NTNU – Trondheim
Norwegian University of
Science and Technology

Effects of Climate and Animal Density on Adult Sex Ratio Variation in a Large Herbivore

Bart Peeters

Biology

Submission date:	September 2014
Supervisor:	Bernt-Erik Sæther, IBI
Co-supervisor:	Brage Bremset Hansen, IBI Åshild Ønvik Pedersen, NPI Vebjørn Veiberg, NINA

Norwegian University of Science and Technology
Department of Biology

Abstract

Adult sex ratio is often biased in natural populations, and its variation is known to influence different demographic components at the population level. The causes of variation in adult sex ratio remain, however, poorly understood. Using time series from 1979 to 2013, I investigated sex-specific adult population growth rates and mortality indices (based on carcass counts) of Svalbard reindeer (*Rangifer tarandus platyrhynchus*) to explain variation in adult sex ratio in response to climate variability and animal density. Food limitation due to harsh winter conditions and high animal density was expected to have a stronger effect on males relative to females due to a higher energy requirement related to body size and reproductive strategy. Accordingly, when accounting for the delayed effect of population-level fecundity (i.e. input from new cohorts) and the positive effect of summer temperature (directly determining vascular plant biomass), I found that increased winter precipitation (i.e. reduced forage accessibility) had a stronger negative effect on adult population growth rate in males than in females. Additionally, the mortality index increased more strongly in response to increased winter precipitation in males than in females. Increased winter precipitation, therefore, lead to a more female-biased ASR. High animal density, however, had a stronger negative effect on female adult population growth rate and increased the mortality index more strongly in females than in males, which could be related to sex-differences in density-dependent age structure. The present study is the first to demonstrate the effects of climate variability and animal density on adult sex ratio variation in an Arctic ungulate, which has important implications for management and harvest regimes of populations facing climate change.

Key Words: Arctic, environment, growth rate, mortality, population structure, *Rangifer tarandus platyrhynchus*, ungulate

Sammendrag

Kjønnsfordeling blant voksne dyr er ofte skjevt fordelt i naturlige populasjoner og variasjonen i kjønnsratene påvirker ulike demografiske parametre på populasjonsnivå. Fremdeles er årsakene til variasjon i kjønnsrate hos voksne lite kjent. I oppgaven bruker jeg populasjons- og strukturtellinger av svalbardrein (*Rangifer tarandus platyrhynchus*) (1979 til 2013) for å undersøke kjønnsspesifikke populasjonsvekstrater for voksne dyr og mortalitetsindekser (basert på kadavertellinger) for å forklare variasjon i kjønnsfordeling som en respons til klimavariabilitet og tetthet av reinsdyr. Begrenset tilgang til mat som følge av dårlige vinterforhold og høy tetthet av reinsdyr ble forventet å ha sterkere påvirkning på populasjonsvekstraten hos voksne bukker enn simler på grunn av et høyere næringsbehov i relasjon til kroppsstørelse og reproduktiv strategi. Økt vinternedbør (som reduserer mattilgang) hadde en sterkere negativ effekt på populasjonsvekstrate hos voksne bukker enn simler etter å ha tatt hensyn til både en forsinket effekt av fekunditet (dvs. input fra nye årsklasser [kohorter]) og en positiv effekt av sommertemperatur (som direkte påvirker vaskulær plantebiomasse). I tillegg hadde økt vinternedbør en sterkere positiv effekt på mortalitetsindeks hos bukker enn simler. Økt vinternedbør førte derfor til en mer simlefordelt voksen kjønnsrate. Høy tetthet av dyr hadde derimot en sterkere negativ effekt på populasjonsvekstraten hos simler enn bukker og økte dødeligheten hos simler sterkere sammenlignet med bukker. Disse resultatene kan være knyttet til kjønnsforskjeller i tetthetsavhengig aldersstruktur. Dette studiet er det første til å vise påvirkningene av både klimavariabilitet og tetthet av dyr på voksen kjønnsfordeling hos et arktisk hovdyr, noe som har implikasjoner for forvaltning og bevaring av populasjoner som er utsatt for klimaendring.

Table of Contents

Abstract i

Sammendrag ii

Table of Contents iii

Introduction 1

Methods 4

  Study area and populations 4

  Reindeer census data 5

  Climate data 6

  Data analysis 7

Results 9

Discussion 11

Acknowledgements 16

References 17

Tables 23

Figures 27

Appendix: Model selection 35

Introduction

Studies on sex ratio variation generally focus on adaptive theories on sex allocation and mechanisms affecting primary sex ratio (i.e. the ratio at fertilization) and secondary sex ratio (the ratio at birth) (see e.g. Clutton-Brock and Iason 1986; Frank 1990). The adult sex ratio (ASR) in wild populations is frequently skewed (Donald 2007) and fluctuates significantly over time (Pettersson *et al.* 2004). Donald (2007) reviewed estimates of ASRs on birds and mammals, showing that the majority of populations of bird species are male-biased. Deviation from parity is even stronger in mammals, but generally female-biased. In ungulates, female-biased ASRs are rather the rule than the exception (Owen-Smith and Mason 2005).

Variation in birth sex ratio in ungulates is affected by population density and climate (Clutton-Brock and Iason 1986; red deer *Cervus elaphus*, Kruuk *et al.* 1999), and, in accordance with Trivers and Willard (1973), with maternal condition (e.g. feral horse *Equus caballus*, Cameron *et al.* 1999; Sheldon and West 2004). After birth, juvenile mortality rates remain higher for males than females (red deer, Bonenfant *et al.* 2009). Juvenile males show greater susceptibility to food shortages due to higher energy requirements (Clutton-Brock *et al.* 1985) and are thus more sensitive to high population density than females (e.g. red deer, Bonenfant *et al.* 2002; Alpine chamois *Rupicapra rupicapra*, Willisch *et al.* 2013) both pre-weaning and post-weaning (Bonenfant *et al.* 2009). In reindeer (*Rangifer tarandus*), skewed secondary sex ratios indicate higher neonatal and post-natal mortality rates for males than females (Skogland 1985).

Beside sex ratio variation among recruits, skewed ASRs in birds and mammals can result from higher mortality of the rarer sex as a consequence of sex-differences in behaviour, physiology and genetics (see Donald 2007). Sex-biased mortality rates can be induced by intrinsic (non-environmental) mechanisms, such as through sexual selection (see below), or extrinsic factors such as predation (Berger and Gompper 1999; Christe *et al.* 2006), selective harvesting (e.g. Van Deelen *et al.* 1997; Vidya *et al.* 2003; Solberg *et al.* 2005) and environmental conditions (Toigo and Gaillard 2003). In males, fitness is strongly linked to success in intrasexual competition over matings. Because of this, sexual size dimorphism through sexual selection appears in a wide range of species, and is strongly related to the degree of polygyny (Loison *et al.* 1999). Accordingly, male longevity is found to decrease with sexual size dimorphism (Bro-Jørgensen 2012). However, no direct relationship is found between sexual size dimorphism and ASR (Berger and Gompper 1999), and sex-differences in adult survival were related to sexual size dimorphism only when correcting for environmental conditions (Toigo and Gaillard 2003).

Clutton-Brock and Isvaran (2007) showed that selection for longevity is weaker in males than females in polygynous species. In ungulates, variability in adult survival is also higher for males than females (Toigo and Gaillard 2003). Studies on roe deer show that adult males can reach survival rates equally high as females under good environmental conditions, but sharply declines to rates similar to yearlings under harsh conditions (Cobben *et al.* 2009). Under food-limited environmental conditions, sex-differences in survival increase with sexual size dimorphism due to increased male mortality rather than decreased female mortality (Toigo and Gaillard 2003). Males are thus more prone to starvation due to higher absolute energy requirements as a consequence of larger body size (Demment and Vansoest 1985), and lower fat reserves relative to females (Glucksmann 1974). Adult males commonly exhibit rut-induced hypophagia due to increased energy demands and decreased time foraging (fallow bucks *Dama dama*, Apollonio and Di Vittorio 2004; Alpine chamois, Willisch and Ingold 2007; Alpine ibex *Capra ibex*, Brivio *et al.* 2010) resulting in reduced body condition and hence increased male mortality when facing harsh winters or drought.

Studies on ungulates have shown that altered ASRs can affect population demography by influencing mean parturition date (Holand *et al.* 2003; Sæther *et al.* 2003), female fecundity (Solberg *et al.* 2002), offspring sex ratio (Bjørneraas *et al.* 2009), sexual size dimorphism (Garel *et al.* 2006) and overall population growth rate (Schmidt and Gorn 2013). How variation in ASR is influenced by population density and climate variability is, however, unclear. Because of its sedentary and solitary behaviour and lack of predators, Svalbard reindeer (*Rangifer tarandus platyrhynchus*) is an ideal model organism to study the effects of climate and density on ASR variation. Furthermore, this part of the Arctic is characterised by significant annual fluctuations in winter weather conditions and a rapid change in climate (Christensen *et al.* 2013). For instance, future climate scenarios indicate an increase in the frequency of 'rain-on-snow' events (ROS) causing ground ice (Putkonen and Roe 2003;

Rennert *et al.* 2009) as a consequence of climate warming. ROS events are well-known to have detrimental effects on Arctic ungulates (Forchhammer and Boertmann 1993; Solberg *et al.* 2001; Hansen *et al.* 2011) as it causes ground-icing and impenetrable snowpacks (Kohler and Aanes 2004), having a strong negative effect on population growth rates through the formation of ice-locked pastures (Hansen *et al.* 2010, 2011). However, increased summer temperature and longer growth seasons might counteract this negative effect of climate warming on population dynamics in Arctic ungulates (Aanes *et al.* 2002; Hansen *et al.* 2013).

In this study, I investigated the effects of animal density- and environmentally-induced food limitation on sex-specific adult population growth rates (hereafter, adult growth rates) and adult mortality indices, to explain fluctuations in ASR in two neighbouring Svalbard reindeer populations. Following studies on variability in sex-specific survival under food-limited conditions (e.g. Bonenfant *et al.* 2002; Toigo and Gaillard 2003), I expected males to be more sensitive to (1) increase in food competition through increased animal density, and (2) poorer forage availability due to harsh winter conditions. ASR is hence expected to become more female-biased following years with high animal density and severe winters.

