

Stabilizing selection and adaptive evolution in a combination of two traits in an arctic ungulate

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Stabilizing selection is thought to be common in wild populations and act as one of the main evolutionary mechanisms, which constrain phenotypic variation. When multiple traits interact to create a combined phenotype, correlational selection may be an important process driving adaptive evolution. Here, we report on phenotypic selection and evolutionary changes in two natal traits in a semidomestic population of reindeer (*Rangifer tarandus*) in northern Finland. The population has been closely monitored since 1969, and detailed data have been collected on individuals since they were born. Over the length of the study period (1969–2015), we found directional and stabilizing selection toward a combination of earlier birth date and heavier birth mass with an intermediate optimum along the major axis of the selection surface. In addition, we demonstrate significant changes in mean traits toward earlier birth date and heavier birth mass, with corresponding genetic changes in breeding values during the study period. Our results demonstrate evolutionary changes in a combination of two traits, which agree closely with estimated patterns of phenotypic selection. Knowledge of the selective surface for combinations of genetically correlated traits are vital to predict how population mean phenotypes and fitness are affected when environments change.

KEY WORDS: Breeding values, individual fitness, phenotype, reindeer, selection.

Natural selection can drive adaptive evolution toward phenotypic values of higher mean fitness in wild populations (Simpson 1944; Lande 1976; Arnold et al. 2001; Kinnison and Hendry 2001; Estes and Arnold 2007; Bell 2010; Uyeda et al. 2011). Under long periods of evolutionary stasis, stabilizing selection is thought to be the most important mechanism that counteracts phenotypic changes by genetic drift and mutations (Charlesworth et al. 1982; Estes and Arnold 2007; Uyeda et al. 2011). However, despite frequent observations of stasis in phenotypes, robust evidence for stabilizing selection acting in contemporary populations has been

relatively rare (Travis 1989; Merilä et al. 2001; Kingsolver et al. 2001, 2012).

The fitness function for a trait or combinations of traits can be thought of as a phenotypic adaptive landscape with fitness peaks and valleys (Wright 1932; Simpson 1944; Lande 1976, 1979; Svensson and Calsbeek 2013). A peak in such a landscape represents a phenotypic optimum (Arnold et al. 2001). Several mechanisms, alone or in synergy, may hinder the detection of stabilizing selection in a population that has adapted to a peak in a fitness landscape. For instance, demographic stochasticity

causes random variation between individuals in survival and fecundity (especially at low population sizes; Lande et al. 2003). This process may cause genetic drift and decrease the strength of the signal from stabilizing selection as the population mean phenotype moves randomly under the fitness peak (Engen and Sæther 2014; Haller and Hendry 2014). In addition, fluctuating environments may cause the fitness peak itself to display stochastic shifts between time points (Arnold et al. 2001; Lande 2007). Hence, a population in a stochastic phenotypic adaptive landscape may be subject to fluctuating selection, alternating between directional and stabilizing selection depending on its phenotypic means and variances relative to the position and shape of the peak (Lande 1976, 1979; Merilä et al. 2001; Grant and Grant 2002; Bell 2008, 2010; Engen and Sæther 2014; Chevin et al. 2015, 2017; Gamelon et al. 2018). Only detailed long-term studies may enable us detect such changes in the direction and shape of selection (Bell 2010; Chevin et al. 2015). In addition, detection of stabilizing selection may be hindered by the fact that selection often act on combinations of related traits (Phillips and Arnold 1989; Sinervo and Svensson 2002; Blows and Brooks 2003; Calsbeek and Irschick 2007; Walsh and Blows 2009; Blows and McGuigan 2015). There may be several mechanisms for why selection acts on several traits simultaneously. For instance, due to trade-offs between important life history traits (Morrissey et al. 2012) or functional relationships (Schluter and Nychka 1994). In a two-dimensional adaptive landscape, certain trait combinations are being favored if the major axis of the peak is not parallel to the axis of either trait (Arnold et al. 2001). By failing to recognize such a relationship between traits, stabilizing selection would be underestimated and the true combined trait under selection would remain unidentified (Blows and Brooks 2003).

A fundamental parameter in population ecology is the annual population growth rate. The annual population growth rate is the result of all individual contributions (i.e., fitness) to the next years breeding population (Caswell 2001; Coulson et al. 2003; Engen et al. 2009b). However, many studies of selection investigate only a single component of fitness (i.e., fecundity or survival; Linden et al. 1992; Neff 2004; Martin and Wainwright 2013) or focus on only one part of the life cycle (Kingsolver et al. 2012). Studies of selection also frequently fail to account for changes in individual mean fitness with age. In long-lived organisms, populations often have age structure in individual fitness, where the age classes differ in their mean fecundity and probability of survival (Caughley 1966; Gaillard et al. 2000; Jones et al. 2008). For example, ungulate populations often have lower survival probabilities in the youngest age classes compared to older age classes (e.g., Catchpole et al. 2000; McElligott et al. 2002; Catchpole et al. 2004). In the oldest age classes, fecundity and survival may decline due to senescence (Loison et al. 1999a; Nussey et al. 2007; Hayward et al. 2013). As a result, age structure will have important im-

plications for describing selection and the evolutionary dynamics of a population (Charlesworth 1973, 1993; Lande 1982; Engen et al. 2014). The total strength and form of selection may best be described by an integrated measure of total individual fitness that result in a clear relationship between evolutionary and population dynamics (Lande 1979, 1982; Lande and Arnold 1983; van Tienderen 2000; Caswell 2001; Coulson et al. 2003, 2006; Engen et al. 2009b, 2011; Sæther and Engen 2015).

Phenological events, like timing of reproduction, are among the traits that are most sensitive to fluctuations and temporal changes in environmental conditions (Festa-Bianchet 1988; Both et al. 2004; Visser 2008; Dunn and Møller 2014). For instance, animals living in seasonal environments will normally give birth to their offspring when foraging conditions are plentiful, easily accessible, and nutrient rich to avoid starvation and increased risk of mortality (e.g., Klein 1965; Plard et al. 2014). However, the morphology of individuals may also affect individual fitness such that in seasonal environments there could be selection on both morphology and phenology. For example, Coulson et al. (2003) found that there was selection for earlier birth dates and heavier birth mass simultaneously in red deer, whereas Wilson et al. (2005) found selection for later birth dates and heavier birth mass in Soay Sheep (*Ovis aries*). This raises the question of whether selection could act correlationally to favor an optimal combination of morphology and phenology.

The ability of populations to respond evolutionarily to selection depends on the availability of additive genetic variance (Lande 1979; Blows 2007; Hansen and Houle 2008). When selection acts on more than one trait, the genetic covariance between traits, given by the genetic variance–covariance matrix (**G**), impacts the evolutionary response (Lande 1979, 1982). These covariances may cause genetic trade-offs in phenotypic traits when the major axis of genetic variation does not align well with the direction of selection (Kopp and Matuszewski 2014). For example, Morrissey et al. (2012) found that evolution of important life history traits (adult longevity, fecundity, etc.) in red deer (*Cervus elaphus*) were most likely constrained by genetic covariance between traits. These constraints were not evident at the phenotypic level (Morrissey et al. 2012). The values of phenotypes are a combination of environmental and genetic effects. Hence, an observed change in phenotypes in a population can be due to the environment (i.e., phenotypic plasticity; Via and Lande 1985), genetic effects or a combination of these. Given that phenotypes have an additive genetic basis (i.e., heritability > 0), investigations of breeding values can be used to differentiate between these two sources of change. For example, Pigeon et al. (2016) found a change in estimated breeding values (EBV) for horn length and horn base in male big horn sheep (*Ovis canadensis*), induced by trophy hunting, that correlated with observed mean phenotypic change in the population. However, genetic drift

could not be excluded as a possible cause for the genetic change (i.e., change in EBV) in the population (Pigeon et al. 2016).

Here, we use a long time series from a semidomestic population of reindeer in northern Finland to investigate the strength and shape of selection on two important natal life history traits: individual birth date and birth mass. Birth date has been found to be important for early life survival in ungulates (e.g., Guinness et al. 1978; Wilson et al. 2005; Plard et al. 2015) and also individual fitness as an adult (e.g., Plard et al. 2015; Kvalnes et al. 2016). Similarly, relationships between birth mass and individual fitness have been found in many species (e.g., Guinness et al. 1978; Wilson et al. 2005; LeBel et al. 1997), including humans (Lummaa and Clutton-Brock 2002). Both traits are often presumed linked with early life conditions and development, which may have lifetime fitness consequences (Lindström 1999; Metcalfe and Monaghan 2001). In our study population, each individual was monitored closely throughout its lifetime with detailed, precise, and accurate estimates of individual fitness and phenotypes. Our four main objectives were as follows: (1) quantify the total directional and stabilizing selection on each phenotypic trait separately, (2) separate between direct and indirect selection on each trait and investigate the degree to which a combination of these traits are subject to correlational selection, (3) estimate the change in phenotypes across the study period, and (4) investigate evolutionary changes in breeding values.

