effects which are not accounted for (reviewed in Merilä et al., 2001). Furthermore, 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

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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).

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 4). 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; Wilson et al., 2005a; Kruuk and Hadfield, 2007). 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; Hadfield, 2012). However, estimating maternal genetic effects is 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 be concealed within the additive genetic and 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 individual (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). In such a case, the phenotype of an individual is thought to be a result of its own genes, an environmental effect and a parental effect (Kirkpatrick and Lande, 1989; Lande and Kirkpatrick, 1990; Hadfield, 2012). Hence, the change in a phenotype from one generation to the next would be affected by both selection on the individuals directly and selection that modify the traits of their parents (Hadfield, 2012). Parental effects may have important consequences for evolutionary trajectories, however, there does not yet exist a theoretical framework for dealing with these effects

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in age-structured populations.

 Demographic and evolutionary consequences of harvesting have 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. 3A, Table 3A). Thus, in species with extended parental care, sustainable harvest strategies should not only consider the effects on the phenotypic distribution of individuals, but also consider how harvesting their young may affect their contribution to further generations (Fig. 2; see also Solberg et al., 2000). Accordingly, 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 includ-

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ing 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).

Acknowledgements

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Tables

Table 1: Age-specific fecundity (f_x) and survival (s_{x+1}) (mean±SE) with pre-breeding census for female (A) and male (B) moose on the island of Vega in northern Norway over the years 2000-2012. n_x = number of individuals in age class x. The stable age distribution (u_x) and reproductive values (v_x) for each sex result from the sex-specific projection matrix, $\mathbf{l}$, populated by the age-specific vital rates in the table. Individuals enter age class 1 at 8-9 months old and those that enter 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. 1.

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 and (co)variance of calf body mass (kg, at 8-9 months of age) and birth date (1th of January = day 1) for moose at the island of Vega in northern Norway. Estimates are shown for (A) the whole study period 1992-2011 and (B) the limited period 2000-2011 where selection was analysed. Number of individuals (n) for each estimate is shown. 70 females and 80 males were measured for both traits during the whole study. In (B), the data were limited to individuals measured for both traits. Estimates in (B) are those relevant for standardizing selection gradients in the study. Thus, they were estimated across the whole data set with 188 (females) and 105 (male) individ-years weighted by age-specific reproductive values (see Table 1). The (co)variances in (B) were estimated after centering by the annual weighted means.

	Females				Males			
	Mean±SE	Var	Cov	n	Mean±SE	Var	Cov	n
(A) 1992-2011								
Calf body mass	179±2	342		76	192±2	450		89
Birth date	152±1	97	-35	79	151±1	96	-92	87
(B) 2000-2011 (weighted)								
Calf body mass	177±1	250		49	189±3	759		43
Birth date	152±1	97	-24	49	157±1	96	-174	43

