

Eleonora Lydia Jenisch

Phenotypic selection in an arctic ungulate population under rapid environmental change

Master's thesis in Biology

Supervisor: Henrik Jensen, Brage Bremset Hansen

May 2024

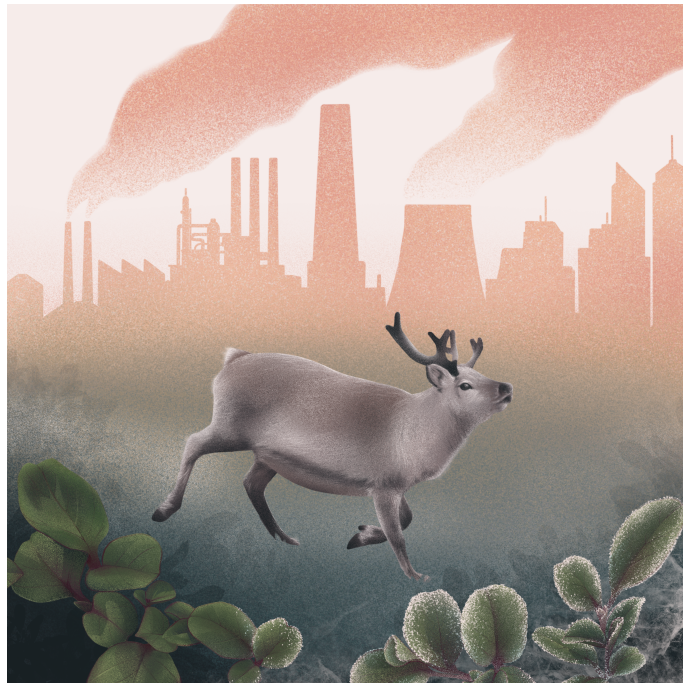


Illustration by Liliانا Jenisch

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Abstract

The rapidly changing climate poses a challenge to many natural populations that cannot disperse elsewhere and must adapt to changing conditions. Ecological factors, population dynamics and genetic background are needed to predict the potential ecological and evolutionary trajectories of these wild populations. Svalbard reindeer are found in a climate change hotspot with little room for range shift and much is known about the population dynamics and ecological interactions, posing an ideal study organism for analysing evolutionary processes. Here, I investigated Svalbard reindeer subpopulations in north-western Spitsbergen for strength and direction of natural selection acting on different phenotypic traits measured in late winter. A mark-recapture study from 2014-2022 with focus on female individuals was used to analyse selection in combination with a genetic pedigree created to support the observation data. Two reproductive fitness components and one viability fitness component were used, namely status of pregnancy in late winter, presence of calf at heel in summer, and survival to the next year. Evidence was found for positive selection on body mass, body condition, leg length and antler size. There was no evidence for selection acting on measurable backfat, however this trait is notoriously hard to measure in the field. Furthermore, there was weak evidence for stabilising selection on antler size with survival as the fitness component. This confirms previous studies that body mass plays an important role in reproductive success of Svalbard reindeer, indicating that higher body mass and better body condition may result in higher population growth rates. Animals in good condition and higher body mass (in late winter) will have an advantage, which is important considering increasing unpredictability in access to forage in winter due to climate change. Results of this study accentuate that individual phenotypic characteristics may influence population dynamics in Svalbard reindeer, and hence emphasize the importance of understanding the evolutionary processes in natural populations inhabiting rapidly changing environments. Crucial future steps are then to investigate the heritable genetic basis of the traits under selection and map the genes for these traits to better understand their genetic architecture and adaptive potential.

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Table of Contents

<i>Abstract</i>	<i>i</i>
<i>Acknowledgements</i>	<i>ii</i>
<i>Introduction</i>	<i>1</i>
Research question and aims	4
<i>Materials & Methods</i>	5
Study area and study species.....	5
Data set and Svalbard reindeer samples.....	5
DNA extractions	6
Genotyping.....	6
SNP filtering	7
Statistical analysis	8
Selection analyses	9
<i>Results</i>	14
Pedigree and CMR comparison	14
Selection analyses	15
<i>Discussion</i>	17
<i>Conclusion</i>	27
<i>Tables</i>	28
<i>Figures</i>	33
<i>References</i>	38
<i>Appendices</i>	47
Appendix A: DNA extraction steps	47
Appendix B: Tables with AIC results – models with or without interactions.....	48
Appendix C: Table with pedigree results.....	51
Appendix D: Correlation of morphological traits for different age classes.....	60
Appendix E: Model results with quadratic term of the phenotypic trait measure	62
Appendix F: Overview table of different combinations in selection models	66

Introduction

Climate change is causing a rapid shift in environmental conditions worldwide, which can be seen especially in Arctic environments (Hinzman *et al.*, 2005). Change in environmental conditions will also change selection pressures on populations, but genetic evidence of evolutionary changes in wild populations due to climate change is sparse (Merilä, 2012). Predicting the ecological and evolutionary responses of a population to climate change is extremely difficult and requires extensive information on the population's genetics, ecology, and population dynamics as well as interactions of factors (Holt, 1990). When dealing with changing environments, species may need to move to a more favourable environment to survive or must adapt to the changing conditions. In natural populations that are not able to disperse to other environments in response to rapid climate change, evolutionary adaptation will likely play an important role (Hoffmann and Sgró, 2011). Natural selection acts on phenotypes and effects can be seen, regardless of heredity of traits and separate from evolution (Arnold and Wade, 1984). Evolutionary responses to natural selection are, however, considered as changes in allele frequencies of genes underlying phenotypic traits from one generation to the other, and evolutionary responses are therefore reliant on heritable genetic variation (Lande and Arnold, 1983; Falconer and Mackay, 1996). Evolutionary response to selection is thus differentiated from phenotypic selection. With that in mind, calculating the direction and strength of any phenotypic selection is an important step in evaluating the future evolutionary response to natural selection of a population (Lande and Arnold, 1983).

There is a growing number of studies on the strength and direction of selection in wild populations of many different species (as reviewed in e.g. Hoekstra *et al.*, 2001). Still, calculating selection gradients in natural populations is challenging. It is often difficult to obtain individual measures of important phenotypic traits and fitness-components in natural populations (Mcgraw and Caswell, 1996). Long-term data of fitness-related phenotypic traits and reliable fitness measures of populations are needed. This requires observation data over a long period or genetic data with which fitness can be estimated (Ellegren and Sheldon, 2008). It can be challenging for species that are not easily accessible or where costs limit the genotyping of large numbers of individuals.

Fitness of an individual can be measured by survival or reproduction of the individual (Benton and Grant, 2000; Sæther and Engen, 2015). Higher reproduction of an individual over its

lifetime compared to other individuals in the population approximates to a higher fitness. To measure reproductive fitness, studies can make use of detailed pedigrees to confirm relatedness of certain individuals and count the number of offspring. Pedigrees can be constructed with the use of observation and documentation of offspring and parents (Alif *et al.*, 2022). More recently, methods have been developed to create genetic pedigrees that can be constructed by using single nucleotide polymorphism (SNP) data providing relationship details between individuals (Glaubitz, Rhodes and Dewoody, 2003; Huisman, 2017). Genetic pedigrees have been used to complete observational pedigrees and genomic data can be an important tool for estimating relatedness and parental relationships in conservation programmes (Galla *et al.*, 2020).

One of the roadblocks inhibiting populations to adapt to changing environments and climatic conditions is reduced genetic diversity (Lande and Barrowclough, 1987). A study using genetic data of wild Svalbard reindeer (*Rangifer tarandus platyrhynchus*) by Peeters *et al.* (2020) showed that sea ice loss due to climate change contributes to genetic isolation of subpopulations. Recent insights in genetic diversity and genomic consequences on the Svalbard reindeer have been achieved related to implications of colonisation (Hold *et al.*, 2024), long-term isolation (Dussex *et al.*, 2023), overharvesting (Kellner *et al.*, 2024) and anthropogenic reintroduction (Burnett *et al.*, 2023) of the high-arctic reindeer. Analysing the genetic makeup of species and which phenotypic traits correspond to which genes will be important in analysing their potential for adapting to the changing environment (Barrett and Schluter, 2008). To do so, knowing which phenotypic traits are important for fitness, i.e. under selection, is the first step before one needs to estimate the adaptive potential of these traits.

Svalbard reindeer – found in a climate change hotspot in the Arctic (Peeters *et al.*, 2019) – are limited in the distance they can migrate (Peeters *et al.*, 2020), and will need to adapt to their future environment in order to survive. Population dynamics and ecological interactions in Svalbard reindeer have been extensively studied (e.g., Solberg *et al.*, 2001; Hansen *et al.*, 2013; Albon *et al.*, 2017; Brage B. Hansen *et al.*, 2019; Brage Bremset Hansen *et al.*, 2019). Svalbard reindeer population sizes are mostly determined by density dependent factors and stochastic variation in weather (Aanes, Sæther and Øritsland, 2000) and the interaction between these (Brage B. Hansen *et al.*, 2019). Warming of the climate enhances plant growth in the Arctic and it is expected that the carrying capacity of Svalbard reindeer will increase due to more food availability in the summer (Albon *et al.*, 2017), and a longer season (Loe *et al.*, 2021).

Meanwhile, another increasingly occurring effect of climate change in the Arctic, rain-on-snow (ROS) events in winter, can cause an ice cover to form over vegetation, thereby reducing the foraging access to reindeer (Hansen, Aanes and Sæther, 2010). This may result in starvation and reduced body mass (Albon *et al.*, 2017), and thereby reduced survival and calf production during and following those winters (Brage B. Hansen *et al.*, 2019). Warm weather spells (periods) combined with ROS events are becoming more common in wintertime in the Arctic and these will have continued effects on populations depending on access to food sources beneath the snowy now-ice pack (Hansen *et al.*, 2014). All these observed environmental effects are likely to generate associations between several phenotypic traits and fitness components and could link ecological and evolutionary processes. The ecological dynamics of Svalbard reindeer have not yet been linked to selection and evolutionary outcomes and it is urgently needed for understanding the trajectory of the subspecies in face of rapid climate change.

With extensive knowledge on their population dynamics and ecology (e.g. Aanes, Sæther and Øritsland, 2000; Albon *et al.*, 2017; Brage B. Hansen *et al.*, 2019) and increasing access to genetic tools and information (e.g. Peeters *et al.*, 2020; Burnett *et al.*, 2023; Dussex *et al.*, 2023; Kellner *et al.*, 2024), as well as their geographic location, the Svalbard reindeer could thus potentially be an excellent model system to examine how rapid climate change affects ecological and evolutionary processes in natural populations. In the arctic environment, multiple questions arise about how natural selection may be acting on any given phenotypic trait in Svalbard reindeer and how strong the selection may be. The variation in late winter body mass – driven by food availability, affected by weather/climate events and, in turn, affecting survival and reproductive success (Albon *et al.*, 2017) – has demographic consequences (Brage B. Hansen *et al.*, 2019). Hence, body mass is likely to be under selection and a trait that may act as a link between ecological and evolutionary dynamics. Other traits such as backfat, associated with energy reserves, and body condition, strongly related to body mass, are also expected to be important fitness related traits. Body (skeletal) size is, in addition with body mass, used to calculate body condition and thus likely tied to fitness. Similarly, the costly growth of antlers in female reindeer used for defence of feeding grounds has been connected to general condition of the animal (Espmark, 1964; Thomas and Barry, 2005). All of these phenotypic traits are likely particularly important for survival in food scarce environments. Therefore, all of these traits should be considered in affecting individual fitness and thus expected to likely be under selection. Quantitative genetic analyses of selection on

morphological and life history traits in Svalbard reindeer will provide crucial insight into the need for evolution of Svalbard reindeer in a rapidly changing environment. Furthermore, they will enable future exploration of how the process of adaptation to certain climate conditions interact with ecological dynamics to influence the growth and viability of populations.

Research question and aims

The main aim of this study was to use quantitative methods to investigate selection on phenotypic traits by using data on morphological traits as well as data collected on individual fitness (survival and reproduction) in a mark-recapture study across three sub-populations of Svalbard reindeer. The two main research questions I asked in this project were: What is the strength and direction of selection on key fitness-related morphological traits of Svalbard reindeer? And does direction of selection differ for different phenotypic traits, such as body mass, leg length, body condition, antler size, or backfat? I used observation data collected during a period of several years and used generalized linear mixed models to estimate selection. To support the accuracy and correctness of observation data obtained from the field, I constructed a genetic pedigree based on a single-nucleotide-polymorphism (SNP) array and compared the two datasets.

Materials & Methods

Study area and study species

The study area is found on the island of Spitsbergen in the High Arctic archipelago of Svalbard. The three main study sites, Brøggerhalvøya (78°53'N, 11°34'E), Sarsøyra (78°44'N, 11°42'E) and Kaffiøyra (78°38'N, 11°58'E) are peninsulas situated north-west on the coast of Spitsbergen (Figure 1). The study area will be subsequently referred to as the Ny-Ålesund area, named after a small research settlement, found on the peninsula of Brøggerhalvøya.

The study species is Svalbard reindeer, a subspecies of reindeer endemic to Svalbard. Svalbard reindeer live a predator free life on the arctic tundra – with the exception of rare predation by polar bears (*Ursus maritimus*) (Derocher, Wiig and Bangjord, 2000). Svalbard reindeer were not present in the Ny-Ålesund area for ~ 100 years before the species was reintroduced to the Brøgger peninsula in 1978 (Aanes, Sæther and Øritsland, 2000). The population size increased, and reindeer later migrated to the other peninsulas, Sarsøyra and Kaffiøyra, in the 1990's. Around 500 reindeer are now found in these three sub-populations (Brage Bremset Hansen *et al.*, 2019), but population sizes are highly fluctuating (Aanes, Sæther and Øritsland, 2000). The occurrence of ROS events in Ny-Ålesund (Putkonen and Roe, 2003) and the stepwise recolonization of the area by the reindeer make it convenient for studying interactions between spatial demographic and selection processes.