Materials and Methods

STUDY SYSTEM

The data were collected from reindeer kept in the Kutuharju Experimental Reindeer Station (owned by the Reindeer Herders Association) in Kaamanen, northern Finland (69°08'N, 26°60'E) in the period 1969–2016. The population was free ranging within large enclosures dominated by pine and birch forest, marshes, moorland, and freshwater lakes (total size = 43.8 km²). Supplementary feeding was made available during winter (Holand et al. 2003), which ensured that there was no density dependence. The data included the female segment of the population, but calves of both sexes were included when recording female fecundity. All reindeer were systematically monitored and females were kept in smaller paddocks (ca. 0.50 km²) during calving to record birth dates (as yearly day number, where 1 = January 1) and mass (± 0.1 kg) of the calves shortly after birth (for more detailed description of fieldwork procedures see, Eloranta and Nieminen 1986; Holand et al. 2003; Weladji et al. 2010). Maternity of calves was determined either by observation (1969–1996) or by genetic analyses (from 1997 onward, for details, see Eloranta and Nieminen 1986; Røed et al. 2002; Engelhardt et al. 2016). Slaughtering accounted for 59% of the mortality of both calves and adult females during the study period. There was no system-

atic human influence on the fecundity of females during the study period.

PHENOTYPIC SELECTION ANALYSES

We estimated phenotypic selection on individual birth date and birth mass (i.e., the date an individual was born and the body mass it had as a newborn). Both traits are fixed throughout the life of an individual and were available for all individuals in the dataset. The dataset for selection analyses had one record for each census year an individual was alive, with a total of 4133 records of 906 individuals for the years 1969–2015 (the dataset stops with the census in 2016). An obvious impact of human activity in our study system was slaughtering, which affected individual survival. To obtain a more precise estimate of natural selection, we excluded the last record in the dataset for individuals in the census year they were culled by humans (number of records = 4133 after 797 records of culled individuals were removed). Thus, all observations of individual deaths in the dataset we used for selection analyses were due to natural causes (predators, exposure, injury, etc.). However, we note that we observed almost no phenotypic difference between the group of individuals that died from natural causes and the group of individuals killed by humans (see Fig. S1). The data were structured according to postbreeding census, recording annual survival and fecundity for all individuals immediately after the calving season (Caswell 2001). Hence, the first age class in our data was new-born calves and the oldest individual ($n = 1$) was 16 years old. For an individual i in year t , survival (J_i) was recorded as 1 if it was alive just after next years breeding season (otherwise 0) and fecundity (B_i) was defined as the number of offspring produced in the breeding season of year $t + 1$ (April–June).

Selection was estimated following Kvalnes et al. (2016, 2017) and Lande and Arnold (1983) using the demographic framework developed by Engen et al. (2009a, 2011, 2012, 2014). This method accounts for fluctuations in age-structure by weighting components of individual fitness and trait values by age-specific reproductive values (rv-weighting) (see Engen et al. 2009a, 2011, 2012, 2014; Kvalnes et al. 2016, 2017, for in depth descriptions and empirical examples). Unaccounted for, such fluctuations introduce a between-age class component to the true selection differential (Engen et al. 2014). The result of utilizing weighting by age-specific reproductive values is that a population with overlapping generations becomes mathematically similar to a population with discrete generations (Price and Smith 1972; Lande 1982). The demographic framework is made up of three stages. First, age-specific reproductive values (\mathbf{v}) and the stable age distribution (\mathbf{u}) are estimated as the left and right eigenvector associated with the dominant eigenvalue (λ) of the mean projection matrix (\mathbf{I}), scaled to $\Sigma u_x = 1$ and $\Sigma v_x = 1$ for age classes $x = (1, 2, \dots, k)$. The elements of \mathbf{I} are age-specific means of fecundity and survival over the study period. Second, for an

individual i in age class x , the contribution to the next years breeding population (individual fitness) is given by $W_i = J_i v_{x+1} + B_i v_x / 2$ (Engen et al. 2009a). Here, J_i is a dichotomous (1/0) indicator of survival, B_i is the number of offspring, and v 's are age-specific reproductive values. The division by two accounts for the shared contribution from each sex to B . Engen et al. (2009a, 2011, 2012, 2014) have shown that W_i is the relevant measure of individual contributions to the future growth rate of the population with age-independent expectation, $E(W_i / v_x) = E(\Lambda_i) = \lambda$. Third, directional (β) and nonlinear (γ) phenotypic selection is estimated from the linear (b) and nonlinear (q) coefficients from rv-weighted multiple least squares regression of relative fitness on trait values. For two traits $\mathbf{z} = (z_1, z_2)$, we then have $\beta = (b_1, b_2)^T$ (where T denotes matrix transposition) and

$$\boldsymbol{\gamma} = \begin{bmatrix} 2q_{11} & q_{12} \\ q_{12} & 2q_{22} \end{bmatrix}, \quad (1)$$

for the model with directional and nonlinear selection on each trait and nonlinear (correlational) selection on the combined traits (Stinchcombe et al. 2008).

Given an estimated $\boldsymbol{\gamma}$ matrix, we used canonical analysis to investigate if a combination of the two traits was the target of nonlinear selection (Box and Wilson 1951; Box and Draper 1987; Phillips and Arnold 1989). This method finds the major axes of the response surface by determining the normalized eigenvalues (ψ_i) and eigenvectors (\mathbf{m}_i) of $\boldsymbol{\gamma}$. The ψ_i 's then give the strength of nonlinear selection along the respective \mathbf{m}_i 's, which may be non-parallel to the original trait axes. The sign of the ψ_i 's describes the shape of the nonlinear selection along these axes, where a positive ψ_i indicates a concave selection (disruptive if a local minimum is present) and a negative ψ_i indicates a convex selection (stabilizing if a local maximum is present).

Individual birth date and birth mass were centered by the annual rv-weighted mean and scaled by the global rv-weighted standard deviation of the centered traits ($\tilde{\sigma}_{\text{birth date}} = 6.17$, $\tilde{\sigma}_{\text{body mass}} = 0.78$, $\tilde{\rho}_{\text{body mass, birth date}} = -0.15$). The global rv-weighted means \pm SE for the traits were $\tilde{\mu}_{\text{birth date}} = 138.27 \pm 0.09$ and $\tilde{\mu}_{\text{body mass}} = 5.73 \pm 0.01$. The resulting SD-scaled selection gradients are indicated using subscript σ . Mean standardized traits often have preferable properties for interpretation of parameters and comparisons across evolutionary studies (see Houle 1992). However, mean standardization was not suitable here as it is not meaningful for traits such as birth date, which is on an interval measurement scale and has an arbitrary choice of zero. Selection acts and is measured on an annual basis, hence, relative fitness was calculated on an annual basis dividing by rv-weighted mean absolute fitness, $\Lambda_{\text{rel},t} = \Lambda_t / \bar{\Lambda}_t$.

We estimated selection using multiple regression in two parts. First, univariate analyses of directional and nonlinear selection was made in a model for each trait. Second, a multivariate

analysis was made where we in addition to the linear and nonlinear parameter for each trait also included the interaction between traits (birth date \times birth mass) to estimate correlational selection. Uncertainties were quantified by resampling (with replacement) for 10,000 bootstrap replicates of the estimated parameters (Mitchell-Olds and Shaw 1987). From these nonparametric bootstrap replicates, we calculated the 95% percentile confidence intervals (CI) for each estimate. The estimated $\boldsymbol{\gamma}_\sigma$ matrix from the multivariate analysis was subjected to canonical analysis to estimate the strength of nonlinear selection along the canonical axes. To account for uncertainty in the estimated selection gradients in the $\boldsymbol{\gamma}_\sigma$ matrix, the canonical analysis was performed for each bootstrap replicate to generate the distribution for the eigenvalues. The nonlinear selection was deemed significantly different from zero if the 95% confidence interval of the eigenvalues did not overlap zero. To investigate if any curvature in the selection surface was due to chance (Reynolds et al. 2010), we performed permutation tests of the two eigenvalues produced from the $\boldsymbol{\gamma}_\sigma$ matrix. The mean projection matrix with elasticities for each element of fecundity and survival with respect to population growth rate (λ) is given in Table S1 and estimated age-specific multivariate nonlinear selection is shown in Table S2.

OBSERVED PHENOTYPIC CHANGES

We investigated if there were any temporal changes in observed rv-weighted birth date and birth mass during the study period (1969–2015, 4930 records of 1455 individuals). This was done by univariate rv-weighted linear regressions where the response variable was one of the traits and year was the sole explanatory variable. The reproductive value weighting accounted for the effect of fluctuating age structure on trait values (Engen et al. 2014). Thus, we investigated if the observed annual weighted mean birth date and birth mass had changed significantly during the study period.

