

"This is the peer reviewed version of the following article: Kvalnes, T., Sæther, B. E., Haanes, H., Røed, K. H., Engen, S., & Solberg, E. J. (2016). Harvest-induced phenotypic selection in an island population of moose, Alces alces. Evolution, 70(7), 1486-1500., which has been published in final form at 10.1111/evo.12952. This article may be used for non-commercial purposes in accordance with Wiley Terms and Conditions for Self-Archiving."

1 Harvest-induced phenotypic selection in an 2 island population of moose, *Alces alces*

3 Thomas Kvalnes^{1,2}, Bernt-Erik Sæther¹, Hallvard Haanes³, Knut H. Røed⁴, Steinar Engen⁵
4 and Erling J. Solberg⁶

5 ¹Centre for Biodiversity Dynamics (CBD), Department of Biology, Norwegian University
6 of Science and Technology (NTNU), NO-7491 Trondheim, Norway

7 ³Norwegian Radiation Protection Authority, NO-1361 Østerås, Norway

8 ⁴Department of Basic Sciences and Aquatic Medicine, Norwegian University of Life Sci-
9 ences, PO-8146 Dep, NO-0033 Oslo, Norway

10 ⁵Centre for Biodiversity Dynamics (CBD), Department of Mathematical Sciences, Nor-
11 wegian University of Science and Technology (NTNU), NO-7491 Trondheim, Norway

12 ⁶Norwegian Institute for Nature Research (NINA), NO-7485 Trondheim, Norway

13 ²Kvalnes (corresponding author): thomas.kvalnes@ntnu.no

14 Sæther: bernt-erik.sather@bio.ntnu.no

15 Haanes: hallvard.haanes@nrpa.no

16 Røed: knuth.roed@nmbu.no

17 Engen: steinaen@math.ntnu.no

18 Solberg: erling.solberg@nina.no

19 Running head: Harvest-induced selection

20 Data archival location: Dryad (datadryad.org)

21 Word count: 6120, Figures: 3, Tables: 4

22 **KEY WORDS:** Age structure, animal model, microevolution, reproductive value, un-
23 gulate

24 revised May 11, 2016

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.

39 Introduction

40 Adaptive evolution on ecological time scales (microevolution) is strongly influenced by
41 the standing level of additive genetic variance and selection expressed as the covariance of
42 phenotype and fitness (Price, 1972; Lande, 1979). In exploited populations, the natural
43 direction of evolutionary changes may be substantially affected by the phenotypic charac-
44 teristics of harvested individuals and the increased mortality added by harvesting (Sæther
45 et al., 2001; Law, 2007; Proaktor et al., 2007; Allendorf and Hard, 2009; Darimont et al.,
46 2009; Engen et al., 2014b). Sustainable harvest strategies should consequently include
47 considerations of how harvest selection might interfere with natural selection and how
48 this in turn will affect phenotypic evolution (Dunlop et al., 2009; Hutchings, 2009; Hendry
49 et al., 2011; Kuparinen and Hutchings, 2012; Laugen et al., 2014).

50 In many heavily exploited mammalian populations, harvest may be the largest source
51 of mortality (e.g. Solberg et al., 2000; Stubsjøen et al., 2000; reviewed in Collins and Kays,
52 2011). As harvesting is often non-random with respect to individual characteristics, this
53 mortality will have the potential for shifting the distribution of phenotypes (Law, 2000;
54 Allendorf and Hard, 2009; Mysterud, 2011; Garcia et al., 2012). Such harvest-induced
55 selection may occur through several mechanisms (Mysterud, 2011). For instance, the use
56 of harvest equipment that select some types of individuals more than others (e.g. size
57 selective fishing nets, Law, 2000; Carlson et al., 2007; Enberg et al., 2012; Kuparinen and
58 Merilä, 2007; Kendall et al., 2009), or hunters that are choosy due to individual variation
59 in harvesting value or attractiveness (e.g. trophy-hunting in ungulates, Coltman et al.,
60 2003; Hedrick, 2011; Pigeon et al., 2016). In addition, there could be individual differences
61 in vulnerability or exposure to hunters (e.g. bold vs less conspicuous behaviour, Ciuti
62 et al., 2012). Several traits affected by harvesting may be heritable (Law, 2000; Kruuk and
63 Hadfield, 2007; Allendorf et al., 2008; Carlson and Seamons, 2008; Sasaki et al., 2009).
64 Thus, there is a growing body of empirical evidence on how harvest-induced selection
65 may cause rapid evolutionary changes (Olsen et al., 2004; Garel et al., 2007; Law, 2007;
66 Allendorf and Hard, 2009; Darimont et al., 2009; Sharpe and Hendry, 2009). In bighorn
67 sheep *Ovis canadensis*, Coltman et al. (2003) found that trophy hunting had induced a

68 decrease in body weight and horn size over time (see also Pigeon et al., 2016). In wild boar
69 *Sus scrofa scrofa*, Gamelon et al. (2011) showed that birth date had advanced in response
70 to harvest selection for early maturation. Also Sasaki et al. (2009) found that harvested
71 populations of Japanese Mamushi Snake *Gloydius blomhoffii* were smaller, matured earlier
72 and displayed stronger anti-predator behaviour than unharvested populations.

73 The strength and form of selection resulting from harvest-induced and natural causes
74 of mortality and fecundity, and which age classes are more strongly affected, are impor-
75 tant determinants for the outcome of selective harvest (Carlson et al., 2007; Edeline et al.,
76 2007; Proaktor et al., 2007; Mysterud, 2011; Olsen and Moland, 2011; Engen et al., 2012,
77 2014b). In age-structured populations, the contribution of an individual to future genera-
78 tions (reproductive value) depends on age-specific transitions among different phenotypic
79 categories affecting their fecundity and survival (Caughley, 1966; Caswell, 2001; Coulson
80 et al., 2010; Sæther et al., 2013). For instance, natural mortality rates in large ungulates
81 are typically low for prime aged adults, and higher for young and old individuals (Gail-
82 lard et al., 1998; Loison et al., 1999). Exploited populations will have harvest mortality
83 interfering with natural mortality, changing the distribution of reproductive values by
84 affecting age classes differently (Langvatn and Loison, 1999; Solberg et al., 2000; Engen
85 et al., 2014b). Thus, the total selection imposed through harvest and natural mortality
86 will be a complex function of annual age-specific covariances of traits and fitness, which
87 best can be understood in a demographic framework (Lande, 1982; van Tienderen, 2000;
88 Coulson et al., 2003, 2006, 2010; Engen et al., 2011, 2012, 2014a; Morrissey et al., 2012).
89 This allows fitness to be defined through both fecundity and survival, and describes
90 how selection at different stages of the life cycle affects both ecological and evolutionary
91 dynamics (Wilson and Nussey, 2010; Engen et al., 2009, 2012, 2014a).

92 In this paper we investigated selective and evolutionary effects of harvesting on two
93 fitness-related traits in ungulates, body mass as a calf and birth date (see also Coulson
94 et al., 2003). We used data from a population of radio-collared moose in northern Norway,
95 where most individuals have been followed in detail with life histories monitored from
96 birth (Sæther et al., 2003, 2004, 2007; Solberg et al., 2007, 2010; Haanes et al., 2013). This

97 enabled us to partition out the effects of harvest from other environmental factors that
98 affect individual phenotype and fitness. Both traits investigated are closely associated
99 with individual fitness. An individuals own calf body mass can explain a large proportion
100 of individual variation in recruitment (Wilson et al., 2005b; Grøtan et al., 2009; Milner
101 et al., 2013), age at maturity (Sæther and Haagenrud, 1983, 1985; Sæther and Heim, 1993;
102 Sæther et al., 1996; Sand, 1996) and early life fecundity (Sæther and Haagenrud, 1985;
103 Schwartz and Hundertmark, 1993; Sand, 1996) in moose as well as in other ungulates
104 (Gaillard et al., 2000b). Furthermore, calf body mass is positively correlated with adult
105 body mass at all age classes in our population (Solberg et al., 2008). Individual birth
106 date is considered a key trait influencing early growth and recruitment in several species
107 of ungulates (Festa-Bianchet, 1988; Coulson et al., 2003; Wilson et al., 2005b; Solberg
108 et al., 2007; Plard et al., 2015). Timing of births has profound population dynamic effects
109 under seasonal variation in resource abundance (Albon and Langvatn, 1992; Sæther and
110 Heim, 1993; Clutton-Brock and Coulson, 2002; Solberg et al., 2007; Plard et al., 2014).
111 If the individual phenotypic variation in these traits causes some individuals to be more
112 attractive or susceptible to hunters, harvest may be an important selective force driving
113 phenotypic changes in this population. For instance, hunters may target individuals with
114 large calf body mass for high yield, preferably shoot barren females (with on average
115 low calf body mass) to avoid shooting calves or females with calves, or may actively
116 select on other cues of individual quality affected by individual differences in birth date.
117 Our objectives were to (1) reveal whether there were temporal trends in the two traits
118 while controlling for other confounding factors, (2) estimate phenotypic selection across
119 years separating between harvest-induced and natural selection, (3) estimate the additive
120 genetic variation for each trait and (4) predict evolutionary responses under the current
121 harvest regime.

122 Material and methods

123 Study system and data collection

124 The data were collected on the island of Vega in northern Norway (65°40'N, 11°55'E, see
125 map in Solberg et al., 2008). The island has an area of 119 km², of which approximately
126 80 km² are preferred moose habitat, and had a human population of 1250-1500 during
127 the study (Solberg et al., 2008, 2010). The moose population was founded by one male
128 and two female yearlings immigrating from the mainland in 1985, with an additional
129 24 immigrants recorded between 1986 and 2011. Starting in 1989, annual hunting has
130 been allowed throughout October, with a break around peak ovulation (Garel et al.,
131 2009). During the first four years hunting intensity was low (2-4 individuals annually),
132 but increased since 1993 (Sæther et al., 2003), keeping the population at winter densities
133 of 25 to 43 individuals annually (Solberg et al., 2007). With this regime, less than 5%
134 of calves and adults are known to have died from causes other than hunting (Figs 1 and
135 2) (see also Solberg et al., 2007). Thus, we assume that density dependence has a minor
136 influence on the dynamics of this population.