Methods

Study area and populations

The Svalbard archipelago is located in the High Arctic at 74 – 81°N and 10 – 30°E (Fig. 1). The terrain is characterized by wide U-shaped valleys, coastal plains and steep mountains, and approximately 60% of the land area is covered by glaciers (Johansen *et al.* 2012). In general, the vegetation is characterized by polar desert and Arctic tundra (Jónsdóttir 2005). Because of the North Atlantic Current, winters are relatively mild compared to other Arctic regions at these latitudes.

The two Svalbard reindeer populations investigated in this study are located in Nordenskiöld Land, Spitsbergen (Fig. 1). The Adventdalen valley system consists of one main valley, Adventdalen, with several small side valleys. The Reindalen valley system consists of three main valleys: Reindalen, Colesdalen and Semmeldalen (Fig. 1). Adventdalen (AD) and Reindalen (RD) are adjacent valley systems and reindeer migration between them occurs (Stien *et al.* 2012), but is limited due to physical barriers (Aanes *et al.* 2003; Loe et al. unpubl.). The endemic Svalbard reindeer along with Svalbard rock ptarmigan (*Lagopus muta hyperborea*) are the only overwintering native herbivores in Svalbard. During the snow free period, reindeer show some habitat overlap with two migratory geese species (*Anser brachyrhynchus* and *Branta leucopsis*; Tyler and Øritsland 1999). The effect of interspecific resource competition with geese on reindeer population dynamics is considered to be low due to the seasonal and local occurrence of geese. Despite the presence of polar bears (*Ursus maritimus*) and Arctic foxes (*Vulpes lagopus*), predation on Svalbard reindeer is very limited. Derocher *et al.* (2000) described observations of polar bears preying on Svalbard reindeer, while only one observation of an Arctic fox killing a Svalbard reindeer calf has been reported (Prestrud 1992).

Hunting on Svalbard reindeer is restricted to Reindalen and Colesdalen and four other valleys outside the study area (Governor of Svalbard 2009) and the annual quota is very limited (range 1983 to 2013 [117 – 235]; Pedersen *et al.* (2014)). Stien *et al.* (2012) estimated that since 1998 yearly harvest rates varied between 6–14% of yearlings and adults, and 4–

9% of calves, for the entire harvest area. Note, however, that these rates are most likely overestimated (Pedersen *et al.* 2014) due to underestimation of population sizes (Lee *et al.* subm.). Males (yearlings and adults) were twice as likely to get shot as females (9–20% and 4–10% respectively). No significant long-term effects of harvest on the population dynamics were found (Stien *et al.* 2012).

Reindeer census data

Reindeer population censuses were conducted annually since 1979 in summer after calving and included total or transect counts of live animals and carcasses (Table 1). During counts, animals were categorized by age (calf, yearling, or adult 2 years and older). The two latter age classes were also categorized by sex.

The AD census consists of total population counts conducted by four to six persons during late June-early July over a period of 7–10 days. Observers walk separate predefined routes (see Tyler 1987b) scanning the entire area with binoculars, and only deviating from the route when necessary to optimize visibility for detection and classification. Reindeer still have parts of their winter fur during this period, making them conspicuous against the barren landscape (Tyler 2008). Due to the open landscape, counts are assumed to be close to the actual population number for AD (Tyler and Øritsland 1999; Tyler *et al.* 2008).

The RD census consists of fixed transect counts conducted by two people during late July-early August over a period of 5–8 days (see Solberg *et al.* 2001). Observers use binoculars and telescopes to scan the area. In contrast to the AD census, reindeer have acquired their summer fur in this period, making them less distinct in the landscape. Sexing and aging is, however, easier since sexual characteristics are more apparent, due to nearly fully developed antlers and visible sexual organs in males. Due to deviating area coverage during counts in RD in 1990 and 1993, data for these years were only used to estimate fecundity (see below).

The number of animals unclassified to age and sex never exceeded 11.4% (mean ± SD, 4.7 ± 3.0) for AD for the period of 1998–2013 (data on unclassified animals were not available for the earlier period 1979–1997), and 11.4% (4.2 ± 3.2) for RD. However, misclassification of sex and age, especially for yearlings and young adults, is not very uncommon during early summer and depends on observer experience and distance to the animal (Peeters et al., unpubl. data).

Carcasses of reindeer that died during the last 12 months were aged to calf, yearling or adult based on tooth eruption pattern (Reimers and Nordby 1968), and sexed based on antler morphology for older individuals and sexual dimorphism in the pelvic bone (Tyler 1987a). Carcasses from adult individuals from RD were in addition aged by year based on analysis of tooth cementum layers (Reimers and Nordby 1968). A considerable proportion of the population in RD consists of marked individuals of known sex and age (mainly females). Marked dead animals could be accurately sexed and aged based on the capture history data. Although the exact time of death is unknown, the majority of carcasses are from individuals that died from starvation during the previous winter and early spring (Reimers 1983). Antlers attached to the carcass from older males indicate they died during or shortly after the rut, as adult males shed their antlers in early winter. Due to the open landscape and their light fur contrasting the landscape of rocks and tundra vegetation, carcasses are easy to observe.

Climate data

Daily precipitation (mm) and average temperature (°C) for the winter period (defined here as 1 November – 30 April) and summer period (1 July – 31 August) were collected at the Norwegian Meteorological Institute's weather station at Longyearbyen airport (Fig. 1; http://eklima.met.no). The number of days with precipitation as rain in winter (temperature ≥ 1°C and precipitation ≥ 1 mm, in accordance with Hansen *et al.* (2013)), representing the number of 'rain-on-snow' events (ROS), was included as a ground ice index. Total winter precipitation (mm) was used as another index of winter harshness conditions (Solberg *et al.* 2001), integrating the effects of both rain and snow on forage availability. Note that the proportion of winter precipitation falling as rain was positively correlated with the amount of precipitation (Pearson's r = 0.49, d.f. = 32, $P < 0.01$). The mean summer temperature (°C) was used as an index of summer forage availability, since summer temperature directly affects above-ground green vascular biomass (Van der Wal and Hessen 2009; Van der Wal and Stien In press) and has a positive effect on the next year's population growth rate of Svalbard reindeer (Aanes *et al.* 2002; Hansen *et al.* 2013).

Data analysis

The following variables were derived from the census data: (1) Adult sex ratio (ASR) was calculated as the proportion of males per total sexed adult (i.e. ≥ 2 years) (Fig. 2A); (2) change in ASR (ΔASR) from year *t* to *t+1*, i.e. $ASR_{t+1} - ASR_t$; (3) the logistic population growth rate (R_t) for both male and female adults (≥ 2 years), calculated as $X_{t+1} - X_t$, with X_t being the natural logarithm of the number of either adult male or female reindeer in year *t* (Figs 2B-C); (4) total number of animals counted, hereafter referred to as total population size (*N*; Fig. 2D); (5) fecundity, measured as the number of calves per adult female (Fig. 2E); (6) a mortality index, calculated as the number of adult male or female carcasses in year *t* divided by the total number of live animals from each respective sex counted in year *t-1* (Fig. 3). Mortality indices calculated based on the number of carcasses versus live animals for the period 1980–1998 in Adventdalen (Fig. 3A) were obtained from Tyler and Øritsland (1999) and multiplied by the total number of live animals in year *t-1* to obtain the number of carcasses in year *t* for both adult males and females. The climatic variables summer temperature, winter precipitation and ROS are illustrated in Fig. 2F.

Reindeer populations in AD and RD showed a positive trend in population size during the study period (Fig. 2D), indicating an increase in carrying capacity, possibly as a result of increased green biomass due to a long-term increase in summer temperature (Fig. 2F) (Van der Wal and Hessen 2009; Hansen *et al.* 2013). Population size and summer temperature were, therefore, detrended.

To investigate the effect of climate and animal density on male and female growth rate, multiple linear regression analysis was used with the following predictor variables in the global model: sex (male or female) as a categorical variable; detrended total population size in year *t* as a relative measure of animal density; fecundity in year *t-1* to control for input from new cohorts; detrended mean summer temperature; total winter precipitation; and ROS, which was ln-transformed after adding one unit in the analysis. To detect differences in the effects between sexes two-way interactions between sex and either one of the covariates were included. Sex was included in all candidate models. All covariates were standardized in the analysis to make relative effects of parameters comparable. Pearson rank correlation coefficients between covariates were $|r| < 0.60$ for all combinations of covariates.

To investigate the effects of climate and animal density on the mortality index, a logistic regression analysis with a logit link was used. The mortality index was entered as response variables in matrix-form with the number of carcasses and estimated survivors (i.e. number of live adults in year *t-1* – number of carcasses in year *t*), representing "successes" and "failures" respectively, for either sex. The previous year's variables (*t-1*) of detrended total population size, detrended summer temperature, total winter precipitation and ROS were standardized and included as predictor variables (in the global model) in interaction with sex, which was included in all candidate models. Due to high overdispersion (8.1 and 7.7 for the global models for AD and RD, respectively) from a generalized linear model, a generalized linear mixed effect model (GLMM, binomial family) was used with Year as a random effect on the intercept.

Finally, to investigate the effects of climate and density on ΔASR, multiple linear regression was used with the following predictor variables in the global model: detrended population size, fecundity, detrended summer temperature, total winter precipitation and ROS.

All statistical analyses were conducted in R version 3.0.2 (R Core Team 2013). The regression analyses were conducted separately for AD and RD, because of the difference in time periods (see Table 1) and differences in sampling methods (see above) for the censuses. Model selection was performed using the corrected Akaike's Information Criterion (AIC_c) based on the models maximum likelihood (ML), which was facilitated by generating full model sets using the 'dredge'-function in the MuMIn package (Barton 2013). Overparameterization was avoided by not allowing models where the number of cases was less than four times the number of parameters. Winter precipitation and ROS, both indices for winter harshness, were not allowed in the same candidate models. Models were checked for approximate normality and constant variance of residuals. The arm package (Gelman and Su 2013) was used for simulating the estimates of the regression parameters to include confidence intervals in the regression plots.