Data set and Svalbard reindeer samples

Data was collected during an ongoing capture-mark-recapture (CMR) study across several years (2014-2022), led by the Norwegian Polar Institute, in collaboration with the Norwegian University of Science and Technology and the Norwegian Institute for Nature Research. Individual reindeer were captured in the three study locations in late winter and observed in summer. During the late winter (April) capture, reindeer (calves, yearlings, and female adults) were captured by researchers via net from snowmobiles (Albon *et al.*, 2017). The focus of the CMR study was on female reindeer, and only few male calves were captured and marked every year. Morphological information was collected from the reindeer. This included leg length (in mm), body mass (in kg), antler length (left and right; measures in cm on the outside curvature) and back fat depth (mm). Status of pregnancy (live foetus or not) was recorded via ultrasound on yearlings and adults. Yearlings and calves of both sexes were differentiated from adults via size of the individual as well as tooth eruption patterns. Female adults captured in early years

of the study were of unknown age, but as mark-recapture went on the number and proportion of marked adult females of known age increased. Date and location of each capture was recorded. Hair and tissue samples were collected at each capture and made available for DNA extractions in this study. Resighting surveys were performed in all three populations every August by three persons on foot traversing the entire peninsulas. The resighting surveys were an integrated part of total count surveys, as any marked individual seen during the count was identified (by binocular and telescope). For marked adult females it was recorded whether they were seen with calf at heel or not.

DNA extractions

Reindeer DNA extractions from all over the Svalbard archipelago as well as mainland Norway reindeer were used in the following DNA extraction and genotyping process. The genotyping data will be used for other projects performed by other researchers, in addition to the present study, which is why samples of other study locations were included in the extraction and genotyping process. In the present study, 228 samples, originating from the three study subpopulations (Brøgger, Sarsøyra and Kaffiøyra), were included. DNA for SNP (Single Nucleotide Polymorphism) genotyping was extracted from tissue, hair, and bone samples. 34 reindeer samples from the study populations had already been extracted by Peeters *et al.* (2020) and were used for genotyping after sufficient DNA quantity and quality was ensured. This was estimated via NanoDrop® spectrophotometry. All new DNA extractions from the Ny-Ålesund study area (n = 194) were taken from hair or tissue samples and followed the same protocol as previous extractions. Hair extractions were carried out according to procedures done by Peeters *et al.* (2020) following (Walsh, Metzger and Higuchi, 1991) using Chelex® 100 resin from BIORAD (Bio-Rad Laboratories, CA, USA). Tissue sample DNA extractions were performed following the Qiagen DNeasy® Blood & Tissue Handbook and using the Qiagen DNeasy® 96 Blood & Tissue Kit (Qiagen, Valencia, CA) (see Appendix A: DNA extraction steps).

Genotyping

Preparation of samples for genotyping involved arranging plates of 96 samples per plate with DNA concentrations of 40 ng/μl per sample. Correct nucleic acid concentrations were assured by using NanoDrop® spectrophotometry to measure DNA concentrations and adjusting concentrations by adding Buffer AE (for tissue DNA extractions) or nuclease-free water (for hair DNA extractions) to samples that needed dilution. The plates were then transported to the

Centre for Integrative Genetics (CIGENE) laboratory in Ås, Norway, which conducted the genotyping using a custom designed Axiom 625K SNP array (M. Martin, H. Jensen, and B.B. Hansen unpublished). Five plates of 96 samples – including Reindeer DNA extractions from the Ny-Ålesund populations (228 samples) as well as the other reindeer from Svalbard and the mainland – were sent to be genotyped by CIGENE. This also included positive controls (10 pairs of duplicate samples), and one negative control (with only nuclease-free water in the plate well). The duplicate samples from randomly chosen individuals (positive controls) were added to have additional quality control of extraction and SNP-genotyping processes. Quality control (QC) was performed throughout the genotyping procedure by CIGENE to ensure the samples met the quality criteria necessary for good outcome. Four individuals from the Ny-Ålesund study populations were excluded from genotyping after not meeting quality control checks (Dish QC threshold of 0.82 and QC call rate threshold value of 0.97; details found in Axiom™ Genotyping Solution Data Analysis User Guide (Thermo Fisher Scientific Inc.)).

The 10 duplicate samples (positive controls) added to control genotyping processes were checked for IBD values of 0.9800 and higher to pass as the same (duplicate) individuals. Initial analysis of genotyping results showed that one pair of duplicate samples (positive control; 158_1 and 158_2) were instead two genetically different individuals (IBD 0.1383 and IBS value 0.7982; B. Whitley, Unpublished). Both samples were therefore included in the further processing and pedigree building. Two samples supposed to be genetically different (159 and 160) showed up as samples from the same individual (IBD of 0.9969 and IBS 0.9991; B. Whitley, Unpublished), and therefore only one of the duplicate individuals were kept for pedigree building. Other positive controls (duplicate samples) passed quality check and only one of the duplicate samples (same individual) was included in further processing and building of the pedigree. Altogether 222 genotyped individuals from the Ny-Ålesund study population were available for pedigree construction after quality checks and after removing duplicate individuals.

SNP filtering

SNPs were filtered for best quality and usability for future analysis. Accordingly, 237,148 of the 625,857 SNPs on the custom Axiom SNP array passed quality filtering by CIGENE and were recommended for use. Quality criteria included the presence of clear SNP clustering and filtering for Poly High Resolution (PHR) SNPs. Further SNP filtering was done using the open-

source whole genome association analysis toolset, PLINK (Purcell et al., 2007) and later the statistical software R (R Core Team, 2022). The reference genome used for SNP mapping was that of a North American caribou, belonging to the same species as Svalbard reindeer.

In PLINK, a bash script was adapted (H. Burnett, unpublished) for further processing of the genotyping files. The PED file was first converted into a binary format for faster processing. SNPs located on sex chromosomes were excluded from the data. The R package “Sequoia” version 2.4.1 (Huisman, 2017) was used for the parentage analyses and pedigree construction. Sequoia is most efficient when a relatively small (in the order of 1000) number of independent and informative SNPs are used (Huisman, 2017). Hence, prior to Sequoia analyses, the SNP genotype data of the Ny-Ålesund individuals were linkage disequilibrium (LD) pruned in windows of 1000 kilobases (kb) and a step size of 10 kb that greedily pruned any pair of SNPs within the window which had $r^2 > 0.05$. Only SNPs with a minor allele frequency (MAF) > 0.25 were included. The number of SNPs were reduced to 1838 high quality SNPs during the PLINK filtering process. The original file format was then converted into a .RAW format which was imported into R where the final filtering step was carried out.

Statistical analysis

Pedigree construction using SEQUOIA

Prior to parentage and pedigree construction analyses in Sequoia the SNP-genotype data were converted into the Sequoia compatible 1-column-per-marker format. The estimated genotyping error rate was presumed constant across SNPs and the error rate was set to 0.002. A life history file was constructed for all 222 genotyped individuals from the Ny-Ålesund study area using data collected during the CMR study. This included information on ID, sex, birth year (for individuals of known birth year) as well as birth year range (for individuals of unknown birth year) on the 222 individuals. Birth year range consisted of possible minimum and maximum birth years for individuals with unknown birth year. In R, SNPs with high Mendelian error rates (>0.03) were removed, which reduced the number of SNPs to 1599 in the final SNP genotype data set. Using that final SNP genotype data set and the life history file, the pedigree was constructed. Assignments of parent-offspring were made by Sequoia if the likelihood ratio (LLR) between the focal relationship and the most likely alternative were higher than the minimum LLR required for acceptance of the proposed relationship, compared to the next most likely relationship (Huisman, 2017). The default threshold of 0.5 was used.

Quality checks of pedigree and comparison to CMR dataset

The genetic pedigree outcome was cross checked and compared to the capture-mark-recapture (CMR) dataset to rule out any biologically impossible parents and evaluate the quality of both the pedigree and the CMR dataset. Quality checks for the pedigree included that no female was assigned as mother to more than one calf in a given year, as Svalbard reindeer females give birth to only one calf in a year (usually in June (Tyler, 1987)) with no twinning recorded as of yet. Additionally, no female should have been assigned as mother to a calf in years after the female was reported dead (e.g., marked carcass found in the field). Once these criteria had been met, the pedigree was used to assess the quality of the CMR dataset, to determine if it could be used as reliable basis for fitness components in the selection analyses. Several quality checks were performed for the CMR dataset. Females assigned as mothers in the pedigree would most likely have been observed pregnant, if they were measured for pregnancy that late winter. I.e., if the CMR dataset indicated a female as pregnant, it was expected to be true. Females assigned as mothers in the pedigree would normally have been observed with calf at heel, if sighted the previous summer. I.e., if the CMR dataset indicated a female as having a calf at heel, it was expected to be true. Lastly, the physical distance of the (capture location of the) calf to (the capture location of) its genetically assigned mother would be expected to be on average smaller than to other females in the population at that time. Most calves stay close to their mothers during that time of year, but there are exceptions (no quantitative data is available on this; B.B. Hansen, pers. comm.). The reindeer are sometimes in pairs of mother-calf, but more often they are found in larger groups, making it difficult to establish mother-calf relationships just by observations. This is true both in April (during capture time, year t) and in August (during the resighting survey, also year t). These mother-calf distances were compared to distances of calves to all other females captured within the same year (April capture campaign) and same sub-population (excluding the assigned mother). The probability of mother-calf relationship is assumed to decrease with physical distance. This factor was not used as direct validation of the mother assignment but added qualitatively to other ways of checking. A mother far from its calf in April may have been due to differences in the two capture times and movements between them and therefore not necessarily a direct sign of wrong assignment.

Selection analyses

Multiple regression to measure strength and direction of selection

The multivariate version of the Breeder's equation, predicts the evolution of a set of correlated traits:

$$\Delta\mathbf{z} = \mathbf{G}\boldsymbol{\beta}$$

With $\Delta\mathbf{z}$ being a vector of changes in trait mean between generations, \mathbf{G} being a matrix of additive genetic variances and covariances (G-matrix), and $\boldsymbol{\beta}$ a vector of selection gradients, the strength and direction of selection acting on each of the traits (Lande, 1979; Lande and Arnold, 1983).

Selection gradients can be estimated based on individual data using multiple linear regression with phenotypic traits as explanatory variables and a fitness component as the response. In multiple regression, the regression coefficients (the slope of the regression line) represent the selection gradients. The selection gradient shows how much the relative fitness of an individual changes when the morphological trait changes. A unit increase in the trait may decrease or increase the fitness of the individual depending on the selection gradient. A positive value of the selection gradient indicates that an increase in the trait (e.g. a unit increase in leg length) will increase the fitness of the individual by the amount given by the regression coefficient. A negative value of the selection gradient indicates that an increase in the trait (e.g. a unit increase in leg length) will decrease the fitness of the individual by the amount given by the regression coefficient. The standard errors of the regression coefficient represent the uncertainty of the estimate, as estimated by the model.

The Lande and Arnold (1983) approach of measuring natural selection using multiple linear regression rests on several assumptions. The capture-mark-recapture dataset provided morphological as well as fitness data, which was used to measure strength and direction of selection in Svalbard reindeer. Since the fitness components (i.e., pregnancy, calf at heel, individual annual survival) and hence response variables in this study were binary in nature, the assumptions of normality of residuals applied to ordinary least squares estimation were violated. Therefore, generalized linear mixed effect models (GLMMs) with logistic link function were used for the selection analyses. This accounted for the binomial format of the response variable and the random effects (repeated measures) of individual (ID) and year.

Whether selection was stabilizing or disruptive was examined by including the quadratic term of the predictor variable and interpreted accordingly if models resulted in statistically

significant positive or negative quadratic estimates (γ). Positive quadratic selection gradients would represent disruptive selection while negative quadratic selection gradients would represent stabilizing selection.

Status of pregnancy of the female reindeer in late winter (pregnant or not pregnant) as well as observation of female with or without calf at heel in summer were used as fitness components reflecting reproductive fitness of female reindeer. Since Svalbard reindeer do not become pregnant in their first autumn, calves (i.e., the youngest age group) were excluded from the selection analysis using reproductive fitness data. Yearlings - those that become two years old at the time of calving - may on some occasions become pregnant (and still be pregnant in April) and have a calf at heel in the subsequent summer and were therefore included in reproductive fitness models. Reindeer capture occurred in late winter months while calf at heel observations were recorded in summer months. To analyse selection using calf at heel observations from the August resighting survey, morphological trait measurements from April that same year were used.

Survival of the individual from the latest observation (capture or resighting year t) to next recorded year ($t+1$) was used as a fitness component reflecting viability and was assessed by estimating if the animal survived to the next recorded year or not, using observation records. This was possible due to a high rate of April recapture and (especially) August resighting in the three subpopulations (B.B. Hansen pers. comm.). An animal observed was assumed to be alive, i.e. variable "1" for that recorded year and all recorded years until its most recent observation, after which it was assumed to not have survived to the next recorded year, i.e. variable "0" for that recorded (last observation) year. This latter assumption is conservative and will tend to underestimate survival, since not all alive and marked reindeer are recaptured or resighted every year. Unfortunately, no estimates were available on detection probabilities. Since the mean survival for Svalbard reindeer after reaching adulthood is very high (Reimers, 1983; Lee *et al.*, 2015), only the youngest age group (calves and yearlings under 1 year 10 months old in April of that year) was included in selection analysis using survival data. Morphological measurements were taken from the same year of the recorded "alive" observation. Additionally, male and female individuals were included in the survival selection analysis, as opposed to the female only measurements in reproduction models. Pedigree results and male sample size did not allow for quantitative studies and thereby excluded a male analysis on the reproductive side.