QUANTITATIVE GENETIC ANALYSES

In the final analyses, we explored if there was any directional evolutionary changes in the two traits by estimating annual mean breeding values using quantitative genetic animal models (Mrode 1996; Kruuk 2004). We used data from $n = 1483$ females that had a known birth date and birth mass. The pedigree was pruned to 1702 informative individuals. Muuttoraanta et al. (2013) performed a quantitative genetic analysis of birth mass and birth date and found support for additive genetic and maternal genetic variance components in these traits. We constructed a bivariate Bayesian animal model for birth date and mass, building on the best model found by Muuttoraanta et al. (2013). Numbering the traits 1 and 2, the model in matrix notation was

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Zu} + \mathbf{Wm} + \mathbf{Sc} + \mathbf{e}, \quad (2)$$

where $\mathbf{y} = (\mathbf{y}_1, \mathbf{y}_2)^T$ is a vector of records for all individuals, $\mathbf{b} = (\mu_1, \mu_2)^T$ is the intercept for each trait, $\mathbf{u} = (\mathbf{u}_1, \mathbf{u}_2)^T$ is a vector of random animal effects, $\mathbf{m} = (\mathbf{m}_1, \mathbf{m}_2)^T$ is a vector of random maternal genetic effects, $\mathbf{c} = (\mathbf{c}_1, \mathbf{c}_2)^T$ is a vector of random cohort effects, and $\mathbf{e} = (\mathbf{e}_1, \mathbf{e}_2)^T$ is a vector of residuals. \mathbf{X} , \mathbf{Z} , \mathbf{W} , and \mathbf{S} are 2×2 block matrices with zero in the off-diagonal elements and design matrices on the diagonal, which relate records of each trait to fixed and random effects. For instance, the \mathbf{Z} matrix has the design matrices \mathbf{Z}_1 and \mathbf{Z}_2 on the diagonal, which relates traits 1 and 2 to random animal effects. \mathbf{u} , \mathbf{m} , \mathbf{c} , and \mathbf{e} were assumed to independently follow a bivariate normal distribution with expectations 0 and covariance matrices $\mathbf{G} \otimes \mathbf{A}$, $\mathbf{M} \otimes \mathbf{A}$, $\mathbf{C} \otimes \mathbf{I}$, and $\mathbf{R} \otimes \mathbf{I}$, where \otimes denotes the Kronecker product, \mathbf{A} is the relationship matrix, and \mathbf{I} is an identity matrix. Thus, the phenotypic covariance matrix (\mathbf{P}) was partitioned into additive genetic (\mathbf{G}), maternal genetic (\mathbf{M}), cohort (\mathbf{C}), and residual (\mathbf{R}) covariance matrices. The inclusion of cohort effects in the model accounted for any temporal changes in phenotypes due to nonrandom environmental variation (Postma 2006). Although the inclusion of maternal genetic effects allowed us to separate direct and maternal additive genetic variance components (Muuttoranta et al. 2014).

The model was fitted using the R package *MCMCglmm* version 2.22.1 with Gaussian distribution and identity link function (Hadfield 2010). Both traits were scaled by their global standard deviation ($\sigma_{\text{birth date}} = 7.56$, $\sigma_{\text{birth mass}} = 0.98$) to ensure good model mixing and simplify the construction of priors. To ensure adequate sample sizes and low autocorrelation (generally < 0.05), we ran the model with a “burn-in” of 3000 and a thinning rate of 500 for a total of 1000 independent random samples of the posterior distributions for the parameters.

To estimate selection directly on the breeding values, we performed a multivariate analysis similar to the one performed on phenotypes (Robertson 1966; Price 1970). Specifically, we fitted a multiple regression with the breeding values for each trait, their quadratic terms, and an interaction to estimate the $\boldsymbol{\gamma}$ matrix with nonlinear selection gradients (see eq. 1). Then we performed a canonical analysis as described previously. Temporal change in annual rv-weighted mean EBV during the study period was investigated following Hadfield et al. (2010), as the slope in regressions of annual rv-weighted EBV on years. As previously, the reproductive value weighting was used to account for fluctuations in age structure. The uncertainty in EBVs was propagated to analyses of selection and temporal change by running separate regressions for each realization of the MCMC chain (Hadfield et al. 2010). We deemed selection gradients and estimates of temporal change in EBVs as significantly different from zero if the 95% Bayesian credibility intervals (BCI) for the estimates did not include zero. In addition, we investigated the probability that temporal changes in EBVs of a trait were due to random genetic drift. This was done

Table 1. SD-standardized estimates of univariate selection on birth date and birth mass of female reindeer in a semidomestic population in northern Finland.

| Trait | β_σ | γ_σ |
|------------|-----------------------------------|------------------------------------|
| Birth date | -0.028 (-0.041, -0.015) | 0.001 (-0.014, 0.020) |
| Birth mass | 0.039 (0.026, 0.053) | -0.018 (-0.036, -0.0004) |

Gradients include both direct and indirect selection on each trait separately. Estimates are given with lower and upper limits of their 95% confidence interval in parenthesis. Statistically significant estimates are given in bold.

by simulating random breeding values (RBVs) down the pedigree and extracting the slope in regressions of rv-weighted RBVs on year for each realization of the \mathbf{G}_σ -matrix in the MCMC chain. The *rbv* function in the *MCMCglmm* package (Hadfield 2010) was used to simulate RBVs. We then performed a two-tailed test comparing the posterior distribution under random genetic drift with the estimated slope from the data. All analyses in our study were done using the statistical software package R version 3.3.3 (R Core Team 2019).

RESULTS

Phenotypic selection

The birth date in the population had a mean of 139.53 ± 0.2 ($n = 1483$), with a variance of 57.10 and a range of 122–195. Birth mass had a mean of 5.52 ± 0.03 kg ($n = 1483$), a variance of 0.96 and a range of 1.8–10.4 kg. The covariance between body mass and birth date was -1.90 ($n = 1483$), which corresponds to a correlation of -0.26 .

Univariate analyses revealed significant directional and stabilizing selection toward heavier birth mass (Table 1), with an optimum within the observed phenotypic range at $2.14 \sigma_{kg}$. In addition, we found significant directional selection toward earlier birth date (Table 1)

In the multivariate analyses, the canonical analysis of nonlinear selection gradients ($\boldsymbol{\gamma}_\sigma$ matrix, Table 2) revealed significant correlational stabilizing selection along the second major axis (Table 3 and Fig. 1, permutation test: $P = 0.002$). Eigenvalue ψ_2 loaded positively on birth mass and negatively on birth date (see Table 3). Thus, heavy individuals born early and light individuals born late suffered a reduced fitness (Table 3 and Fig. 1). Along the first major axis, there was no significant nonlinear selection (Table 3), indicating that the selective landscape had a fitness ridge where the optimum birth mass increased with later birth dates (Fig. 1). The overall pattern of selection agreed most strongly with estimates from the youngest age classes (Table S2). The survival probabilities in the younger age classes also had the largest elasticities with respect to population growth rate (see Table S1).

Table 2. SD-standardized linear (β_σ), quadratic and correlational (γ_σ) selection gradients from a multivariate model for female reindeer in a semidomestic population in northern Finland.

| Trait | β_σ | γ_σ |
|-----------------------------------|-----------------------------------|---------------------------|
| Birth date | -0.023 (-0.031, -0.008) | 0.001 (-0.010, 0.018) |
| Birth mass | 0.035 (0.019, 0.042) | -0.015 (-0.028, 0.004) |
| Birth date \times birth mass | | 0.011 (-0.001, 0.022) |

Estimates are given with lower and upper limits of their 95% confidence interval in parenthesis. Statistically significant estimates are given in bold.

Table 3. Matrix of eigenvectors and eigenvalues from the canonical analysis of γ_σ for female reindeer in a semidomestic population in northern Finland.

| i | ψ_i | m_i | |
|-----|--------------------------------|------------|------------|
| | | Birth date | Birth mass |
| 1 | 0.007 (-0.005, 0.026) | -0.890 | -0.455 |
| 2 | -0.021 (-0.033, -0.004) | -0.455 | 0.890 |

Estimates of the eigenvalue (ψ_i) for each eigenvector (m_i) is given with lower and upper limits of the 95% confidence interval in parenthesis.

Phenotypic changes

The annual rv-weighted mean birth date advanced significantly during the study period ($\beta = -0.162$, $t = -20.216$, d.f. = 4928, $P < 0.001$), with a range of 21 May in 1972 to 13 May 2015 (Fig. 2A). In addition, the annual observed rv-weighted mean birth mass also increased during the same period ($\beta = 0.028$, $t = 28.328$, d.f. = 4928, $P < 0.001$), with a range of 4.5 kg in 1973 to 6.2 kg in 2010 (Fig. 2B).