137 During 1992 and 1993 all individuals in the population were radio collared for the first
138 time. In January-March every year until present (except 2003 and 2008), this procedure
139 was repeated to mark all new calves (born in May-June) which survived the annual
140 hunting. At the same time, calf body mass was recorded with an accuracy of ± 2 kg by
141 use of an analogue or digital scale installed on a helicopter. At this stage, calves were
142 8-9 months of age and follow their mothers closely for another 2-4 months. No data are
143 available on live body mass of calves at earlier ages. Calf body mass was standardised by
144 simple linear regression as there was significant weight loss by date during the period of
145 fieldwork ($b = -0.166$, $t = -1.85$, $P = 0.067$), which was similar for both sexes ($sex \times$
146 $date$ interaction: $t = -0.23$, $P = 0.818$). The adjusted calf body mass (z) was estimated
147 by $z = z' - bd$, where d equals date of measurement relative to 15th of February and
148 b is the slope of calf body mass (z') on date of measurement. Pregnant females were
149 approached during May-July at 3-5 days intervals until calving, when birth date (± 1

150 day, 1st of January = day 1) was determined for all calves based on calf size, behaviour,
151 and the condition of the mother (Sæther et al., 2003). In total over the years 1992-
152 2011, there were 181 individuals phenotyped for calf body mass, birth date or both (see
153 Table 2). The high intensity of fieldwork combined with relative small area and open
154 landscape of the study site, ensured that >90% of individuals were radio collared at
155 all times during the study and could have survival determined with a high degree of
156 certainty (Stubsjøen et al., 2000; Solberg et al., 2007, 2010). Furthermore, with tissue
157 samples from all marked and hunted individuals, a genetic pedigree with a total of 499
158 individuals born in the period 1984-2012 was constructed (for details see Haanes et al.,
159 2013). This enabled the number of offspring to be determined genetically for both sexes.
160 The diagram in Fig. 1 indicates the chronological order of events during a time step and
161 relevant demographic parameters monitored.

162 **Temporal phenotypic trends**

163 We tested for temporal trends across the years 1992-2011 in calf body mass and birth
164 date by constructing linear mixed effects models with year as a continuous effect and
165 mother identity as random effect to account for non-independence of siblings. Previous
166 investigations in this population has found the age of the mother, twin status (1 = twin,
167 0 = singleton) and degree of inbreeding, f , to account for some of the phenotypic variance
168 in calf body mass and birth date (Solberg et al., 2007; Haanes et al., 2013). Thus, we
169 included them as covariates in our models. With these models a significant year effect was
170 taken as evidence for a temporal trend. However, we also fitted a quadratic effect of year
171 in our models to test whether any trends found displayed an effect-reduction over time,
172 as predicted if caused by manipulations of sex ratio and age structure that were made in
173 the early years (Sæther et al., 2003). All adult males were shot after the rut in 1994 and a
174 high off-take of males in all age classes followed in 1996, which kept the sex ratio strongly
175 biased towards females until 1999 (Sæther et al., 2003, 2004). Statistical significance was
176 assessed by likelihood ratio tests, in which twice the difference in log likelihood between
177 two nested models (fitted by maximum likelihood), is χ^2 -distributed with degrees of

178 freedom (df) equal to $df_1 - df_2$. Model assumptions were checked graphically using
179 diagnostic plots. Estimates are provided with standard errors in the text. All analyses
180 were performed using the R package *lme4*, version 1.1.12 (Bates et al., 2014) with R
181 version 3.2.5 (R Core Team, 2014).

182 **Phenotypic selection analyses**

183 We estimated selection on individual calf body mass and birth date, keeping these traits
184 fixed throughout an individuals life. Hence, calf body mass is an individuals own body
185 mass measured as calf and birth date is the date on which an individual was born. The
186 selection analyses were restricted to the years 2000-2011 and included only individuals
187 with both traits of interest. Thus, we avoided the period of sex ratio and age structure
188 manipulations, and ensured that phenotypes (as calf) were available within most age
189 classes.

190 Selection was analysed in males and females separately using the demographic frame-
191 work developed by Engen et al. (2009, 2011, 2012, 2014a) to account for age structure.
192 Hence, for each sex, the data were structured with pre-breeding census (Caswell, 2001)
193 for survival and fecundity (Fig. 1). Calves (aged 8-9 months) constituted the first age
194 class and the oldest individuals were collected in age class 11 (females) and 7 (males),
195 as only 4 females and 3 males survived these age classes. An individual was recorded as
196 surviving from year t to $t + 1$ if recorded in year $t + 1$, and had fecundity equal to half
197 the number of calves produced in year t which were alive in year $t + 1$ (i.e. recruits,
198 see Fig. 1). Emigrants were treated as dead individuals. In this framework, fecundity
199 includes both the number of calves produced and their survival until 8-9 months of age
200 (Fig. 2). There are potential issues with assigning offspring viability to their parents
201 fitness (e.g. Wolf and Wade, 2001; Hadfield, 2012, and references therein). However, the
202 viability of calves are largely dependent on characteristics of the female. Moose calves
203 are weaned at approx. 6 months of age, and follow their mothers closely until just before
204 the next calving season.

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

206 ing components of individual fitness and trait values by age-specific reproductive values
 207 from the mean population projection matrix (Caswell, 2001; Engen et al., 2012, 2014a).
 208 Hence, for each sex, the mean age-specific fecundity and survival were estimated across
 209 the years 2000-2012 to populate the sex-specific projection matrix, \mathbf{l} . The real dominant
 210 eigenvalue of \mathbf{l} is the multiplicative growth rate (λ) of the population. The corresponding
 211 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
 212 age distribution and reproductive values (Table 1 and Fig. 1; Caswell, 2001; Engen et al.,
 213 2009, 2012).

214 Within each sex, the annual individual fitness of an individual i in age class x was
 215 defined as $\Lambda_i = W_i/v_x$, where v_x is the sex- and age-specific reproductive value and W_i
 216 is the individual reproductive value (Engen et al., 2009). W_i estimate the individual
 217 contribution to the total reproductive value of the population next year (Engen et al.,
 218 2009, 2014a) and is defined by,

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

219 where J_i is a dichotomous indicator of survival (0/1), B_i is the number of recruits pro-
 220 duced and the v 's are the sex- and age-specific reproductive values. The B 's were always
 221 divided by 2 to account for the contribution from each sex. This definition of annual
 222 individual fitness was used to estimate the total selection on a trait. We also estimated
 223 viability and fecundity selection separately by using the first and second part of equation
 224 1 as measures of viability (W_{si}) and fecundity (W_{fi}) fitness (Engen et al., 2011). Any
 225 selection that is detected on survival is by definition harvest-induced, as there are almost
 226 no natural mortality in this population (Fig. 2). However, to investigate the effects of
 227 harvest on fecundity, we repeated the fecundity selection analyses while ignoring harvest
 228 mortality among recruits (s_x^h in Fig. 1) in fecundity fitness. That is, using $f_x = m_x s_1^{n1} s_1^{n2}$
 229 for fecundity in projection matrices and adding the number of harvested calves to the
 230 number of recruits (B_i) produced by an individual i in the selection analyses. In each
 231 case, relative fitness was defined using the annual weighted mean fitness (Engen et al.,
 232 2014a).

233 To separate direct from indirect selection, we estimated selection gradients across
 234 years as a set of weighted partial regression coefficients (weights v_x) of relative fitness
 235 on trait values (Lande and Arnold, 1983; Engen et al., 2012, 2014a). Within each sex,
 236 both traits were centred by the annual weighted mean and scaled by the global weighted
 237 standard deviation (SD-scaled) of the centred traits (see Table 2). Directional ($\beta_{\sigma 1}$), cor-
 238 relational ($\gamma_{\sigma 12}$) and quadratic ($\gamma_{\sigma 11}$) selection gradients were estimated. Uncertainties
 239 in the estimates were assessed by resampling with replacement for 10000 bootstrap repli-
 240 cates (Mitchell-Olds and Shaw, 1987). Standard errors and confidence intervals (CI) were
 241 estimated as the standard deviations and adjusted bootstrap percentile intervals of the
 242 bootstrap replications. Quadratic selection gradients and standard errors were doubled
 243 from the least squares estimates (Stinchcombe et al., 2008). *Post hoc* tests adding the
 244 individual inbreeding coefficient, f , to the models revealed no inflation of estimated selec-
 245 tion gradients due to heterogeneity among individuals in f (Kvalnes et al. unpublished
 246 results; see Willis, 1996). Standard errors of weighted means were estimated by the ratio
 247 variance approximation as recommended by Gatz and Smith (1995).

248 Quantitative genetics analyses

249 Pruning the pedigree to only the phenotyped individuals and connecting pedigree links,
 250 we ended up with an informative pedigree of 210 individuals born in the period 1992-
 251 2011. This pedigree information was utilized in univariate animal models (Lynch and
 252 Walsh, 1998; Kruuk, 2004). This is a form of mixed model which expresses the vector
 253 (\mathbf{y}) of measurements on the individuals own calf body mass or birth date in terms of
 254 their additive genetic effects and other random and fixed effects. Pooling the sexes and
 255 mean-scaling the traits across years (see Table 2), we constructed models of the following
 256 structure

$$\mathbf{y} = \mathbf{X}\mathbf{b} + \mathbf{Z}_a\mathbf{a} + \mathbf{Z}_m\mathbf{m} + \mathbf{e}, \quad (2)$$

257 where \mathbf{b} is a parameter vector with the fixed effects of sex and the individual inbreeding
 258 coefficient, \mathbf{a} is a vector of additive genetic effects and \mathbf{m} is a vector of maternal envi-

259 ronment effects. \mathbf{X} is a design matrix relating fixed predictors to each individual, each
260 \mathbf{Z} is a design matrix relating random predictors to each individual, and \mathbf{e} is a vector of
261 residuals (Lynch and Walsh, 1998; Kruuk, 2004). Hence, in this model the total phe-
262 notypic variance (σ_P^2) was partitioned into three additive components such that $\sigma_P^2 =$
263 $\sigma_A^2 + \sigma_M^2 + \sigma_R^2$, where each component is the estimated variance for the corresponding
264 vector in equation 2. Individual f -values were included to avoid inflated additive genetic
265 effects due to correlations among close relatives (Reid and Keller, 2010; Haanes et al.,
266 2013), while sex was included to have estimates of heritability on the same scale as the
267 estimated selection gradients (Wilson, 2008).