April morphological traits used in the selection analysis were hind leg length (to the closest mm), body mass (to the closest 0.5 kg), body condition (see below), antler size (to the closest mm; the mean length of left and right antler measured along the antler from base to furthest tip) and backfat, measured by ultrasound. Due to the zero inflated nature of backfat depth and low precision, backfat depth measurements were converted into a binary variable, with a measured backfat depth of up to 5 millimetres treated as no backfat. Body condition was calculated by using the residuals from the regression of $\log_{10}(\text{body mass})$ on $\log_{10}(\text{leg length})$, with age (as well as sex for the survival analysis) included as a fixed factor. The logarithm of body mass and leg length was used to account for the allometric relationship between body mass and body length (Huxley, 1932). Antler lengths of zero centimetres were removed before analysis, as these individuals had shed one or both antlers. Antler lengths of 0.5 centimetres and above were included in analysis. Additionally, calves were removed from the antler analysis as their antlers are often worn down.

Statistical model selection

Morphological data and fitness data across all years with April capture data (2014-2019 and 2021-2022) were used in statistical models. Data from the three subpopulations (Sarsøyra, Brøggerhalvøya and Kaffiøyra) were pooled to achieve a higher number of observations. Before selecting appropriate models, the morphological traits were checked for any collinearity between traits. Back fat depth and body mass, as well as leg length and body mass were expected to covary, but with varying degree of covariation between age classes. Correlation coefficients ranged from -0.02 for correlation between leg length and back fat depth and up to 0.68 for correlation between body mass and mean antler size in age class 2 (Appendix D). Due to strong collinearity across some traits (Appendix D), one model was fitted for each predictor variable, as to avoid any confounding effects. Year and repeated measures of individuals were accounted for by including year and ID as random factors. Due to the strong age effect on morphological traits, age was always included as a fixed factor. Similarly, sex was included as fixed effect in survival models, as both males and females were included in that analysis.

Individuals were classified into three age classes: Age class 1, 2 and 3. Age class 1 was made up of calves, i.e. 10 months old, at the time of capture in April and yearlings, i.e. 14 months old at the time of resighting in summer. Age class 2 included yearlings, i.e. 22 months old at the time of capture in April and adults, i.e. 26 months old at the time of resighting in summer.

Age class 3 then included any adults of 34 months and older (up to 11 years old) at the time of capture in April.

Different models were first fitted with age class as an interaction between age class (factor) and the phenotypic trait, which gives separate slopes for the different age classes. To decide if models should be run with or without interactions between the phenotypic trait and age class, model selection was performed according to Akaike's Information Criteria (AIC) (Sakamoto, Ishiguro and Kitawaga, 1987; Burnham and Anderson, 1998; Forstmeier and Schielzeth, 2011). Models with the lowest AICc were selected as the "best" model (Appendix B). The same procedure was repeated for sex as fixed factor in survival models. Other factors were also taken into consideration, such as weight of model and p-value of the interaction. Additionally, age class (or sex) interactions were removed if model convergence was influenced by it and caused any problems. Each model (combination of phenotypic trait and fitness component) was also fitted with the quadratic term of the phenotypic trait measure included, to test whether there was evidence for either stabilizing or disruptive selection (Appendix E). Unless otherwise stated, all statistical analyses and modelling were performed in R (R Core Team, 2022) and results are presented in the statistical language of evidence (Muff *et al.*, 2022).

Results

Pedigree and CMR comparison

The full pedigree resulted in 50 mothers (dams) and 6 fathers (sires) assigned among the 222 genotyped individuals (Appendix C). As this result included all parental relationships over the span of 2014 to 2022, the pedigree-based individual reproductive fitness estimates were considered as too low to be used for selection analysis. However, the genetic pedigree was used to perform a quality check of the capture-mark-recapture (CMR) dataset. The quality checks as well as cross comparison between CMR and genetic pedigree increased confidence in the accuracy of the dataset as well as the pedigree and helped validate the use of the observation data for the selection analysis. The occurrence of impossible mothers was ruled out as an important first step to validating the genetic pedigree. The parentage analyses did not assign any females as a mother to more than one calf in a given year (Appendix C). The pedigree did not assign any females as a mother to a calf in the years after the female had died. Additionally, all female adults and calves that had been assigned as mother-calf pairs were from the same subpopulations, thereby adding to the trustworthiness of the parentage assignment and pedigree construction.

When comparing the CMR dataset with the pedigree results, false negatives in the pregnancy section – i.e. a mother assigned in the genetic pedigree, but pregnancy not detected in the CMR dataset – only happened on one occasion (Table 1). False positives – a female that was genotyped and indicated as pregnant by the ultrasound but not as a mother in the genetic pedigree – were not found. False negatives in the calf at heel section – a mother assigned in the genetic pedigree, but not observed with “calf at heel” that summer – were found, as well as (fewer) false positives (Table 1). An estimated 6% false negatives for calf at heel in the CMR dataset was calculated by crosschecking with the pedigree results (sub-setting for calves with genetically known mothers).

For every capture season (April) the distance was calculated between each genotyped calf with known mother (if the mother was also captured with GPS coordinates that same year). The distribution of the mother-calf distances appeared to have predominantly relatively short distances and was right-skewed, i.e., with a few exceptions of long distances (Figure 2). The mean distance of calf to assigned mother was 1433 m (median 463 m), however this included outliers of mothers and calves caught on different days. Considering only mothers and calves

caught on the same day, the mean distance was 1158 m (median 0 m). The distances of calves to all other females captured in the same subpopulation (excluding the assigned mother) appeared to be markedly longer than the distances of the calf to assigned mother (Figure 2). The mean distance of calves (with known mothers) to other female adults in the sub-population was 5241 m (median 5073 m).

Selection analyses

Leg length

My analyses showed no evidence for selection on leg length with either the fitness components pregnancy ($\beta=0.02\pm0.02$, $n=282$, $p=0.70$; Table 2) or calf at heel ($\beta=0.04\pm0.03$, $n=212$, $p=0.20$; Table 3). However, there was evidence for positive selection on leg length with survival as fitness component in the youngest age group ($\beta=0.10\pm0.03$, $n=224$, $p=0.01$; Table 4; Figure 4A). No evidence was found for either stabilizing or disruptive selection on leg length with any of the fitness components.

Body mass

There was strong evidence for positive selection gradients on body mass using fitness components pregnancy ($\beta=0.80\pm0.26$, $n=287$, $p=0.002$; Figure 3A) and calf at heel ($\beta=0.16\pm0.05$, $n=218$, $p=0.001$; Figure 3D). Furthermore, there was evidence for an interaction between body mass and age class (-0.55 ± 0.25 , $p=0.02$) when fitted in the pregnancy model. The interaction term showed that selection gradients in the pregnancy model were equal to $\beta=(0.80-0.55)=0.25\pm\text{SE}$ for age class 3 and $\beta=0.80\pm0.26$ for age class 2. The analysis with survival as fitness component also showed evidence for positive selection on body mass ($\beta=0.22\pm0.08$, $n=224$, $p=0.01$; Figure 4B). No evidence was found for stabilizing or disruptive selection on body mass with any of the fitness components.

Backfat

There seemed to be weak evidence for positive selection on backfat with pregnancy as fitness component ($\beta=0.78\pm0.42$, $n=266$, $p=0.06$). Whereas there was no selection on backfat with either calf at heel ($\beta=-0.26\pm0.64$, $n=191$, $p=0.68$), or survival ($\beta=-0.22\pm0.63$, $n=281$, $p=0.73$) as fitness components. Since backfat was made into a binary variable (having backfat or not), determining stabilising or disruptive selection was not possible.

Antler size

There was weak evidence for positive selection on antler size ($\beta=0.09\pm0.04$, $n=142$, $p=0.04$; Figure 3B) with pregnancy as the fitness component. There was no evidence for any selection acting on antler size with calf at heel ($\beta=-0.01\pm0.03$, $n=117$, $p=0.69$) or survival ($\beta=-0.08\pm0.08$, $n=174$, $p=0.33$) as fitness components. However, there was strong evidence for stabilising selection on antler size ($\gamma=-0.02\pm0.01$, $n=174$, $p=0.004$; Figure 5) with survival as fitness component (Table 5). There was no evidence for either stabilizing or disruptive selection on antler size with any of the other fitness components.

Body condition

There was strong evidence for positive selection on body condition ($\beta: 39.32\pm12.38$, $n=281$, $p=0.001$; Figure 3C) with pregnancy as the fitness component. However, there was no evidence for any selection on body condition in models with calf at heel ($\beta=-4.09\pm10.92$, $n=211$, $p=0.71$) or survival ($\beta=3.32\pm2.53$, $n=223$, $p=0.19$) as fitness components. Here, too, I found no evidence for either stabilizing or disruptive selection on body condition with any of the fitness components.

Discussion

By using a genetic pedigree to verify CMR data and obtain individual measures of three different fitness components I could quantify the strength and direction of selection on five morphological traits in Svalbard reindeer. My analyses showed that there was very strong to moderate evidence for positive selection on body mass, body condition and antler size as well as leg length (Table 2; Table 3; Table 4). I found that there appeared to be considerable variation in the evidence of strength of selection acting on the different phenotypic traits. There was strong evidence for positive selection on body mass acting through all three fitness components (pregnancy Figure 3 (Figure 3A), calf at heel (Figure 3D), and survival (Figure 3B)). There was also evidence for strong positive selection on body condition (Figure 3C), as well as moderate evidence for positive selection on antler size acting through pregnancy (Figure 3B). In contrast, no evidence for any selection on backfat or on leg length with reproductive fitness components was found. Nonetheless, there was moderate evidence for positive selection on leg length in age class 1 with survival as a fitness component and both sexes included (Figure 4A). Additionally, strong evidence was found for stabilising selection on antler size acting through survival (Figure 5).

Strong positive selection was found to act on body mass, with individuals of higher body mass having higher fitness as estimated by all fitness components. Body mass is commonly used as a measure to assess physical condition of ungulates (Parker, Barboza and Gillingham, 2009). Higher body mass usually reflects better physical condition of the animals as well as higher levels of energy reserves (Parker, Barboza and Gillingham, 2009). In Rocky Mountain elk (*Cervus canadensis nelsoni*) the larger the calves are at onset of winter the more days they are likely to survive (Cook *et al.*, 2004). Similar results were found in the white tailed deer (*Odocoileus virginianus*) fawns (Taillon, Sauvé and Côté, 2006). This is emphasized by results in my analyses where positive selection on body mass was found on the youngest age class using the survival fitness component and with both sexes included. Reindeer mortality in wild populations, as well as semi-domesticated reindeer, due to starvation in winter has recently been linked to ROS events in the Arctic tundra with ice restricting access to forage grounds (Hansen, Aanes and Sæther, 2010; Hansen *et al.*, 2011; Forbes *et al.*, 2016). ROS events are expected to become more frequent in the future which will have further implications on population dynamics of reindeer as well as other species in areas affected. Differences in energy reserves – and therefore body mass and overall condition – have previously been found

to play an important role in survival and reproduction of Svalbard reindeer (Pigeon *et al.*, 2022), and the evidence found in this study corroborates this with strong positive selection found especially on body mass.

A study on wild Soay sheep (*Ovis aries*) of St. Kilda showed that with climate change – milder winters and a longer season of grass growth – a higher proportion of small and slow-growing sheep survived the winters, which consequently reduced the average growth of individuals (famously called the “shrinking sheep”) and increased the population size (Ozgul *et al.*, 2009). This is a great example of the demographic change that climate change can induce, and how changing selection pressures (milder winters for the Soay sheep) can affect wild living populations. The warmer and longer seasons of plant growth on Svalbard (Albon *et al.*, 2017; Loe *et al.*, 2021) as well as contrasting ice cover of vegetation due to ROS events in winter (Hansen, Aanes and Sæther, 2010) may similarly change selection pressures on reindeer, and on body mass especially, but more work needs to be done to analyse effects on the wild reindeer.

In female Svalbard reindeer, energy allocation may decide future reproductive success, with body mass and condition being strong determinants (Pigeon *et al.*, 2022). Pregnant individuals have to be heavier due to increased fat (energy) needs to get through the winter and keep/grow the foetus (Pigeon *et al.*, 2022), before giving birth to the calf in the first week of June (Tyler, 1987). Therefore, positive selection on that trait through reproductive fitness components is to be expected and in accordance with the results found here. This also supports studies on ungulates (e.g. Milner *et al.*, 2003; Veiberg *et al.*, 2017) as well as other species (e.g. ground squirrels (Wells *et al.*, 2019) or dabbling ducks (Gloutney and Clark, 1991)), showing the importance of body mass for reproduction of female individuals. Higher body mass in Svalbard reindeer is especially important when environmental conditions are uncertain as, during poor conditions, body mass loss worsens chances of reproductive success (Pigeon *et al.*, 2022). The rate at which reindeer and caribou get pregnant is also highly dependent on weight in autumn (Reimers, 1997). The reindeer are heaviest in autumn, after a summer of grazing on abundant vegetation, and use most of their fat storage in winter. Additional weight of the foetus in influencing effects of body mass on reproductive fitness components is most likely negligible, however should be noted. Overall, my analyses indicate high importance of body mass for all fitness components, regardless of age and most likely in both sexes.

Similar to body mass, body condition, calculated from the regression of body mass on body length, can be used as a direct indication of general condition of the animal (Reist, 1985; Milner *et al.*, 2003). Body condition takes into account the length of the animal, which will reflect overall body size and hence reflect how heavy the individual is (Reist, 1985). Larger/longer and therefore heavier animals are not necessarily in better condition than smaller/shorter and therefore lighter individuals, for example if they are emaciated. Here, evidence was found for positive selection acting on body condition using the pregnancy fitness component, which means that an increase in body condition gives an increase in fitness for the animal. This is expected, as body mass and therefore condition - especially throughout the winter - is a big factor contributing to the ability of the female reindeer to being pregnant and giving birth in June (Veiberg *et al.*, 2017).

