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# Climate and density dependence cause changes in adult sex ratio in a large Arctic herbivore

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**Abstract.** Variation in adult sex ratio (ASR) affects population demography and dynamics of large mammals. The mechanisms behind this variation are largely unclear, but may be partly related to climatic drivers and density dependence operating differently on the adult male and female segments of the population. Here, we examine such drivers of annual changes in ASR in the predator-free wild Svalbard reindeer (*Rangifer tarandus platyrhynchus*), a high Arctic subspecies whose population dynamics are shaped by climate. Using up to 35 year long time-series of population count data from two populations, we disentangle drivers of fluctuations in ASR by first analyzing how climate and density dependence affect sex-specific adult population growth rates through effects on mortality. There were a positive population size trend and an overall female bias in ASR throughout the study period. Increased winter precipitation, a proxy for the harshness of winter feeding conditions, was found to significantly reduce adult population growth rates through reduced survival in males, but not in females. However, increased population size tended to cause a stronger immediate decline in female than in male adult population growth rates. As a consequence, the female bias in ASR increased with harsher winter conditions and declined with higher population size. As expected from the increased frequency of rainy and icy winters due to climate warming, a recent trend toward increased female bias in ASR was evident. This demonstrates that climatic drivers of both short-term fluctuations and long-term trends in demography need to be accounted for in the management and population dynamic predictions of Arctic ungulates.

**Key words:** caribou; climate change; density dependence; environment; icing; management; population structure; rain-on-snow (ROS); reproductive strategy; survival; ungulate.

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## INTRODUCTION

In ungulates, alterations in the adult sex ratio (ASR) are likely to influence population characteristics such as mean parturition date (Mysterud et al. 2002, Holand et al. 2003), female fecundity (Solberg et al. 2002), offspring sex ratio (Sæther et al. 2004), sexual size dimorphism (Garel et al. 2006), timing of the rut, and mean age of males holding harems (Clutton-Brock et al. 1997).

Variation in ASR may thus influence population growth rate (Milner et al. 2007, Lee et al. 2011, Schmidt and Gorn 2013). In managed populations, ASR is often biased toward females as a result of male trophy hunting and sex-specific harvest quotas (Solberg et al. 2005, Milner et al. 2007), leading to a higher per-capita growth rate (but see Mysterud et al. 2002, Milner et al. 2007). Understanding how ASR is influenced by population size and environmental variability, such as climate change, is therefore of relevance for the conservation, management, and harvest quota setting of vulnerable populations, and in particular small populations that are sensitive to demographic stochasticity (Lee et al. 2011).

Although offspring sex ratio can deviate from parity according to maternal condition (Trivers and Willard 1973, Clutton-Brock and Iason 1986), density dependence (Kruuk et al. 1999, Mysterud et al. 2000) as well as climate (Post et al. 1999, Mysterud et al. 2000), offspring sex ratio in mammals is generally even (but see Clutton-Brock and Iason 1986). In contrast, ASR in wild populations is frequently skewed and, in ungulates, generally toward females (Berger and Gompper 1999). The observed skew in ASR results mainly from a higher average mortality in the rarer sex. Both juvenile and adult mortality rates are typically higher for male than for female ungulates due to higher energy requirements and, hence, higher susceptibility to food shortage (Clutton-Brock et al. 1985, Toigo and Gaillard 2003). Although survival of the two sexes can be equally high under good environmental conditions (Cobben et al. 2009), it is typically more variable in males than in females (Toigo and Gaillard 2003). Extrinsic factors such as predation (Berger and Gompper 1999) can also induce sex-biased mortality rates.

While previous studies on ungulates have addressed climate and density effects on sex-specific survival (Coulson et al. 2001, Toigo and Gaillard 2003, Willisch et al. 2013), offspring sex ratio (Kruuk et al. 1999, Mysterud et al. 2000), and spatial variation in ASR (Manning et al. 2015), we are not aware of any study investigating the combined effects of density dependence and weather variability on year-to-year fluctuations in ASR. This is challenging because of difficulties in disentangling effects of juvenile sex ratio from sex-specific survival, as well as climate from density-dependent effects during periods of population trends. Accordingly, while ungulate ASR is generally believed to be more female-biased during periods of high population abundance (e.g., red deer *Cervus elaphus*, Clutton-Brock et al. 1997), the opposite has been observed as well (Soay sheep *Ovis aries*, Clutton-Brock et al. 1991, Alpine ibex *Capra ibex*, Jacobson et al. 2004).

The wild Svalbard reindeer (*Rangifer tarandus platyrhynchus*) is an ideal model species to study the effects of climate and population size on demography. Predation on Svalbard reindeer is negligible (Tyler 1987, Derocher et al. 2000), and harvest is spatially restricted with a very low annual outtake and no apparent effect on local population dynamics (Stien et al. 2012*a*). However, huge annual fluctuations in winter weather conditions combined with density dependence generate strong variation in survival, fecundity, and population sizes (Hansen et al. 2011, 2013, Stien et al. 2012*b*, Lee et al. 2015). While longer and warmer snow-free seasons have increased the carrying capacity and average population sizes (Hansen et al. 2013, Van der Wal and Stien 2014, Albon et al. 2016), current trends and future climate scenarios indicate an increase in the frequency of "rain-on-snow" (ROS) events, causing ground ice (Hansen et al. 2014) and, in turn, starvation and population crashes (Solberg et al. 2001, Kohler and Aanes 2004, Hansen et al. 2011, 2013). Similar effects of winter climate events have been observed in other ungulates across the Arctic (Parker et al. 1975, Forchhammer and Boertmann 1993, Rennert et al. 2009).