Quantitative genetics

The quantitative genetic analysis indicated that there was a heritability of 0.208 (BCI = 0.087, 0.318) for birth date and 0.332 (BCI = 0.225, 0.467) for birth mass, with a genetic correlation of -0.099 (BCI = -0.17, -0.003). Table 4 gives the estimates for all covariance matrices. A multivariate analysis of selection on breeding values revealed that the pattern of selection was similar to the selection on the phenotypes (Tables 5 and 6). However, having accounted for the uncertainty in EBV there was a wide CI around the second major axis identified in the canonical analysis, which included zero (Table 5). Similar to the results on phenotypes, eigenvalue ψ_2 loaded positively on breeding values for birth mass and negatively on breeding values for birth date. Although uncertain, taken together with the selection on phenotypes this indicates that individuals with breeding values for large

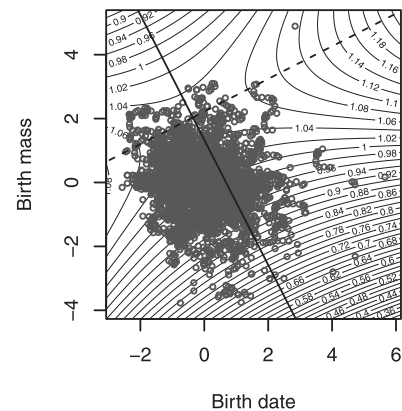


Figure 1. Estimated selection on birth date and birth mass of females in a semidomestic reindeer population in northern Finland. Dashed line denotes the axis of the first eigenvector of the γ_σ -matrix. Solid line denotes the axis of the stabilizing correlational selection (second eigenvector of the γ_σ -matrix) between the two traits. Contours give the shape of the predicted individual selection landscape. Observed fitness values are given as open circles. One observation was excluded to improve clarity (at birth date = 9.238 and birth mass = -0.781).

body mass and early birth or light body mass and late birth were at a disadvantage. There was a significant temporal decrease in EBVs for birth date ($\beta = -0.007$, BCI = [-0.012, -0.001], Fig. 2B), corresponding to advanced birth date. The probability that this temporal change in EBVs for birth date was due to random genetic drift was calculated to be 0.047%. We also found a significant temporal increase in EBVs for birth mass ($\beta = 0.011$, BCI = [0.004, 0.017], Fig. 2D), corresponding to increased birth mass during the study period. The probability that a change of this magnitude was due to random genetic drift alone was 0.01%. Accordingly, the changes in EBVs for the two traits were in the same directions as the observed phenotypic changes (Fig. 2B, D). Corresponding results were found for changes in breeding values among cohorts (Fig. S2).

DISCUSSION

Selection is a continuous process that affects populations in the present and may result in adaptive evolution on ecological time scales (Hendry and Kinnison 1999; Grant and Grant 2002; Hendry 2016). In this regard, annual estimates of individual fitness has many advantages over life-time measures of fitness, as highlighted by, for instance, Coulson et al. (2006) and Sæther and Engen (2015). However, fluctuating age distribution complicates the use of annual measures of fitness and may obscure the detection of true selection (or lack thereof) in age-structured populations (Hill 1974; Engen et al. 2014). In this study, we observed clear variation in both mean fecundity and survival probability among age classes in the population (Table S1). The survival probability was low for

Table 4. Estimated variance components for a population of semidomestic reindeer in northern Finland.

| Variance component | Birth mass | Birth date | Birth date : Birth mass |
|--------------------|----------------------|----------------------|-------------------------|
| Additive genetic | 0.332 (0.225, 0.467) | 0.208 (0.087, 0.318) | -0.099 (-0.17, -0.003) |
| Maternal genetic | 0.109 (0.061, 0.165) | 0.059 (0, 0.105) | -0.014 (-0.046, 0.023) |
| Cohort | 0.183 (0.112, 0.341) | 0.222 (0.126, 0.346) | -0.102 (-0.216, -0.035) |
| Residual | 0.354 (0.272, 0.45) | 0.494 (0.402, 0.58) | -0.026 (-0.086, 0.043) |

Estimates are given with lower and upper limits of their 95% Bayesian credibility interval in parenthesis. Additive genetic variance for the two traits are given as heritability, whereas the interaction between the two traits is given as genetic correlation. Phenotypic means and variances are provided in the main text of the results.

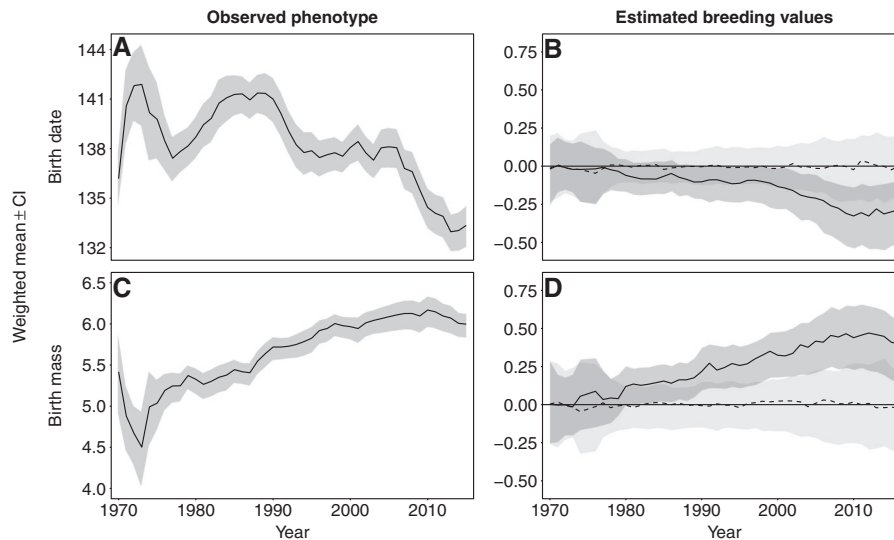


Figure 2. The observed annual change in mean female birth date (A) and mean female birth mass (C) during the study period of a semidomestic reindeer population in northern Finland. The corresponding annual changes in estimated breeding values (solid line) for birth date (B) and birth mass (D) are shown together with simulated estimates of expected change due to random genetic drift alone (dashed line). All estimates are weighted by the reproductive values for each respective age class. Shaded areas denote the 95% confidence interval (A and C) or 95% credibility interval (B and D) for each respective estimate. Birth date is denoted as yearly day number (A), where day 138 is May 18.

calves and decreased markedly in the oldest age classes (ages 10 and older), and fecundity was zero in calves and increased toward prime aged individuals (ages 3 and older, Table S1). These patterns are similar to observations from other ungulate species (e.g., Loison et al. 1999a; Nussey et al. 2007; Hayward et al. 2013). To overcome the problem of age structure, we applied a well-established demographic framework, weighting by age-specific reproductive values, for estimating selection (Engen et al. 2011, 2012, 2014; Kvalnes et al. 2016, 2017). Reproductive values were first introduced by Fisher (1930) to deal with fluctuating age distribution in age-structured population dynamic models. For an individual in a given age class, the reproductive value is defined as the expected contribution to future population growth rate (Fisher 1930; Leslie 1948). The distribution of reproductive values among age classes depends on the life history of the species (Lande et al. 2003). In species where survival rates are lower for juveniles than for adults, the reproductive value generally peaks

at age of first reproduction and decrease toward older age classes (Lande et al. 2003; Sæther et al. 2013). This demographic framework enabled us to combine annual individual contributions of survival and fecundity into a single measure of annual individual fitness, account for age structure, and make inferences about the overall pattern of natural selection in the population. The selection estimated within each age (Table S2) class did not strongly reflect the total selection pattern found in the population (Tables 2 and 3). Accordingly, if we were only able to estimate the strength and shape of selection within each age class, this would have obscured the overall pattern of selection (Fig. 1).

In this study, we found stabilizing selection on a combination of two natal traits, birth date and birth mass (Tables 1–3). The same patterns were also found in our multivariate analyses of selection on breeding values (Tables 5 and 6). The estimated selective surface with correlational selection on birth date and birth mass had a pronounced curvature along the birth mass axis

Table 5. Estimates of linear, quadratic, and correlational selection on estimated breeding values (EBV) for two traits in female reindeer in a semidomesticated population in northern Finland.

| Trait (EBV) | β_{σ} | γ_{σ} |
|-----------------------------------|-----------------------------------|---------------------------|
| Birth date | -0.028 (-0.053, -0.002) | 0.028 (-0.174, 0.282) |
| Birth mass | 0.046 (0.028, 0.065) | -0.063 (-0.198, 0.080) |
| Birth date \times birth mass | | 0.040 (-0.017, 0.115) |

Estimates are given as their median with 95% credibility intervals in parenthesis. Uncertainty in estimated breeding values was propagated to selection gradients by performing the selection analysis for each realization of the MCMC chain. Statistically significant estimates are given in bold.

Table 6. Matrix of eigenvectors and eigenvalues from the canonical analysis of nonlinear selection on estimated breeding values (EBV) for two traits in female reindeer in a semidomesticated population in northern Finland.

| i | ψ_i | m_i | |
|-----|------------------------|-------------------|-------------------|
| | | Birth date EBV | Birth mass EBV |
| 1 | 0.053 (-0.091, 0.312) | -0.922 | -0.351 |
| 2 | -0.096 (-0.233, 0.011) | -0.207 | 0.608 |

Estimates of the eigenvalue for each eigenvector are given as their median with 95% credibility intervals in parenthesis.