Table 3: SD-scaled directional ($\beta_{\sigma i}$), quadratic ($\gamma_{\sigma ii}$) and correlational ($\gamma_{\sigma ij}$) 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 significantly different from zero. Selection gradients are estimated using total fitness (the combinations of survival and fecundity according to equation 1), viability fitness and two measures of fecundity fitness. In the analyses with fecundity fitness excluding harvest mortality among calves, the number of recruits was 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 4: 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: 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 2: 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. 1 and Table 1). The mean annual natural probabilities of survival after harvest ($\overline{s^{n2}}$ in Fig. 1), 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 3: 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 se-
lection 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
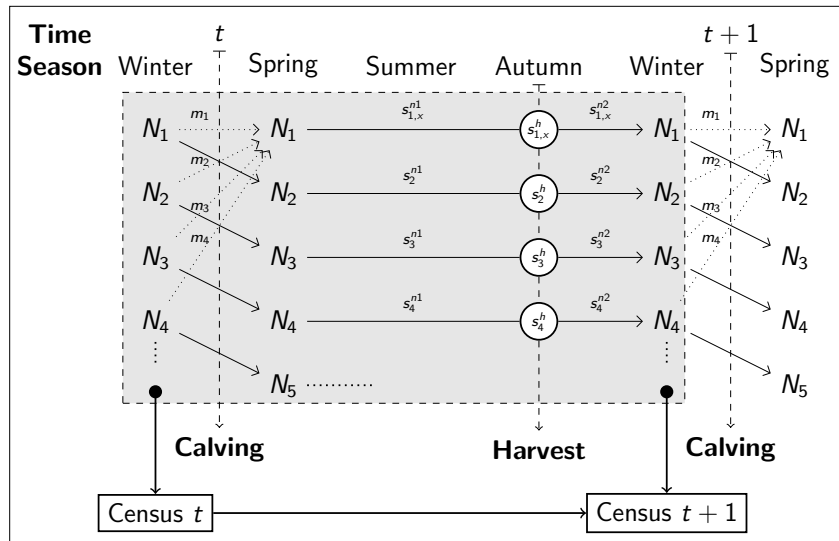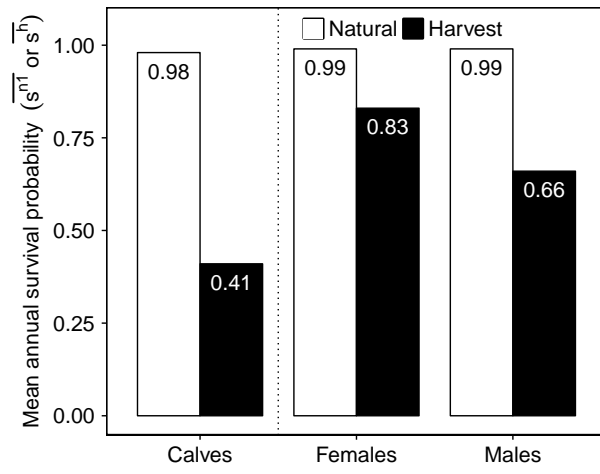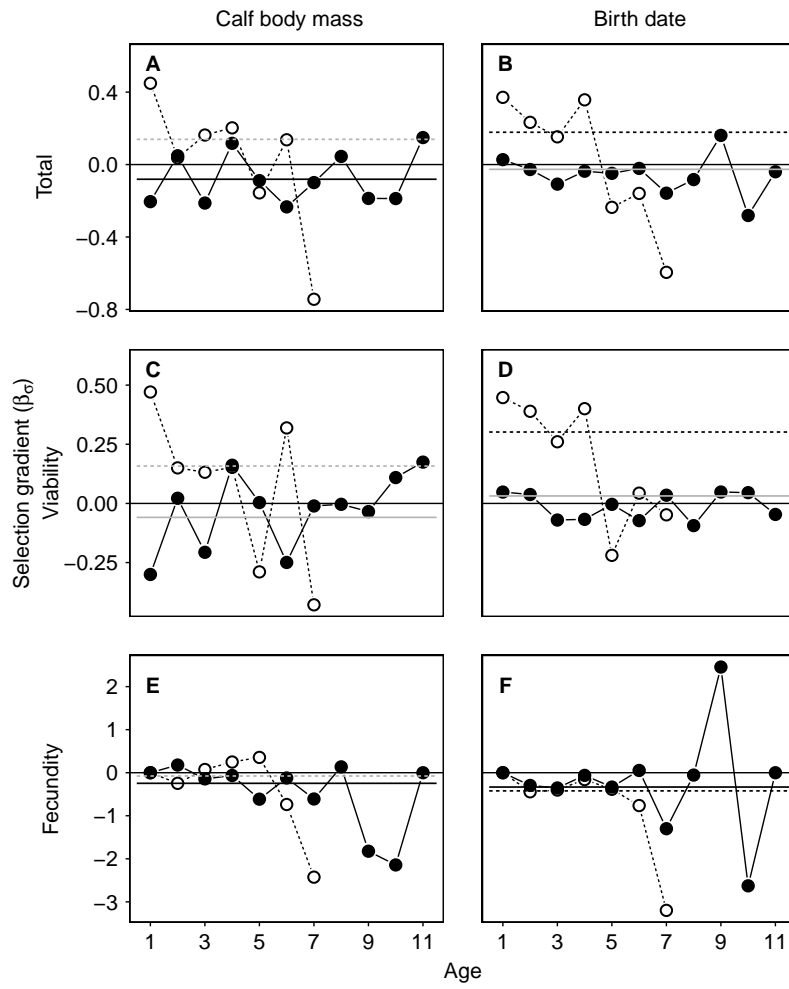given in the text and in Table 3.

Figures

Figure 1

Figure 2

Figure 3