268 The models were fitted using Bayesian methods implemented in MCMCglmm version
269 2.22.1 (Hadfield, 2010) with Gaussian distribution and identity link function. Priors
270 for the fixed effects were the normal distribution with zero mean and large variance
271 (10^{10}), while a non-informative improper prior was used for the variance components by
272 specifying $V = 0$ and $\text{nu} = -2$. Care was taken to ensure good mixing of the chains
273 and that specified priors did not have exaggerated influence on posterior distributions by
274 graphical examinations of different priors. In the analyses, runs with a burn-in period of
275 10 000 and a thinning interval of 200 ensured low autocorrelation (generally < 0.1) for a
276 total of 10 000 independent random samples from the stationary posterior distribution.
277 The deviance information criterion (DIC) was calculated (Spiegelhalter et al., 2002) to
278 determine the statistical support for variance components by comparing the full model
279 with reduced models where the component of interest was left out. Unscaled variance
280 components (σ^2) were reported in the results by back-transforming with the square of
281 the mean across years (Table 2), accompanied by variance-scaled estimates to obtain the
282 narrow sense heritability ($h^2 = \sigma_A^2/\sigma_P^2$). All estimates are reported as the posterior mode
283 and 95 % credibility intervals from the full model.

284 **Predicting responses to selection**

285 We separated direct and indirect selection on calf body mass and birth date in the selec-
286 tion analyses, but were limited by sample size to univariate analyses of quantitative genet-

287 ics. Hence, to predict responses to selection we obtained the vector of unscaled selection
288 differentials by $\mathbf{S} = \mathbf{P}\boldsymbol{\beta}_\sigma \circ \boldsymbol{\sigma}^{-1}$, where \mathbf{P} is the weighted phenotypic (co)variance matrix,
289 $\boldsymbol{\beta}_\sigma$ is the vector of estimated SD-scaled selection gradients, $\boldsymbol{\sigma}$ the vector of weighted
290 phenotypic standard deviations and \circ denotes element-wise multiplication (Lande and
291 Arnold, 1983). Then the predicted response (R) in the weighted mean of each trait fol-
292 lows from the breeders equation $R = h^2 S$, where h^2 is the narrow sense heritability of a
293 trait (Lush, 1937).

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

299 Results

300 Temporal phenotypic trends

301 Males were heavier than than females ($\chi^2 = 25.40$, $df = 1$, $P < 0.001$), but there was no
302 sexual difference in birth date ($\chi^2 = 0.66$, $df = 1$, $P = 0.418$, Table 2). In both sexes
303 calf body mass decreased with later birth date (males: $r_p = -0.456$, $t = -4.522$, $df = 78$,
304 $P < 0.001$, females: $r_p = -0.220$, $t = -1.864$, $df = 68$, $P = 0.067$). Accounting for the
305 differences between sexes, we found no significant directional change in calf body mass
306 across years ($b = 0.25 \pm 0.30$, $\chi^2 = 0.73$, $df = 1$, $P = 0.394$), whereas birth dates delayed
307 with a rate of 0.81 ± 0.20 days per year ($\chi^2 = 15.47$, $df = 1$, $P < 0.001$). The annual
308 delay was similar in both sexes ($\chi^2 = 1.52$, $df = 1$, $P = 0.218$) and did not deviate from
309 linearity ($\chi^2 = 0.47$, $df = 1$, $P = 0.493$).

310 Phenotypic selection

311 For females, there was significant negative directional selection on calf body mass (Fig.
312 3A, Table 3A, CI = [-0.16, 0.00]), but no significant directional selection on birth date
313 (Fig. 3B, Table 3A, CI = [-0.10, 0.04]). When considering only survival (see Fig. 2), the
314 estimates of directional viability selection were non-significant for calf body mass (Fig.
315 3C, Table 3A, CI = [-0.14, 0.02]) and birth date (Fig. 3D, Table 3A, CI = [-0.04, 0.11]).
316 In contrast, there was evidence for directional fecundity selection towards lighter calf
317 body mass (Fig. 3E, Table 3A, CI = [-0.52, 0.01]) and earlier birth date (Fig. 3F, Table
318 3A, CI = [-0.56, -0.13]). Hence, small and early born females produced more recruits.
319 However, the confidence interval for the directional fecundity selection on calf body mass
320 marginally crossed zero.

321 Re-analysing fecundity selection while excluding the effect of harvesting (see Figs 1
322 and 2), i.e. adding harvested calves to fecundity fitness, indicated no significant direc-
323 tional selection on calf body mass before the hunting season (Table 3A, CI = [-0.20,
324 0.05]). Hence, the variation in the number of calves born and their natural mortality
325 were not the causes of selection on female calf body mass. The estimates of directional

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

332 In males, there was significant positive directional selection for later birth date (Fig.
333 3B, Table 3B, CI = [0.00, 0.35]). The estimated directional selection on calf body mass
334 was also positive, however, the confidence interval crossed zero (Fig. 3A, Table 3B, CI
335 = [-0.02, 0.28]). In accordance with the estimated total selection, there was significant
336 directional viability selection for later birth date (Fig. 3D, Table 3B, CI = [0.11, 0.49]).
337 Almost all deaths were harvest-induced (see Fig. 2) and males born early in the season
338 were more likely to be shot. The mean difference in birth date between killed and sur-
339 viving individuals within years was 9 days. The estimated directional viability selection
340 on calf body mass had a confidence interval which crossed zero (Fig. 3C, Table 3B, CI
341 = [-0.03, 0.32]). In the analyses of fecundity selection in males there was found signifi-
342 cant negative directional selection for earlier birth date (Fig. 3F, Table 3B, CI = [-0.86,
343 -0.09]). Early born males had a higher reproductive success, hence, fecundity and via-
344 bility selection on birth date acted in opposite directions. There was not any significant
345 fecundity selection on calf body mass in males (Fig. 3E, Table 3B, CI = [-0.44, 0.29]). Re-
346 analysing fecundity selection for males while excluding the effect of harvesting on recruit
347 production (see Figs 1 and 2), did not indicate any harvest-induced fecundity selection.
348 No significant estimates of correlational or quadratic selection were found (Table 3B).

349 **Predictions of phenotypic evolution**

350 There was high support for an additive genetic component in calf body mass and birth
351 date (Table 4). In addition, there was high support for a maternal environment effect in
352 both traits as judged by DIC (Table 4). The heritability of calf body mass was 18.4 %, a
353 little larger than the heritability of birth date. Maternal environment effects contributed

354 to more than 50 % of the phenotypic variation in birth date (Table 4B), while calf body
355 mass had a much smaller maternal variance component (Table 4A). Estimates for fixed
356 effects were $b_f = -0.14$ (CI = [-0.32, 0.04]) and $b_{sex} = 0.07$ (CI = [0.04, 0.10]) for calf
357 body mass, and $b_f = -0.01$ (CI = [-0.11, 0.09]) and $b_{sex} = 0.00$ (CI = [-0.02, 0.01]) for
358 birth date.

359 Using the total selection differentials, which include direct and indirect selection on
360 traits, we predicted the response to selection on calf body mass as -0.22 (CI = [-0.85,
361 0.01]) kg/year in females and 0.12 (CI = [-0.62, 1.12]) kg/year in males, and on birth date
362 as -0.02 (CI = [-0.25, 0.13]) days/year in females and 0.12 (CI = [-0.06, 0.65]) days/year
363 in males. The uncertainty in the estimates of heritability were large, thus, the confidence
364 intervals for these prediction are wide. Furthermore, these predictions do not account for
365 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;

395 Sasaki et al., 2009; Mysterud, 2011; Ciuti et al., 2012; but see Moe et al., 2009). Whatever
396 mechanism, the increased risk of losing a calf among large females may explain the neg-
397 ative harvest-induced selection on female body mass as calf and will modify any natural
398 fecundity selection (Fig. 3, Table 3A).

399 Our results indicated no selection on calf body mass in males in our population (Fig.
400 3, Table 3B). Thus, hunters were non-selective in their harvest of yearlings and adults
401 with respect to their calf body mass, and males with large calf body mass did not have
402 larger reproductive success than males with smaller calf body mass. These results seems
403 surprising as only a small proportion of males are often found to mate with most of the
404 females in polygamous ungulates (Clutton-Brock, 1982; Mysterud et al., 2002) and body
405 mass is usually seen as an important trait explaining variation among males in mating
406 success (Stewart et al., 2000). Solberg et al. (2008) found that calf body mass generally
407 predicts adult body mass well in our population. However, male moose grow for a long
408 period and do not reach their asymptotic body mass until old ages (Solberg and Sæther,
409 1994; Solberg et al., 2004). Large individual deviations from the predicted relationship
410 between calf and adult body mass could reduce the power of detecting any selection on
411 body mass. Alternatively, in small and isolated populations under high harvest pressure,
412 demographic stochasticity will be large and few males will reach the size at which they
413 might compete successfully for females (Langvatn and Loison, 1999; Solberg et al., 2000;
414 Stewart et al., 2000; Darimont et al., 2009; Engen et al., 2014b). Hence, individuals
415 that enter older age classes might not be those that were large as calves, indicating
416 that age is a major determinant of reproductive success (see Table 1; Sæther et al., 2003;
417 Coulson et al., 2010; Sæther et al., 2013). This also implies that hunters can appear to be
418 selective with respect to body mass across age classes, but that this selective harvest may
419 not have any direct evolutionary effect on body mass if the mechanism is a preference for
420 old individuals that are large (Solberg et al., 2000; Ericsson and Wallin, 2001; Mysterud,
421 2011). Indeed, from Table 1 we see that survival rates, which are almost exclusively
422 determined by harvest mortality (see Fig. 2), are lowest among yearling and prime aged
423 (above age 5) males. The oldest male in our population was 11 years old at harvest, and

424 only 3 males got older than 7 years. The demographic approach used to estimate selection
425 in this study correctly accounted for the dependency between age and fitness. Generally,
426 estimates of selection will contain a component of false selection when age-structure is
427 ignored. This is caused by transient changes in the age-distribution and differences in
428 the mean phenotype between age classes (Engen et al., 2014a).