Here, we investigate the extent to which sex-specific effects of climate and density dependence cause fluctuations in ASR in two neighboring, yet semi-isolated Svalbard reindeer populations that are subject to first-order density dependence (Solberg et al. 2001, Albon et al. 2002, Hansen et al. 2013) and fluctuate in synchrony due to common climatic drivers (Aanes et al. 2003). In this highly sexually dimorphic ungulate, we expect that ASR becomes more female-biased after winters with heavy precipitation due to a stronger effect of food-limited conditions on mortality in the adult male segment (Toigo and Gaillard 2003). Because changes in ASR result from mechanisms affecting the adult male and female segment of the population differently, we first analyze sex-specific adult population growth rates in response to weather variables and population size, with a mechanistic

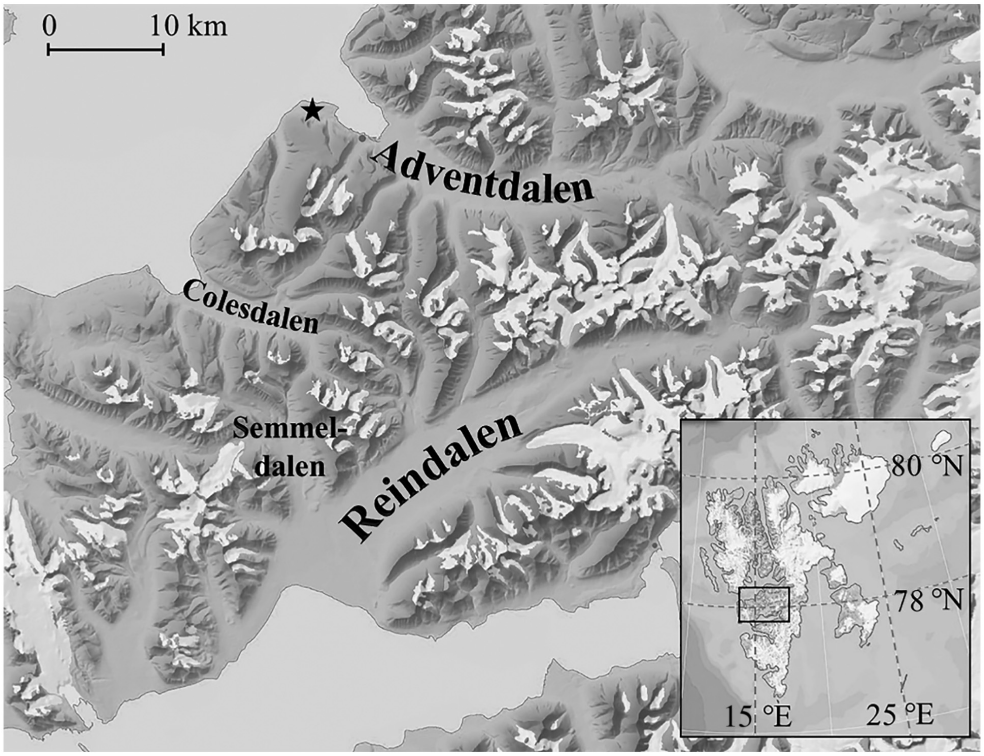

Fig. 1. The two study populations of Svalbard reindeer are located in Adventdalen and the Reindalen valley system in Nordenskiöld Land on the Svalbard archipelago (inset). The star indicates the location of the Norwegian Meteorological Institute's weather station at Svalbard Airport, Longyearbyen.

support from mortality analyses. We then investigate how this is reflected in annual changes and longer-term trends in ASR related to recent climate change.

## 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. Because of the warm North Atlantic Current, winters are relatively mild for the latitude, but annual precipitation is low (~195 mm in Longyearbyen). The two study populations of Svalbard reindeer are located in Nordenskiöld Land, Spitsbergen (Fig. 1). The Adventdalen (AD) valley system consists of one main valley with several small side valleys. The neighboring Reindalen (RD) valley system consists of three main valleys RD, Colesdalen, and Semmeldalen, with adjacent side valleys (Fig. 1). Unlike most other caribou and reindeer subspecies, the Svalbard reindeer is more or less solitary and sedentary with low exchange of animals between neighboring valley systems (Côté et al. 2002). The endemic Svalbard reindeer, along with Svalbard rock ptarmigan (*Lagopus muta hyperborea*), are the only overwintering native herbivores in Svalbard. In addition, there is a local population of the introduced sibling vole (*Microtus levis*), which only occurs in a small area close to a bird colony. The effect of interspecific resource competition with migratory 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 appears to be negligible (Tyler 1987, Derocher et al. 2000). Reindeer harvesting in the study area is restricted to only parts of RD and Colesdalen. The regulations related to the hunting of Svalbard reindeer state that the harvest should not affect the population development or the population demography. In line with this goal, sex and age distribution of annual harvest quotas aim to reflect the demographic structure of the population. The annual quota is low, that is, probably less than 5% of the total pre-harvest population, and there appears to be no significant effects of harvest on the population dynamics (Stien et al. 2012*a*).

### *Reindeer data*

Annual population censuses of Svalbard reindeer were conducted in summer after calving. During counts, animals were categorized by age as calves, yearlings, or adults (≥2 yr old) based on body size and antler characteristics. The two latter age classes were also categorized by sex. For AD, we used population count data from 1979 to 2013 (1979–1996, Tyler and Øritsland 1999, 1997–2013, this study). The AD census consists of total population counts conducted by four to six people during late June–early July over a period of 7–10 d. Observers walk separate, predefined routes scanning the entire area with binoculars, and only deviate from the routes 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. Due to the open landscape and their stationary behavior, counts are assumed to be close to the actual population number for AD (Tyler 1987, Tyler and Øritsland 1999).

The RD census consists of fixed transect counts conducted by two people during late July–early August over a period of 5–8 d (Solberg et al. 2001). Observers use binoculars and telescopes to scan the area. In contrast to the AD census, reindeer have lost their winter fur in this period, making them less distinct in the landscape. Annual RD censuses were performed over the period 1979–2013 (Solberg et al. 2001); however, in 1979–1990 and 1993, the counts covered different areas than other years. For consistency and to avoid bias due to, for example, effects of sexual segregation in space (Loe et al. 2006), we used the data from 1991 to 1992 and 1994 to 2013.