No evidence was found that body condition affected either the presence of calf at heel in summer or survival of young (age class 1) individuals to the next year. This is contrary to expectations, as body condition would be expected to have a similar, or possibly even stronger, effect as body mass in all fitness models. The discrepancy may be explained by the fact that in order to become pregnant females must already be in good body condition, yet once they have given birth their body condition may decrease due to the energetic demands of nursing and the mass lost at parturition. Body weight and condition was found to be strongly correlated in red deer (*Cervus elaphus*) and deer in good condition had higher pregnancy rates (Mitchell, McCowan and Nicholson, 1976). That study found a difference in body condition of adult females who were pregnant and lactating versus those who did not have an offspring that year, with lower body weights and fat reserves found in deer that were pregnant and lactating, showing the toll it takes on females to reproduce (Mitchell, McCowan and Nicholson, 1976). It may be possible, therefore, that body condition does not take into account the specific life stage of the adult female, and this could be the case with Svalbard reindeer. Taillon *et al.* (2012) showed that, in caribou, maternal body mass and calf body condition were positively related. Similar results in energetic costs during the lactation period have been found in other mammals, such as the southern right whales (*Eubalaena australis*) where calf growth rate was positively related to body volume loss in the maternal female (Christiansen *et al.*, 2018). The models analysing selection on body condition using the survival fitness component in my study were done on young individuals of both sexes. The body condition of the youngest age class, age class 1, may depend on the body condition of the mother nursing them the previous summer. This may account for the difference in evidence of selection seen in body condition with

pregnancy versus survival as fitness component in my study. Other factors, not included in my analysis may also affect results seen here, and which would need to be investigated. It may be that this type of measure of body condition is not necessarily the best way to capture body condition of Svalbard reindeer and more measures should be explored. As body condition takes into account body size, the difference in calf at heel and survival may be more pronounced here, and not observable in models only looking at selection on body mass.

Moderate evidence for positive selection on antler size was found in models with the pregnancy fitness component. In the antler size model it was important to account for age as a fixed factor since antler growth is age specific (Thomas and Barry, 2005). Growing antlers is a costly feature of female Svalbard reindeer in the sparse arctic environment and may come at a cost in reproduction for the female (Loe *et al.*, 2019). Growing antlers above a certain size may come with high energy demands which would oppose positive selection on antler size. There may thus be advantages as well as disadvantages for females to grow antlers. The advantage has been linked to female reindeer with larger antlers as being able to score better foraging grounds for themselves and their calf (Espmark, 1964). In my analyses, the antler size model with the pregnancy fitness component showed evidence for positive selection in adult females. This may reflect advantages gained from competing for foraging grounds by growing antlers as being enough to offset any energy needs of growing antlers that may as well be allocated to the growing offspring, or its own body mass or fat reserves. It is important to note that antler size could also reflect the conditions of the local environment at the time (Kavan and Anděrová, 2019).

While no evidence for directional selection was found on antler size in survival models, strong evidence for stabilising selection on antler size was shown with the survival fitness component. As mentioned above, antlers above a certain size may be too costly to grow. Antlers of too small a size on the other hand may not bring any advantage in competition, and those individuals may lose out on access to valuable high quality foraging grounds. Interestingly, we can see differences in optimal antler size between the two age classes included in the stabilising selection model using survival as fitness component (Figure 5). There is a cut-off at which point it appears that the younger age group (age class 2) loses any advantage of growing antlers larger than ca. 30 cm, and at which point survival to the next year drops drastically. On the other hand, older individuals (age class 3) have an increasing advantage in growing antlers larger than 30 cm until about 35 cm, when survival to next year also drops, yet not as fast and

as far as younger individuals. Differences here may suggest different strategies in cost allocations as well as perhaps status of pregnancy, which could be included in the model as a next step in further analysis. Yearlings, which are part of age class 2, additionally have smaller antlers than adults, which may be reflected in results found here and not unexpected.

Many factors contribute to leg length in *Rangifer*. Leg length in ungulates is relatively stable once individuals reach adulthood, however there may be variation in leg length due to environmental factors during growth (Terada, Tatsuzawa and Saitoh, 2012) as well as genetic variation (Milner *et al.*, 2000). The interaction of ground and snow conditions and the animal's morphology influences the locomotor movements of ungulates (Parker, Robbins and Hanley, 1984). With increasing leg length an advantage can be found in net energy cost when considering walking and running stretches on hard surfaces and even more so in deep snow (Klein, Meldgaard and Fancy, 1987). While there was moderate evidence for positive selection on leg length, showing higher survival of young individuals with longer legs in both sexes, leg length does not appear to affect reproductive fitness of older individuals. The advantage of increased leg length may be offset by the energy cost of growing longer legs, when foraging on ground devoid of snow cover, as well as heat loss during winter (Klein, Meldgaard and Fancy, 1987). Lack of selection for longer legs across different fitness components in adults would make sense, considering a thin snow cover (snow depths) often found around shore areas and especially if more rain on snow events instead make for a hard ice cover (López-Moreno *et al.*, 2016). The benefit of having longer legs in deep snow cover may be countered by the benefit of having shorter legs for foraging on hard surfaces without snow cover, thereby equalizing any positive or negative selection that could be acting on leg length. An important advantage that Svalbard reindeer have compared to its mainland relative is the lack of predators – except for rare cases (e.g. predation of polar bears; Derocher, Wiig and Bangjord, 2000) – and therefore lack of need for predator avoidance behaviour (Loe *et al.*, 2006). There is no need for speed (with exceptions) and therefore long legs to run fast. Shorter legs also means less energy lost through heat loss due to their high surface to volume ratio and thin insulating hair (Klein, Meldgaard and Fancy, 1987), which would be an argument in favour of no positive selection found on leg length.

It is interesting to see a difference in evidence for selection results between young individuals of both sexes regarding survival, and older, female-only reindeer regarding reproduction models. Since skeletal growth in mammals slows down once reaching adulthood (Lui and

Baron, 2011), differences in skeletal leg length may not be affecting reproductive fitness once females have reached mature age. Leg length is not expected to affect survival in the two older age classes (age class 2 and 3) either, as survival after reaching adulthood is considered very high (Lee *et al.*, 2015), and no selection (variation in fitness) would be observed regarding survival. Hence, why survival has not been used as a fitness component in older age classes in my analyses. Instead, fitness advantages are seen in the youngest age group, which may reflect a multitude of factors mentioned above. Important to note is that body mass and leg length are rather highly correlated in the youngest age group ($r=0.62$; Appendix D). Here, survival of their first winter is highly dependent on energy reserves, and evidence for selection on body mass was found using all three fitness components. Selection observed on leg length in the youngest age group with the survival component may thus reflect selection acting on the highly correlated trait body mass. An option to take a closer look could be to quantify the relative direct and indirect strengths of selection on leg length and body mass for survival in the youngest age class by running a bivariate model that includes both leg length and body mass as covariates. It would make sense that selection on leg length in the youngest age class mirrors selection on body mass (for survival) as they grew both skeleton (leg length) and other tissue (body weight) in parallel during the preceding summer and autumn.

No evidence of selection acting on presence/absence of backfat (depth) was found in this study. Backfat depth is a difficult trait to assess regarding selection, as this trait is zero inflated and considered problematic, also when it comes to measuring in the field. It may introduce problems in the models. The advantage of using backfat depth is that it in theory should be a good indicator of fat reserve of the animal and therefore of energy storage (Nieminen and Laitinen, 1986), which is needed to survive the winter. As with body mass, backfat can be seen as a measure of condition of the animal (Stien *et al.*, 2003). In Svalbard reindeer, the major cause of winter mortality is due to starvation (Reimers, 1983). It would therefore be expected that there is strong selection for increased backfat. The problem with the model results lies more with the inaccuracy of the measurement and the highly zero inflated pattern of the observations. The many zero observations may be explained by the fact that fat is being used up during winter, when forage for food is scarce (Reimers, 1982). There may be nothing left to measure via ultrasound in spring when the reindeer are captured, and back fat depth is measured.

A downside of my analyses is that I did not account for costs of previous reproduction status. Females that have a calf through the summer will spend a lot of energy on lactation/nursing, which will affect their body mass in winter (Mitchell, McCowan and Nicholson, 1976). Costs of previous reproduction status may especially affect results of selection analyses on body mass, backfat and antler size, as these are all closely connected to energy allocation (Nieminen and Laitinen, 1986; Loe *et al.*, 2019; Pigeon *et al.*, 2022). Future analysis could take this into account by splitting analyses into individuals that were recorded with calf at heel and those that were recorded without calf at heel the previous summer (August). However, accounting for costs of previous reproduction would mean a further reduction in sample size, which has to be factored in.

Limitations

Parentages assigned by the Sequoia pedigree are expected to be correct, given the high number of high-quality SNP-genotypes and assignment procedures in Sequoia, which results in high confidence in the outcome. No expected error percentage could be calculated from the pedigree outcome, as it depends on many things such as population structure and variation in genotyping error rates. Extremely low error rates (of < 0.0001) were found by Huisman (2017) when running Sequoia on simulated datasets, where all assumptions are met. Even though this error rate is probably higher in real life datasets, confidence in the outcome is high given the accuracy of the life history data and the low genotyping error rates. As the genetic pedigree is based on likelihood of observed genotypes, the outcome will be more unbiased than field observation of reproductive fitness. Ideally, the pedigree should be used directly as basis for reproductive fitness in the selection analyses. In this study, however, only 50 calves were assigned mothers and six calves were assigned sires over the span of 2014-2021, and this would give extremely low statistical power in the selection analyses. Therefore, I did not attempt to produce a dataset with fitness parameters based on the pedigree. A genetic pedigree with a higher outcome of parentage assignment would be useful in future selection analysis studies as well as other genetic methods such as animal models, to control for relatedness of individuals. To construct such a pedigree many more calves and a higher proportion of adult females (potential mothers) and adult males (potential fathers) in the populations would have to be genotyped. This is slowly being achieved as the CMR is continuously extended with on average close to 50% of the (female) calves being captured annually, thereby increasing the sample size as well as the proportion marked (and sampled for DNA).

Overall, the low error rates found by comparing the genetic pedigree with fitness data collected during the CMR study support the observation data. As with many observation datasets, there is a chance of erroneous observations made by researchers in the field which would affect results of the selection study. The advantage of the study performed here with the CMR dataset is that a crosscheck with the genetically constructed pedigree increases the confidence that observation data from the CMR study can be trusted. False negatives, genetic mothers not shown as pregnant in the CMR dataset, were possible if pregnancy was not detected by ultrasound. As it was expected to only happen on rare occasions, this was not interpreted as an indication of incorrect mother assignment. False positives, pregnant and genotyped females in the CMR but not assigned as mothers in the genetic data were not expected to happen, since if a genetic mother had been assigned as a mother, she would match genetically with the calf. Given that the ages of the mother and calf are correct, the calf could not have been assigned as the mother of what was believed to be its mother. If a calf had another mother that was not genotyped, there would be no “mother” assigned to it. No calf at heel, instead of the expected according to the pedigree assignments, could stem from incorrect observations in summer, with a calculated probability of 6% false negatives (Table 1). This could have happened when the calf was lying somewhere away (unseen) or closer to another female (misleading observation, possibly also leading to false positives). Due to reasons stated above, it happened more likely due to wrong observations in the field than due to wrong genetic assignment. Individuals with large spatial distances to their assigned mother were likely attributed to the fact that mother and calf were captured on different days. The distribution in space could also have been disturbed when the animals were chased around during capture, sometimes several times during the capture season. Confidence in the correctness of both CMR and genetic pedigree was additionally increased since all mother-calf pairs were found to be from the same subpopulations, in spite of very low genetic differentiation between them (Burnett *et al.*, 2023).

Finally, the survival fitness component in my analyses had been determined based on observations of individuals “not seen alive”. An animal observed was assumed to be alive until its most recent observation, after which it was assumed to not have survived to the next year. This latter assumption is highly conservative and will underestimate survival, since not all live marked reindeer are recaptured or resighted. A (future) improvement of the study would be to combine the analyses with mark-recapture models that provide “likelihood” for being alive at any point in time and for each individual. Survival is difficult to assess via the mark-recapture data set used here, as death of an individual is rarely observed, and therefore has been

substituted with “not seen alive” the year before. This can be accurate enough, considering the CMR study has an estimated high recapture rate. The mean survival for Svalbard reindeer, as for most ungulates, after reaching adulthood is very high (Lee *et al.*, 2015), which is why older age groups were not included in the survival selection analysis. Difference in fitness among individuals in older age groups is more likely seen through which individuals get pregnant and give birth to a calf in June.

Further research

Populations experiencing extreme selection pressures due to climate change will increase with the increasing unpredictability of climate conditions world-wide. Species continuously experience changing environmental conditions which changes selection pressures. This has been shown before extensively, as for example in the well-known study on a population of Darwin’s finches experiencing extreme selection pressure on bill shape after a very rainy period followed by two years of drought (Grant and Grant, 1989). Understanding the different selection pressures acting on key morphological traits of populations is important in informing the potential evolutionary trajectories of species. This may be especially important for conservation strategies and mitigating impacts of environmental change on vulnerable species.

My results have shown varying degrees of evidence of selection on morphological traits in Svalbard reindeer. How this has impacted, currently impacts, and will impact the wild population in the future depends on a myriad of factors that still need to be analysed. For example, while strong selection on body weight has been measured in the Soay sheep on St. Kilda (Milner *et al.*, 1999), an evolutionary response by shifting to higher overall body mass does not necessarily follow selection events. Evolutionary change depends on additive genetic variance of the trait (Lande and Shannon, 1996) and opposing selection on correlated traits could limit the evolutionary response to even strong selection acting on heritable traits (Price and Langen, 1992). The strong selection on beak shape observed in the Grant and Grant (1989) study on large cactus finches (*Geospiza conirostris*) has resulted in little to no evolutionary change even though high levels of additive genetic variance was present. Here, selection on beak shape was constraint by phenotypic and genetic correlations in beak morphometrics. Correspondingly, selection on antler size was analysed in a wild population of red deer and had estimated selection and high levels of heritability of the trait, yet no evolutionary response was observed (Kruuk *et al.*, 2002). There, body condition and nutritional state are suggested to affect the potential evolutionary response. More research is crucial in determining the fate and

analysing the future trajectory of isolated populations that will have to adapt to rapid environmental change.