Results

The sex-specific adult growth rate was best described as a function of total winter precipitation, animal density (i.e. detrended population size), previous year's fecundity and a two-way interaction between sex and total winter precipitation for both AD and RD reindeer populations (Table 2; for model selection, see Appendix Table A1). In addition, there was an effect of summer temperature and a two-way interaction between sex and animal density for AD (Table 2). Total winter precipitation had a stronger negative effect on adult growth rate in males than in females (Figs 4A-B). Animal density had a negative effect on adult growth rate in both AD and RD, and was significantly stronger in females than in males for AD (Figs 4C-D). Adult growth rate increased with increasing summer temperature in AD (Fig. 4E) and previous year's fecundity in both AD and RD (Table 2).

The median age at which Svalbard reindeer died, given that they survived until the age of 1 year, was 7 years for males ($n = 124$) and 9 years for females ($n = 169$; Fig. 5), based on the aged carcasses from RD for the period 1996–2012. Female reindeer became significantly older than males (given survival until age 1; Wilcoxon rank sum test; $W = 7475$, $P < 0.001$). Of female and male carcasses aged ≥ 1 year, respectively 27 and 37% were unclassified by age, and 6% of carcasses aged ≥ 1 year were unsexed. Among the total number of carcasses found, 45% were from calves (0 year), indicating a high mortality risk during their first year.

The mortality index was best described as a function of sex, and previous year's animal density and winter precipitation, with a two-way interaction between sex and previous year's winter precipitation for AD, and a two-way interaction between sex and previous year's animal density for RD (Table 3; for model selection, see Table A2). The mortality index was significantly higher for adult males than for adult females. For AD, the previous year's winter precipitation had a significantly stronger positive effect on the mortality index of adults in males than in females (Fig. 6A). For RD, the previous year's winter precipitation had a strong positive effect on the mortality index with no significant difference between adult males and females (Fig. 6B). The mortality index increased with increasing animal density the previous year both in AD (Table 3, model 2) and RD, and increased more strongly for adult females than males for RD (Figs 6C-D).

ASR for AD ranged from 0.32 – 0.49 (mean ± SD, 0.39 ± 0.04, n = 35), and ASR for RD ranged from 0.31 – 0.49 (0.40 ± 0.06, n = 21) (Fig. 2A). ASR was clearly female-biased throughout the time series for both populations (AD: $\chi^2 = 96.24$, d.f. = 34, $P < 0.001$; RD: $\chi^2 = 130.10$, d.f. = 20, $P < 0.001$). The most parsimonious models describing ΔASR included an effect of both winter precipitation and animal density for AD and an effect of winter precipitation for RD (Table 4; for model selection, see Table A3). The negative effect of increased winter precipitation on ΔASR (Figs 7A-B) caused ASR to become more female-biased. However, as seen in AD, ASR would become more even with increasing animal density due to a positive effect on ΔASR (Fig. 7C). Note that the variables used in the regression analysis were standardized to make their effect size directly comparable. Thus, for AD, the effect size of winter precipitation and animal density on ΔASR are of approximatly the same size, but of opposite sign (Table 4).

Discussion

By decomposing long-term time series of population monitoring data into sex-specific components, this study has demonstrated that annual variation in Svalbard reindeer ASR (i.e. the proportion of males per total sexed adults) is affected by both winter climate variability and animal density (Fig. 7). Increased winter precipitation leads to a stronger decrease in male adult population growth rate (Figs 4A-B) and a stronger increase in male adult mortality index (based on carcass counts) compared to females (in AD; Fig. 6A) and, therefore, a decline in ASR (Figs 7A-B). On the other hand, increased population density had a stronger negative effect on female adult growth rate (in AD; Fig. 4C) and a stronger positive effect on female adult mortality index compared to males (in RD; Fig. 6D), which consequently increased the ASR (in AD; Fig. 7C).

Based on sex-differences in reproductive strategy (Kastnes 1979; Bårdsen *et al.* 2008) and studies on variability in sex-specific survival under food-limited conditions (e.g. Bonenfant *et al.* 2002; Toigo and Gaillard 2003), males were expected to be more sensitive to food limitation due to harsh winter conditions and animal density compared to females. Accordingly, ASR was expected to become more female-biased following years with harsh winter conditions and high animal density.

Conforming to my predictions, increased winter precipitation as an indicator of winter harshness conditions decreased male adult growth rate and increased male adult mortality index more strongly compared to females. ASR became, therefore, more female-biased following years with increased winter precipitation. Winters with increased precipitation are characterized by large amounts of rain forming ice-blocked pastures (Hansen *et al.* 2010). Adult males of Svalbard reindeer, particularly old large males, spend little time grazing and resting during the rutting period (Kastnes 1979; Vestues 2009) resulting in a reduced body condition at the onset of winter. Adult female reindeer, on the other hand, adopt a risk-sensitive reproductive allocation strategy in response to winter conditions (Bårdsen *et al.* 2008, 2010, 2011). In addition, female reindeer retain their antlers during winter and are, therefore, superior to males in competition over forage patches (Holand *et al.* 2004). During extreme winters with high rainfall and ground icing, part of the reindeer population will seek out forage opportunities at higher altitudes (Hansen *et al.* 2010). Due to intra-sexual competition, it could be that a higher proportion of adult males than females are driven to high and steep habitat in search for food. Males seem more determined than females to climb up mountains in search for food, making them more exposed to avalanche risks or falling off cliffs (see Reimers 1983). Because of these sex-differences in behavioural ecology, increased winter precipitation and, thus, ground icing had a stronger negative effect on adult survival of males relative to females, resulting in an increased female-biased ASR.

Total winter precipitation had a strong positive effect on the mortality index of adult reindeer in RD, but no difference in the effect between sexes (Table 2; Fig. 6B). This is presumably due to noise in the monitoring data related to, for instance, differences in detection probability of carcasses between sexes due to sexual habitat segregation during years with increased icing (see above). Overall, winters with increased precipitation forming ground ice (Hansen *et al.* 2010, 2011) are known to have strong negative effects on reindeer population growth rates (Hansen *et al.* 2011, 2013) and are predicted to become more frequent due to climate warming (Hansen *et al.* 2011). Given that other factors are kept constant, my results indicate that this might lead to an overall more female-biased ASR in the future.

In contradiction to my predictions, animal density influenced both female adult growth rate and mortality index more strongly compared to males. Therefore, ASR increased in response to increased animal density. This is a rather unexpected result regarding studies on sex- and age-dependent survival in relation to population density (reindeer, Skogland 1985; red deer, Bonenfant *et al.* 2002; Alpine chamois, Willisch *et al.* 2013). However, in ungulates, the proportion of senescent individuals is typically higher at high compared to low animal density (Festa-Bianchet *et al.* 2003; Bonenfant *et al.* 2009) and adult survival declines more rapidly for males than females with increasing age (Clutton-Brock and Isvaran 2007). Therefore, it is possible that a stronger impact of animal density on female adult growth rate and mortality index compared to males could be associated with sex-differences in density-dependent age structure effects.

Adult males of Svalbard reindeer showed a higher average mortality (Table 3) and a lower median life span (Fig. 5) compared to females. While most female carcasses found during the summer counts apparently died during mid-late winter, approximately 30% of male carcasses in age class 5-8 years have been registered with intact antlers during the survey in RD (Veiberg pers. comm.). Prime-aged males shed their antlers at the onset of the winter, and it is therefore likely that those males died during early winter from starvation or injuries related to the rutting activity. For instance, eight adult male carcasses in RD were found with interlocked antlers, indicating that they died after getting stuck during the rut (see also Reimers 1983). It is, therefore, possible that the proportion of senescent individuals dying during winter increases more strongly for females than males after years with high animal density. Alternatively, male energy expenditure during the rut might decrease with increasing animal density due to easier access to females or decreased effort in harem holding, in particular amongst young adult males. This would consequently increase the survival probability of (young) adult males during the upcoming winter.

The effect of animal density on ΔASR and its interaction with sex on adult growth rate was not included in the top models for RD (Table 2 and 4; see also Table A1 and A3). For the mortality index analysis, however, the interaction effect of sex with animal density was strongly significant for RD, but not included in the model for AD (Table 3; see also Table A2). These slight differences in results between AD and RD can be related to sample size and the restricted number of parameters allowed in the model to avoid overparameterization (particularly for the mortality index analysis), and observation error. Lee *et al.* (subm.) indicated that transect counts of reindeer in RD are uncertain due to sampling error. Differences in observation methods (time of season, handheld binoculars vs. telescopes) between AD and RD can also give different sources of observation error. Since the census in AD is conducted early in the summer season, young males could be misclassified as adult females and vice versa. The amount of such misclassifications can vary greatly between years due to large annual variation in the fecundity (Fig. 2E), i.e. either due to annual variation in cohort size and, therefore, the number of young males in the population, or simply because females with a calf are easy to classify. Additionally, the sex-specific adult growth rate and mortality index can be influenced by sex-differences in migration probability related to animal density (red deer, Clutton-Brock *et al.* 2002). Nevertheless, the results from the AD and RD population monitoring data were overall consistent.

In general, winter precipitation had a stronger negative effect on adult survival in males, while animal density had a stronger negative effect on adult survival in females. Years with good winter conditions (i.e. little or no rain causing ground ice) and high animal density would lead to an increase in ASR (e.g. AD year 1994–1995, Fig. 2), while years with poor winter conditions and relatively low animal density would lead to a strong decline in ASR (e.g. year 1995–1996, Fig. 2).

A positive effect of summer temperature on Svalbard reindeer population dynamics has been reported in only a few previous studies (Aanes *et al.* 2002; Hansen *et al.* 2013). Using the Arctic Oscillation index rather than summer temperature per se, Aanes *et al.* (2002) indicated that Svalbard reindeer population dynamics were influenced by summer weather conditions through a trophic bottom-up effect. Since fecundity in year *t-1* was included to correct for input from new cohorts, the adult growth rate analysis indicated a significant, positive effect of summer temperature on adult survival.

The effects of biased ASRs and ASR variation on demographic components and the implications for population management have been emphasized in previous studies (Solberg *et al.* 2002; Holand *et al.* 2003; Sæther *et al.* 2003; Mysterud *et al.* 2005; Garel *et al.* 2006; Bjørneraas *et al.* 2009; Schmidt and Gorn 2013). For instance, studies on moose (*Alces alces*) have shown that the proportion of male calves in a population declined with high animal densities and with low proportions of adult males (Bjørneraas *et al.* 2009). High population density can cause a decline in maternal body condition (Sæther 1997) and consequently lower recruitment rates (Solberg *et al.* 2002), particularly lower male recruitment (Bjørneraas *et al.* 2009).