429 For herbivores in seasonal environments, getting the timing right with respect to the
430 advance of spring vegetation is important to achieve optimal foraging conditions for lac-
431 tating females and their calves (Klein, 1965; Albon and Langvatn, 1992; Mysterud et al.,
432 2001; Solberg et al., 2007). Being born too early or late may increase calf mortality due to
433 low amounts of available high quality food and have negative developmental consequences
434 which lasts into adulthood (Solberg et al., 2004, 2008; Rödel et al., 2009). Accordingly,
435 Schmidt et al. (2001) found antler size in red deer *Cervus elaphus* to be negatively related
436 to birth date and Plard et al. (2015) found higher probability of recruitment and larger
437 adult body mass for early-born roe deer. In our study, we found significant negative
438 fecundity selection on birth date in both sexes (Fig. 3, Table 3). Thus, supporting the
439 idea that early-born individuals possess qualities which increase their reproductive perfor-
440 mance (Rödel et al., 2009; Plard et al., 2015; but see Wilson et al., 2005a). However, the
441 response to fecundity selection depends on its interaction with survival (Coulson et al.,
442 2003, 2006; Wilson and Nussey, 2010). In our study, we found strong opposing harvest-
443 induced viability selection on birth date in males (Fig. 3, Table 3B), where early-born
444 males were shot more frequently than late-born males. There are two not mutually exclu-
445 sive hypotheses for such a pattern. Phenotypic variation in birth date could make some
446 individuals (1) more attractive (hunter preference) or (2) more susceptible to hunters
447 (Law, 2000; Coltman et al., 2003; Carlson et al., 2007; Allendorf and Hard, 2009; Sasaki
448 et al., 2009; Ciuti et al., 2012). As adult moose generally are solitary and the population
449 is subject to high hunting pressure during a relatively short hunting season, the possibil-
450 ity for hunters to be choosy might be restricted (Solberg et al., 2000; Mysterud, 2011).
451 However, at present we are not able to rule out this possibility from the susceptibility
452 hypothesis, where early-born males are more frequently shot due to increased exposure.

453 Possible mechanisms by which the latter could occur, include variation in rates and pat-
454 tern of movement or size of home range and habitat use in relation to distribution of
455 hunters, and variation in other behaviour traits (e.g. shyness) during the rutting season
456 that affect susceptibility (Law, 2000; Sasaki et al., 2009; Mysterud, 2011; Ciuti et al.,
457 2012). In either case, the harvest-induced viability selection caused the total selection
458 in males in favour of later births. This contrasts with females, where harvest mortality
459 was non-selective with respect to birth date and confounded negative fecundity selection
460 by increased demographic stochasticity (Table 3). Probably hunters have less opportu-
461 nities to selectively shoot females than males, because they expose themselves less often
462 to hunters (Solberg et al., 2010; Ericsson and Wallin, 2001) and are followed by one or
463 more calves (see also Table 1 and Fig. 2). Previous studies has suggested that hunters
464 preferably shoot females without calves, and if they are to shoot females with calves the
465 calves have to be shot first, thus, allowing females to escape (Solberg et al., 1999, 2000;
466 Ericsson, 2001).

467 We found evidence for additive genetic variance in both traits in this study (Table
468 4). The heritability estimated for birth date and calf body mass were of the same order
469 as previously recorded with similar analyses of reindeer (both traits, Muuttoranta et al.,
470 2013), bighorn sheep (parturition date, Feder et al., 2008), soay sheep *Ovis aries* (both
471 traits, Wilson et al., 2005a) and red deer (body mass, Kruuk and Hadfield, 2007). Our
472 sample sizes of less than 170 individuals (see Table 2) limited the quantitative genetic
473 analyses to univariate models (Kruuk, 2004; de Villemereuil et al., 2013). Hence, we
474 used the univariate breeders equation to predict a negative response in calf body mass in
475 females and a positive response in birth date in males over the years (see *Results*). These
476 predictions ignore genetic covariances between traits within and between sexes (Morrissey
477 et al., 2010) which certainly would have been important in shaping the observed change
478 towards later births at a rate of 0.81 days per year and the lack of change in calf body
479 mass. Generally, unmeasured additive genetic covariance between selected traits limit
480 the additive genetic variation in each trait that is available for unconstrained phenotypic
481 evolution (Hansen and Houle, 2008; Morrissey et al., 2010). In previous studies on un-

482 gulates, a negative genetic covariance between birth mass and date has been found for
483 instance in reindeer (Muuttoranta et al., 2013), while a positive genetic covariance has
484 been found in soay sheep (Wilson et al., 2005a). In this study, we found a negative phe-
485 notypic covariance between calf body mass (at 8-9 months of age) and birth date (Table
486 2; see also Solberg et al., 2008). A quantitative genetic analysis would be required to
487 separate genetic effects from environmental effects due to higher foraging quality for early
488 born individuals. However, the negative phenotypic covariance could be taken to indicate
489 the presence of a negative genetic covariance (Cheverud, 1988). A strong negative genetic
490 covariance would constrain the evolutionary response in traits selected in the same di-
491 rection, while a positive genetic covariance would have the opposite effect (Lande, 1979).
492 In this study, a negative genetic covariance between body mass as calf and birth date
493 could constrain the evolutionary responses in females to negative directional selection on
494 body mass as calf, while causing a response of delayed birth date (see Table 3). In males,
495 a negative covariance would constrain evolutionary responses in both traits and if suffi-
496 ciently strong could even cause predicted responses in the opposite direction of selection.
497 However, the final response to selection on a suite of traits within each sex will generally
498 also depend on intersexual genetic covariances (Lande, 1980; Gosden et al., 2012). The
499 intersexual genetic covariance for each trait in this study seems likely to be positive and
500 may even be quite strong. Hence, our inability to estimate all of these additive genetic
501 components, could be an important cause of differences between predicted and observed
502 phenotypic changes. However, other explanations for differences between observed and
503 predicted phenotypic changes which are difficult to rule out should also be mentioned.
504 For instance, selection on a unmeasured genetically correlated trait could constrain evo-
505 lutionary responses and responses could be masked by environmental effects which are
506 not accounted for (reviewed in Merilä et al., 2001). Furthermore, in our population with
507 such a long life expectancy, estimated responses will only be observable if consistent in
508 direction over several years (Engen et al., 2014a). At any time, the population will consist
509 of reproducing individuals in different age classes which has been exposed to potentially
510 fluctuating selection pressures over their life span (Engen et al., 2012). The full response

511 to selection will in such populations only be observable when all individuals under se-
512 lection in the population has stopped reproducing (i.e. achieved lifetime reproduction;
513 Engen et al., 2011, 2014a).

514 Both traits in this study are to some degree likely to be maternally determined.
515 Accordingly, approximately 50 % of the variance in birth date and 20 % of the variance
516 in calf body mass were attributed to maternal environmental effects (Table 4). The
517 maternal environment effects estimated in these models contains an environmental source
518 of phenotypic variation, but also parts of this variation is likely to have a genetic origin
519 (Mousseau and Fox, 1998; Wilson et al., 2005a; Kruuk and Hadfield, 2007). Such maternal
520 genetic effects represent a heritable component of phenotypic variation, inherited through
521 maternal inheritance, which contribute to the rate and direction of evolutionary changes
522 in a trait (Kirkpatrick and Lande, 1989; Lande and Kirkpatrick, 1990; Hadfield, 2012).
523 However, estimating maternal genetic effects is not a trivial matter and requires extensive
524 sample sizes in a well connected pedigree (Kruuk and Hadfield, 2007; Wilson et al., 2010).
525 When not directly estimated these effects will be concealed within the additive genetic
526 and maternal environment effects (e.g. Wilson et al., 2005a; Kruuk and Hadfield, 2007;
527 Wilson et al., 2010). Antagonistic selection through mothers and offspring on calf body
528 mass or birth date could act to constrain evolutionary changes (Kirkpatrick and Lande,
529 1989). Thus, while we find directional selection on both calf body mass and birth date
530 from the perspective of the individual (i.e. an individuals own trait values), there could
531 also be selection on these traits through their maternal analogues, offspring body mass
532 and parturition date (the trait values of an individuals offspring; e.g. Wilson et al., 2005b;
533 Janzen and Warner, 2009). In such a case, the phenotype of an individual is thought to
534 be a result of its own genes, an environmental effect and a parental effect (Kirkpatrick
535 and Lande, 1989; Lande and Kirkpatrick, 1990; Hadfield, 2012). Hence, the change in
536 a phenotype from one generation to the next would be affected by both selection on
537 the individuals directly and selection that modify the traits of their parents (Hadfield,
538 2012). Parental effects may have important consequences for evolutionary trajectories,
539 however, there does not yet exist a theoretical framework for dealing with these effects

540 in age-structured populations.

541 Demographic and evolutionary consequences of harvesting have been investigated in
542 several populations, however, thus far only as separate processes (Law, 2000; Solberg
543 et al., 2000). The demographic framework which we utilize here enable us to investigate
544 harvest-induced selection and phenotypic evolution while keeping track of the relation-
545 ships to demographic parameters such as population growth rate and the age structure of
546 the population (Engen et al., 2009, 2011, 2012, 2014a; Morrissey et al., 2012; Sæther and
547 Engen, 2015). Thus, the general implications of our results can more readily be related
548 to demography of the population and be available for developing better harvest strate-
549 gies over short and long time scales (Dunlop et al., 2009). In this study we demonstrate
550 how harvesting can result in phenotypic selection through non-random hunting of calves
551 from females which differ in fecundity rates and calf body mass (Fig. 3A, Table 3A).
552 Thus, in species with extended parental care, sustainable harvest strategies should not
553 only consider the effects on the phenotypic distribution of individuals, but also consider
554 how harvesting their young may affect their contribution to further generations (Fig. 2;
555 see also Solberg et al., 2000). Accordingly, our measure of fitness consists of both fe-
556 cundity (production and early survival of calves) and own survival (Engen et al., 2014a).
557 We clearly demonstrate how non-selective harvesting might effectively mask any natural
558 selection occurring (e.g. fecundity selection on birth date in females) by introducing ad-
559 ditional demographic stochasticity through mortality (Engen and Sæther, 2014; Sæther
560 and Engen, 2015). Under the high hunting pressures which many exploited populations
561 experience, this effect will be considerable (Solberg et al., 2000; Stubsjøen et al., 2000;
562 Darimont et al., 2009; Collins and Kays, 2011).