In my analyses I looked at total selection acting on each phenotypic trait. However, it would be interesting to quantify the importance of direct and indirect selection in future studies. After direct and indirect selection has been determined for certain traits, the next step could be to study the heritable genetic basis of any traits under selection. This is necessary to predict rate and direction of evolution. Additive genetic variation underlying the traits under selection is needed for any potential evolutionary impacts of selection acting on populations (Lande and Shannon, 1996). Estimates of additive genetic variance and heritability can be obtained using animal models (Kruuk, 2004; Wilson *et al.*, 2010). Additionally, it is important to map genes of traits under selection to understand better the genetic architecture of these traits (Slate *et al.*, 2010), i.e. to understand how many genes affect these traits, where the genes are found in the genome and how they interact with other genes and the environment. Genetic maps are created to find quantitative trait loci (QTL) which are regions in the genome associated with certain phenotypic traits (Geldermann, 1975), and which will be important in further research analysing the potential of evolutionary adaptation to environmental changes.

Important to note is that the selection slopes estimated in my analyses were based on logistic regression, to accommodate for the binary nature of my fitness components. To use the multivariate breeder's equation to predict expected rate and direction of evolutionary change across generations the parameter estimates from the models in my analyses would first need to be transformed (i.e. converted) into selection gradients using appropriate formulas (Janzen and Stern, 1998; Morrissey and Sakrejda, 2013).

Conclusion

This study provides varying degrees of evidence of selection on phenotypic traits in a natural population located in a climate change hotspot. Selection on body mass was found using all three fitness components: pregnancy, calf at heel and survival. This emphasizes the importance of body mass for populations that must survive a harsh winter with reduced access to forage in winters with unpredictable climate events such as rain-on-snow events. Other fitness related traits have shown evidence of selection, such as body condition, antler size and leg length. To evaluate the response to selection and potential adaptation of the natural population, more research on the genetic architecture and heritability of the traits under selection should be done. Further, possible opposing selection on correlated traits should be analysed, as this can dampen the potential response to selection acting on the traits studied here. Nevertheless, evidence found here can pinpoint future direction on which traits to start looking at first. Most importantly it has been shown that individual phenotypic characteristics may influence population dynamics in Svalbard reindeer, and hence emphasizes the importance of understanding the evolutionary processes and their effects on population dynamics in natural populations inhabiting rapidly changing environments.

Tables

Table 1: Overview of number of females and calves recorded during the CMR study in each respective year (2014-2022) as well as number of females and calves that were genotyped, number of calves that have been assigned to a mother and the number of unlikely mothers found for each year.

Year t	N calves Aug t-1	N calves genotyped (year t)	N genotyped calves with assigned mother (year t)	N ad females Aug t-1	N ad females genotyped and assumed alive that year t	N assigned mothers not observed pregnant in t-1	N assigned mothers not observed with calf in t-1
2014	143	20	4	203	22	0	0
2015	35	10	2	126	37	0	0
2016	53	21	5	191	49	1	0
2017	174	57	17	220	66	0	1
2018	46	15	4	175	107	0	1
2019	115	35	6	232	116	0	1
2020	31	0	0	231	141	0	0
2021	159	27	11	219	139	0	0
2022	62	0	0	192	152	0	0

The year (*t*) represents the year of calf capture. Other columns represent: Number of counted calves of both sexes (*N calves Aug t-1*) as the calves counted in the three populations the summer before the capture. Number of calves genotyped from that field season (*N calves genotyped*). Number of calves genotyped that field season, with a genotyped mother assigned (*N genotyped calves with assigned mother*). Number of counted adult (2+ yr) females in the three populations the summer before the capture (*N ad females Aug t-1*). Accumulated number of adult (at time of sampling) females, that were genotyped and assumed still alive later that year (*N ad females genotyped and alive*). The number of calves that were assigned to "impossible" mothers i.e. not pregnant the previous April (*N assigned mothers not observed pregnant in t-1*). And, lastly, the number of calves that were assigned to "very-unlikely" mothers i.e. not seen with a calf at heel in August (*N assigned mothers not observed with calf in t-1*).

Table 2: Summary of GLMM model results (on logit scale) with pregnancy as the response variable (fitness component). The predictor variables are the morphological traits with age class as a fixed factor (+ without interaction, * with interaction). Parameter estimates represent the slopes of the regression (selection gradients). “Intercepts” are the intercept values of the fixed effects. The slope of body condition is on log of logit scale.

Model name	Fitness component	Predictor variables	Random effects	Intercepts (±SE)	Parameter estimate for the slope β (± SE)	Fixed effects p-values for the slope(s)	Number of observations
Model 1	Pregnancy	leg length + age class	id, year	-3.46 (±5.39) Age class 3: 2.14 (±0.43)	0.02 (±0.02)	0.70	282 (id: 137, year: 8)
Model 2	Pregnancy	body mass * age class	id, year	-31.08 (±9.78) Age class 3: 20.36 (±9.21)	0.80 (±0.26) Body mass:Age class3 -0.55 (±0.25)	0.002 Body mass:Age class 3 0.02	287 (id: 139, year: 8)
Model 3	Pregnancy	backfat + age class	id, year	-1.20 (±0.40) Age class 3: 1.80(±0.40)	0.78 (±0.42)	0.06	266 (id: 136, year: 8)
Model 4	Pregnancy	antler size + age class	id, year	-2.85 (±1.60) Age class 3: 1.13 (±0.91)	0.09 (±0.04)	0.04	142 (id: 89, year: 7)
Model 5	Pregnancy	body condition * age class	id, year	-2.28 (±0.77) Age class 3: 1.13 (±0.91)	39.32 (±12.38) Body condition:Age class3 -20.36 (±11.94)	0.001 0.09	281 (id: 137, year: 8)

Table 3: Summary GLMM model results (on logit scale) with calf at heel as the response variable (fitness component). The predictor variables are the morphological traits with age class as a fixed factor (+ without interaction, * with interaction). Parameter estimates represent the slopes of the regression (selection gradients). “Intercepts” are the intercept values of the fixed effects. The slope of body condition is on log of logit scale.

Model name	Fitness component	Predictor variables	Random effects	Intercepts (\pm SE)	Parameter estimate for the slope β (\pm SE)	Fixed effects p-values for the slope(s)	Number of observations
Model 6	Calf at heel	leg length + age class	id, year	-12.90 (\pm 8.45) Age class 3: 1.10 (\pm 0.65)	0.04 (\pm 0.03)	0.20	212 (id: 109, year: 7)
Model 7	Calf at heel	body mass + age class	id, year	-8.16 (\pm 2.17) Age class 3: -0.44 (\pm 0.75)	0.16 (\pm0.05)	0.001	218 (id: 110, year: 7)
Model 8	Calf at heel	backfat + age class	id, year	-2.35 (\pm 0.72) Age class 3: 1.80 (\pm 0.71)	-0.26 (\pm 0.64)	0.68	191 (id: 105, year: 7)
Model 9	Calf at heel	antler size + age class	id, year	-0.24 (\pm 1.63) Age class 3: -0.11(\pm 1.29)	-0.01 (\pm 0.03)	0.69	117 (id: 70, year: 7)
Model 10	Calf at heel	body condition * age class	id, year	-2.24 (\pm 0.75) Age class 3: 1.37 (\pm 0.64)	-4.09 (\pm 10.92) Body condition:Age class3 15.71 (\pm 11.81)	0.71 0.18	211 (id: 108, year: 7)

Table 4: Summary of GLMM model results (on logit scale) with survival to the next year as the response variable (fitness component). The predictor variables are the morphological traits with sex or age class as a fixed factor (+ without interaction, * with interaction). Parameter estimates represent the slopes of the regression (selection gradients). “Intercepts” are the intercept values of the fixed effects. No repeated measures of individuals in Model 15, therefore “id” was not included as a random effect. The slope of body condition is on log of logit scale.

Model name	Fitness component	Predictor variables	Random effects	Intercepts (\pm SE)	Parameter estimate for the slope β (\pm SE)	Fixed effects p-values for the slope(s)	Number of observations
Model 11	Survival	leg length + sex (only age class 1)	id, year	-22.14 (\pm 8.39) Male: -2.05 (\pm 0.55)	0.10 (\pm0.03)	0.01	224 (id: 224, year: 8)
Model 12	Survival	body mass + sex (only age class 1)	id, year	-3.65 (\pm 2.29) Male: -1.93 (\pm 0.55)	0.22 (\pm0.08)	0.01	224 (id: 224, year: 8)
Model 13	Survival	backfat + age class (only females, no age class 1)	id, year	3.06 (\pm 1.33) Age class 3: -1.44 (\pm 0.76)	-0.22 (\pm 0.63)	0.73	281 (id: 142, year: 8)
Model 14	Survival	antler size * age class (only females, no age class 1)	id, year	3.97 (\pm 2.61) Age class 3: -3.44 (\pm 2.78)	-0.08 (\pm 0.08) Antler size:Age class3 0.11 (\pm 0.09)	0.33 0.24	174 (id: 101, year: 8)
Model 15	Survival	body condition + sex (only age class 1)	year	1.79 (\pm 1.10) Male: -1.42 (\pm 0.48)	3.32 (\pm 2.53)	0.19	223 (year: 8)

Table 5: Summary of the quadratic GLMM result (on logit scale) with strong evidence of selection acting on leg length and survival to the next year as the response variable (fitness component). The predictor variables are antler size, and the quadratic term of antler size, with age class as a fixed factor (* with interaction). “Intercepts” are the intercept values of the fixed effects.

Model name	Fitness component	Predictor variables	Random effects	Intercepts (\pmSE)	Parameter estimate for the slope γ (\pm SE)	Fixed effects p-values for the slope(s)	Number of observations
Model 16	Survival	antler size + antler size ² * age class	id, year	2.95 (\pm 4.03) Age class 3: -11.09 (\pm 4.81)	0.59 (\pm0.21) antler size ² -0.02 (\pm0.01) antler size ² :Age class3 0.01 (\pm0.00)	0.004 0.003 0.01	174 (id: 101, year: 8)

Figures

Figure 1: Map showing the location of the three main study sites (Brøggerhalvøya, Sarsøyra, Kaffiøyra) within the archipelago of Svalbard (inset). The smallest inset shows the location of Svalbard on the world map. The maps were obtained from <https://toposvalbard.npolar.no/> (©Norwegian Polar Institute).



Figure 2: Scatterplot distribution of distances in meters between capture sites of calves of assigned mother-calf pairs with UTM coordinates available and adult females. Different shapes show the capture sites (location). Y-axis shows the mean distance of the genotyped calf to all (genotyped and non-genotyped) adult females in that location in that year. X-axis shows the distance of the calf to its genetically assigned mother. Sample size is reduced since not all of the calf-mother pairs had UTM coordinates available to calculate distance.

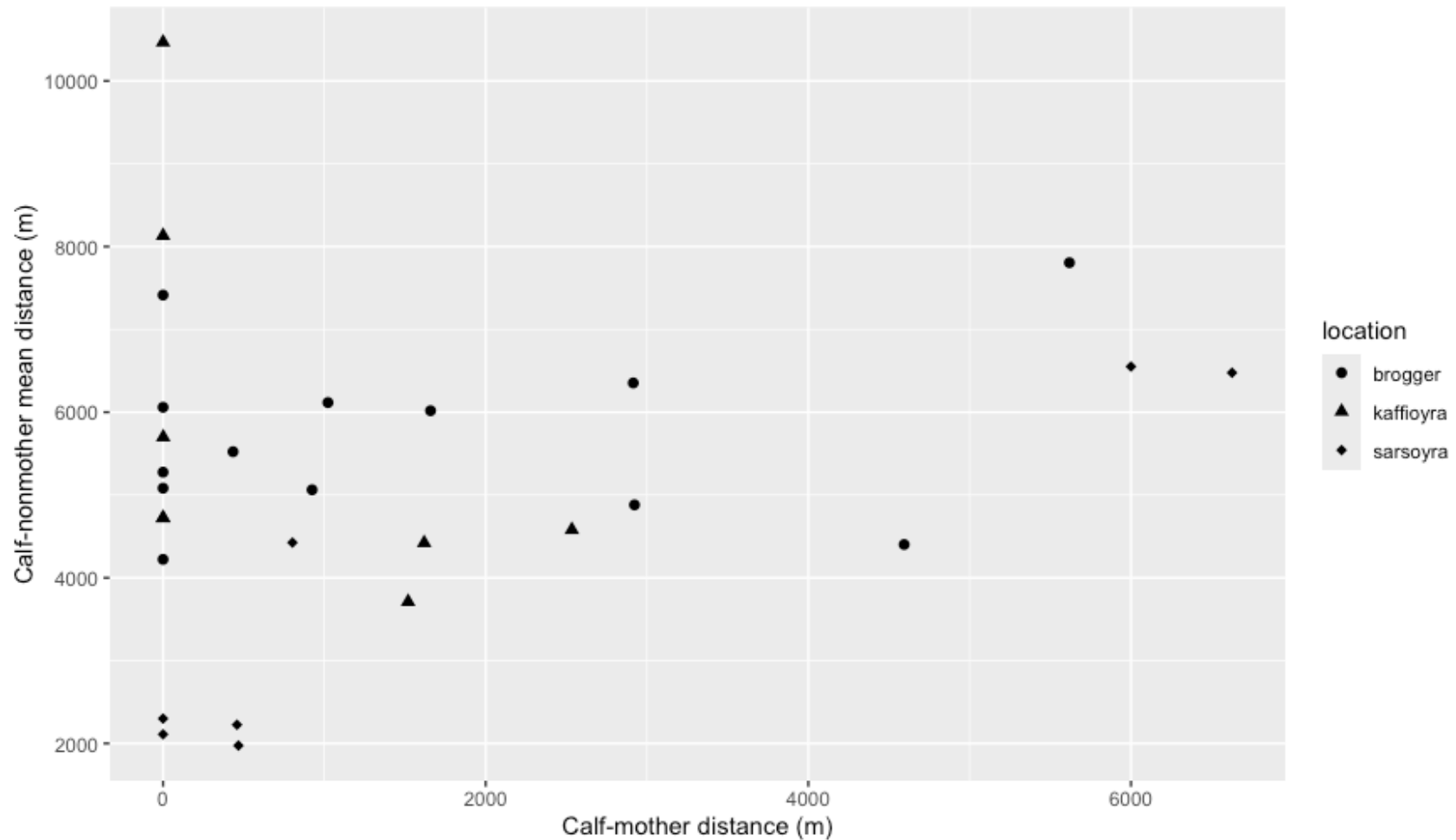


Figure 3: Predicted probabilities of being pregnant in April as a function of (A) body mass, (B) antler size, and (C) log(body condition), and predicted probability of having a calf at heel as a function of (D) body mass. Colour red represents age class 2. Colour blue represents age class 3. Shaded areas represent the 95% confidence interval. Panel (A) shows relationship where evidence for interaction was found between body mass and age class.