Hunting on Svalbard reindeer is restricted to some areas (see methods; Governor of Svalbard 2009) and is assumed to have limited effects on total population size (Stien *et al.* 2012). However, the yearly harvest has been relatively stable (6-12% of the estimated total population from 1997-2012), while the proportion of harvested calves has been adjusted based on the calf-per-female ratio during counts (4.2-38.6% of the total harvest) (Pedersen *et al.* 2014). During years with strong declines in population size (due to e.g. high animal density or harsh winter conditions), mortality rates increase drastically for calves and senescent individuals in particular (Lee *et al.* subm.). In addition, fecundity rates in such years are very low. Prime-aged individuals will thus be more strongly targeted during the hunting season, partly because very few calves are in the quota at the expense of other demographic groups. Thus, hunting quotas can be adjusted taking the results from this study and information on changes in population size due to animal density and winter weather into consideration. This is to avoid that, for instance, a high proportion of prime-aged animals is shot after crash years due to high animal density or harsh winter conditions.

The results of this study provide empirical evidence on how ASR variation is influenced by both climate variability and animal density. While ASR in Svalbard reindeer was overall female-biased, this bias increased with increasing winter harshness. Higher animal density, on the other hand, reduced this bias in ASR, possibly due to sex-differences in density-dependent age structure effects. It is reasonable to believe that climate variability and animal density may have similar effects on the ASR variation of other Rangifer populations and even other species, particularly those with a polygynous mating system. Considering Arctic winters to become warmer and wetter in the future (Christensen *et al.* 2013) and the consequences on population dynamics (Hansen *et al.* 2011, 2013), these results provide valuable insights on the response of demographic structure to climate warming. Harvest regimes and conservation strategies can accordingly be optimized to sustain viable populations.

Acknowledgements

This study was part of the project “Predicting effects of climate change on Svalbard reindeer populations: a mechanistic approach” funded by Norwegian Research Council (NORKLIMA) and the Centre for Biodiversity Dynamics (Norwegian University of Science and Technology). Data collection was financed by the Norwegian Polar Institute, Norwegian Institute for Nature Research and Svalbard Science Forum (Arctic Field Grant). I thank the Norwegian Meteorological Institute for providing weather data. Ronny Aanes (formerly at the Norwegian Polar Institute) is acknowledged for collecting the reindeer population and mortality data during 2001–2010.

I thank all of my supervisors for accepting me as their master student and for all the feedback they have given. Particularly, I want to thank Brage for proposing me the interesting topic of my master’s thesis, the many long discussions we had and for always telling me to “keep my tongue straight in my mouth”. Thanks to Marit, Mathilde, Aino, Åshild, Brage and Lukasz for the time spent counting reindeer and facing harsh outdoor conditions together during our field work on Svalbard. Thanks to Ivar Herfindal and Vidar Grøtan for giving me statistical advice, and thank you, Ivar, for helping me out with the estimation plots. I thank Oddveig Øien Ørvoll and Anders Skoglund for helping me out with the map on the study population so quickly. Thanks to Rakel for proof-reading and thanks to Chris and Odd Helge for the many statistical, biological and random discussions during our daily coffee breaks.

Last but not least, I thank my parents, brothers and sister – just because.

References

Aanes R, Sæther B-E, Smith FM, Cooper EJ, Wookey PA & Øritsland NA (2002) The Arctic Oscillation predicts effects of climate change in two trophic levels in a high-arctic ecosystem. *Ecol Lett* **5**:445-453.

Aanes R, Sæther B-E, Solberg EJ, Aanes S, Strand O & Øritsland NA (2003) Synchrony in Svalbard reindeer population dynamics. *Can J Zool* **81**:103-110.

Apollonio M & Di Vittorio I (2004) Feeding and reproductive behaviour in fallow bucks (*Dama dama*). *Naturwissenschaften* **91**:579-584.

Barton K (2013) MuMIn: Multi-model inference. R package version 1.9.13.

Berger J & Gompper ME (1999) Sex ratios in extant ungulates: Products of contemporary predation or past life histories? *J Mammal* **80**:1084-1113.

Bjørneraas K, Solberg EJ, Herfindal I & Sæther B-E (2009) Large-scale spatiotemporal variation in calf sex ratio in moose (*Alces alces*): an effect of density-dependent decrease in maternal condition? *Can J Zool* **87**:346-355.

Bonenfant C, Gaillard J-M, Klein F & Loison A (2002) Sex- and age-dependent effects of population density on life history traits of red deer *Cervus elaphus* in a temperate forest. *Ecography* **25**:446-458.

Bonenfant C, Gaillard J-M, Coulson T, Festa-Bianchet M, Loison A, Garel M, Loe LE, Blanchard P, Pettorelli N, Owen-Smith N, Du Toit J & Duncan P (2009) Empirical Evidence of Density-Dependence in Populations of Large Herbivores. *Adv Ecol Res* **41**:313-357.

Brivio F, Grignolio S & Apollonio M (2010) To feed or not to feed? Testing different hypotheses on rut-induced hypophagia in a mountain ungulate. *Ethology* **116**:406-415.

Bro-Jørgensen J (2012) Longevity in Bovids is Promoted by Sociality, But Reduced by Sexual Selection. *PLoS ONE* **7**:e45769.

Bårdsen B-J, Fauchald P, Tveraa T, Langeland K, Yoccoz NG & Ims RA (2008) Experimental evidence of a risk-sensitive reproductive allocation in a long-lived mammal. *Ecology* **89**:829-837.

Bårdsen B-J, Tveraa T, Fauchald P & Langeland K (2010) Observational evidence of risk-sensitive reproductive allocation in a long-lived mammal. *Oecologia* **162**:627-639.

Bårdsen B-J, Henden J-A, Fauchald P, Tveraa T & Stien A (2011) Plastic reproductive allocation as a buffer against environmental stochasticity - linking life history and population dynamics to climate. *Oikos* **120**:245-257.

Cameron EZ, Linklater WL, Stafford KJ & Veltman CJ (1999) Birth sex ratios relate to mare condition at conception in Kaimanawa horses. *Behav Ecol* **10**:472-475.

Christe P, Keller L & Roulin A (2006) The predation cost of being a male: implications for sex-specific rates of ageing. *Oikos* **114**:381-394.

Christensen JH, Krishna Kumar K, Aldrian E, An S-I, Cavalcanti IFA, de Castro M, Dong W, Goswami P, Hall A, Kanyanga JK, Kitoh A, Kossin J, Lau N-C, Renwick J, Stephenson DB, Xie S-P & Zhou T (2013) Climate Phenomena and their Relevance for Future Regional Climate Change. - In: Stocker TF, Qin D, Plattner G-K, Tignor M, Allen SK, Boschung J, Nauels A, Xia Y, Bex V& Midgley PM (eds) Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK and New York, NY, USA.

Clutton-Brock TH & Iason GR (1986) Sex-ratio variation in mammals. *Q Rev Biol* **61**:339-374.

Clutton-Brock TH & Isvaran K (2007) Sex differences in ageing in natural populations of vertebrates. *Proc R Soc B* **274**:3097-3104.

Clutton-Brock TH, Albon SD & Guinness FE (1985) Parental investment and sex-differences in juvenile mortality in birds and mammals. *Nature* **313**:131-133.

Clutton-Brock TH, Coulson TN, Milner-Gulland EJ, Thomson D & Armstrong HM (2002) Sex differences in emigration and mortality affect optimal management of deer populations. *Nature* **415**:633-637.

Cobben MMP, Linnell JDC, Solberg EJ & Andersen R (2009) Who wants to live forever? Roe deer survival in a favourable environment. *Ecol Res* **24**:1197-1205.

Demment MW & Vansoest PJ (1985) A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. *Am Nat* **125**:641-672.

Derocher AE, Wiig O & Bangjord G (2000) Predation of Svalbard reindeer by polar bears. *Polar Biol* **23**:675-678.

Donald PF (2007) Adult sex ratios in wild bird populations. *Ibis* **149**:671-692.

Festa-Bianchet M, Gaillard J-M & Cote SD (2003) Variable age structure and apparent density dependence in survival of adult ungulates. *J Anim Ecol* **72**:640-649.

Forchhammer M & Boertmann D (1993) The muskoxen *Ovibos moschatus* in the North and Northeast Greenland - population trends and the influence of abiotic parameters on population-dynamics. *Ecography* **16**:299-308.

Frank SA (1990) Sex allocation theory for birds and mammals. *Annu Rev Ecol Syst* **21**:13-55.

Garel M, Solberg EJ, Sæther B-E, Herfindal I & Hogda KA (2006) The length of growing season and adult sex ratio affect sexual size dimorphism in moose. *Ecology* **87**:745-758.

Gelman A & Su Y-S (2013) arm: Data Analysis Using Regression and Multilevel/Hierarchical Models. R package version 1.6-10.

Glucksmann A (1974) Sexual dimorphism in mammals. *Biol Rev* **49**:423-475.

Governor of Svalbard (2009) Plan for forvaltning av svalbardrein, kunnskaps- og forvaltningsstatus. Rapport 1/2009, pp 47 (in Norwegian).

Hansen BB, Aanes R & Sæther B-E (2010) Feeding-crater selection by high-arctic reindeer facing ice-blocked pastures. *Can J Zool* **88**:170-177.

Hansen BB, Aanes R, Herfindal I, Kohler J & Sæther B-E (2011) Climate, icing, and wild arctic reindeer: past relationships and future prospects. *Ecology* **92**:1917-1923.

Hansen BB, Grøtan V, Aanes R, Sæther B-E, Stien A, Fuglei E, Ims RA, Yoccoz NG & Pedersen ÅØ (2013) Climate Events Synchronize the Dynamics of a Resident Vertebrate Community in the High Arctic. *Science* **339**:313-315.

Holand O, Røed KH, Mysterud A, Kumpula J, Nieminen M & Smith ME (2003) The effect of sex ratio and male age structure on reindeer calving. *J Wildl Manag* **67**:25-33.

Holand O, Gjostein H, Losvar A, Kumpula J, Smith ME, Røed KH, Nieminen M & Weladji RB (2004) Social rank in female reindeer (*Rangifer tarandus*): effects of body mass, antler size and age. *J Zool* **263**:365-372.