563 In conclusion, we here demonstrate how selective harvest led to directional selection
564 in a population of ungulates, and show how this may lead to evolutionary changes on an
565 ecological time-scale. Even though several previous studies have demonstrated selective
566 harvest, this has only rarely been manifested into harvest-induced directional selection
567 due to a lack of knowledge on fitness and phenotypic distributions in most harvested
568 populations (Mysterud, 2011). We emphasise the importance of considering and includ-

569 ing the potential for harvest-induced selection through both viability and fecundity to
570 develop sustainable harvest strategies. Even under non-selective harvest the increased de-
571 mographic stochasticity due to harvesting might affect the evolutionary potential of the
572 population by diminishing the strength of natural selection (Sæther and Engen, 2015).

573 **Acknowledgements**

574 We are grateful to I. Herfindal, S.S. Markussen and T.H. Ringsby for discussions during
575 the work of this manuscript, to M.B. Morrissey, M. Festa-Bianchet and Associate Editor
576 Dr. Andrew McAdam for excellent comments on earlier versions of this manuscript, and
577 to the local moose hunters and managers for their most helpful cooperation in collecting
578 and coordinating tissue sampling in the field. The authors of this study has no conflicts
579 of interest to declare. This study was financially supported by the Research Council of
580 Norway (project no. 10357100 and SFF-III 223257/F50), the European Research Council
581 (ERC-2010-AdG 268562) and the Norwegian Environment Agency.

References

- 582
583 Albon, S. D. and R. Langvatn. 1992. Plant phenology and the benefits of migration in a
584 temperate ungulate. *Oikos* 65:502–513.
- 585 Allendorf, F. W., P. R. England, G. Luikart, P. A. Ritchie, and N. Ryman. 2008. Genetic
586 effects of harvest on wild animal populations. *Trends Ecol. Evol.* 23:327–337.
- 587 Allendorf, F. W. and J. J. Hard. 2009. Human-induced evolution caused by unnatural
588 selection through harvest of wild animals. *Proc. Natl. Acad. Sci. USA* 106:9987–9994.
- 589 Bates, D., M. Maechler, B. Bolker, and S. Walker. 2014. *lme4: Linear mixed-effects*
590 *models using eigen and s4*. Tech. rep.
- 591 Carlson, S. M., E. Edeline, L. A. Vollestad, T. O. Haugen, I. J. Winfield, J. M. Fletcher,
592 J. B. James, and N. C. Stenseth. 2007. Four decades of opposing natural and human-
593 induced artificial selection acting on windermere pike (*Esox lucius*). *Ecol. Lett.* 10:512–
594 521.
- 595 Carlson, S. M. and T. R. Seamons. 2008. A review of quantitative genetic components
596 of fitness in salmonids: implications for adaptation to future change. *Evol. Appl.*
597 1:222–238.
- 598 Caswell, H. 2001. *Matrix population models: Construction, analysis, and interpretation*.
599 2nd ed. Sinauer Associates, Sunderland, Massachusetts.
- 600 Caughley, G. 1966. Mortality patterns in mammals. *Ecology* 47:906–918.
- 601 Cheverud, J. M. 1988. A comparison of genetic and phenotypic correlations. *Evolution*
602 42:958–968.
- 603 Ciuti, S., T. B. Muhly, D. G. Paton, A. D. McDevitt, M. Musiani, and M. S. Boyce.
604 2012. Human selection of elk behavioural traits in a landscape of fear. *Proc. R. Soc.*
605 B 279:4407–4416.
- 606 Clutton-Brock, T. H. 1982. The functions of antlers. *Behaviour* 79:108–124.

607 Clutton-Brock, T. H. and T. Coulson. 2002. Comparative ungulate dynamics: the devil
608 is in the detail. *Phil. Trans. R. Soc. B* 357:1285–1298.

609 Collins, C. and R. Kays. 2011. Causes of mortality in North American populations of
610 large and medium-sized mammals. *Anim. Conserv.* 14:474–483.

611 Coltman, D. W., P. O'Donoghue, J. T. Jorgenson, J. T. Hogg, C. Strobeck, and M. Festa-
612 Bianchet. 2003. Undesirable evolutionary consequences of trophy hunting. *Nature*
613 426:655–658.

614 Coulson, T., T. G. Benton, P. Lundberg, S. R. X. Dall, B. E. Kendall, and J. M. Gaillard.
615 2006. Estimating individual contributions to population growth: evolutionary fitness
616 in ecological time. *Proc. R. Soc. B* 273:547–555.

617 Coulson, T., L. E. B. Kruuk, G. Tavecchia, J. M. Pemberton, and T. H. Clutton-Brock.
618 2003. Estimating selection on neonatal traits in red deer using elasticity path analysis.
619 *Evolution* 57:2879–2892.

620 Coulson, T., S. Tuljapurkar, and D. Z. Childs. 2010. Using evolutionary demography to
621 link life history theory, quantitative genetics and population ecology. *J. Anim. Ecol.*
622 79:1226–1240.

623 Darimont, C. T., S. M. Carlson, M. T. Kinnison, P. C. Paquet, T. E. Reimchen, and
624 C. C. Wilmers. 2009. Human predators outpace other agents of trait change in the
625 wild. *Proc. Natl. Acad. Sci. USA* 106:952–954.

626 Dunlop, E. S., K. Enberg, C. Jorgensen, and M. Heino. 2009. Toward darwinian fisheries
627 management. *Evol. Appl.* 2:246–259.

628 Edeline, E., S. M. Carlson, L. C. Stige, I. J. Winfield, J. M. Fletcher, J. Ben James,
629 T. O. Haugen, L. A. Vollestad, and N. C. Stenseth. 2007. Trait changes in a harvested
630 population are driven by a dynamic tug-of-war between natural and harvest selection.
631 *Proc. Natl. Acad. Sci. USA* 104:15799–15804.

- 632 Enberg, K., C. Jørgensen, E. S. Dunlop, O. Varpe, D. S. Boukal, L. Baulier, S. Eliassen,
633 and M. Heino. 2012. Fishing-induced evolution of growth: concepts, mechanisms and
634 the empirical evidence. *Mar. Ecol.* 33:1–25.
- 635 Engen, S., T. Kvalnes, and B.-E. Sæther. 2014a. Estimating phenotypic selection in age-
636 structured populations by removing transient fluctuations. *Evolution* 68:2509–2523.
- 637 Engen, S., R. Lande, and B.-E. Sæther. 2011. Evolution of a plastic quantitative trait in
638 an age-structured population in a fluctuating environment. *Evolution* 65:2893–2906.
- 639 ———. 2014b. Evolutionary consequences of nonselective harvesting in density-
640 dependent populations. *Am. Nat.* 184:714–726.
- 641 Engen, S., R. Lande, B.-E. Sæther, and S. F. Dobson. 2009. Reproductive value and the
642 stochastic demography of age-structured populations. *Am. Nat.* 174:795–804.
- 643 Engen, S. and B.-E. Sæther. 2014. Evolution in fluctuating environments: Decomposing
644 selection into additive components of the Robertson-Price equation. *Evolution* 68:854–
645 865.
- 646 Engen, S., B.-E. Sæther, T. Kvalnes, and H. Jensen. 2012. Estimating fluctuating selec-
647 tion in age-structured populations. *J. Evol. Biol.* 25:1487–1499.
- 648 Ericsson, G. 2001. Reduced cost of reproduction in moose *Alces alces* through human
649 harvest. *Alces* 37:61–69.
- 650 Ericsson, G. and K. Wallin. 2001. Age-specific moose (*Alces alces*) mortality in a predator-
651 free environment: Evidence for senescence in females. *Ecoscience* 8:157–163.
- 652 Feder, C., J. G. A. Martin, M. Festa-Bianchet, C. Berube, and J. Jorgenson. 2008. Never
653 too late? Consequences of late birthdate for mass and survival of bighorn lambs.
654 *Oecologia* 156:773–781.
- 655 Festa-Bianchet, M. 1988. Birthdate and survival in bighorn lambs (*Ovis canadensis*). *J.*
656 *Zool.* 214:653–661.