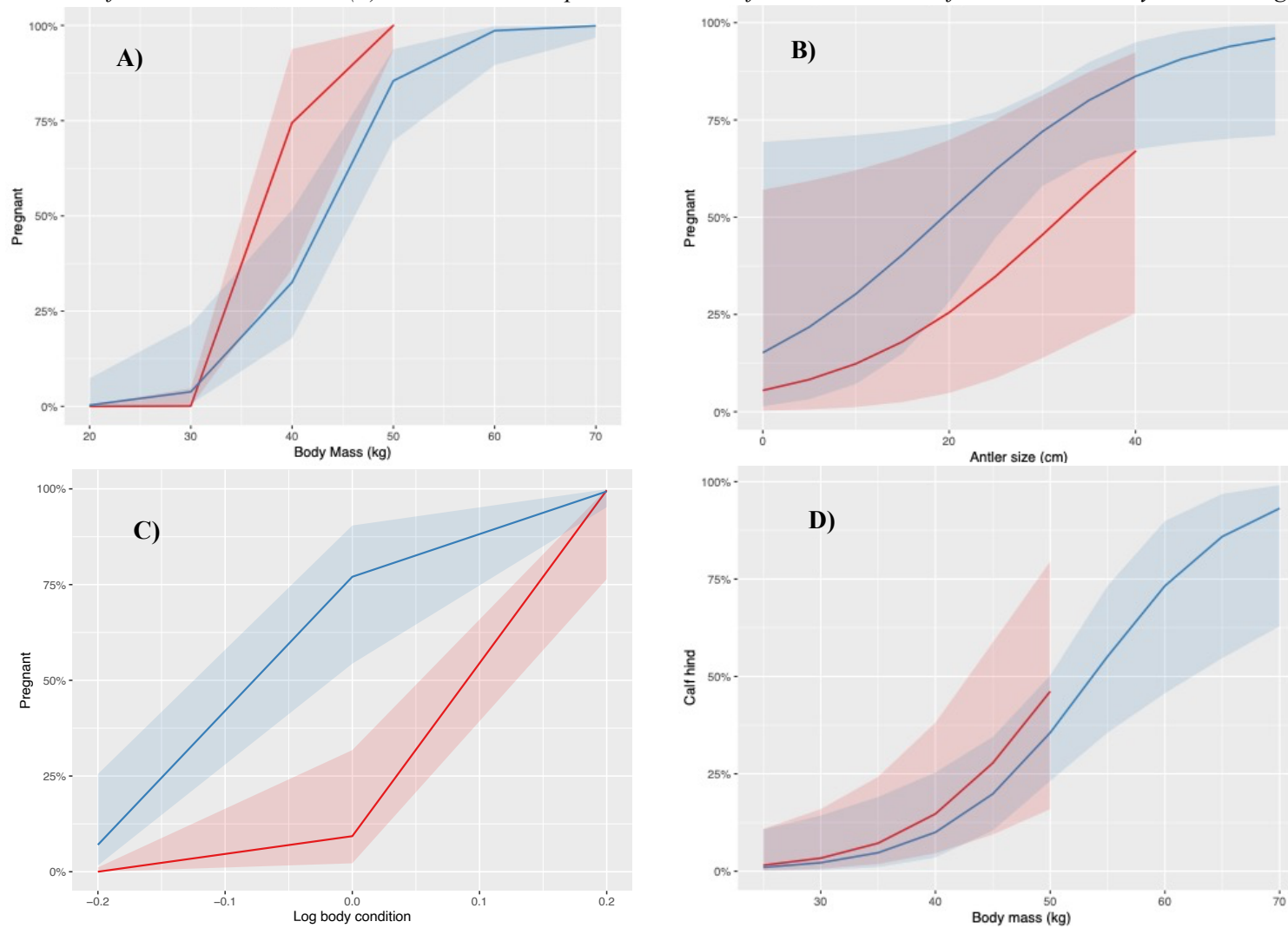


Figure 4: Predicted probabilities of survival from the last observation to the next recorded year as a function of (A) leg length (in mm) and (B) body mass (in kg). Colour red represents the selection curve for females, colour blue represents the selection curve for males. Only age class 1 is included in both analyses. Shaded areas represent the 95% confidence interval.

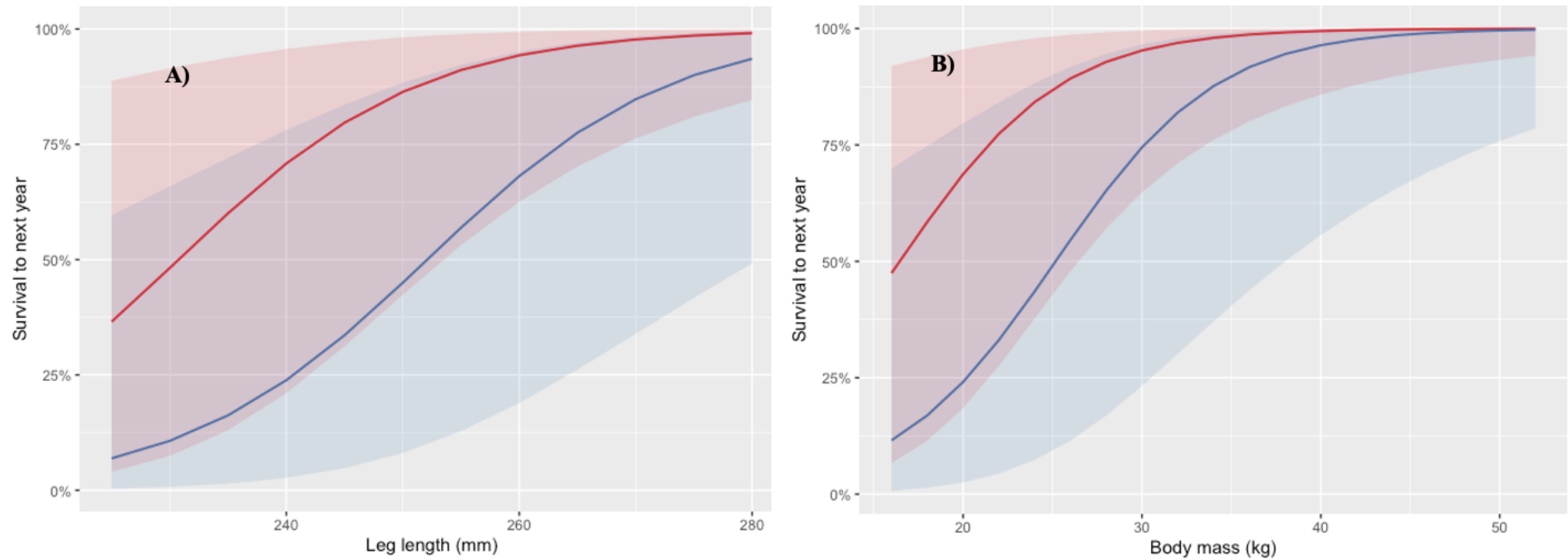
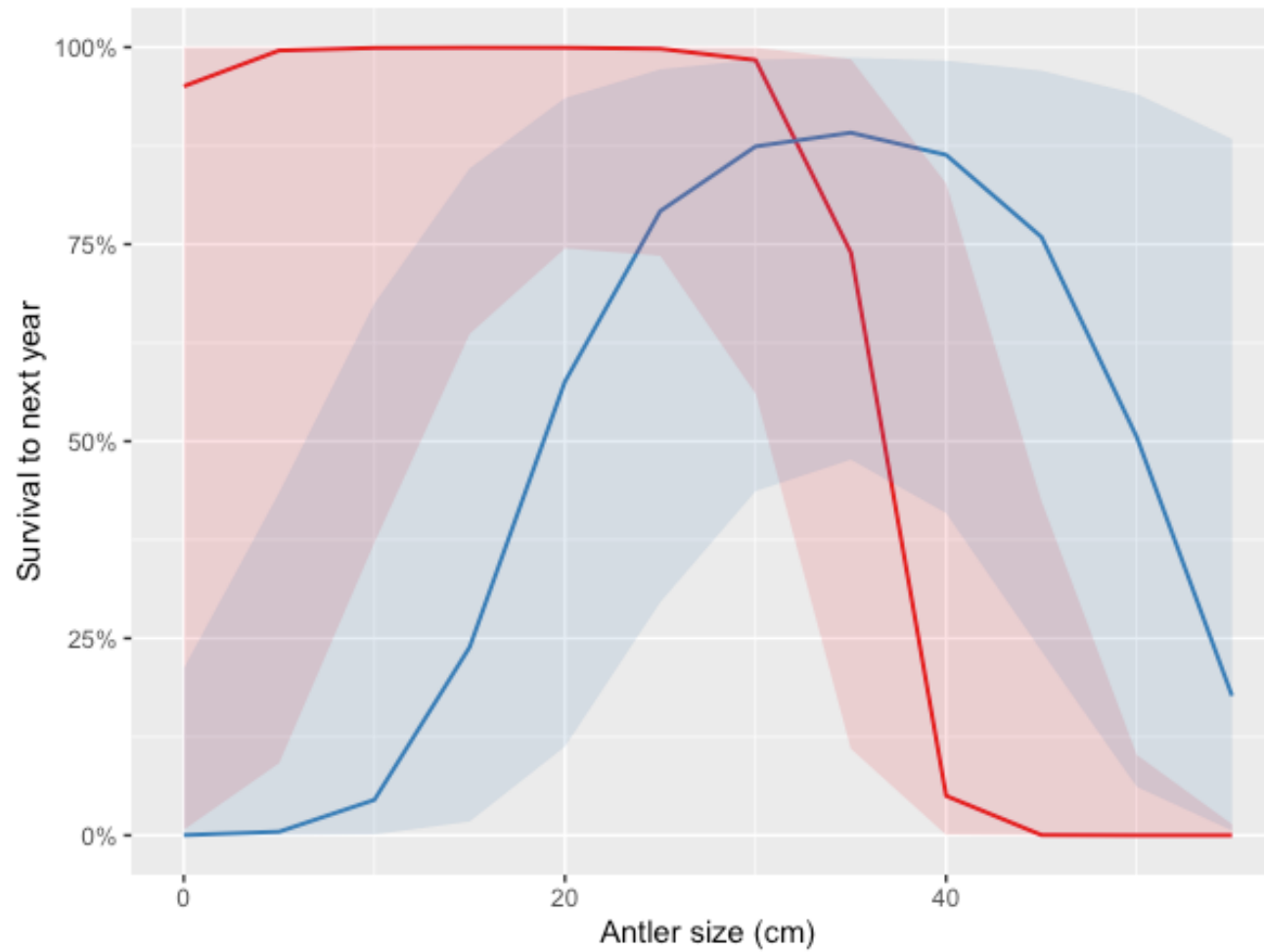


Figure 5: Quadratic relationship between predicted probability of survival of females of reproductive age from the last observation (year t) to the next recorded year (year $t+1$) and antler size (in cm). Here, colour red represents age class 2, colour blue represents age class 3. Shaded areas represent the 95% confidence interval.



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Appendices

Appendix A: DNA extraction steps

Hair sample DNA extraction

Preparation of hair samples involved cutting around 20-30 Svalbard reindeer hair as close to the hair root as possible. To deal with electrostatic, hair was cut on aluminium foil and placed into Eppendorf tubes using tweezers. For each sample, 100 μ l of 14 μ l of proteinase K (20 mg/ml) mixed with 5% Chelex® 100 resin was added to Eppendorf tubes with 20-30 reindeer hair roots. The tubes were incubated in a thermo shaker for one hour at 56°C and subsequently incubated at approximately 95°C for 15 minutes to deactivate the proteinase K. After centrifuging at 20 krpm for one minute, the supernatant was placed in a fresh Eppendorf tube and measured for its DNA concentration using NanoDrop® spectrophotometry. Successfully extracted DNA samples were then stored at -20°C until used for genotyping.