Johansen BE, Karlsen SR & Tommervik H (2012) Vegetation mapping of Svalbard utilising Landsat TM/ETM plus data. *Polar Rec* **48**:47-63.

Jónsdóttir IS (2005) Terrestrial ecosystems on Svalbard: heterogeneity, complexity and fragility from an Arctic Island perspective. *Biol Environ* **105B**:155-165.

Kastnes K (1979) Svalbard-reinens aktivitetsmønster gjennom året, (*Rangifer tarandus platyrhynchus*). PhD dissertation, University of Oslo, Oslo, Norway.

Kohler J & Aanes R (2004) Effect of winter snow and ground-icing on a Svalbard reindeer population: Results of a simple snowpack model. *Arct Antarct Alp Res* **36**:333-341.

Kruuk LEB, Clutton-Brock TH, Albon SD, Pemberton JM & Guinness FE (1999) Population density affects sex ratio variation in red deer. *Nature* **399**:459-461.

Lee AM, Bjørkvoll EM, Hansen BB, Albon SD, Stien A, Sæther B-E, Engen S, Veiberg V, Loe LE & Grøtan V (subm.) An integrated population model for a long-lived ungulate: more efficient data use with Bayesian methods. *Oikos*.

Loison A, Gaillard J-M, Pelabon C & Yoccoz NG (1999) What factors shape sexual size dimorphism in ungulates? *Evol Ecol Res* **1**:611-633.

Mysterud A, Solberg EJ & Yoccoz NG (2005) Ageing and reproductive effort in male moose under variable levels of intrasexual competition. *J Anim Ecol* **74**:742-754.

Owen-Smith N & Mason DR (2005) Comparative changes in adult vs. juvenile survival affecting population trends of African ungulates. *J Anim Ecol* **74**:762-773.

Pedersen ÅØ, Bårdsen B-J, veiberg V & Hansen BB (2014) Jegernes egne data. Analyser av jaktstatistikk og kjevemateriale fra svalbardrein. Norwegian Polar Institute Kortrapport/Brief Report Series 027, pp 28 (in Norwegian).

Pettersson LB, Ramnarine IW, Becher SA, Mahabir R & Magurran AE (2004) Sex ratio dynamics and fluctuating selection pressures in natural populations of the Trinidadian guppy, *Poecilia reticulata*. *Behav Ecol Sociobiol* **55**:461-468.

Prestrud P (1992) Food-habits and observations of the hunting behavior of Arctic foxes, *Alopex lagopus*, in Svalbard. *Can Field-Nat* **106**:225-236.

Putkonen J & Roe G (2003) Rain-on-snow events impact soil temperatures and affect ungulate survival. *Geoph Res Lett* **30**:1188.

R Core Team (2013) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Reimers E (1983) Mortality in svalbard reindeer. *Holarct Ecol* **6**:141-149.

Reimers E & Nordby O (1968) Relationship between age and tooth cementum layers in Norwegian reindeer. *J Wildl Manag* **32**:957-961.

Rennert KJ, Roe G, Putkonen J & Bitz CM (2009) Soil Thermal and Ecological Impacts of Rain on Snow Events in the Circumpolar Arctic. *J Clim* **22**:2302-2315.

Schmidt JH & Gorn TS (2013) Possible Secondary Population-Level Effects of Selective Harvest of Adult Male Muskoxen. *PLoS ONE* **8**:e67493.

Sheldon BC & West SA (2004) Maternal dominance, maternal condition, and offspring sex ratio in ungulate mammals. *Am Nat* **163**:40-54.

Skogland T (1985) The effects of density-dependent resource limitations on the demography of wild reindeer. *J Anim Ecol* **54**:359-374.

Solberg EJ, Jordhoy P, Strand O, Aanes R, Loison A, Sæther B-E & Linnell JDC (2001) Effects of density-dependence and climate on the dynamics of a Svalbard reindeer population. *Ecography* **24**:441-451.

Solberg EJ, Loison A, Ringsby TH, Sæther B-E & Heim M (2002) Biased adult sex ratio can affect fecundity in primiparous moose *Alces alces*. *Wildl Biol* **8**:117-128.

Solberg EJ, Grøtan V, Rolandsen CM, Broseth H & Brainerd S (2005) Change-in-sex ratio as an estimator of population size for Norwegian moose *Alces alces*. *Wildl Biol* **11**:163-172.

Solberg EJ, Strand O, Veiberg V, Andersen R, Heim M, Rolandsen CM, Langvatn R, Holmstrøm F, Solem MI, Eriksen R, Astrup R & Ueno M (2012) Moose, red deer and reindeer - Results from the monitoring program for wild cervids, 1991-2011. NINA report 885, pp 156 (in Norwegian).

Stien A, Bårdsen B-J, Veiberg V, Andersen R, Loe LE & Pedersen ÅØ (2012) Jakt på svalbardrein - kunnskapsstatus og evaluering av aktuelle forvaltningsmodeller. Rapport til Svalbards Miljøvernfond, pp 21 (in Norwegian).

Sæther B-E (1997) Environmental stochasticity and population dynamics of large herbivores: A search for mechanisms. *Trends Ecol Evol* **12**:143-149.

Sæther B-E, Solberg EJ & Heim M (2003) Effects of altering sex ratio structure on the demography of an isolated moose population. *J Wildl Manag* **67**:455-466.

Toigo C & Gaillard J-M (2003) Causes of sex-biased adult survival in ungulates: sexual size dimorphism, mating tactic or environment harshness? *Oikos* **101**:376-384.

Trivers RL & Willard DE (1973) Natural-selection of parental ability to vary sex-ratio of offspring. *Science* **179**:90-92.

Tyler NJC (1987a) Sexual dimorphism in the pelvic bones of Svalbard reindeer. *J Zool* **213**:147-152.

Tyler NJC (1987b) Natural limitation of the abundance of the High Arctic Svalbard reindeer. PhD Dissertation, Cambridge University, Cambridge, UK.

Tyler NJC & Øritsland NA (1999) Varig ustabilitet og bestandsregulering hos Svalbardrein. *Nor Polarinst Medd* **150**:125-139 (in Norwegian).

Tyler NJC, Forchhammer MC & Øritsland NA (2008) Nonlinear effects of climate and density in the dynamics of a fluctuating population of reindeer. *Ecology* **89**:1675-1686.

Van Deelen TR, Campa H, Haufler JB & Thompson PD (1997) Mortality patterns of white-tailed deer in Michigan's upper peninsula. *J Wildl Manag* **61**:903-910.

Van der Wal R & Hessen DO (2009) Analogous aquatic and terrestrial food webs in the high Arctic: The structuring force of a harsh climate. *Perspect Plant Ecol Evol Syst* **11**:231-240.

Van der Wal R & Stien A (In press) High arctic plants like it hot: a long-term investigation of between-year variability in plant biomass. *Ecology*.

Vestues G (2009) The mating system of Svalbard reindeer. Effects of male age and antler size on harem size, behaviour during the rutting season and reproductive effort. Master thesis, Norwegian University of Science and Technology, Trondheim, Norway.

Vidya TNC, Kumar VR, Arivazhagan C & Sukumar R (2003) Application of molecular sexing to free-ranging Asian elephant (*Elephas maximus*) populations in southern India. *Current Science* **85**:1074-1077.

Willisch CS & Ingold P (2007) Feeding or resting? The strategy of rutting male Alpine chamois. *Ethology* **113**:97-104.

Willisch CS, Bieri K, Struch M, Franceschina R, Schnidrig-Petrig R & Ingold P (2013) Climate effects on demographic parameters in an unhunted population of Alpine chamois (*Rupicapra rupicapra*). *J Mammal* **94**:173-182.

Tables

Table 1: Data sources for reindeer population and carcass data used in this study. Population data includes total and transect reindeer counts and structured counts by sex and age. Carcass data includes sexed adult carcasses for Adventdalen, and sexed and aged carcasses for Reindalen. NPI = Norwegian Polar Institute, NINA = Norwegian Institute for Nature Research.

	Data	Time period	Source
Adventdalen	Population	1979 – 1997	Tyler and Øritsland (1999)
		1998 – 2010	Hansen *et al.* (2013)†
		2011 – 2013	NPI unpubl.
	Carcass	2001 – 2013	NPI unpubl.
Reindalen	Population	1990 – 2011	Solberg *et al.* (2012)†
		2012	NINA unpubl.
	Carcass	1996 – 2012	NINA unpubl.

† Structured counts by sex and age are unpublished (data courtesy of NPI and NINA for Adventdalen and Reindalen, respectively).

Table 2: Parameter estimates (β), standard error (SE) and test statistics (*t*- and *P*-values) of the top ranking models ($\Delta AIC_c > 2$ for all other alternative models) for the sex-specific adult growth rate analysis of Svalbard reindeer in Adventdalen and Reindalen. The reference level for Sex is females. Covariates were standardized. Fec_{t-1} = fecundity in year *t-1*; dtr_N = detrended population size; Prec= total winter precipitation (1 November – 30 April); dtr_sumT = detrended summer temperature (1 July – 31 August).

	Adventdalen		**Reindalen**	
	β ± SE	***t* (*P*)**	**β ± SE**	***t* (*P*)**
Intercept	0.014 ± 0.029	0.48 (0.63)	0.034 ± 0.050	0.77 (0.45)
Sex	0.000 ± 0.040	0.00 (1.00)	–0.047 ± 0.070	–0.67 (0.51)
Fec_{t-1}	0.071 ± 0.022	3.28 (<0.01)	0.119 ± 0.038	3.14 (<0.01)
dtr_N	–0.181 ± 0.030	–6.05 (<0.001)	–0.138 ± 0.035	–3.97 (<0.001)
Prec	0.008 ± 0.029	0.26 (0.79)	–0.038 ± 0.050	–0.76 (0.45)
dtr_sumT	0.056 ± 0.021	2.61 (<0.05)		
Sex × dtr_N	0.093 ± 0.041	2.24 (<0.05)		
Sex × Prec	–0.084 ± 0.040	–2.07 (<0.05)	–0.159 ± 0.070	–2.28 (<0.05)
Adjusted R^2	0.554		0.555	

Table 3: Parameter estimates (β), standard error (SE) and test statistics (*z*- and *P*-values) of the top ranking models for the mortality index analysis of adult Svalbard reindeer in Adventdalen and Reindalen. Only the most parsimonious models with $\Delta AIC_c < 1$ are shown (see table A2 for model selection). Estimates and standard errors (β ± SE) are on the logit scale. Standard deviation (SD) for the residual variability and the number of groups (i.e. years) are given for the random effects on the intercept. The reference level for Sex is females. Covariates were standardized. dtr_N_{t-1} = detrended population size in year *t-1*; $Prec_{t-1}$= total winter precipitation in year *t-1* (1 November – 30 April).