For a given annual census, the number of animals unclassified to age and sex never exceeded 11.4% ($\mu = 5.0\%$, $\sigma = 3.1\%$) for AD for the period of 1998–2013 (data on unclassified animals were not available for the period 1979–1997), and 11.3% ($\mu = 4.1\%$, $\sigma = 3.2\%$) for RD. However, misclassifications may occur depending on observer experience and distance to the animal, particularly for yearlings and young adults during the early summer count in AD.

### *Climate data*

Daily precipitation (mm) and average temperature (°C) for the winter period (defined here as November–April) and summer period (July–August) were obtained from the Norwegian Meteorological Institute's weather station at Svalbard airport (see Fig. 1 for location; http://eklima.met.no). According to geographical distances, weather data may be more representative for AD than for RD, but annual variability in weather was assumed to be strongly correlated between valley systems (Solberg et al. 2001). Precipitation falling on days with a mean temperature ≥1°C during the winter period was defined as ROS (Stien et al. 2012*b*, Hansen et al. 2013). Three alternative indices for winter harshness condition were used: (1) total winter precipitation (mm, Fig. 2a; Solberg et al. 2001), (2) amount of ROS (mm; Appendix S1: Fig. S1; Stien et al. 2012*b*), and (3) the number of days with ROS, hereafter referred to as ROS-days (daily mean temperature ≥ 1°C and precipitation ≥ 1 mm, in accordance with Hansen et al. 2013; Appendix S1: Fig. S1). Rain-on-snow and ROS-days are both indices for icing conditions, while total winter precipitation integrates the effects of both rain and snow on forage availability. All three indices were positively correlated (Appendix S1: Table S1). Mean summer temperature (°C; Fig. 2a) was used as an index of forage abundance, since summer temperature directly determines above-ground green vascular biomass the same year (Van der Wal and Stien 2014) and has a positive effect on the next year's population growth rate of Svalbard reindeer (Hansen et al. 2013).

### *Data analysis*

The following variables were derived from the census data in each population: (1) ASR calculated as the proportion of males per total sexed adults (i.e., ≥2 yr; Fig. 2b), (2) change in ASR (ΔASR) from year $t$ to $t + 1$, that is, $\text{ASR}_{t+1} - \text{ASR}_t$, (3) the sex-specific logistic population growth rate ($R_t$) for adults (≥2 yr), calculated as $X_{t+1} - X_t$, with $X_t$