(Fig. 1). Similar results was also revealed in the univariate selection analyses (Table 1) that quantified the total selection on each trait, including both the direct and indirect selection. Thus, there was clear indications of directional and stabilizing selection on birth mass (Fig. 1). Univariate analyses of selection were of special interest in this study as Klein (1965) proposed that the main determinant for growth in ungulate populations is the availability of nutrient rich plant material. In seasonal environments, plants become less easy to digest later in summer (Albon and Langvatn 1992) and ungulates should give birth during the early stages of plant phenology to maximize the energy and nutrients that are available to their calves. The degree to which there is selection on birth date alone and the degree to which this is due to selection on other traits is thus of special interest as it can have effects on life history and population dynamics (e.g., Plard et al. 2014, 2015). Birth mass influences the energy requirements for the developing calf (Andersen and Sæther 1992), and is a likely trait to modify the pattern of selection on birth date.

Considering birth mass on its own, there may be several reasons for why a relatively low birth mass (microsomia) may be disadvantageous. One example of an immediate effect is that

small/light calves may be more susceptible to harsh environmental conditions due to their relatively large body surface area to volume ratio (Clutton-Brock et al. 1982; Loison et al. 1999b). In addition, low birth mass may have long-term effects as low birth mass may lead to a low body mass as an adult (Gaillard et al. 2003; Solberg et al. 2008), which may in itself cause a reduced fitness (see Tyler 1987). Individuals may potentially avoid a low adult body mass by so-called "catch-up" or compensatory growth (Hornick et al. 2000; Hector and Nakagawa 2012). However, "catch-up" or compensatory growth may also have negative effects on individuals later in their life (Hector and Nakagawa 2012). For example, compensatory growth in humans have been linked with higher prevalence of disease as an adult (Cottrell and Ozanne 2008). In the other end of the spectrum, calves with a relatively large birth mass (macrosomia) may suffer from dystocia (i.e., complications at birth) due to their large size. This could result in death or injury for both the calf and the mother (Alexander 1974). A positive relationship between large birth mass and dystocia has been found in domestic ungulates (Alexander 1974; Mee 2012), primates (Stockinger et al. 2011), and humans (Adesina and Olayemi 2003). To the best of our knowledge, there has been no earlier reports of stabilizing selection on birth mass in ungulates. However, examples of intermediate optima have been reported for birth mass in humans (Ridley 2004), offspring size in amphibians (Kaplan 1992), egg size in fish (Einum and Fleming 2000), and egg size in reptiles (Janzen and Warner 2009).

The timing of birth to the availability and quality of food may be of great importance for animals in seasonal environments (Klein 1965; Albon and Langvatn 1992; Rutberg 1987; Post et al. 2003). However, several studies have found a simple linear negative relationship between birth date and fitness in ungulates (e.g., Coulson et al. 2003; Wilson et al. 2005; Plard et al. 2015). Thus, the negative effects associated with being born too early seems to be absent or of minor importance compared to the severe effects of being born too late (Côte and Festa-Bianchet 2001; Feder et al. 2008). The results in the present study seems to conform to this pattern, with univariate analyses of selection revealing negative directional selection toward earlier birth date (Table 1). There are two main processes thought to cause these results: Individuals born relatively late may miss the emergence of vegetation with high nutrient content (Klein 1970; Rutberg 1987; Albon and Langvatn 1992) and in addition they have a shorter time in which to grow and accumulate resources before their first winter (Festa-Bianchet 1988; Côte and Festa-Bianchet 2001). In contrast, individuals born very early may be buffered against adverse environmental effects if they are born by mothers in better condition compared to mothers who give birth later (e.g., Mitchell and Lincoln 1973; Clutton-Brock et al. 1986; Berger 1992). However, in a two-year study of pronghorn sheep (*Antilocapra americana*),

Gregg et al. (2001) found indications of an optimum in birth date with respect to survival of fawns.

Previous studies on ungulates have shown that there may be directional selection on both birth date and birth mass (e.g., Coulson et al. 2003; Wilson et al. 2005; Plard et al. 2015). However, our results indicated that there was stabilizing correlational selection favoring a combination of these two traits (Table 2 and Fig. 1). Light individuals born late and heavy individuals born early seemed to be at a disadvantage. We believe there are several causes for these results. Andersen and Sæther (1992) found that food intake of moose calves (*Alces alces*) increased with body mass of calves. Therefore, large calves may require more resources than are available early in the spring (Rutberg 1987; Skogland 1989; Post et al. 2003). Even though the mother may be able to partly compensate for an increased resource requirement for the calf, there may be limits to the amount of milk that she is able to produce as the lactation period in ungulates has been found to be the period where females expend the most amount of energy per day (Parker et al. 2009). Conversely, individuals born relatively late and with a low birth mass may suffer from a combination of missing the emergence of vegetation with high nutrient content and the negative effects of microclimate (see above). To our knowledge, this is the first study to find stabilizing correlational selection on birth date and birth mass in an ungulate species.

Directional and stabilizing selection may cause changes in both the mean and the variance of traits across generations, where a reduction in the genetic variation in a population is expected when extreme trait values are selected against (Lande 1979, 1980; Plabon et al. 2010; Sztepanacz and Blows 2017). When a combination of traits are under selection, the phenotypic and genetic covariance matrix may change as variation in each trait and their covariation is shaped in response to the shape of the selective landscape and the direction of selection (Arnold et al. 2001, 2008; Revell et al. 2010). The rate to which the genetic covariance matrix may change under selection have important implications for predictions of adaptive evolution (Arnold et al. 2008; Revell et al. 2010; Eroukhanoff and Svensson 2011; Björklund et al. 2013; Kopp and Matuszewski 2014). Although this issue could not be handled in sufficient detail within the current study, future studies may be able to shed some light on the stability of the genetic covariance matrix and the degree to which the selective landscape may have shaped trait variation in our study population.

There was a phenotypic change in our study population over the study period toward earlier births and heavier birth mass (Fig. 2). To evaluate the degree to which this represented evolutionary changes (genetic), we estimated the temporal changes in breeding values for the two traits. Analyses of EBV can give anticonservative estimates of both selection and temporal changes unless uncertainty in the estimates and temporal environmental changes in the phenotype across relatives are accounted for in the

analyses (Postma 2006; Hadfield et al. 2010). Here, we follow the recommendations from Hadfield et al. (2010) and perform the analyses for each iteration of the MCMC chain to obtain a full posterior distribution for the parameters of interest and specifically include cohort in the model to account for environmental changes when estimating breeding values (Postma 2006). We found that the observed phenotypic change was matched by a genetic change (i.e., change in EBV) in the same direction for both traits (Fig. 2). Taken together with our selection results, these patterns indicated that there have been substantial directional selection (Tables 2 and 5) that have resulted in evolution of the mean phenotype in the population. Although the overall selection was found to be stabilizing (Fig. 1), the majority of the individuals in the population had phenotypes located to one side of the predicted optimum (Fig. 1) and we found significant directional selection in the population (Table 2). Thus, in addition to stabilizing selection the population seems to have experienced directional selection for earlier birth date and increased birth mass for the majority of the study period. To have continued directional selection over the long study period given the rapid response observed in the population requires that the fitness peak and the adaptive landscape have changed over time, gradually or in larger steps, keeping the population tracking a moving optimum throughout the study period. A possible driver of such a change in the optimum could be temperature. Indeed, the average temperature in Finland have been found to increase $0.14^{\circ}\text{C}/\text{decade}$ over the period 1847–2013 with larger than average changes during spring and the most rapid changes occurring in the period since the late 1960s (Mikkonen et al. 2015). Also, the observed phenotypic changes in our study coincide with an overall change in spring temperature for the region (A. P. Paoli et al., unpubl. results) and Skogland (1989) found a positive relationship between the start of the vegetation growth season and the start of the calving period in reindeer and caribou populations. Thus, the observed changes could be the direct result of changes in spring temperatures on the optimum phenotype to match the emergence of the vegetation (Rutberg 1987; Post and Forchhammer 2008; Post et al. 2009). Temperatures may continue changing in the future due to global climate changes, an important topic is therefore to investigate the degree to which populations are able to reduce their risk of extinction by adaptive evolution when selection acts correlationally on fitness-related traits.

AUTHOR CONTRIBUTIONS

HH wrote the manuscript together with TK. HH conducted the phenotypic analyses and TK conducted the quantitative genetic analyses. All authors contributed with edits and comments to analyses and writing.

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DATA ARCHIVING

Data archival location: Data will be archived on Dryad ([datadryad.org](https://doi.org/10.5061/dryad.m37pvmcxz)) following acceptance <https://doi.org/10.5061/dryad.m37pvmcxz>.