	Adventdalen				**Reindalen**	
	Model 1		Model 2		Model 1	
Fixed effects	**β ± SE**	***z* (*P*)**	**β ± SE**	***z* (*P*)**	**β ± SE**	***z* (*P*)**
Intercept	–3.79 ± 0.25	–15.33 (<0.001)	–3.80 ± 0.22	–17.13 (<0.001)	–3.89 ± 0.30	–13.13 (<0.001)
Sex	0.65 ± 0.12	5.24 (<0.001)	0.65 ± 0.12	5.26 (<0.001)	0.35 ± 0.12	2.79 (<0.01)
dtr_N_{t-1}			0.44 ± 0.23	1.95 (0.051)	0.56 ± 0.29	1.98 (<0.05)
$Prec_{t-1}$	–0.23 ± 0.25	–0.91 (0.37)	–0.11 ± 0.23	–0.49 (0.63)	0.81 ± 0.30	2.76 (<0.01)
Sex × dtr_N_{t-1}					–0.33 ± 0.10	–3.42 (<0.001)
Sex × $Prec_{t-1}$	0.49 ± 0.13	3.79 (<0.001)	0.49 ± 0.13	3.77 (<0.001)		
Random effects	**SD**	**No. groups**	**SD**	**No. groups**	**SD**	**No. groups**
Year	0.81	13	0.71	13	1.11	17
AIC_c	179.78		179.80		216.31	
ΔAIC_c	0.00		0.02		0.00	

Table 4: Parameter estimates (β), standard error (SE) and test statistics (*t*- and *P*-values) of the top ranking models ($\Delta AIC_c > 2$ for all other alternative models) for the analysis of change in adult sex ratio (ΔASR) of Svalbard reindeer in Adventdalen and Reindalen. Covariates were standardized. dtr_N = detrended population size; Prec= total winter precipitation (1 November – 30 April).

	Adventdalen		**Reindalen**	
	β ± SE	***t* (*P*)**	**β ± SE**	***t* (*P*)**
Intercept	0.001 ± 0.008	0.11 (0.91)	–0.011 ± 0.017	–0.67 (0.52)
dtr_N	0.022 ± 0.008	2.70 (<0.05)		
Prec	–0.020 ± 0.008	–2.43 (<0.05)	–0.038 ± 0.017	–2.24 (<0.05)
Adjusted R^2	0.277		0.182	

Figures

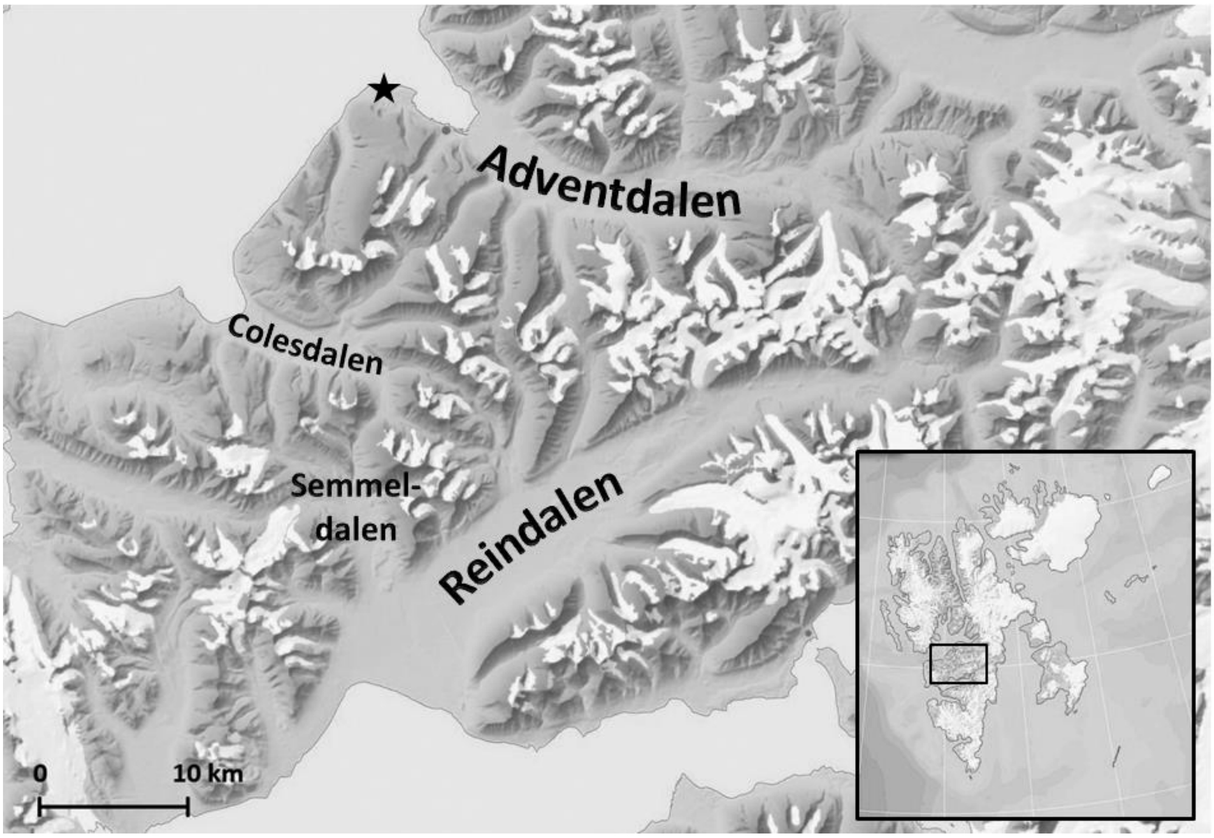

Figure 1: The two study populations of Svalbard reindeer are located in Adventdalen and Reindalen in Nordenskiöld Land on the Svalbard archipelago (inset). The valley systems Colesdalen and Semmeldalen are part of the Reindalen population. The star indicates the location of the Norwegian Meteorological Institute's weather station at Svalbard Airport, Longyearbyen.

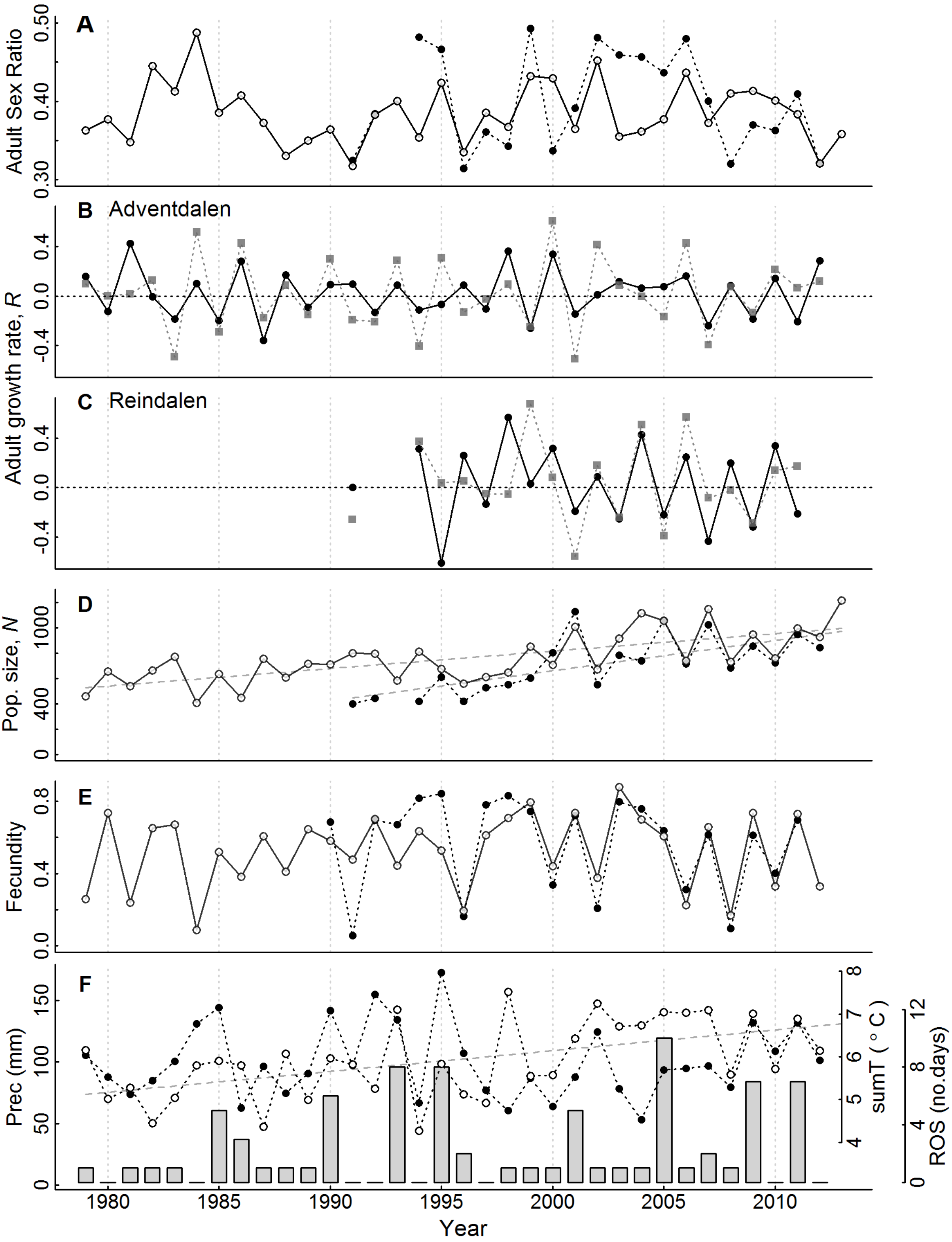

Figure 2: Time series of (A) adult sex ratio (i.e. the proportion of males per total sexed adults) for Adventdalen (1997–2013; white circles, straight lines) and Reindalen (1991–2012; black circles, dotted lines); (B-C) adult logistic population growth rates (*R*) from year *t* to *t+1* for males (black circles, straight lines) and females (grey squares, dotted lines) for

Adventdalen (B) and Reindalen (C); (D) total population size (*N;* grey dashed lines indicate the positive trends), and (E) population-level fecundity (i.e. the number of calves per female) for Adventdalen (white circles, straight lines) and Reindalen (black circles, dotted lines); (F) climate data used for all analyses: total winter precipitation (mm) (Prec; black circles, dotted lines), average summer temperature (°C) (sumT ; white circles, dotted lines with the positive trend in summer temperature indicated by the grey dashed line), and the number of days with 'rain-on-snow' (ROS; grey bars).