- 657 Gaillard, J. M., M. Festa-Bianchet, D. Delorme, and J. Jorgenson. 2000a. Body mass
658 and individual fitness in female ungulates: bigger is not always better. *Proc. R. Soc.*
659 *B* 267:471–477.
- 660 Gaillard, J. M., M. Festa-Bianchet, and N. G. Yoccoz. 1998. Population dynamics of
661 large herbivores: variable recruitment with constant adult survival. *Trends Ecol. Evol.*
662 13:58–63.
- 663 Gaillard, J. M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Toigo. 2000b. Tem-
664 poral variation in fitness components and population dynamics of large herbivores.
665 *Annu. Rev. Ecol. Syst.* 31:367–393.
- 666 Gamelon, M., A. Besnard, J. M. Gaillard, S. Servanty, E. Baubet, S. Brandt, and
667 O. Gimenez. 2011. High hunting pressure selects for earlier birth date: Wild boar
668 as a case study. *Evolution* 65:3100–3112.
- 669 Garcia, S. M., J. Kolding, J. Rice, M. J. Rochet, S. Zhou, T. Arimoto, J. E. Beyer,
670 L. Borges, A. Bundy, D. Dunn, E. A. Fulton, M. Hall, M. Heino, R. Law, M. Makino,
671 A. D. Rijnsdorp, F. Simard, and A. D. M. Smith. 2012. Reconsidering the consequences
672 of selective fisheries. *Science* 335:1045–1047.
- 673 Garel, M., J. M. Cugnasse, D. Maillard, J. M. Gaillard, A. J. M. Hewison, and D. Dubray.
674 2007. Selective harvesting and habitat loss produce long-term life history changes in a
675 mouflon population. *Ecol. Appl.* 17:1607–1618.
- 676 Garel, M., E. J. Solberg, B.-E. Sæther, V. Grøtan, J. Tufto, and M. Heim. 2009. Age, size,
677 and spatiotemporal variation in ovulation patterns of a seasonal breeder, the Norwegian
678 moose (*Alces alces*). *Am. Nat.* 173:89–104.
- 679 Gatz, D. F. and L. Smith. 1995. The standard error of a weighted mean concentration -
680 1. Bootstrapping vs other methods. *Atmos. Environ.* 29:1185–1193.
- 681 Gosden, T. P., K. L. Shastri, P. Innocenti, and S. F. Chenoweth. 2012. The B-matrix
682 harbors significant and sex-specific constraints on the evolution of multicharacter sexual
683 dimorphism. *Evolution* 66:2106–2116.

- 684 Grøtan, V., B.-E. Sæther, M. Lillegard, E. J. Solberg, and S. Engen. 2009. Geographical
685 variation in the influence of density dependence and climate on the recruitment of
686 Norwegian moose. *Oecologia* 161:685–695.
- 687 Haanes, H., S. S. Markussen, I. Herfindal, K. H. Røed, E. J. Solberg, M. Heim, L. Midth-
688 jell, and B.-E. Sæther. 2013. Effects of inbreeding on fitness-related traits in a small
689 isolated moose population. *Ecol. Evol.* 3:4230–4242.
- 690 Hadfield, J. D. 2010. MCMC methods for multi-response generalized linear mixed models:
691 The MCMCglmm R package. *J. Stat. Softw.* 33:1–22.
- 692 ———. 2012. The quantitative genetic theory of parental effects. *in* N. J. Royle, P. T.
693 Smiseth, and M. Kölliker, eds. *The evolution of parental care*. Oxford university press,
694 Oxford.
- 695 Hansen, T. F. and D. Houle. 2008. Measuring and comparing evolvability and constraint
696 in multivariate characters. *J. Evol. Biol.* 21:1201–1219.
- 697 Hedrick, P. W. 2011. Rapid decrease in horn size of bighorn sheep: Environmental
698 decline, inbreeding depression, or evolutionary response to trophy hunting? *J. Hered.*
699 102:770–781.
- 700 Hendry, A. P., M. T. Kinnison, M. Heino, T. Day, T. B. Smith, G. Fitt, C. T. Bergstrom,
701 J. Oakeshott, P. S. Jørgensen, M. P. Zalucki, G. Gilchrist, S. Southerton, A. Sih,
702 S. Strauss, R. F. Denison, and S. P. Carroll. 2011. Evolutionary principles and their
703 practical application. *Evol. Appl.* 4:159–183.
- 704 Hewison, A. J. M. 1996. Variation in the fecundity of roe deer in Britain: effects of age
705 and body weight. *Acta Theriol.* 41:187–198.
- 706 Hutchings, J. A. 2009. Avoidance of fisheries-induced evolution: management implica-
707 tions for catch selectivity and limit reference points. *Evol. Appl.* 2:324–334.
- 708 Janzen, F. J. and D. A. Warner. 2009. Parent-offspring conflict and selection on egg size
709 in turtles. *J. Evol. Biol.* 22:2222–2230.

- 710 Kendall, N. W., J. J. Hard, and T. P. Quinn. 2009. Quantifying six decades of fishery
711 selection for size and age at maturity in sockeye salmon. *Evol. Appl.* 2:523–536.
- 712 Kirkpatrick, M. and R. Lande. 1989. The evolution of maternal characters. *Evolution*
713 43:485–503.
- 714 Klein, D. R. 1965. Ecology of deer range in Alaska. *Ecol. Monogr.* 35:259–284.
- 715 Kruuk, L. E. B. 2004. Estimating genetic parameters in natural populations using the
716 'animal model'. *Phil. Trans. R. Soc. B* 359:873–890.
- 717 Kruuk, L. E. B. and J. D. Hadfield. 2007. How to separate genetic and environmental
718 causes of similarity between relatives. *J. Evol. Biol.* 20:1890–1903.
- 719 Kuparinen, A. and J. A. Hutchings. 2012. Consequences of fisheries-induced evolution
720 for population productivity and recovery potential. *Proc. R. Soc. B* 279:2571–2579.
- 721 Kuparinen, A. and J. Merilä. 2007. Detecting and managing fisheries-induced evolution.
722 *Trends Ecol. Evol.* 22:652–659.
- 723 Lande, R. 1979. Quantitative genetic analysis of multivariate evolution, applied to
724 brain:body size allometry. *Evolution* 33:402–416.
- 725 ———. 1980. The genetic covariance between characters maintained by pleiotropic mu-
726 tations. *Genetics* 94:203–215.
- 727 ———. 1982. A quantitative genetic theory of life history evolution. *Ecology* 63:607–615.
- 728 Lande, R. and S. J. Arnold. 1983. The measurement of selection on correlated characters.
729 *Evolution* 37:1210–1226.
- 730 Lande, R. and M. Kirkpatrick. 1990. Selection response in traits with maternal inheri-
731 tance. *Genet. Res.* 55:189–197.
- 732 Langvatn, R. and A. Loison. 1999. Consequences of harvesting on age structure, sex ratio
733 and population dynamics of red deer *Cervus elaphus* in central Norway. *Wildlife Biol.*
734 5:213–223.

- 735 Laugen, A. T., G. H. Engelhard, R. Whitlock, R. Arlinghaus, D. J. Dankel, E. S.
736 Dunlop, A. M. Eikeset, K. Enberg, C. Jørgensen, S. Matsumura, S. Nusslé, D. Ur-
737 bach, L. Baulier, D. S. Boukal, B. Ernande, F. D. Johnston, F. Mollet, H. Pardoe,
738 N. O. Therkildsen, S. Uusi-Heikkilä, A. Vainikka, M. Heino, A. D. Rijnsdorp, and
739 U. Dieckmann. 2014. Evolutionary impact assessment: accounting for evolutionary
740 consequences of fishing in an ecosystem approach to fisheries management. *Fish Fish.*
741 15:65–96.
- 742 Law, R. 2000. Fishing, selection, and phenotypic evolution. *ICES J. Mar. Sci.* 57:659–668.
743 ———. 2007. Fisheries-induced evolution: present status and future directions. *Mar.*
744 *Ecol. Prog. Ser.* 335:271–277.
- 745 Loison, A., M. Festa-Bianchet, J. M. Gaillard, J. T. Jorgenson, and J. M. Jullien. 1999.
746 Age-specific survival in five populations of ungulates: Evidence of senescence. *Ecology*
747 80:2539–2554.
- 748 Lush, J. L. 1937. *Animal breeding plans*. Iowa State College Press, Ames, Iowa.
- 749 Lynch, M. and B. Walsh. 1998. *Genetics and analysis of quantitative traits*. Sinauer
750 Associates, Sunderland, Mass.
- 751 Merilä, J., B. C. Sheldon, and L. E. B. Kruuk. 2001. Explaining stasis: microevolutionary
752 studies in natural populations. *Genetica* 112:199–222.
- 753 Milner, J. M., F. M. van Beest, E. J. Solberg, and T. Storaas. 2013. Reproductive success
754 and failure: the role of winter body mass in reproductive allocation in Norwegian moose.
755 *Oecologia* 172:995–1005.
- 756 Mitchell-Olds, T. and R. G. Shaw. 1987. Regression analysis of natural selection: Statis-
757 tical inference and biological interpretation. *Evolution* 41:1149–1161.
- 758 Moe, T., E. J. Solberg, I. Herfindal, B.-E. Sæther, K. Bjørnerås, and M. Heim. 2009. Sex
759 ratio variation in harvested moose (*Alces alces*) calves: does it reflect population calf
760 sex ratio or selective hunting? *Eur. J. Wildlife Res.* 55:217–226.

- 761 Morrissey, M. B., L. E. B. Kruuk, and A. J. Wilson. 2010. The danger of applying
762 the breeder's equation in observational studies of natural populations. *J. Evol. Biol.*
763 23:2277–2288.
- 764 Morrissey, M. B., C. A. Walling, A. J. Wilson, J. M. Pemberton, T. H. Clutton-Brock,
765 and L. E. B. Kruuk. 2012. Genetic analysis of life-history constraint and evolution in
766 a wild ungulate population. *Am. Nat.* 179:E97–E114.
- 767 Mousseau, T. A. and C. W. Fox. 1998. The adaptive significance of maternal effects.
768 *Trends Ecol. Evol.* 13:403–407.
- 769 Muuttoranta, K., O. Holand, K. H. Røed, M. Tapio, M. Nieminen, and A. Maki-Tanila.
770 2013. Genetic and environmental effects affecting the variation in birth date and birth
771 weight of reindeer calves. *Rangifer* 33:25–35.
- 772 Mysterud, A. 2011. Selective harvesting of large mammals: how often does it result in
773 directional selection? *J. Appl. Ecol.* 48:827–834.
- 774 Mysterud, A., T. Coulson, and N. C. Stenseth. 2002. The role of males in the dynamics
775 of ungulate populations. *J. Anim. Ecol.* 71:907–915.
- 776 Mysterud, A., R. Langvatn, N. G. Yoccoz, and N. C. Stenseth. 2001. Plant phenology,
777 migration and geographical variation in body weight of a large herbivore: the effect of
778 a variable topography. *J. Anim. Ecol.* 70:915–923.
- 779 Olsen, E. M., M. Heino, G. R. Lilly, M. J. Morgan, J. Brattey, B. Ernande, and U. Dieck-
780 mann. 2004. Maturation trends indicative of rapid evolution preceded the collapse of
781 northern cod. *Nature* 428:932–935.
- 782 Olsen, E. M. and E. Moland. 2011. Fitness landscape of atlantic cod shaped by harvest
783 selection and natural selection. *Evol. Ecol.* 25:695–710.
- 784 Pachkowski, M., S. D. Côte, and M. Festa-Bianchet. 2013. Spring-loaded reproduction:
785 effects of body condition and population size on fertility in migratory caribou (*Rangifer*
786 *tarandus*). *Can. J. Zool.* 91:473–479.