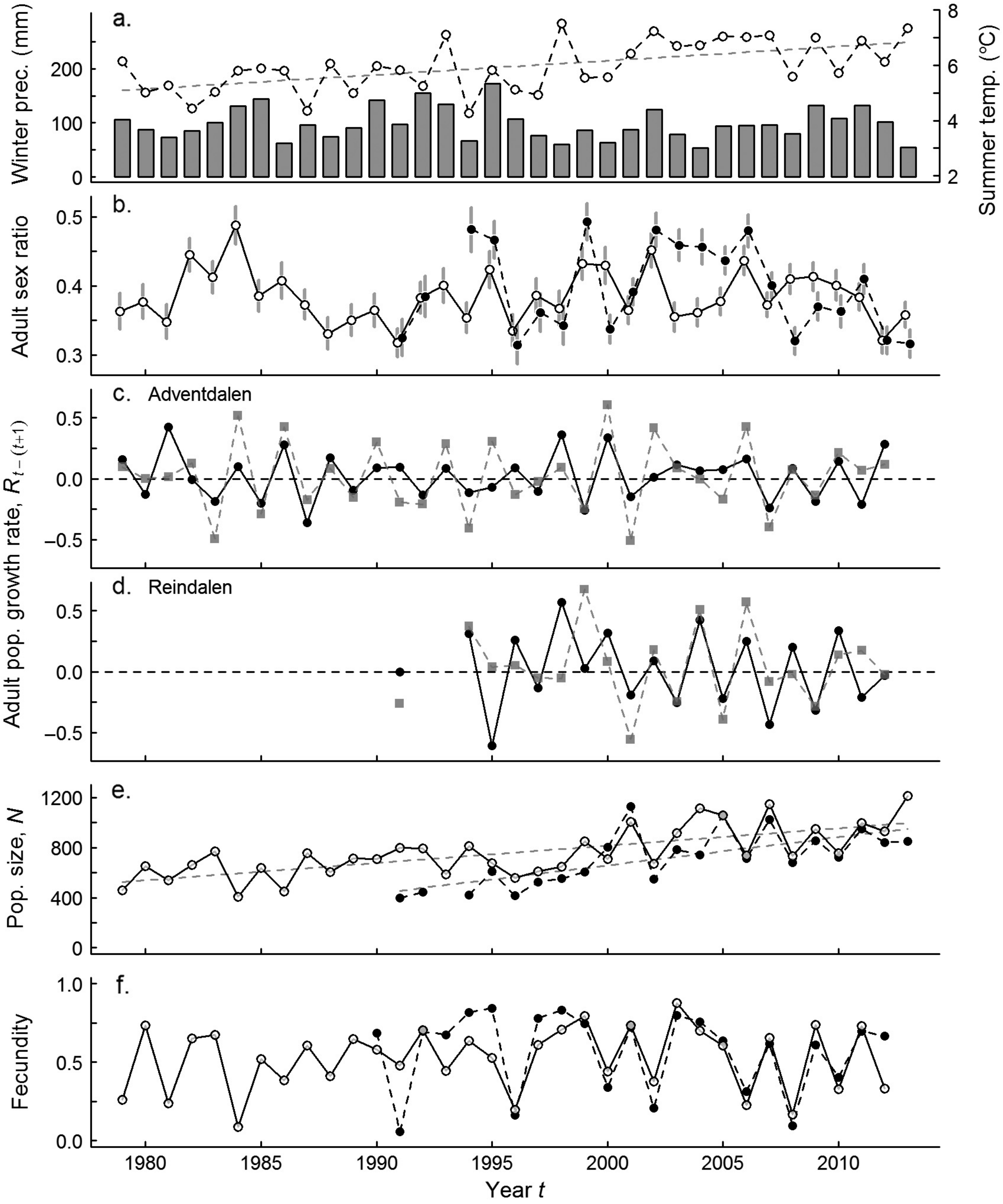

Fig. 2. Time-series of (a) total winter precipitation (gray bars) and mean summer temperature (white circles and dashed line; positive trend indicated by the gray dashed line). (b) Adult sex ratio, that is, the male proportion of adults (≥2 yr), in Adventdalen (AD; white circles, solid line) and Reindalen (RD; black circles, dashed line). Standard errors indicated by gray lines. (c, d) Adult logistic population growth rates ($R$) from year $t$ to $t + 1$ for males (black circles, solid line) and females (gray squares, dashed line) in AD and RD. (e) Population size ($N$; gray dashed lines indicate positive trends) in AD (white circles, solid line) and RD (black circles, dashed line). (f) Population-level fecundity (i.e., the number of calves per female) in AD (white circles, solid line) and RD (black circles, dashed line).

being the natural logarithm of the number of either adult male or female reindeer in year $t$ (Fig 2c, d), (4) population size ($N$), that is, total number of animals counted (Fig. 2e), (5) fecundity, calculated as the number of calves per adult female (Fig. 2f). The reindeer population sizes showed positive trends during the study period (Fig. 2e), indicating a likely increase in carrying capacity due to increasing summer temperatures (Fig. 2a) and available plant biomass (Hansen et al. 2013, Van der Wal and Stien 2014). Therefore, population size and mean summer temperature were detrended by using the residuals from a linear model of population size and mean summer temperature against year (Albon et al. 2016). Population size hereafter refers to detrended population size, unless stated otherwise.

We used multiple linear regression analysis to disentangle the effects of climate and population size on sex-specific adult population growth rate and ΔASR, with particular emphasis on the population with the longest time-series (AD). Analyzing variation in ΔASR rather than variation in annual ASR per se was preferred as the latter would represent deviations from the mean ASR and thus underestimate the strength of climate and population size effects on changes in ASR. Predictor variables in the global models were population size in year $t$, summer temperature in year $t$, total winter precipitation, ROS, and ROS-days, which was ln-transformed after adding one unit in the analysis to avoid logs of zero. Total winter precipitation, ROS, and ROS-days covered the period from November in year $t$ to April in year $t + 1$ and were not included in the same candidate models as the former also captures the extent of ROS, and they are all indices for winter harshness conditions. Fecundity in year $t - 1$ was included as a covariate in the adult population growth rate analysis to control for input from new cohorts (i.e., calves born in year $t - 1$ will enter the adult population in year $t + 1$, given that they survive). Also, for the adult population growth rate analysis, sex was included in all candidate models and two-way interactions between sex and the covariates were included in the global model. All covariates were standardized for comparison. Pearson's correlation coefficients were $|r| \leq 0.56$ for all pairwise combinations of covariates included in the models (Appendix S1: Table S1). Model selection was performed using the corrected Akaike's information criterion (AICc) based on the models' maximum likelihood (Burnham and Anderson 2002). Corrected Akaike's information criterion was preferred over AIC due to low sample size (35 and 22 yr of data for AD and RD, respectively) relative to the potential number of parameters estimated. The top-ranked model for the population with the longest time-series (AD) was applied on the RD population for comparison. Model residuals were checked for approximate normality using a Shapiro–Wilk test and $Q$–$Q$ plot. Furthermore, we analyzed carcass count data to provide mechanistic support for the results on sex-specific adult population growth rates and ASR (Appendix S3). The number of carcasses found each year reflects annual mortalities rather well, particularly in years with high mortality (Lee et al. 2015), although indices based on counts of carcasses vs. live population are underestimates of mortality. Carcass data were only available for a shorter length of the time-series (2001–2013 for AD and 1996–2013 for RD). To investigate for trends in ASR (Fig. 2b), we fitted a linear regression model for ASR with year as an explanatory variable. Since the trend estimate depends on the starting point (yr), we fitted the regression to multiple time-series with starting point in 1979, 1980, etc., up to 2006 (each time-series ending with 2013).

All analyses were conducted separately for AD and RD because of the differences in time periods covered and sampling methods (see *Reindeer data* in *Methods* section), and to avoid complex three-way interactions (e.g., sex, population and ROS). However, we did perform a post hoc analysis of adult population growth rate and ΔASR combining data for AD and RD in the same model for the period in which the time-series overlap (Appendix S4). Since harvest of Svalbard reindeer does not occur in AD and the annual harvest in RD has no apparent effects on population dynamics (Stien et al. 2012*a*), we did not attempt to control for the effect of harvest. All statistical analyses were conducted in R version 3.1.0 (R Core Team 2014).