Tissue sample DNA extraction

Preparation for tissue samples involved cutting a small piece of sample tissue (ca. 0.3-0.6 cm) and placing it into individual tubes from the tube rack provided by the Qiagen DNeasy® Blood & Tissue kit. Steps were followed according to the Qiagen DNeasy® protocol and involved overnight incubation of samples. First, 20 μ l of Proteinase K was mixed with 180 μ l of Buffer ATL and added to each sample. Incubation of the samples took place at 56°C overnight in a thermo-shaker at low shake setting. Once centrifuged to collect any matter, 410 μ l of Buffer AL-ethanol was added to the samples and briefly shaken to mix. Using a pipette, 900 μ l of that solution was placed into wells of fresh DNeasy® 96 plates. The plates were sealed with Airpore Tape sheets and, on top of S-Blocks, centrifuged at 4krpm for 15 minutes. The centrifugation was intentionally longer than in the protocol, as the centrifuge in use could not go to as high a speed as indicated in the manual. The next step included adding 500 μ l of Buffer AW1 to each sample and centrifugation at 4krpm for 25 minutes, after resealing. This step was repeated for Buffer AW2 at 4krpm for 10 minutes, but without sealing. Placing the DNeasy® 96 plates on Elution Microtubes, 200 μ l of Buffer AE per sample was added and sealed. After incubating for one minute at room temperature the samples were centrifuged (4krpm) for approximately five minutes. Finally, the microtubes were sealed and kept at -20°C until further use for genotyping.

Appendix B: Tables with AIC results – models with or without interactions

The tables show outcome of model selection, where each response and predictor variable combination was analysed according to Akaike’s Information Criteria (AIC) (Sakamoto, Ishiguro and Kitawaga, 1987; Burnham and Anderson, 1998; Forstmeier and Schielzeth, 2011). Models with the lowest AICc were selected as the “best” model, here shown in bold.

Model name	Response variable	Predictor variables	Random effects	AICc	ΔAIC	Weight	df
Model 1	Pregnancy	leg length + age class	id, year	350.4	0.00	0.65	5
Model 1.2	Pregnancy	leg length * age class	id, year	351.7	1.27	0.35	6
Model 2	Pregnancy	body mass * age class	id, year	304.9	0.00	0.96	6
Model 2.2	Pregnancy	body mass + age class	id, year	311.1	6.26	0.04	5
Model 3	Pregnancy	backfat + age class	id, year	328.6	0.00	0.62	5
Model 3.2	Pregnancy	backfat * age class	id, year	329.5	0.95	0.38	6
Model 4	Pregnancy	antler size + age class	id, year	169.4	0.00	0.59	5
Model 4.2	Pregnancy	antler size * age class	id, year	170.1	0.74	0.41	6
Model 5	Pregnancy	log body condition * age class	id, year	279.7	0.00	0.70	7
Model 5.2	Pregnancy	log body condition + age class	id, year	281.4	1.69	0.30	6

Model name	Response variable	Predictor variables	Random effects	AICc	ΔAIC	Weight	df
Model 6	Calf at heel	leg length + age class	id, year	242.5	0.00	0.74	5
Model 6.2	Calf at heel	leg length * age class	id, year	244.6	2.06	0.26	6
Model 7	Calf at heel	body mass + age class	id, year	236.3	0.00	0.74	5
Model 7.2	Calf at heel	body mass * age class	id, year	238.3	2.08	0.26	6
Model 8	Calf at heel	backfat + age class	id, year	224.2	0.00	1.00	5
Model 8.2	Calf at heel	backfat * age class	id, year	279.7	55.55	0.00	7
Model 9	Calf at heel	antler size + age class	id, year				
Model 9.2	Calf at heel	antler size * age class	id, year	-	-	-	-
Model 10	Calf at heel	log body condition * age class	id, year	234.0	0.2	0.48	6
Model 10.2	Calf at heel	log body condition + age class	id, year	233.8	0.0	0.52	5

Model name	Response variable	Predictor variables	Random effects	AICc	ΔAIC	Weight	df
Model 11	Survival	leg length + sex	id, year	156.7	0.0	0.74	5
Model 11.2	Survival	leg length * sex	id, year	158.8	2.1	0.26	6
Model 12	Survival	body mass + sex	id, year	157.8	0.00	0.67	5

Model 12.2	Survival	body mass * sex	id, year	159.2	1.42	0.33	6
Model 13	Survival	backfat + age class	id, year	179.3	0.00	0.72	5
Model 13.2	Survival	backfat * age class	id, year	181.2	1.88	0.28	6
Model 14	Survival	antler size * age class	id, year	130.2	1.16	0.36	6
Model 14.2	Survival	antler size + age class	id, year	129.0	0.00	0.64	5
Model 15	Survival	log body condition + sex	id, year	161.0	0.00	0.81	4
Model 15.2	Survival	log body condition * sex	id, year	163.8	2.87	0.19	7

Model name	Response variable	Predictor variables	Random effects	AICc	ΔAIC	Weight	df
Model 16	Survival	antler size + antler size² * age class	id, year	123.4	0.00	0.86	7
Model 16.2	Survival	antler size + antler size ² + age class	id, year	127.0	3.56	0.14	6

Appendix C: Table with pedigree results

Table shows outcome of pedigree results with information on the 222 individuals included in the genetic pedigree. “DNA ID” shows individual ID names used during genotyping, while “id” shows individual ID name used in the CMR dataset. “Age” has been sorted into calves (c), yearlings (y), and adults (a). “Cohort” represents the individual’s birth year. If no birth year (cohort) is available, then a minimum and maximum possible birth year has been established. “Mother DNA ID”, “Father DNA ID” and “Offspring DNA ID” are the respective mother, father and offspring assigned to the individual by the Sequoia pedigree.

Sampling year	Location	DNA ID	id	Sex	Age	Cohort	Min. birth year	Max. birth year	Mother DNA ID	Father DNA ID	Offspring DNA ID	Offspring born in year	Comment
2017	Kaffiøyra	100	100	f	c	2016							
2017	Kaffiøyra	101	101	f	c	2016							
2017	Kaffiøyra	102	102	f	c	2016			B115				
2017	Kaffiøyra	103	103	f	c	2016							
2017	Kaffiøyra	104	104	f	c	2016			B99				
2017	Kaffiøyra	105	105	f	c	2016							
2017	Kaffiøyra	106	106	f	c	2016			B111				
2017	Kaffiøyra	107	107	f	c	2016							
2017	Kaffiøyra	108	108	f	c	2016			B116				
2017	Kaffiøyra	109	109	f	c	2016							
2017	Kaffiøyra	110	110	f	c	2016			NyA 39				
2017	Kaffiøyra	111	111	f	c	2016			B102				
2017	Kaffiøyra	112	112	f	c	2016							
2017	Kaffiøyra	113	113	f	a	NA	2000	2014					
2017	Kaffiøyra	114	114	f	c	2016			B101				
2017	Kaffiøyra	115	115	f	a	NA	2013	2015					

2017	Kaffiøyra	116	116	f	c	2016			B9				
2017	Kaffiøyra	117	117	f	a	NA	2000	2014			118	2016	
2017	Kaffiøyra	118	118	f	c	2016			117				
2017	Kaffiøyra	119	119	f	c	2016							
2017	Kaffiøyra	120	120	f	c	2016							
2017	Sarsøyra	121	121	f	c	2016							
2017	Sarsøyra	122	122	f	c	2016							
2017	Sarsøyra	123	123	f	c	2016							
2017	Sarsøyra	124	124	f	c	2016					211	2020	
2017	Sarsøyra	125	125	f	c	2016					205	2020	
2017	Sarsøyra	126	126	f	c	2016							
2017	Sarsøyra	127	127	f	c	2016							
2017	Sarsøyra	128	128	f	c	2016							
2017	Sarsøyra	129	129	f	c	2016							
2017	Sarsøyra	130	130	f	c	2016							
2017	Sarsøyra	131	131	f	c	2016					208	2020	
2017	Sarsøyra	132	132	f	c	2016			T27				
2017	Sarsøyra	133	133	f	c	2016							
2017	Sarsøyra	134	134	f	c	2016							
2017	Sarsøyra	135	135	f	c	2016							
2017	Sarsøyra	136	136	f	c	2016							
2017	Brøgger	138	138	f	c	2016							
2017	Brøgger	139	139	f	c	2016							
2017	Brøgger	140	140	f	c	2016							
2017	Brøgger	141	141	f	c	2016							
2017	Brøgger	142	142	f	c	2016							
2017	Brøgger	143	143	f	c	2016							
2017	Brøgger	145	145	f	c	2016			B124				
2017	Brøgger	146	146	f	c	2016			B15				

2017	Brøgger	147	147	f	c	2016							
2017	Brøgger	148	148	f	c	2016							
2017	Kaffiøyra	14	14	m	c	2016							
2017	Brøgger	151	151	f	c	2016							
2018	Brøgger	152	152	f	c	2017			Y41 2				
2018	Brøgger	153	153	f	c	2017			B18				
2018	Brøgger	154	154	f	c	2017							
2018	Kaffiøyra	155	155	f	c	2017							
2018	Kaffiøyra	156	156	f	c	2017							
2018	Sarsøyra	157	157	f	c	2017							
2018	Kaffiøyra	158 1	158	f	c	2017					220	2020	
2018	Brøgger	159	159	f	c	2017							genetically identical to NyA 160*
2017	Kaffiøyra	15	15	m	c	2016			B109				
2018	Brøgger	161	161	f	c	2017							
2018	Brøgger	162	162	f	c	2017					224	2020	
2019	Brøgger	163	163	f	c	2018							
2019	Brøgger	164	164	f	c	2018							
2019	Sarsøyra	165	165	f	c	2018							
2019	Sarsøyra	166	166	f	c	2018							
2019	Sarsøyra	167	167	f	c	2018							
2019	Sarsøyra	168	168	f	c	2018					206	2020	
2019	Sarsøyra	169	169	f	y	2017							
2017	Kaffiøyra	16	16	m	c	2016							
2019	Sarsøyra	170	170	f	c	2018							
2019	Brøgger	171	171	f	c	2018							
2019	Brøgger	172	172	f	c	2018							
2019	Brøgger	173	173	f	c	2018							

2019	Brøgger	174	174	f	c	2018			B81				
2019	Sarsøyra	175	175	f	c	2018							
2019	Sarsøyra	176	176	m	c	2018							
2019	Sarsøyra	177	177	m	c	2018							
2019	Kaffiøyra	178	178	m	c	2018			NyA 39				
2019	Kaffiøyra	179	179	f	c	2018							
2017	Kaffiøyra	17	17	m	c	2016			B106				
2019	Kaffiøyra	180	180	f	c	2018			B9				
2019	Kaffiøyra	181	181	f	c	2018							
2019	Kaffiøyra	182	182	f	c	2018							
2019	Kaffiøyra	183	183	m	c	2018							
2019	Kaffiøyra	184	184	f	c	2018							
2019	Kaffiøyra	185	185	f	c	2018							
2019	Kaffiøyra	186	186	f	c	2018							
2019	Kaffiøyra	187	187	f	c	2018							
2019	Kaffiøyra	188	188	f	c	2018			T29				
2019	Kaffiøyra	189 2	189	f	c	2018							
2017	Kaffiøyra	18	18	m	c	2016							
2019	Kaffiøyra	190	190	f	c	2018							
2019	Kaffiøyra	191	191	f	c	2018							
2019	Kaffiøyra	192	192	f	c	2018							
2019	Brøgger	193	193	f	c	2018							
2019	Brøgger	194	194	f	c	2018			B14				
2019	Brøgger	195	195	m	c	2018			B96	B88			
2019	Sarsøyra	196	196	m	c	2018							
2019	Sarsøyra	197	197	m	c	2018							
2019	Brøgger	198	198	m	c	2018				B90			
2021	Brøgger	199	199	f	c	2020							
2021	Brøgger	201	201	m	c	2020			Y98				

2021	Brøgger	202	202	f	c	2020			B16	NyA 12			
2021	Brøgger	203	203	f	c	2020							
2021	Sarsøyra	204	204	f	c	2020							
2021	Sarsøyra	205	205	f	c	2020			125				
2021	Sarsøyra	206	206	f	c	2020			168				
2021	Sarsøyra	207	207	f	c	2020			B105				
2021	Sarsøyra	208	208	f	c	2020			131				
2021	Sarsøyra	209	209	m	c	2020							
2021	Sarsøyra	210	210	m	c	2020							
2021	Sarsøyra	211	211	f	c	2020			124				
2021	Sarsøyra	212	212	f	c	2020							
2021	Sarsøyra	213	213	f	c	2020			T41				
2021	Sarsøyra	214	214	m	c	2020							
2021	Brøgger	215	215	f	c	2020							
2021	Brøgger	216	216	f	c	2020							
2021	Sarsøyra	217	217	f	c	2020				T32			
2021	Sarsøyra	218	218	m	c	2020				T36			
2021	Sarsøyra	219	219	m	c	2020							
2021	Brøgger	220	220	f	c	2020			158 1				
2021	Brøgger	221	221	f	c	2020							
2021	Brøgger	222	222	m	c	2020							
2021	Brøgger	223	223	m	c	2020							
2021	Brøgger	224	224	m	c	2020			162	X9			
2021	Brøgger	225	225	f	c	2020							
2021	Brøgger	226	226	m	c	2020			B18				
2014	Kaffiøyra	B100	Y51	m	c	2013							
2014	Kaffiøyra	B101	Y52	f	c	2013					114	2016	
2014	Kaffiøyra	B102	Y53	f	c	2013					111	2016	
2014	Kaffiøyra	B103	Y59	f	a	NA	2006	2011					