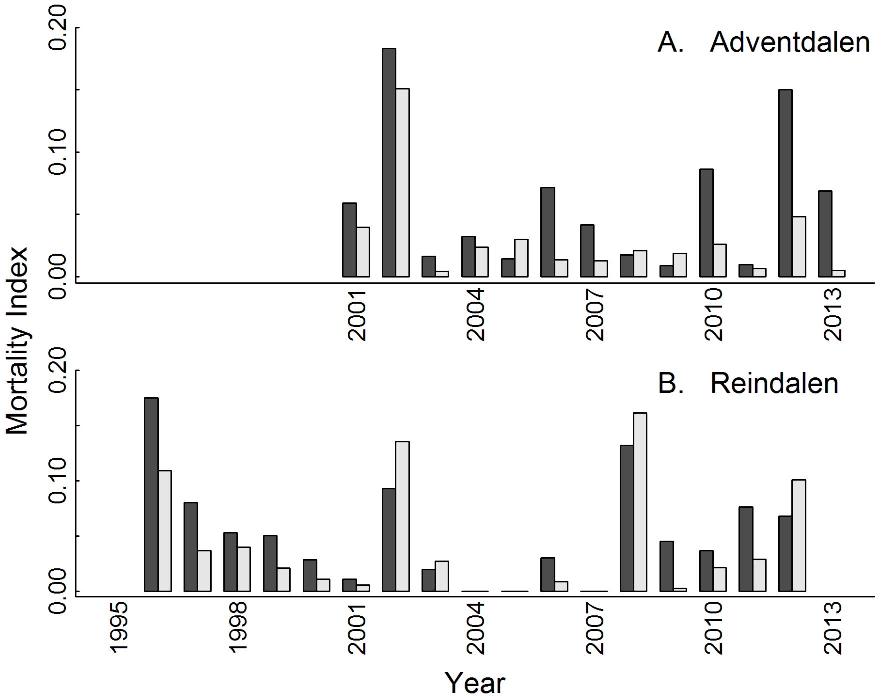

Figure 3: Yearly adult mortality index for male (dark bars) and female reindeer (light bars) in (A) Adventdalen and (B) Reindalen. Mortality indices were calculated by dividing the number of carcasses of adult animals from each sex (died within 12 months from the previous year's census) by the previous year's number of live adults of each respective sex.

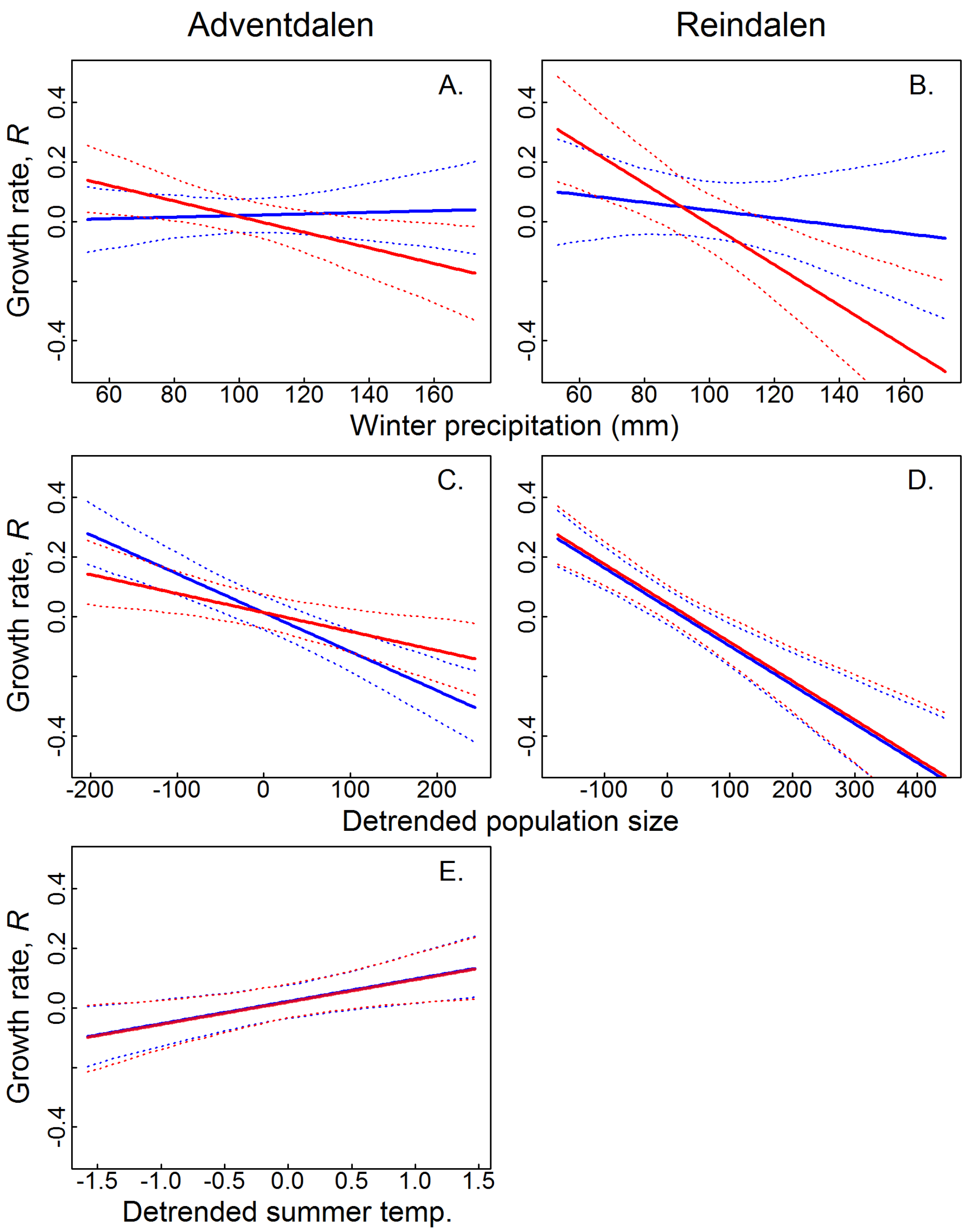

Figure 4: Estimated response of adult population growth rate (*R*) to (A-B) total winter precipitation (mm; 1 November – 30 April), (C-D) detrended population size, and (E) detrended summer temperature (1 July – 31 August) for Adventdalen (A, C, E) and Reindalen (B, D). Red and blue lines are for adult males and females, respectively. Dotted lines indicate 95% confidence intervals based on 1000 simulations of the estimated coefficients from the most parsimonious regression model (Table 2). For each estimated response illustrated in the graphs, all other variables included in the model were kept constant at their average value.

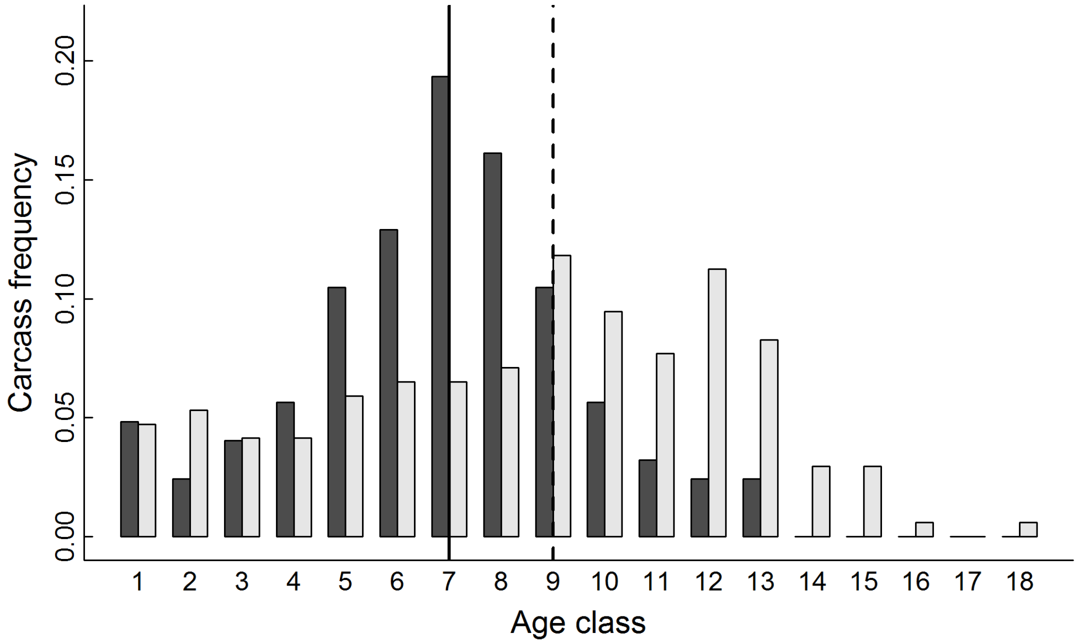

Figure 5: Age class distribution for male (dark bars, n = 124) and female (light bars, n = 169) reindeer carcasses of age ≥ 1 year from Reindalen over the period 1996–2012. Vertical lines indicate median age at death for males (straight line) and females (dashed line), given that they survived until the age of 1 year. Note that 45% of total carcasses were from calves (0 year), which were usually not sexed. Of female and male carcasses aged ≥ 1 year, respectively 27 and 37% were unclassified by age, and 6% of carcasses aged ≥ 1 year were unsexed. Only carcasses of known age and sex are shown in the figure.