## RESULTS

In both populations, ASR was female-biased (AD: $\mu = 0.39$, $\sigma = 0.04$, $\chi^2 = 96.24$, df = 34, $P < 0.001$; RD: $\mu = 0.40$, $\sigma = 0.06$; $\chi^2 = 144.48$,

Table 1. Parameter estimates (β), standard errors (SE), and test statistics ($t$ and $P$ values) of the analysis of (a) sex-specific adult population growth rate and (b) change in adult sex ratio (ΔASR) of Svalbard reindeer in Adventdalen and Reindalen.

| | Adventdalen | | | | Reindalen | | | |
|---|---|---|---|---|---|---|---|---|
| Parameters | β | SE | $t$ | $P$ | β | SE | $t$ | $P$ |
| (a) Adult population growth rate | | | | | | | | |
| Intercept | 0.015 | 0.029 | 0.510 | 0.611 | 0.037 | 0.050 | 0.737 | 0.467 |
| Sex(male) | 0.004 | 0.040 | 0.094 | 0.925 | −0.038 | 0.070 | −0.538 | 0.594 |
| $\text{Fec}_{t-1}$ | 0.071 | 0.022 | 3.288 | 0.002 | 0.111 | 0.038 | 2.900 | 0.007 |
| winPrec | 0.008 | 0.030 | 0.260 | 0.796 | −0.041 | 0.052 | −0.779 | 0.442 |
| dtr_N | −0.181 | 0.030 | −6.069 | <0.001 | −0.136 | 0.050 | −2.706 | 0.011 |
| dtr_sumT | 0.056 | 0.021 | 2.650 | 0.010 | 0.006 | 0.035 | 0.157 | 0.877 |
| Sex(male) × winPrec | −0.085 | 0.041 | −2.072 | 0.043 | −0.162 | 0.071 | −2.204 | 0.035 |
| Sex(male) × dtr_N | 0.093 | 0.041 | 2.241 | 0.029 | 0.009 | 0.068 | 0.134 | 0.894 |
| (b) ΔASR | | | | | | | | |
| Intercept | 0.002 | 0.008 | 0.222 | 0.826 | −0.009 | 0.016 | −0.566 | 0.579 |
| winPrec | −0.020 | 0.008 | −2.434 | 0.021 | −0.038 | 0.017 | −2.230 | 0.040 |
| dtr_N | 0.022 | 0.008 | 2.700 | 0.011 | 0.003 | 0.016 | 0.215 | 0.833 |

*Notes:* The reference level for Sex is females. Covariates were standardized. The adjusted coefficient of determination (adj. $R^2$) was 0.555 (Adventdalen) and 0.505 (Reindalen) for (a), and 0.277 (Adventdalen) and 0.138 (Reindalen) for (b). $\text{Fec}_{t-1}$, fecundity in year $t - 1$; winPrec, winter precipitation; dtr_N, detrended population size; dtr_sumT, detrended summer temperature.

df = 21, $P < 0.001$) with annual estimates in the range of 0.31–0.49 (Fig. 2b). Both ASR and ΔASR were positively correlated between AD and RD (ASR: Pearson's $r = 0.44$, df = 20, $P = 0.040$; ΔASR: $r = 0.54$, df = 20, $P = 0.013$). In addition, there was a positive correlation between AD and RD in annual population size (i.e., not detrended; $r = 0.71$, df = 20, $P < 0.001$) and fecundity ($r = 0.75$, df = 21, $P < 0.001$). Likewise, the sex-specific adult population growth rates in the two populations were positively correlated, yet not statistically significant for females (males: $r = 0.59$, df = 18, $P < 0.01$; females: $r = 0.30$, df = 18, $P = 0.21$).

For the population with the longest count time-series (AD), model selection suggested that the sex-specific adult population growth rate was best described as a function of winter precipitation, population size, previous year's fecundity, summer temperature, and two-way interactions between sex and winter precipitation, and sex and population size (Table 1a; see Appendix S2: Table S1 for model selection). Winter precipitation had no significant effect on females, but a negative effect on males (Table 1a, Fig. 3a), which was supported by the adult mortality index analysis (Appendix S3). In contrast, the overall negative effect of population size was significantly stronger in females than in males (Table 1a, Fig. 3b). In addition, adult population growth rate increased with increasing summer temperature and previous year's fecundity (Table 1a). The most parsimonious model describing ΔASR in AD included a negative effect of winter precipitation and a positive effect of population size (Table 1b, Fig 4a, b; Appendix S2: Table S2 for model selection), which was consistent with the adult population growth rate analysis. Thus, harsher winter conditions and reduced population size led to a more female-biased ASR.

As for AD, sex-specific adult population growth rate in RD was related to winter precipitation, population size, previous year's fecundity, and a two-way interaction between sex and winter precipitation (Table 1a, Fig 3c, d). In contrast to AD, there was no evidence for a summer temperature effect or an interaction effect of sex and population size on adult population growth rate in RD (Table 1a, Fig. 3d; see Appendix S2: Table S1 for model selection and Table S3 for parameter estimates from the top-ranked model). However, a stronger effect of population size on female than on male mortality was evident in RD from the adult mortality index analysis (Appendix S3). ΔASR in RD was best described as a function of winter precipitation only (Table 1b, Fig 4c, d; Appendix S2: Tables S2, S3).