LITERATURE CITED

- Adesina, O. A., and O. Olayemi. 2003. Fetal macrosomia at the university college hospital, Ibadan: a 3-year review. *J. Obstet. Gynaecol.* 23:30–33.
- Albon, S. D., and R. Langvatn. 1992. Plant phenology and the benefits of migration in a temperate ungulate. *Oikos* 65:502–513.
- Alexander, G. 1974. Birth weight of lambs influences and consequences. John Wiley & Sons, Ltd, Chichester, U.K.
- Andersen, R., and B. E. Sæther. 1992. Functional-response during winter of a herbivore, the moose, in relation to age and size. *Ecology* 73:542–550.
- Arnold, S. J., M. E. Pfrender, and A. G. Jones. 2001. The adaptive landscape as a conceptual bridge between micro- and macroevolution. *Genetica* 112:9–32.
- Arnold, S. J., R. Burger, P. A. Hohenlohe, B. C. Ajie, and A. G. Jones. 2008. Understanding the evolution and stability of the G-matrix. *Evolution* 62:2451–2461.
- Bell, G. 2008. Selection: the mechanism of evolution. Oxford biology. 2nd ed. Oxford Univ. Press, Oxford, U.K.
- . 2010. Fluctuating selection: the perpetual renewal of adaptation in variable environments. *Phil. Trans. R. Soc. B* 365:87–97.
- Berger, J. 1992. Facilitation of reproductive synchrony by gestation adjustment in gregarious mammals: a new hypothesis. *Ecology* 73:323–329.
- Björklund, M., A. Husby, and L. Gustafsson. 2013. Rapid and unpredictable changes of the G-matrix in a natural bird population over 25 years. *J. Evol. Biol.* 26:1–13.
- Blows, M. W., and R. Brooks. 2003. Measuring nonlinear selection. *Am. Nat.* 162:815–820.
- Blows, M. W., and K. McGuigan. 2015. The distribution of genetic variance across phenotypic space and the response to selection. *Mol. Ecol.* 24:2056–2072.
- Both, C., A. V. Artemyev, B. Blaauw, R. J. Cowie, A. J. Dekhuijzen, T. Eeva, A. Enemar, L. Gustafsson, E. V. Ivankina, A. Järvinen, et al. 2004. Large-scale geographical variation confirms that climate change causes birds to lay earlier. *Proc. R. Soc. B* 271:1657–1662.
- Box, G. E. P., and N. R. Draper. 1987. Empirical model-building and response surfaces. John Wiley & Sons, Inc., Chichester, U.K.
- Box, G. E. P., and K. B. Wilson. 1951. On the experimental attainment of optimum conditions. *J. R. Stat. Soc. Ser. B-Stat. Methodol.* 13:1–45.
- Calsbeek, R., and D. J. Irschick. 2007. The quick and the dead: correlational selection on morphology, performance, and habitat use in island lizards. *Evolution* 61:2493–2503.
- Caswell, H. 2001. Matrix population models: construction, analysis, and interpretation. 2nd ed. Sinauer Associates, Sunderland, MA.
- Catchpole, E. A., Y. Fan, B. J. T. Morgan, T. H. Clutton-Brock, and T. Coulson. 2004. Sexual dimorphism, survival and dispersal in red deer. *J. Agric. Biol. Environ. Stat.* 9:1–26.
- Catchpole, E. A., B. J. T. Morgan, T. N. Coulson, S. N. Freeman, and S. D. Albon. 2000. Factors influencing Soay sheep survival. *J. R. Stat. Soc. Ser. C-Appl. Stat.* 49:453–472.
- Caughley, G. 1966. Mortality patterns in mammals. *Ecology* 47:906–918.
- Charlesworth, B. 1973. Selection in populations with overlapping generations .5. Natural-selection and life histories. *Am. Nat.* 107:303–311.
- . 1993. Natural-selection on multivariate traits in age-structured populations. *Proc. R. Soc. B-Biol. Sci.* 251:47–52.
- Charlesworth, B., R. Lande, and M. Slatkin. 1982. A neo-Darwinian commentary on macroevolution. *Evolution* 36:474–498.
- Chevin, L. M., M. E. Visser, and J. Tufto. 2015. Estimating the variation, autocorrelation, and environmental sensitivity of phenotypic selection. *Evolution* 69:2319–2332.
- Chevin, L. M., O. Cotto, and J. Ashander. 2017. Stochastic evolutionary demography under a fluctuating optimum phenotype. *Am. Nat.* 190:786–802.
- Clutton-Brock, T. H., F. E. Guinness, S. D. Albon, and P. Barrett. 1982. Red deer: behavior and ecology of two sexes. Wildlife behavior and ecology. Edinburgh Univ. Press, Edinburgh.
- Clutton-Brock, T. H., S. D. Albon, and F. E. Guinness. 1986. Great expectations—dominance, breeding success and offspring sex-ratios in red deer. *Anim. Behav.* 34:460–471.
- Cottrell, E. C., and S. E. Ozanne. 2008. Early life programming of obesity and metabolic disease. *Physiol. Behav.* 94:17–28.
- Coulson, T., L. E. B. Kruuk, G. Tavecchia, J. M. Pemberton, and T. H. Clutton-Brock. 2003. Estimating selection on neonatal traits in red deer using elasticity path analysis. *Evolution* 57:2879–2892.
- Coulson, T., T. G. Benton, P. Lundberg, S. R. X. Dall, B. E. Kendall, and J. M. Gaillard. 2006. Estimating individual contributions to population growth: evolutionary fitness in ecological time. *Proc. R. Soc. B* 273:547–555.
- Côte, S. D., and M. Festa-Bianchet. 2001. Birthdate, mass and survival in mountain goat kids: effects of maternal characteristics and forage quality. *Oecologia* 127:230–238.
- Dunn, P. O., and A. P. Møller. 2014. Changes in breeding phenology and population size of birds. *J. Anim. Ecol.* 83:729–739.
- Einum, S., and I. A. Fleming. 2000. Highly fecund mothers sacrifice offspring survival to maximize fitness. *Nature* 405:565–567.
- Eloranta, E., and M. Nieminen. 1986. Calving of the experimental reindeer herd in Kaamanen during 1970–1985. *Rangifer* 6:115–121.
- Engelhardt, S. C., R. B. Weladji, Ø. Holand, K. H. Røed, and M. Nieminen. 2016. Allonursing in reindeer, *Rangifer tarandus*: a test of the kin-selection hypothesis. *J. Mammal.* 97:689–700.
- Engen, S., and B.-E. Sæther. 2014. Evolution in fluctuating environments: decomposing selection into additive components of the Robertson-Price equation. *Evolution* 68:854–865.
- Engen, S., R. Lande, and B.-E. Sæther. 2009a. Reproductive value and fluctuating selection in an age-structured population. *Genetics* 183:629–637.
- Engen, S., R. Lande, B.-E. Sæther, and S. F. Dobson. 2009b. Reproductive value and the stochastic demography of age-structured populations. *Am. Nat.* 174:795–804.
- Engen, S., R. Lande, and B.-E. Sæther. 2011. Evolution of a plastic quantitative trait in an age-structured population in a fluctuating environment. *Evolution* 65:2893–2906.
- Engen, S., B.-E. Sæther, T. Kvalnes, and H. Jensen. 2012. Estimating fluctuating selection in age-structured populations. *J. Evol. Biol.* 25:1487–1499.
- Engen, S., T. Kvalnes, and B.-E. Sæther. 2014. Estimating phenotypic selection in age-structured populations by removing transient fluctuations. *Evolution* 68:2509–2523.