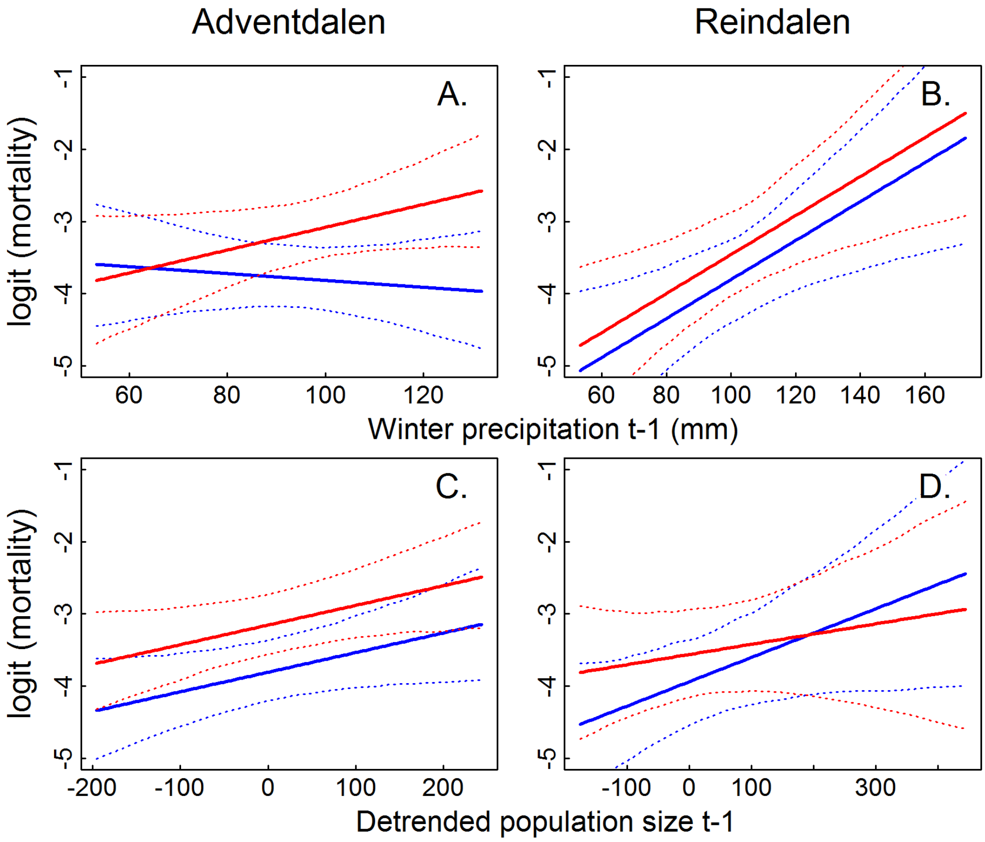

Figure 6: Estimated response of the mortality index (on logit scale) to (A-B) total precipitation (mm; 1 November – 30 April) during the previous winter, and (C-D) detrended population size in year *t-1* for Adventdalen (A, C) and Reindalen (B, D). Red and blue lines are for adult males and females, respectively. Dotted lines indicate 95% confidence intervals based on 1000 simulations of the fixed effects from the first and second ranking models for Reindalen and Adventdalen, respectively (Table 3). For each estimated response illustrated in the graphs, all other variables included in the model were kept constant at their average value.

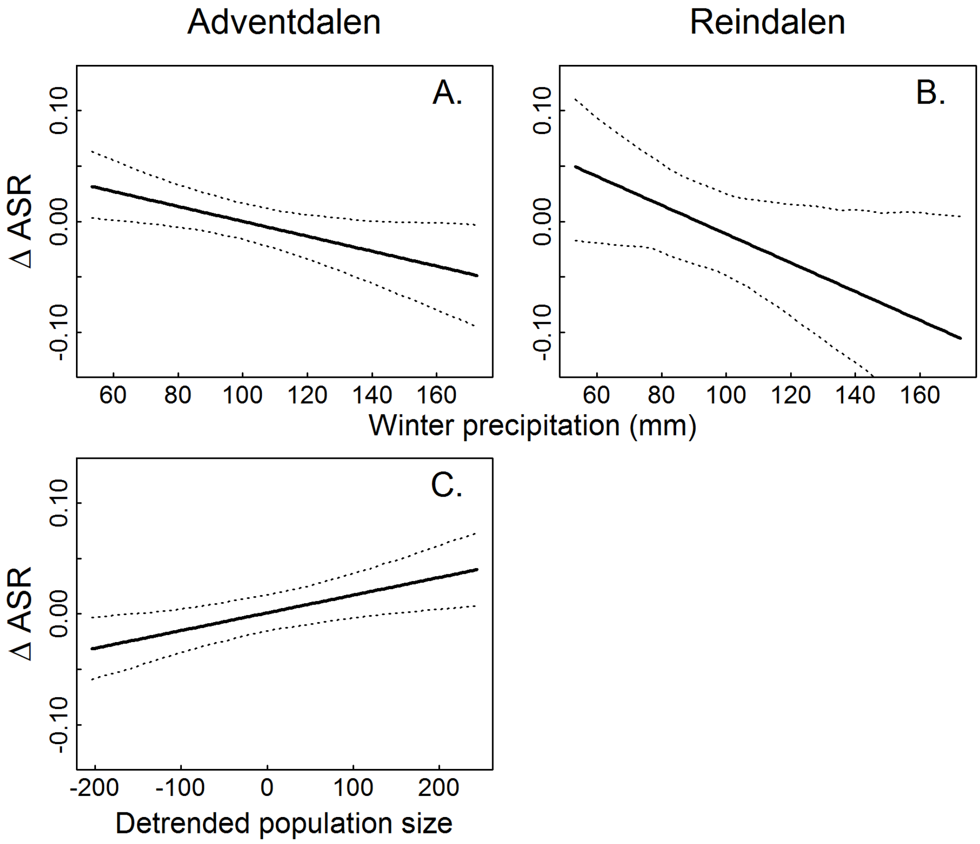

Figure 7: Estimated response of change in adult sex ratio from one year to the next (ΔASR) to (A-B) winter precipitation (mm; 1 November – 30 April), and (C) detrended population size for Adventdalen (A, C) and Reindalen (B). Dotted lines indicate 95% confidence intervals based on 1000 simulations of the estimated coefficients from the most parsimonious regression model (Table 4). For each estimated response illustrated in the graphs, all other variables included in the model were kept constant at their average value.

Appendix: Model selection

Table A1: The five best models according to AIC$_c$ and ΔAIC$_c$ for adult population growth rate analysis of Svalbard reindeer in Adventdalen and Reindalen. 'X' indicates whether a variable was included in a model. Sex was included in all candidate models. Winter precipitation (Prec [mm]; 1 November – 30 April) and the ln-transformed number of days with ROS (logROS = ln[ROS + 1]) were never included in the same model. dtr_N = detrended population size; Fec$_{t-1}$ = fecundity in year *t-1*; dtr_sumT = detrended summer temperature (1 July – 31 August).

Model rank	**Sex**	**dtr_N**	**Fec$_{t-1}$**	**Prec**	**dtr_ sumT**	**logROS**	**Sex × dtr_N**	**Sex × Fec$_{t-1}$**	**Sex × Prec**	**Sex × dtr_ sumT**	**Sex × logROS**	**AIC$_c$**	**ΔAIC$_c$**
Adventdalen													
1	X	X	X	X	X		X		X			–38.37	0.00
2	X	X	X	X	X		X					–36.35	2.01
3	X	X	X		X		X					–36.18	2.19
4	X	X	X	X	X		X		X	X		–35.61	2.76
5	X	X	X	X	X				X			–35.59	2.77
Reindalen													
1	X	X	X	X					X			1.67	0.00
2	X	X	X	X								4.35	2.67
3	X	X	X	X			X		X			4.87	3.20
4	X	X	X	X				X	X			4.91	3.23
5	X	X	X	X	X				X			4.91	3.23

Table A2: The five best models according to AIC_c and ΔAIC_c for mortality index analysis of adult Svalbard reindeer in Adventdalen and Reindalen. 'X' indicates whether a variable was included in a model. Sex was included in all candidate models. Winter precipitation in year *t-1* ($Prec_{t-1}$ [mm]; 1 November – 30 April) and the ln-transformed number of days with ROS in year *t-1* ($logROS_{t-1} = ln[ROS_{t-1} + 1]$) were never included in the same model. dtr_N_{t-1} = detrended population size in year *t-1*; dtr_sumT_{t-1} = detrended summer temperature in year *t-1* (1 July – 31 August).

Model rank	**Sex**	**dtr_N_{t-1}**	**$Prec_{t-1}$**	**dtr_sumT_{t-1}**	**$logROS_{t-1}$**	**Sex × dtr_N_{t-1}**	**Sex × $Prec_{t-1}$**	**Sex × dtr_sumT_{t-1}**	**Sex × $logROS_{t-1}$**	**AIC_c**	**ΔAIC_c**
Adventdalen											
1	X		X				X			179.78	0.00
2	X	X	X				X			179.80	0.02
3	X		X	X			X			182.95	3.17
4	X				X					184.38	4.60
5	X	X			X	X				185.19	5.41
Reindalen											
1	X	X	X			X				216.31	0.00
2	X	X	X	X		X				218.13	1.82
3	X	X	X	X		X		X		218.27	1.96
4	X	X	X			X	X			219.01	2.70
5	X	X				X				219.76	3.45

Table A3: The five best models according to AIC_c and ΔAIC_c for the analysis of change in adult sex ratio (ΔASR) of Svalbard reindeer in Adventdalen and Reindalen. 'X' indicates whether a variable was included in a model. Winter precipitation (Prec [mm]; 1 November – 30 April) and the ln-transformed number of days with ROS (logROS = ln[ROS + 1]) were never included in the same model. dtr_N = detrended population size; Fec_{t-1} = fecundity in year *t-1*; dtr_sumT = detrended summer temperature (1 July – 31 August).

Model rank	**dtr_N**	**Fec_{t-1}**	**Prec**	**dtr_ sumT**	**logROS**	**AIC_c**	**ΔAIC_c**
Adventdalen							
1	X		X			–106.58	0.00
2	X		X	X		–103.81	2.76
3	X					–103.21	3.37
4			X			–101.97	4.60
5	X				X	–101.74	4.83
Reindalen							
1			X			–40.41	0.00
2						–38.36	2.05
3			X	X		–37.70	2.71
4	X		X			–37.22	3.19
5		X	X			–37.16	3.25