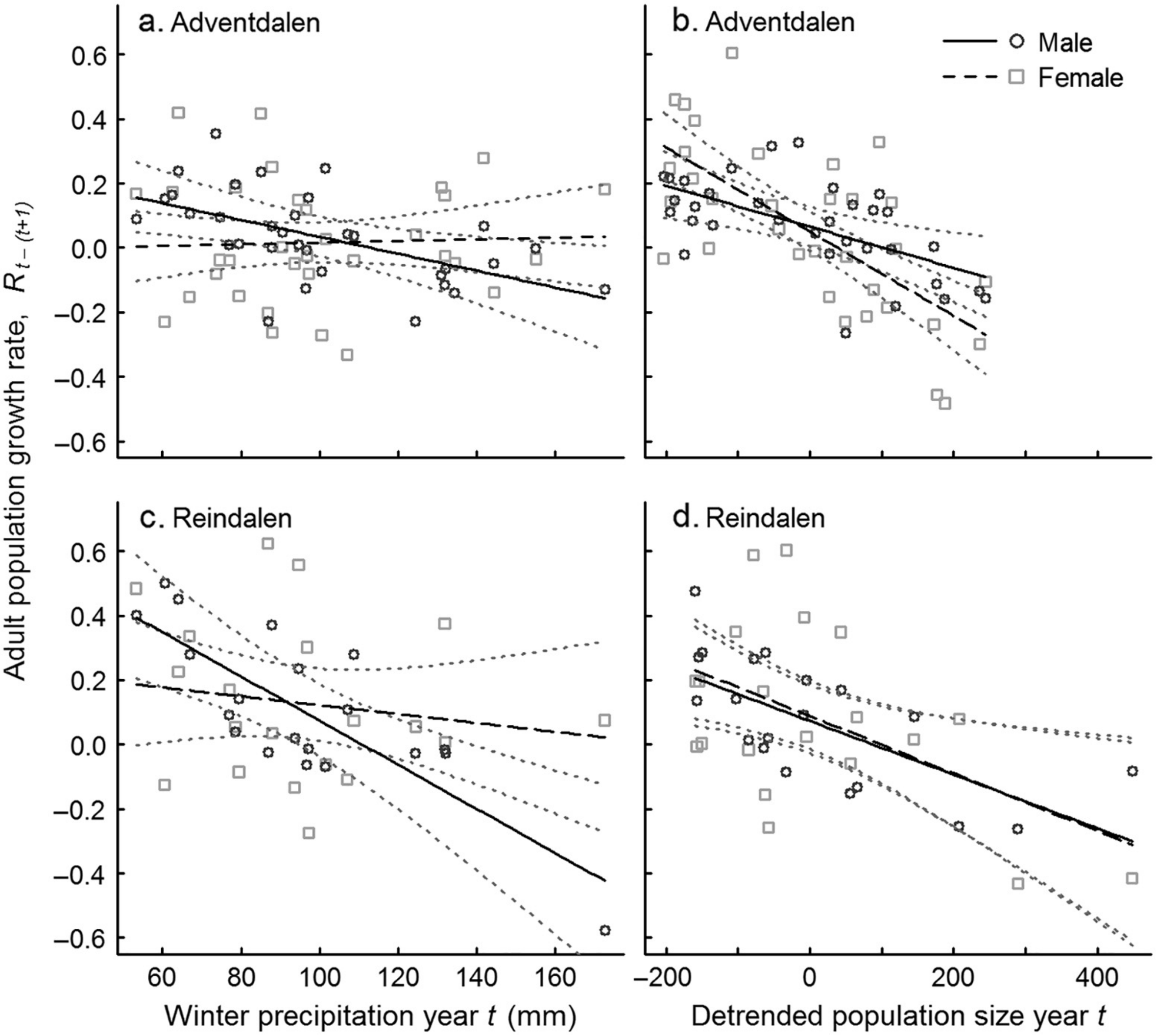

Fig. 3. Estimated effects of (a, c) winter precipitation and (b, d) population size (detrended) on adult population growth rates in males (solid lines) and females (dashed lines) of Svalbard reindeer populations in (a, b) Adventdalen and (c, d) Reindalen. The estimates are from the models in Table 1a. Dotted lines indicate 95% confidence intervals. Partial residuals are shown for males (black circles) and females (gray squares). For each estimated response illustrated in the graphs, all other covariates included in the model were kept constant at their median value. Note that the difference in slopes for males and females in (d) is not significant.

In both populations, the trend in ASR fluctuated around or close to zero, for then to become increasingly negative for the subsets of time-series spanning only the later part of the sampling period (Fig. 5). This temporal trend pattern was particularly evident in RD (Fig. 5b), where the negative trend in ASR was statistically significant from 1999 onward ($r < -0.58$, df = 13–7, $P < 0.05$; for time-series with starting year 2000 and 2006: $r < -0.49$, $P \approx 0.07$). The post hoc analysis that combined the overlapping time-series from both populations revealed no evidence for three-way interaction effects in the adult population growth rates; that is, sex differences in the effects of winter precipitation and population size did not depend on population (Appendix S4). However, the post hoc analysis of ΔASR confirmed that the density effect was mainly evident in AD, while the winter