2014	Kaffiøyra	B104	Y61	f	c	2013			B11				
2014	Kaffiøyra	B105	Y64	f	c	2013					207	2020	
2014	Kaffiøyra	B106	Y65	f	c	2013					17	2016	
2014	Kaffiøyra	B107	Y66	f	c	2013							
2014	Kaffiøyra	B108	Y67	f	c	2013							
2014	Kaffiøyra	B109	Y68	f	c	2013					15	2016	
2014	Kaffiøyra	B10	34	f	a	NA	2000	2011					
2014	Kaffiøyra	B110	Y69	f	c	2013							
2014	Kaffiøyra	B111	Y70	f	c	2013					106	2016	
2015	Kaffiøyra	B112	1	m	c	2014							
2015	Kaffiøyra	B113	2	m	c	2014							
2015	Kaffiøyra	B114	3	m	c	2014							
2015	Kaffiøyra	B115	29k	f	a	NA	2000	2012			102 and B122	2016 and 2014	
2015	Kaffiøyra	B116	30k	f	a	NA	2000	2012			108 and B118	2016 and 2014	
2015	Kaffiøyra	B117	Y74	f	c	2014							
2015	Kaffiøyra	B118	Y75	f	c	2014			B116				
2015	Kaffiøyra	B119 2	Y76	f	c	2014							
2014	Kaffiøyra	B11	35	f	a	2003					B104 and B12	2013 and NA	
2015	Kaffiøyra	B120	Y77	f	c	2014							
2015	Kaffiøyra	B121	Y78	f	c	2014							
2015	Kaffiøyra	B122	Y79	f	c	2014			B115				
2015	Brøgger	B123	4	m	c	2014							
2015	Brøgger	B124	Y80	f	a	NA	2000	2012			145	2016	
2014	Kaffiøyra	B12	36	f	a	NA	2000	2011	B11				
2014	Kaffiøyra	B13	37	f	a	NA	2000	2011					
2014	Brøgger	B14	21	f	a	NA	2000	2011			194 and Y95	2018 and 2015	

2014	Brøgger	B15	22	f	a	NA	2000	2011			146, B94, X8, Y41 2	2016, 2013, 2017, 2015	
2014	Brøgger	B16	23	f	a	NA	2000	2011			202 and X9	2020 and 2017	
2014	Brøgger	B17	24	f	a	NA	2000	2011			NyA 150	2016	
2014	Brøgger	B18	25	f	a	NA	2000	2011			153 and 226	2017 and 2020	
2014	Brøgger	B81	Y60	f	c	2013					174 and NyA X5	2018 and 2016	
2014	Brøgger	B82	26	f	a	NA	2000	2011			B91, NyA 149, Y98	2013, 2016, 2015	
2014	Brøgger	B83	27	f	a	NA	2000	2011					
2014	Brøgger	B84	28	f	a	NA	2000	2011			B88	2013	
2014	Brøgger	B85	29b	f	a	NA	2000	2011					
2014	Brøgger	B86	30b	f	a	2011							
2014	Brøgger	B87	32	f	a	NA	2000	2011					
2014	Brøgger	B88	Y50	m	c	2013			B84				
2014	Brøgger	B89	Y54	m	c	2013							
2014	Brøgger	B90	Y55	m	c	2013							
2014	Brøgger	B91	Y62	f	c	2013			B82				
2014	Brøgger	B92	Y63	f	c	2013							
2014	Brøgger	B93	Y71	f	c	2013							
2014	Brøgger	B94	Y72	f	c	2013			B15				
2014	Brøgger	B95	Y73	f	c	2013							
2014	Brøgger	B96	31	f	a	NA	2000	2011			195	2018	
2014	Kaffiøyra	B97	38	f	a	NA	2000	2011					
2014	Kaffiøyra	B98	40	f	a	NA	2000	2011					
2014	Kaffiøyra	B99	41	f	a	NA	2000	2011			104	2016	
2014	Kaffiøyra	B9	33	f	a	NA	2000	2011			116 and 180	2016 and 2018	

2016	Brøgger	NyA 11	11	m	c	2015							
2016	Brøgger	NyA 12	12	m	c	2015							
2017	Brøgger	NyA 149	149	f	c	2016			B82				
2017	Brøgger	NyA 150	150	f	c	2016			B17				
-	-	158_2	NA	-	-	-	-	-	-	-	-	-	158_1 and 158_2 genetically different *
2014	Kaffiøyra	NyA 39	39	f	a	NA	2000	2011			110 and 178	2016 and 2018	
2017	Brøgger	NyA X5	X5	m	c	2016			B81				
2016	Brøgger	NyA Y42	Y42	f	c	2015							
2016	Brøgger	NyA Y43	Y43	f	c	2015							
2016	Sarsøyra	NyA Y82	Y82	f	a	NA	2000	2013					
2016	Sarsøyra	NyA Y91	Y91	f	c	2015							
2016	Sarsøyra	T27	Y83	f	a	NA	2000	2013			132	2016	
2016	Sarsøyra	T29	Y81	f	a	NA	2000	2013			188	2018	
2016	Sarsøyra	T30	Y84	f	a	NA	2000	2013			T31	2015	
2016	Sarsøyra	T31	6	m	c	2015			T30				
2016	Sarsøyra	T32	10	m	c	2015							
2016	Sarsøyra	T33	7	m	c	2015							
2016	Sarsøyra	T34	Y90	f	c	2015							
2016	Sarsøyra	T35	9	m	c	2015			T40				
2016	Sarsøyra	T36	5	m	c	2015							
2016	Sarsøyra	T37	Y89	f	c	2015							
2016	Sarsøyra	T38	Y86	f	a	NA	2000	2013					
2016	Sarsøyra	T40	Y88	f	a	NA	2000	2013			T35	2015	
2016	Sarsøyra	T41	Y94	f	c	2015					213	2020	
2016	Sarsøyra	T42	Y93	f	c	2015							
2017	Sarsøyra	X1	X1	m	c	2016							

2017	Sarsøyra	X2	X2	m	c	2016							
2017	Sarsøyra	X3	X3	m	c	2016							
2017	Sarsøyra	X4	X4	m	c	2016							
2018	Brøgger	X6	X6	m	c	2017							
2018	Sarsøyra	X7	X7	m	c	2017							
2018	Brøgger	X8	X8	m	c	2017			B15				
2018	Brøgger	X9	X9	m	c	2017			B16				
2016	Brøgger	Y41 2	Y41	f	c	2015			B15		152	2017	
2016	Brøgger	Y44	Y44	f	a	NA	2000	2013					
2016	Brøgger	Y45	Y45	f	c	2015							
2016	Brøgger	Y46	Y46	f	c	2015							
2016	Brøgger	Y47 2	Y47	f	c	2015							
2016	Brøgger	Y95	Y95	f	c	2015			B14				
2016	Brøgger	Y96	Y96	f	c	2015							
2016	Brøgger	Y97	Y97	f	a	NA	2000	2013					
2016	Brøgger	Y98	Y98	f	c	2015			B82		201	2020	

* Individual with the DNA ID 158_2 was originally supposed to be a duplicate sample of 158_1, but genotyping outcome showed that 158_1 and 158_2 were two genetically different individuals (IBD value of 0.1383 and IBS value of 0.7982; B. Whitley, Unpublished). Most likely an error occurred in the lab or field process. Due to the success of other the controls in the genotyping process, this did not seem to affect other samples and their trustworthiness (H. Burnett, pers. comm.).

* Individual 159 and 160 were supposed to be two different individuals, but genotyping showed that both samples came from the same individual (IBD value of 0.9969 and IBS value of 0.9991; B. Whitley, Unpublished). Most likely an error occurred in the lab or field process. Only one of the samples, 159, was included in the construction of the pedigree.

Appendix D: Correlation of morphological traits for different age classes

Tables show correlations (r; in black) between different morphological traits used in this thesis. P-values and sample size (in light grey) of correlation tests are written underneath the correlation coefficients.

Age class 1 (<1 y 10 months old in April of capture year); No backfat or antler size measurements available in the youngest age group:

	Body mass	Leg length	Backfat
Body mass	-	0.62 p<0.001 n=223	-
Leg length	0.62 p<0.001 n=223	-	-
Backfat	-	-	-
Mean antler size	-	-	-

Age class 2 (yearlings and young adults <2 y 10 months old in April of capture year; females):

	Body mass	Leg length	Backfat
Body mass	-	0.57 p<0.001 n=59	0.09 p=0.48 n=59
Leg length	0.57	-	-0.02

	p<0.001 n=59		p=0.89 n=59
Backfat	0.09 p=0.48 n=59	-0.02 p=0.89 n=59	-
Mean antler size	0.68 p=0.04	0.75 p=0.03	-

Age class 3 (female adults older than 2 y 10 months in April of capture year):

	Body mass	Leg length	Backfat
Body mass	-	0.32 p<0.001 n=267	0.56 p<0.001 n=221
Leg length	0.32 p<0.001 n=267	-	0.17 p=0.01 n=217
Backfat	0.56 p<0.001 n=221	0.17 p=0.01 n=217	-
Mean antler size	0.19 p=0.01	0.07 p=0.40	0.15 p=0.09

Appendix E: Model results with quadratic term of the phenotypic trait measure

Each model (combination of phenotypic trait and fitness component) was also fitted with the quadratic term of the phenotypic trait measure included, to test whether there was evidence for either stabilizing or disruptive selection.

Model name	Fitness component	Predictor variables	Random effects	Parameter estimate for the slope(s) γ (\pm SE)	Fixed effects p-values	Number of observations
Model 1.3	Pregnancy	leg length + leg length ² + age class	id, year	Model error, Could not converge	-	-
Model 2.3	Pregnancy	body mass + body mass ² * age class	id, year	Model error, Could not converge	-	-
Model 3.3	Pregnancy	backfat	-	binary variables, quadratic term not possible	-	-
Model 4.3	Pregnancy	antler size + antler size ² + age class	id, year	0.39 (\pm 0.25) antler size ² -0.00 (\pm 0.00)	0.11 0.19	142 (id: 89, year: 7)
Model 5.3	Pregnancy	body condition + body condition ² * age class	id, year	19.73 (\pm 3.79) body condition ² 308.22 (\pm 169.05) body condition ² :Age class 3 -359.66 (\pm 174.19)	<0.001 0.07 0.04	281 (id: 137, year: 8)

Model name	Fitness component	Predictor variables	Random effects	Parameter estimate for the slope(s) γ (\pm SE)	Fixed effects p-values	Number of observations
Model 6.3	Calf at heel	leg length + leg length ² + age class	id, year	Model error, Could not converge	-	-
Model 7.3	Calf at heel	body mass + body mass ² + age class	id, year	0.57 (\pm 0.28) body mass ² -0.00 (\pm 0.00)	0.04 0.12	218 (id: 110, year: 7)
Model 8.3	Calf at heel	backfat	-	binary variables, quadratic term not possible	-	-
Model 9.3	Calf at heel	antler size + antler size ² + age class	id, year	0.01 (\pm 0.17) antler size ² -0.00 (\pm 0.00)	0.96 0.90	117 (id: 70, year: 7)
Model 10.3	Calf at heel	body condition + body condition ² + age class	id, year	10.59 (\pm 3.65) body condition ² -37.38 (\pm 46.74)	0.004 0.43	211 (id: 108, year: 7)

Model name	Fitness component	Predictor variables	Random effects	Parameter estimate for the slope(s) γ (\pm SE)	Fixed effects p-values	Number of observations
Model 11.3	Survival	leg length + leg length ² + sex (only age class 1)	id, year	Model error, Could not converge	-	-
Model 12.3	Survival	body mass + body mass ² + sex (only age class 1)	id, year	0.70 (\pm 0.36) body mass ² -0.01 (\pm 0.01)	0.05 0.14	224 (id: 224, year: 8)
Model 13.3	Survival	backfat	-	binary variables, quadratic term not possible	-	-
Model 14.3	Survival	antler size + antler size ² * age class	id, year	0.59 (\pm0.21) antler size ² -0.02 (\pm0.01) antler size ² :Age class3 0.01 (\pm0.00)	0.004 0.003 0.01	174 (id: 101, year: 8)
Model 15.3	Survival	body condition + body condition ² * sex (only age class 1)	id, year	3.04 body condition ² -5.60 (\pm 8.16) body condition ² :sex(m) -72.17 (\pm 45.78)	0.22 0.49 0.11	223 (year: 8)

Model name	Fitness component	Predictor variables	Random effects	Parameter estimate for the slope(s) γ (\pm SE)	Fixed effects p-values	Number of observations
Model 16	Survival	antler size + antler size ² * age class	id, year	0.59 (\pm0.21) antler size ² -0.02 (\pm0.01) antler size ² :Age class3 0.01 (\pm0.00)	0.004 0.003 0.01	174 (id: 101, year: 8)

Appendix F: Overview table of different combinations in selection models

Summary of the different combinations of fitness components and morphological traits that were used, showing which age classes (1,2,3) and sexes (male *m* or female *f*), as well as random effects that were included in different models. The column “interaction or no interaction included” shows whether fixed effects interaction (*) were included or not (+), and the column “Direction of selection tested?” shows whether direction of selection could be analysed (with or without significant results). Some quadratic models produced errors and could not converge. Backfat was transformed into a binary variable, therefore direction of selection could not be tested.

Fitness component	Morphological trait	Age classes included	Sex	Interaction (*) or no interaction (+) included	Random effect	Direction of selection tested?
Pregnancy	Leg length	2, 3	f	+ age class	id, year	Error converging
Pregnancy	Body mass	2, 3	f	* age class	id, year	Error converging
Pregnancy	Back fat	2, 3	f	+ age class	id, year	-
Pregnancy	Antler size	2, 3	f	+ age class	id, year	Yes, non-significant
Pregnancy	Body condition	2, 3	f	* age class	id, year	Yes, non-significant
Calf at heel	Leg length	2, 3	f	+ age class	id, year	Error converging
Calf at heel	Body mass	2, 3	f	+ age class	id, year	Yes, non-significant
Calf at heel	Back fat	2, 3	f	+ age class	id, year	-

Calf at heel	Antler size	2, 3	f	+ age class	id, year	Yes, non-significant
Calf at heel	Body condition	2, 3	f	* age class	id, year	Yes, non-significant
Survival to next year	Leg length	1	m, f	+ sex	id, year	Error converging
Survival to next year	Body mass	1	m, f	+ sex	id, year	Yes, non-significant
Survival to next year	Back fat	2, 3	f	+ age class	id, year	-
Survival to next year	Antler size	2, 3	f	* age class	id, year	Yes, significant with interaction
Survival to next year	Body condition	1	m, f	+ sex	id, year	Yes, non-significant



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