- Eroukhmanoff, F., and E. I. Svensson. 2011. Evolution and stability of the G-matrix during the colonization of a novel environment. *J. Evol. Biol.* 24:1363–1373.
- Estes, S., and S. J. Arnold. 2007. Resolving the paradox of stasis: models with stabilizing selection explain evolutionary divergence on all timescales. *Am. Nat.* 169:227–244.
- Feder, C., J. G. A. Martin, M. Festa-Bianchet, C. Berube, and J. Jorgenson. 2008. Never too late? Consequences of late birthdate for mass and survival of bighorn lambs. *Oecologia* 156:773–781.
- Festa-Bianchet, M. 1988. Birthdate and survival in bighorn lambs (*Ovis canadensis*). *J. Zool.* 214:653–661.
- Fisher, R. A. 1930. The genetical theory of natural selection. At the Clarendon Press, Oxford, U.K.
- Gaillard, J. M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Toigo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. *Annu. Rev. Ecol. Syst.* 31:367–393.
- Gaillard, J. M., A. Loison, C. Toigo, D. Delorme, and G. Van Laere. 2003. Cohort effects and deer population dynamics. *Ecoscience* 10:412–420.
- Gamelon, M., J. Tufto, A. L. K. Nilsson, K. Jerstad, O. W. Røstad, N. C. Stenseth, and B.-E. Sæther. 2018. Environmental drivers of varying selective optima in a small passerine: a multivariate, multiepisodic approach. *Evolution* 72:2325–2342.
- Grant, P. R., and B. R. Grant. 2002. Unpredictable evolution in a 30-year study of Darwin's finches. *Science* 296:707–711.
- Gregg, M. A., M. Bray, K. M. Kilbride, and M. R. Dunbar. 2001. Birth synchrony and survival of pronghorn fawns. *J. Wildl. Manage.* 65: 19–24.
- Guinness, F. E., T. H. Cluttonbrock, and S. D. Albon. 1978. Factors affecting calf mortality in red deer (*cervus-elaphus*). *J. Anim. Ecol.* 47:817–832.
- D Hadfield, J. 2010. MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. *J. Stat. Softw.* 33:1–22.
- Hadfield, J. D., A. J. Wilson, D. Garant, B. C. Sheldon, and L. E. B. Kruuk. 2010. The misuse of blup in ecology and evolution. *Am. Nat.* 175:116–125.
- Haller, B. C., and A. P. Hendry. 2014. Solving the paradox of stasis: squashed stabilizing selection and the limits of detection. *Evolution* 68:483–500.
- Hansen, T. F., and D. Houle. 2008. Measuring and comparing evolvability and constraint in multivariate characters. *J. Evol. Biol.* 21:1201–1219.
- Hayward, A. D., A. J. Wilson, J. G. Pilkington, T. H. Clutton-Brock, J. M. Pemberton, and L. E. B. Kruuk. 2013. Reproductive senescence in female soay sheep: variation across traits and contributions of individual ageing and selective disappearance. *Funct. Ecol.* 27:184–195.
- Hector, K. L., and S. Nakagawa. 2012. Quantitative analysis of compensatory and catch-up growth in diverse taxa. *J. Anim. Ecol.* 81:583–593.
- Hendry, A. 2016. *Eco-evolutionary dynamics*. Princeton Univ. Press, Princeton, NJ.
- Hendry, A. P., and M. T. Kinnison. 1999. The pace of modern life: measuring rates of contemporary microevolution. *Evolution* 53:1637–1653.
- G Hill, W. 1974. Prediction and evaluation of response to selection with overlapping generations. *Anim. Prod.* 18:117–139.
- Holand, Ø., K. H. Røed, A. Mysterud, J. Kumpula, M. Nieminen, and M. E. Smith. 2003. The effect of sex ratio and male age structure on reindeer calving. *J. Wildl. Manage.* 67:25–33.
- Hornick, J. L., C. Van Eenaeme, O. Gerard, I. Dufrasne, and L. Istasse. 2000. Mechanisms of reduced and compensatory growth. *Domest. Anim. Endocrinol.* 19:121–132.
- Houle, D. 1992. Comparing evolvability and variability of quantitative traits. *Genetics* 130:195–204.
- Janzen, F. J., and D. A. Warner. 2009. Parent-offspring conflict and selection on egg size in turtles. *J. Evol. Biol.* 22:2222–2230.
- Jones, O. R., J. M. Gaillard, S. Tuljapurkar, J. S. Alho, K. B. Armitage, P. H. Becker, P. Bize, J. Brommer, A. Charmantier, M. Charpentier, et al. 2008. Senescence rates are determined by ranking on the fast-slow life-history continuum. *Ecol. Lett.* 11:664–673.
- H Kaplan, R. 1992. Greater maternal investment can decrease offspring survival in the frog *Bombina orientalis*. *Ecology* 73:280–288.
- Kingsolver, J. G., H. E. Hoekstra, J. M. Hoekstra, D. Berrigan, S. N. Vignieri, C. E. Hill, A. Hoang, P. Gibert, and P. Beerli. 2001. The strength of phenotypic selection in natural populations. *Am. Nat.* 157:245–261.
- Kingsolver, J. G., S. E. Diamond, A. M. Siepielski, and S. M. Carlson. 2012. Synthetic analyses of phenotypic selection in natural populations: lessons, limitations and future directions. *Evol. Ecol.* 26:1101–1118.
- Kinnison, M. T., and A. P. Hendry. 2001. The pace of modern life II: from rates of contemporary microevolution to pattern and process. *Genetica* 112:145–164.
- Klein, D. R. 1965. Ecology of deer range in Alaska. *Ecol. Monogr.* 35:259–284.
- . 1970. Tundra ranges north of the boreal forest. *J. Range Manage.* 23:8–14.
- Kopp, M., and S. Matuszewski. 2014. Rapid evolution of quantitative traits: theoretical perspectives. *Evol. Appl.* 7:169–191.
- B Kruuk, L. E. 2004. Estimating genetic parameters in natural populations using the “animal model.” *Phil. Trans. R. Soc. B* 359:873–890.
- Kvalnes, T., B.-E. Sæther, H. Haanes, K. H. Røed, S. Engen, and E. J. Solberg. 2016. Harvest-induced phenotypic selection in an island population of moose, *Alces alces*. *Evolution* 70:1486–1500.
- Kvalnes, T., T. H. Ringsby, H. Jensen, I. J. Hagen, B. Rønning, H. Parn, H. Holand, S. Engen, and B. E. Sæther. 2017. Reversal of response to artificial selection on body size in a wild passerine. *Evolution* 71:2062–2079.
- Lande, R. 1976. Natural selection and random genetic drift in phenotypic evolution. *Evolution* 30:314–334.
- . 1979. Quantitative genetic analysis of multivariate evolution, applied to brain:body size allometry. *Evolution* 33:402–416.
- . 1980. The genetic covariance between characters maintained by pleiotropic mutations. *Genetics* 94:203–215.
- . 1982. A quantitative genetic theory of life history evolution. *Ecology* 63:607–615.
- . 2007. Expected relative fitness and the adaptive topography of fluctuating selection. *Evolution* 61:1835–1846.
- Lande, R., and S. J. Arnold. 1983. The measurement of selection on correlated characters. *Evolution* 37:1210–1226.
- Lande, R., S. Engen, and B.-E. Sæther. 2003. *Stochastic population dynamics in ecology and conservation*. Oxford Univ. Press, Oxford, U.K.
- LeBel, S., M. Salas, P. Chardonnet, and M. Bianchi. 1997. Rusa deer (*cervus timorensis russa*) farming in new caledonia: impact of different feed levels on herd breeding rate and performance of newborn fawns. *Aust. Vet. J.* 75:199–203.
- H Leslie, P. 1948. Some further notes on the use of matrices in population mathematics. *Biometrika* 35:213–245.
- Linden, M., L. Gustafsson, and T. Part. 1992. Selection on fledging mass in the collared flycatcher and the great tit. *Ecology* 73:336–343.
- Lindström, J. 1999. Early development and fitness in birds and mammals. *Trends Ecol. Evol.* 14:343–348.
- Loison, A., M. Festa-Bianchet, J. M. Gaillard, J. T. Jorgenson, and J. M. Jullien. 1999a. Age-specific survival in five populations of ungulates: evidence of senescence. *Ecology* 80:2539–2554.
- Loison, A., R. Langvatn, and E. J. Solberg. 1999b. Body mass and winter mortality in red deer calves: disentangling sex and climate effects. *Ecography* 22:20–30.