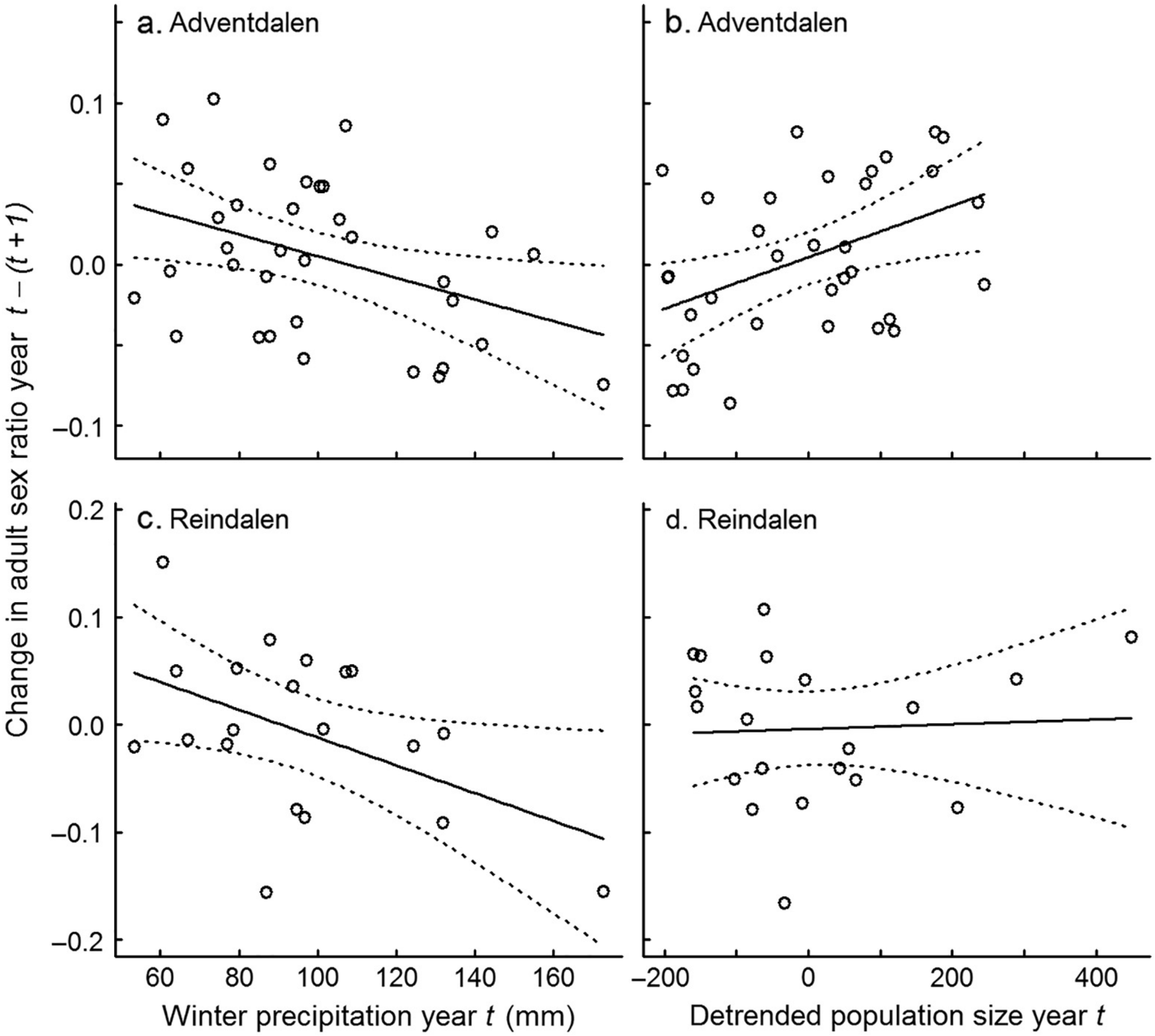

Fig. 4. Estimated effects of (a, c) winter precipitation and (b, d) population size (detrended) on change in adult sex ratio of Svalbard reindeer populations in (a, b) Adventdalen and (c, d) Reindalen. The estimates are from the models in Table 1b. Dotted lines indicate 95% confidence intervals. Partial residuals are shown by the black circles. For each estimated response illustrated in the graphs, the other covariate included in the model was kept constant at its median value. Note that the effect of population size in (d) is not significant.

precipitation effect tended to be stronger in RD than in AD (Appendix S4).

## Discussion

By separating long-term population monitoring data into sex-specific components, we have shown that winter harshness and direct (first-order) density dependence influence the adult male and female segments of Svalbard reindeer populations differently, causing changes in ASR. Increased winter precipitation reduced the adult population growth rates in males, but not in females (Fig. 3a,c), apparently due to a stronger effect on mortality (Appendix S3). Increased population size had an overall negative effect on adult population growth rate, but was considerably stronger in females than in males in our

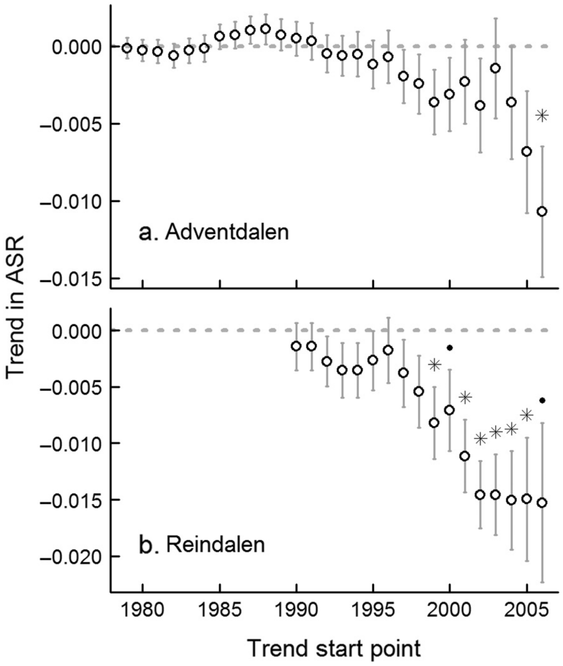

Fig. 5. Estimates of trend in adult sex ratio for time-series with varying starting years for (a) Adventdalen and (b) Reindalen. A negative trend indicates a reduction in the male proportion of adults. Gray bars indicate standard errors of slope estimates. Asterisks and dots indicate trends with *P* values <0.05 and <0.10, respectively.

study population with the longest time-series (Fig. 3b, d) through a stronger effect on female mortality (Appendix S3). Consequently, the female bias in Svalbard reindeer ASR increased with winter severity, but tended to decline with population size (Fig. 4). Thus, the recent negative trend in ASR (Fig. 5) coincided with an increased frequency of winter warm spells and heavy ROS events during the past decade (Appendix S1: Fig. S1; Rennert et al. 2009, Hansen et al. 2011, 2014).