787 Pigeon, G., M. Festa-Bianchet, D. W. Coltman, and F. Pelletier. 2016. Intense selective
788 hunting leads to artificial evolution in horn size. *Evol. Appl.* 9:521–530.

789 Plard, F., J. M. Gaillard, T. Coulson, A. J. M. Hewison, D. Delorme, C. Warnant, and
790 C. Bonenfant. 2014. Mismatch between birth date and vegetation phenology slows the
791 demography of roe deer. *Plos Biol.* 12:e1001828.

792 Plard, F., J. M. Gaillard, T. Coulson, A. J. M. Hewison, M. Douhard, F. Klein, D. De-
793 lorme, C. Warnant, and C. Bonenfant. 2015. The influence of birth date via body mass
794 on individual fitness in a long-lived mammal. *Ecology* 96:1516–1528.

795 Price, G. R. 1972. Extension of covariance selection mathematics. *Ann. Hum. Genet.*
796 35:485–490.

797 Proaktor, G., T. Coulson, and E. J. Milner-Gulland. 2007. Evolutionary responses to
798 harvesting in ungulates. *J. Anim. Ecol.* 76:669–678.

799 R Core Team. 2014. R: A language and environment for statistical computing. Tech. rep.

800 Reid, J. M. and L. F. Keller. 2010. Correlated inbreeding among relatives: Occurrence,
801 magnitude, and implications. *Evolution* 64:973–985.

802 Rödel, H. G., D. von Holst, and C. Kraus. 2009. Family legacies: short- and long-term
803 fitness consequences of early-life conditions in female european rabbits. *J. Anim. Ecol.*
804 78:789–797.

805 Sand, H. 1996. Life history patterns in female moose (*Alces alces*): the relationship
806 between age, body size, fecundity and environmental conditions. *Oecologia* 106:212–
807 220.

808 Sasaki, K., S. F. Fox, and D. Duvall. 2009. Rapid evolution in the wild: Changes in body
809 size, life-history traits, and behavior in hunted populations of the japanese mamushi
810 snake. *Conserv. Biol.* 23:93–102.

- 811 Schmidt, K. T., A. Stien, S. D. Albon, and F. E. Guinness. 2001. Antler length of yearling
812 red deer is determined by population density, weather and early life-history. *Oecologia*
813 127:191–197.
- 814 Schwartz, C. C. and K. J. Hundertmark. 1993. Reproductive characteristics of Alaskan
815 moose. *J. Wild. Manage.* 57:454–468.
- 816 Sharpe, D. M. T. and A. P. Hendry. 2009. Life history change in commercially exploited
817 fish stocks: an analysis of trends across studies. *Evol. Appl.* 2:260–275.
- 818 Solberg, E. J., M. Garel, M. Heim, V. Grøtan, and B.-E. Sæther. 2008. Lack of compen-
819 satory body growth in a high performance moose *Alces alces* population. *Oecologia*
820 158:485–498.
- 821 Solberg, E. J., M. Heim, V. Grøtan, B.-E. Sæther, and M. Garel. 2007. Annual variation
822 in maternal age and calving date generate cohort effects in moose (*Alces alces*) body
823 mass. *Oecologia* 154:259–271.
- 824 Solberg, E. J., A. Loison, J. M. Gaillard, and M. Heim. 2004. Lasting effects of conditions
825 at birth on moose body mass. *Ecography* 27:677–687.
- 826 Solberg, E. J., A. Loison, B.-E. Sæther, and O. Strand. 2000. Age-specific harvest mor-
827 tality in a Norwegian moose *Alces alces* population. *Wildlife Biol.* 6:41–52.
- 828 Solberg, E. J., C. M. Rolandsen, M. Heim, J. D. C. Linnell, I. Herfindal, and B.-E.
829 Sæther. 2010. Age and sex-specific variation in detectability of moose (*Alces alces*)
830 during the hunting season: implications for population monitoring. *Eur. J. Wildlife*
831 *Res.* 56:871–881.
- 832 Solberg, E. J. and B.-E. Sæther. 1994. Male traits as life-history variables: Annual
833 variation in body mass and antler size in moose (*Alces alces*). *J. Mammal.* 75:1069–
834 1079.
- 835 Solberg, E. J., B.-E. Sæther, O. Strand, and A. Loison. 1999. Dynamics of a harvested
836 moose population in a variable environment. *J. Anim. Ecol.* 68:186–204.

- 837 Spiegelhalter, D. J., N. G. Best, B. R. Carlin, and A. van der Linde. 2002. Bayesian
838 measures of model complexity and fit. *J. R. Stat. Soc. B* 64:583–616.
- 839 Stewart, K. M., R. T. Bowyer, J. G. Kie, and W. C. Gasaway. 2000. Antler size relative
840 to body mass in moose: Tradeoffs associated with reproduction. *Alces* 36:77–83.
- 841 Stinchcombe, J. R., A. F. Agrawal, P. A. Hohenlohe, S. J. Arnold, and M. W. Blows.
842 2008. Estimating nonlinear selection gradients using quadratic regression coefficients:
843 Double or nothing? *Evolution* 62:2435–2440.
- 844 Stubsjøen, T., B.-E. Sæther, E. J. Solberg, M. Heim, and C. M. Rolandsen. 2000. Moose
845 (*Alces alces*) survival in three populations in northern Norway. *Can. J. Zool.* 78:1822–
846 1830.
- 847 Sæther, B.-E. 1997. Environmental stochasticity and population dynamics of large her-
848 bivores: a search for mechanisms. *Trends Ecol. Evol.* 12:143–149.
- 849 Sæther, B.-E., R. Andersen, O. Hjeljord, and M. Heim. 1996. Ecological correlates of
850 regional variation in life history of the moose *Alces alces*. *Ecology* 77:1493–1500.
- 851 Sæther, B.-E., T. Coulson, V. Grøtan, S. Engen, R. Altwegg, K. B. Armitage, C. Bar-
852 braud, P. H. Becker, D. T. Blumstein, F. S. Dobson, M. Festa-Bianchet, J. M. Gail-
853 lard, A. Jenkins, C. Jones, M. A. C. Nicoll, K. Norris, M. K. Oli, A. Ozgul, and
854 H. Weimerskirch. 2013. How life history influences population dynamics in fluctuating
855 environments. *Am. Nat.* 182:743–759.
- 856 Sæther, B.-E. and S. Engen. 2015. The concept of fitness in fluctuating environments.
857 *Trends Ecol. Evol.* 30:273–281.
- 858 Sæther, B.-E., S. Engen, and E. J. Solberg. 2001. Optimal harvest of age-structured
859 populations of moose *Alces alces* in a fluctuating environment. *Wildlife Biol.* 7:171–
860 179.
- 861 Sæther, B.-E., S. Engen, E. J. Solberg, and M. Heim. 2007. Estimating the growth of a
862 newly established moose population using reproductive value. *Ecography* 30:417–421.

- 863 Sæther, B.-E. and H. Haagenrud. 1983. Life history of the moose (*Alces alces*): fecundity
864 rates in relation to age and carcass weight. *J. Mammal.* 64:226–232.
- 865 ———. 1985. Life history of the moose *Alces alces*: relationship between growth and
866 reproduction. *Holarctic Ecol.* 8:100–106.
- 867 Sæther, B.-E. and M. Heim. 1993. Ecological correlates of individual variation in age
868 at maturity in female moose (*Alces alces*): the effects of environmental variability. *J.*
869 *Anim. Ecol.* 62:482–489.
- 870 Sæther, B.-E., E. J. Solberg, and M. Heim. 2003. Effects of altering sex ratio structure
871 on the demography of an isolated moose population. *J. Wild. Manage.* 67:455–466.
- 872 Sæther, B.-E., E. J. Solberg, M. Heim, J. E. Stacy, K. S. Jakobsen, and R. Olstad. 2004.
873 Offspring sex ratio in moose *Alces alces* in relation to paternal age: an experiment.
874 *Wildlife Biol.* 10:51–57.
- 875 van Tienderen, P. H. 2000. Elasticities and the link between demographic and evolution-
876 ary dynamics. *Ecology* 81:666–679.
- 877 Tveraa, T., P. Fauchald, C. Henaug, and N. G. Yoccoz. 2003. An examination of a
878 compensatory relationship between food limitation and predation in semi-domestic
879 reindeer. *Oecologia* 137:370–376.
- 880 de Villemereuil, P., O. Gimenez, and B. Doligez. 2013. Comparing parent-offspring re-
881 gression with frequentist and bayesian animal models to estimate heritability in wild
882 populations: a simulation study for gaussian and binary traits. *Methods Ecol. Evol.*
883 4:260–275.
- 884 White, R. G., J. E. Rowell, and W. E. Hauer. 1997. The role of nutrition, body condition
885 and lactation on calving success in muskoxen. *J. Zool.* 243:13–20.
- 886 Willis, J. H. 1996. Measures of phenotypic selection are biased by partial inbreeding.
887 *Evolution* 50:1501–1511.