- Lummaa, V., and T. Clutton-Brock. 2002. Early development, survival and reproduction in humans. *Trends Ecol. Evol.* 17:141–147.
- Martin, C. H., and P. C. Wainwright. 2013. Multiple fitness peaks on the adaptive landscape drive adaptive radiation in the wild. *Science* 339:208–211.
- McElligott, A. G., R. Altwegg, and T. J. Hayden. 2002. Age-specific survival and reproductive probabilities: evidence for senescence in male fallow deer (*Dama dama*). *Proc. R. Soc. B-Biol. Sci.* 269:1129–1137.
- Mee, J. 2012. Prevalence and risk factors for dystocia in dairy cattle—with emphasis on confinement systems. Pp. 113–125 in T. McFadden, ed. *Advances in dairy technology*, Vol. 24. University of Alberta, Department of Agriculture Food & Nutrition Science, Edmonton.
- Merilä, J., B. C. Sheldon, and L. E. B. Kruuk. 2001. Explaining stasis: microevolutionary studies in natural populations. *Genetica* 112:199–222.
- Metcalf, N. B., and P. Monaghan. 2001. Compensation for a bad start: grow now, pay later? *Trends Ecol. Evol.* 16:254–260.
- Mikkonen, S., M. Laine, H. M. Mäkelä, H. Gregow, H. Tuomenvirta, M. Lahtinen, and A. Laaksonen. 2015. Trends in the average temperature in Finland, 1847–2013. *Stoch. Environ. Res. Risk Assess.* 29:1521–1529.
- Mitchell, B., and G. A. Lincoln. 1973. Conception dates in relation to age and condition in 2 populations of red deer in Scotland. *J. Zool.* 171:141–152.
- Mitchell-Olds, T., and R. G. Shaw. 1987. Regression analysis of natural selection: statistical inference and biological interpretation. *Evolution* 41:1149–1161.
- Morrissey, M. B., C. A. Walling, A. J. Wilson, J. M. Pemberton, T. H. Clutton-Brock, and L. E. B. Kruuk. 2012. Genetic analysis of life-history constraint and evolution in a wild ungulate population. *Am. Nat.* 179:E97–E114.
- Mrode, R. A. 1996. *Linear models for the prediction of animal breeding values*. CAB International, Wallingford, U.K.
- Muuttoranta, K., O. Holand, K. H. Røed, M. Tapio, M. Nieminen, and A. Mäki-Tanila. 2013. Genetic and environmental effects affecting the variation in birth date and birth weight of reindeer calves. *Rangifer* 33:25–35.
- Muuttoranta, K., M. Tapio, Ø. Holand, K. H. Røed, M. Nieminen, and A. Mäki-Tanila. 2014. Genetic variation in mean production related traits in reindeer (*Rangifer t. tarandus*). *Rangifer* 34:21–36.
- D Neff, B. 2004. Stabilizing selection on genomic divergence in a wild fish population. *Proc. Natl. Acad. Sci. USA* 101:2381–2385.
- Nussey, D. H., L. E. B. Kruuk, A. Morris, and T. H. Clutton-Brock. 2007. Environmental conditions in early life influence ageing rates in a wild population of red deer. *Curr. Biol.* 17:R1000–R1001.
- Parker, K. L., P. S. Barboza, and M. P. Gillingham. 2009. Nutrition integrates environmental responses of ungulates. *Funct. Ecol.* 23:57–69.
- Phillips, P. C., and S. J. Arnold. 1989. Visualizing multivariate selection. *Evolution* 43:1209–1222.
- Pigeon, G., M. Festa-Bianchet, D. W. Coltman, and F. Pelletier. 2016. Intense selective hunting leads to artificial evolution in horn size. *Evol. Appl.* 9:521–530.
- Plabon, C., T. F. Hansen, A. J. R. Carter, and D. Houle. 2010. Evolution of variation and variability under fluctuating, stabilizing, and disruptive selection. *Evolution* 64:1912–1925.
- Plard, F., J. M. Gaillard, T. Coulson, A. J. M. Hewison, D. Delorme, C. Warnant, and C. Bonenfant. 2014. Mismatch between birth date and vegetation phenology slows the demography of roe deer. *PLoS Biol.* 12:e1001828.
- Plard, F., J. M. Gaillard, T. Coulson, A. J. M. Hewison, M. Douhard, F. Klein, D. Delorme, C. Warnant, and C. Bonenfant. 2015. The influence of birth date via body mass on individual fitness in a long-lived mammal. *Ecology* 96:1516–1528.
- Post, E., and M. C. Forchhammer. 2008. Climate change reduces reproductive success of an arctic herbivore through trophic mismatch. *Philos. Trans. R. Soc. B-Biol. Sci.* 363:2369–2375.
- Post, E., P. S. Boving, C. Pedersen, and M. A. MacArthur. 2003. Synchrony between caribou calving and plant phenology in depredated and non-depredated populations. *Can. J. Zool.-Rev. Can. Zool.* 81:1709–1714.
- Post, E., M. C. Forchhammer, M. S. Bret-Harte, T. V. Callaghan, T. R. Christensen, B. Elberling, A. D. Fox, O. Gilg, D. S. Hik, T. T. Hoye, et al. 2009. Ecological dynamics across the arctic associated with recent climate change. *Science* 325:1355–1358.
- Postma, E. 2006. Implications of the difference between true and predicted breeding values for the study of natural selection and micro-evolution. *J. Evol. Biol.* 19:309–320.
- R Price, G. 1970. Selection and covariance. *Nature* 227:520–521.
- Price, G. R., and C. A. B. Smith. 1972. Fishers Malthusian parameter and reproductive value. *Ann. Hum. Genet.* 36:1–7.
- R Core Team. 2019. *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Revell, L. J., D. L. Mahler, J. R. Sweeney, M. Sobotka, V. E. Fancher, and J. Losos. 2010. Nonlinear selection and the evolution of variances and covariances for continuous characters in an anole. *J. Evol. Biol.* 23:407–421.
- Reynolds, R. J., D. K. Childers, and N. M. Pajewski. 2010. The distribution and hypothesis testing of eigenvalues from the canonical analysis of the gamma matrix of quadratic and correlational selection gradients. *Evolution* 64:1076–1085.
- Ridley, M. 2004. *Evolution*. 3rd ed. Wiley, Oxford, U.K.
- Robertson, A. 1966. A mathematical model of culling process in dairy cattle. *Anim. Prod.* 8:95–108.
- T Rutberg, A. 1987. Adaptive hypotheses of birth synchrony in ruminants: an interspecific test. *Am. Nat.* 130:692–710.
- Røed, K. H., Ø. Holand, M. E. Smith, H. Gjostein, J. Kumpula, and M. Nieminen. 2002. Reproductive success in reindeer males in a herd with varying sex ratio. *Mol. Ecol.* 11:1239–1243.
- Schluter, D., and D. Nychka. 1994. Exploring fitness surfaces. *Am. Nat.* 143:597–616.
- Simpson, G. G. 1944. *Tempo and mode in evolution*. Columbia Univ. Press, New York, NY.
- Sinervo, B., and E. Svensson. 2002. Correlational selection and the evolution of genomic architecture. *Heredity* 89:329–338.
- Skogland, T. 1989. *Comparative social organization of wild reindeer in relation to food, mates and predator avoidance*. P. Parey Scientific Publishers, Berlin, Germany.
- Solberg, E. J., M. Garel, M. Heim, V. Grøtan, and B.-E. Sæther. 2008. Lack of compensatory body growth in a high performance moose *Alces alces* population. *Oecologia* 158:485–498.
- Stinchcombe, J. R., A. F. Agrawal, P. A. Hohenlohe, S. J. Arnold, and M. W. Blows. 2008. Estimating nonlinear selection gradients using quadratic regression coefficients: double or nothing? *Evolution* 62:2435–2440.
- Stockinger, D. E., A. E. Torrence, R. R. Hukkanen, K. W. Vogel, C. E. Hotchkiss, and J. C. Ha. 2011. Risk factors for dystocia in pigtailed macaques (*Macaca nemestrina*). *Comparative Med.* 61:170–175.
- Svensson, E. I., and R. Calsbeek. 2013. *The adaptive landscape in evolutionary biology*. Oxford Univ. Press, Oxford, U.K.
- Sztepanacz, J. L., and M. W. Blows. 2017. Artificial selection to increase the phenotypic variance in gmax fails. *Am. Nat.* 190:707–723.
- Sæther, B.-E., and S. Engen. 2015. The concept of fitness in fluctuating environments. *Trends Ecol. Evol.* 30:273–281.
- Sæther, B.-E., T. Coulson, V. Grøtan, S. Engen, R. Altwegg, K. B. Armitage, C. Barbraud, P. H. Becker, D. T. Blumstein, F. S. Dobson, et al. 2013. How

- life history influences population dynamics in fluctuating environments. *Am. Nat.* 182:743–759.
- H van Tienderen, P. 2000. Elasticities and the link between demographic and evolutionary dynamics. *Ecology* 81:666–679.
- Travis, J. 1989. The role of optimizing selection in natural populations. *Annu. Rev. Ecol. Syst.* 20:279–296.
- C Tyler, N. J. 1987. Fertility in female reindeer the effects of nutrition and growth. *Rangifer* 7:37–41.
- Uyeda, J. C., T. F. Hansen, S. J. Arnold, and J. Pienaar. 2011. The million-year wait for macroevolutionary bursts. *Proc. Natl. Acad. Sci. USA* 108:15908–15913.
- Via, S., and R. Lande. 1985. Genotype-environment interaction and the evolution of phenotypic plasticity. *Evolution* 39:505–522.
- E Visser, M. 2008. Keeping up with a warming world; assessing the rate of adaptation to climate change. *Proc. R. Soc. B-Biol. Sci.* 275:649–659.
- W Blows, M. 2007. A tale of two matrices: multivariate approaches in evolutionary biology. *J. Evol. Biol.* 20:1–8.
- Walsh, B., and M. W. Blows. 2009. Abundant genetic variation plus strong selection = multivariate genetic constraints: a geometric view of adaptation. *Annu. Rev. Ecol. Evol. Syst.* 40:41–59.
- Weladji, R. B., O. Holand, J. M. Gaillard, N. G. Yoccoz, A. Mysterud, M. Nieminen, and N. C. Stenseth. 2010. Age-specific changes in different components of reproductive output in female reindeer: terminal allocation or senescence? *Oecologia* 162:261–271.
- Wilson, A. J., J. G. Pilkington, J. M. Pemberton, D. W. Coltman, A. D. J. Overall, K. A. Byrne, and L. E. B. Kruuk. 2005. Selection on mothers and offspring: whose phenotype is it and does it matter? *Evolution* 59:451–463.
- Wright, S. 1932. The roles of mutation, inbreeding, crossbreeding and selection in evolution. *Proc. Sixth Int. Congr. Genet.* 1:356–366.

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1: Cause of death and morphology in a population of semidomestic reindeer in northern Finland.

Figure S2: The observed change in mean female birth date (A) and mean female birth mass (C) among cohorts during the study period of a semidomestic reindeer population in northern Finland.

Table S1: Demographic estimates of female reindeer in a semidomestic population in northern Finland.

Table S2: Estimates of age-specific selection on birth date (*i*) and birth mass (*j*) per age class in a population of semidomestic reindeer in northern Finland.