- 888 Wilson, A. J. 2008. Why h^2 does not always equal V_A/V_P ? *J. Evol. Biol.* 21:647–650.
- 889 Wilson, A. J., D. W. Coltman, J. M. Pemberton, A. D. J. Overall, K. A. Byrne, and
890 L. E. B. Kruuk. 2005a. Maternal genetic effects set the potential for evolution in a
891 free-living vertebrate population. *J. Evol. Biol.* 18:405–414.
- 892 Wilson, A. J. and D. H. Nussey. 2010. What is individual quality? An evolutionary
893 perspective. *Trends Ecol. Evol.* 25:207–214.
- 894 Wilson, A. J., J. G. Pilkington, J. M. Pemberton, D. W. Coltman, A. D. J. Overall,
895 K. A. Byrne, and L. E. B. Kruuk. 2005b. Selection on mothers and offspring: Whose
896 phenotype is it and does it matter? *Evolution* 59:451–463.
- 897 Wilson, A. J., D. Réale, M. N. Clements, M. M. Morrissey, E. Postma, C. A. Walling,
898 L. E. B. Kruuk, and D. H. Nussey. 2010. An ecologist’s guide to the animal model. *J.*
899 *Anim. Ecol.* 79:13–26.
- 900 Wolf, J. B. and M. J. Wade. 2001. On the assignment of fitness to parents and offspring:
901 whose fitness is it and when does it matter? *J. Evol. Biol.* 14:347–356.

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

Table 2: Mean \pm 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 \pm SE	Var	Cov	n	Mean \pm SE	Var	Cov	n
(A) 1992-2011								
Calf body mass	179 \pm 2	342		76	192 \pm 2	450		89
Birth date	152 \pm 1	97	-35	79	151 \pm 1	96	-92	87
(B) 2000-2011 (weighted)								
Calf body mass	177 \pm 1	250		49	189 \pm 3	759		43
Birth date	152 \pm 1	97	-24	49	157 \pm 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 \pm 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 autumn 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. \times Birth date
	$\beta_{\sigma 1}$	$\gamma_{\sigma 11}$	$\beta_{\sigma 2}$	$\gamma_{\sigma 22}$	$\gamma_{\sigma 12}$
(A) Females					
Total	-0.08\pm0.04	0.08 \pm 0.07	-0.03 \pm 0.04	0.03 \pm 0.11	0.03 \pm 0.05
Viability	-0.06 \pm 0.04	0.10 \pm 0.07	0.03 \pm 0.04	-0.02 \pm 0.10	0.03 \pm 0.05
Fecundity	-0.25\pm0.14	-0.05 \pm 0.23	-0.33 \pm 0.11	0.31\pm0.27	0.07 \pm 0.13
Fecundity (excl. harvest)	-0.07 \pm 0.07	0.16 \pm 0.13	-0.28 \pm 0.07	0.13\pm0.14	-0.04 \pm 0.05
(B) Males					
Total	0.14 \pm 0.08	-0.04 \pm 0.08	0.18 \pm 0.09	-0.15\pm0.13	0.05 \pm 0.08
Viability	0.16 \pm 0.09	-0.05 \pm 0.10	0.30 \pm 0.10	-0.17\pm0.14	0.08 \pm 0.09
Fecundity	-0.08 \pm 0.19	-0.02 \pm 0.23	-0.42 \pm 0.20	-0.12\pm0.20	-0.05 \pm 0.19
Fecundity (excl. harvest)	0.05 \pm 0.22	0.18 \pm 0.25	-0.32 \pm 0.18	-0.23\pm0.21	-0.05 \pm 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)	

903 **Figure legends**

904 **Figure 1:** Diagram showing the life cycle of moose (for one sex) at the island of Vega in
905 northern Norway during one time step (t to $t+1$). For each age class $x = (1, 2, \dots, k)$, N_x
906 = the number of individuals, m_x is the average number of offspring produced divided by
907 2, s_{x+1}^{n1} and s_{x+1}^{n2} are the annual natural probabilities of survival before and after harvest
908 and s_{x+1}^h = the probability of surviving the annual hunting season (*Harvest*). Using
909 pre-breeding census, the grey rectangle indicate the part of the life cycle which are part
910 of the census at time t . Individuals enter out data at age 1 (c. 9 months), and are prior
911 to this included in their parents fecundity. Calves are weaned at the age of approx. 6
912 months, follow their mother closely at the time of census and are not rejected until just
913 before the calving season (*Calving*). The corresponding sex specific projection matrix $\mathbf{1}$
914 (see Table 1) has fecundities, $f_x = m_x s_{1,x}^{n1} s_{1,x}^h s_{1,x}^{n2}$ for all x , in the first row and survivals,
915 $s_{x+1} = s_{x+1}^{n1} s_{x+1}^h s_{x+1}^{n2} = N_{x+1}/N_x$ for $x < k$, in the subdiagonal. For $x = k$ we have
916 survival $s_{k+1} = s_k$ in the lower left corner element of $\mathbf{1}$, because individuals in the final
917 age class stay in this age class until death.

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

926 **Figure 3:** Directional selection gradients (SD-scaled) on calf body mass (A, C, E) and
927 birth date (B, D, F) for female (solid circles and lines) and male (open circles and dashed
928 lines) moose during the years 2000-2011 at the island of Vega in northern Norway. Three
929 different measures of relative fitness, total fitness (A, B), viability fitness (C, D) and fe-
930 cundity fitness (E, F), where used to estimate selection gradients. Age-specific directional

931 selection gradients (circles and lines) are from simple linear regressions. Estimated se-
932 lection gradients of the population (horizontal lines) are coloured black when significant.
933 Weighted means and (co)variances for the traits are given in Table 2. Further details are
934 given in the text and in Table 3.

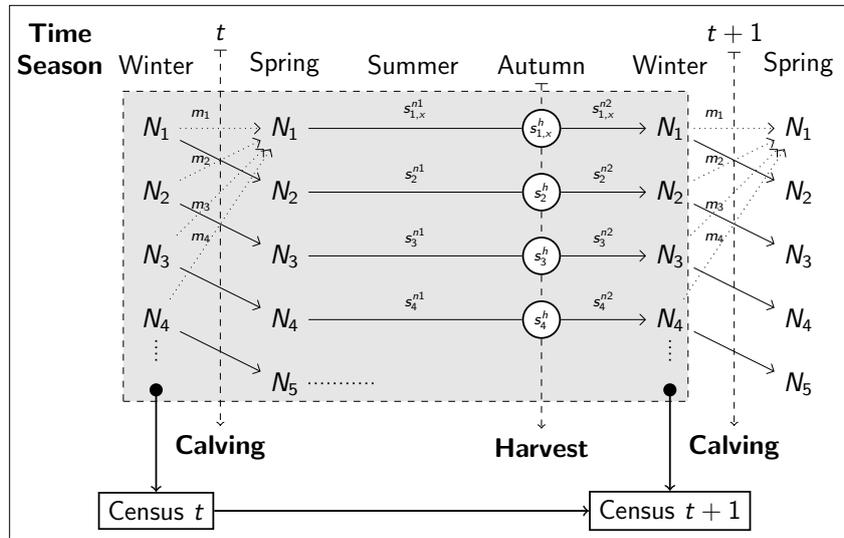


Figure 1

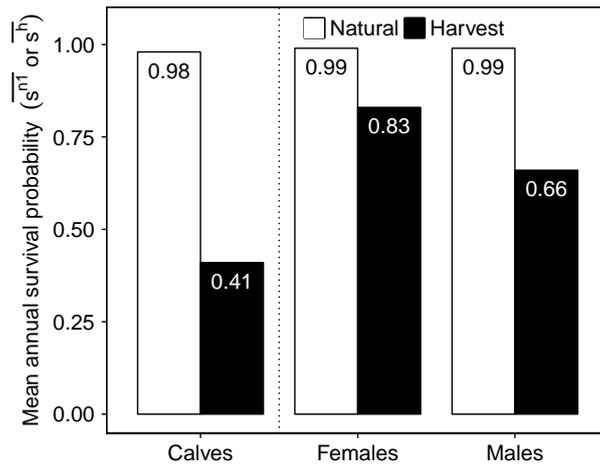


Figure 2

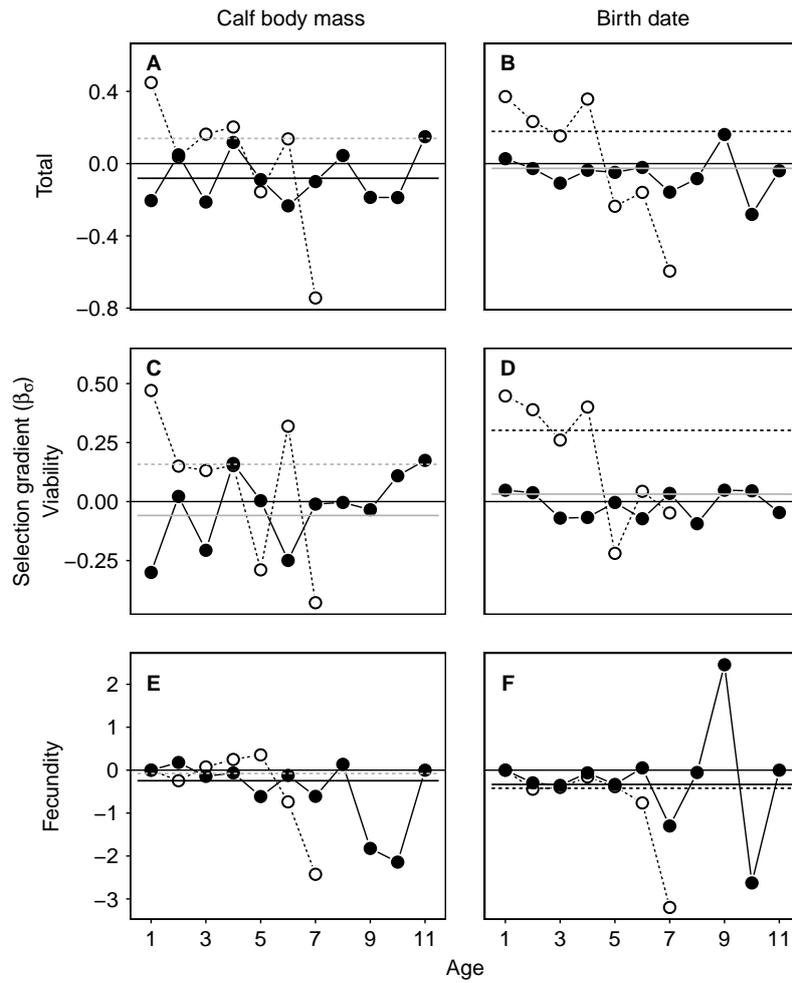


Figure 3