Food limitation during winter is the main driver of population fluctuations in many ungulate populations, varying strongly between years according to annual variation in precipitation and snow-ice conditions (Parker et al. 1975, Forchhammer and Boertmann 1993, Garrott et al. 2003, Hansen et al. 2011). While the snow-pack is rarely deep in Svalbard, crust-ice in the snow-pack and occasional ground-icing due to ROS events are considered the main feeding constraints during winter (Hansen et al. 2010, 2011). Total winter precipitation seems to reflect these conditions, being strongly correlated with ROS and ROS-days (Appendix S1: Table S1). High amount of winter precipitation has previously been shown to negatively affect calving rate, survival, and population growth rate in Svalbard reindeer (Solberg et al. 2001). Since input from new cohorts was accounted for, the sex-specific effect of winter precipitation on adult population growth rate indicates a stronger increase in mortality in adult males than in females during severe winters (see Appendix S3). This led to a more female-biased ASR following harsh winters. Winter weather also influences female survival (in RD; Appendix S3; Albon et al. 2016), but this effect is highly age-specific (Lee et al. 2015). The majority of female reindeer belong to the prime-aged age classes (Lee et al. 2015, Bjørkvoll et al. 2016), for which the mean survival rates are very close to one and even very high during harsh winters. As a likely consequence, the weather effects on our mortality index and population growth rate estimates for the entire adult female segment were found to be weak. For males, this appears not to be the case, possibly due to a stronger average climate effect across ages. These sex-specific differences in the effect of severe winter conditions were also expected based on overall sex differences in reproductive strategy (Barboza et al. 2004, Bårdsen et al. 2008) and survival (Coulson et al. 2001, Toigo and Gaillard 2003, Catchpole et al. 2004, Willisch et al. 2013). Adult male reindeer typically reduce food intake during the autumn rutting period, resulting in reduced body condition at the onset of winter (Barboza et al. 2004). Females, on the other hand, adjust their reproductive resource allocation in summer to prepare for unpredictable winter conditions (Bårdsen et al. 2008) and can even terminate their pregnancy if their body condition becomes too poor (Tyler 1987). Therefore, females seem less prone to mortality from starvation during winters with increased precipitation than males. As female survival is less affected, the potential increase in calf per-capita ratio due to more female-biased ASR can hence improve population recovery rate in the following years.

There was evidence from both populations that the effect of increased population size tended to be stronger in females than in males (Fig. 3b; Appendix S3: Fig. S3d). Density-dependent effects have indeed been reported previously for female fecundity (Albon et al. 2002) and population growth rate (Solberg et al. 2001, Aanes et al. 2003, Hansen et al. 2011, 2013). The weaker effect in males may seem contradictory to previous studies on sex-dependent senescence (Mysterud et al. 2001) and survival rates (Clutton-Brock et al. 1991, 1997, Catchpole et al. 2004). However, a positive correlation between ASR and population size was also demonstrated in alpine ibex during a long-term population growth due to improved winter conditions (Jacobson et al. 2004). In ungulates, so-called apparent density dependence can influence adult female mortality due to density-dependent changes in age structure; that is, the proportion of senescent females typically increases with increasing population size (Festa-Bianchet et al. 2003, Lee et al. 2015). Also, adult mortality rates increase more rapidly with age in males than in females (see Appendix S3: Fig. S1; Tyler and Øritsland 1999, Clutton-Brock and Isvaran 2007). Thus, if the relative proportion of senescent individuals during high-density winters is higher in the female than in the male population segment, differences in age structure may cause sex differences in the level of such apparent density dependence. However, age-structured data were not available for both sexes to evaluate such relations. We thus encourage future studies testing the generality of these patterns of density dependence as well as the mechanisms behind.

Some slight inconsistencies between populations could be related to differences in time-series lengths and sampling methods, that is, total vs. transect counts, early vs. late season, and even the use of handheld binoculars vs. telescopes. For instance, potential shifts in sex-specific space use (Loe et al. 2006) relative to the transect lines in the RD census represent a source of noise in this dataset, while this is less likely for the total counts in AD. On the other hand, the census in AD is conducted earlier in the summer season when young males are possibly more easily misclassified as adult females and vice versa due to a fairly similar body size and antler size. The extent of such misclassifications is likely to be small on average but will vary according to the large annual variation in fecundity and, hence, the number of young males in the population (i.e., cohort size). This may explain why some sex-specific adult population growth rates and year-to-year fluctuations in ASR are unrealistically large. Nevertheless, regardless of these uncertainties in the population count data, we found overall similar sex-specific effects of winter precipitation and population size between the two study populations, as supported by the mortality indices and post hoc analysis (Appendices S3 and S4).

Goal-oriented management of harvested (or otherwise managed) populations relies on updated information about the population's demography and how it is affected by environmental change, density dependence, and age- and sex-specific harvest quotas. Given that our results reflect general patterns, the sex-specific climate effects may be of particular relevance for the management of small populations, which are particularly sensitive to demographic stochasticity (Lee et al. 2011) and, possibly, climate–harvest interaction effects. Most importantly, population growth rate is expected to increase when ASR is more female-biased due to a higher per-capita recruitment (but see Mysterud et al. 2002, Milner et al. 2007). However, a change in the number and age distribution of males (either due to harvest or due to environmental change) could restrict females' access to high-quality mates and thereby affect timing of both conception and calving (Clutton-Brock et al. 1997, Holand et al. 2003, Sæther et al. 2003), as well as offspring sex ratio (Sæther et al. 2003, 2004, Røed et al. 2007). This will in turn have feedback effects on population growth (Milner et al. 2007). However, predicting direct or indirect consequences of changes in ASR resulting from biased harvest or trends in environmental drivers is not straightforward, as these might be buffered by complex mechanisms affecting offspring sex ratio. A recent study on mountain goats (*Oreamnos americanus*) illustrated this, showing that for females in good condition at the time of conception, the probability of producing a male offspring decreased from about 80–20% as ASR became more male-biased (Hamel et al. 2016). Nevertheless, our results indicate a recent negative trend in ASR, which has occurred parallel with more frequent harsh winters (Hansen et al. 2011, 2014). This more female-biased ASR might have contributed to the long-term population growth (see also Coulson et al. 2001) that has previously been linked to summer warming and a longer growing season (Hansen et al. 2013, Albon et al. 2016). Such trends would likely be amplified or buffered under strongly male- and female-biased harvest quotas, respectively. Thus, while our study system is subject to a very low harvest level, a predictive understanding of both short-term fluctuations and long-term trends in ASR is clearly of relevance for a sustainable and adaptive management of harvested populations in general.

Climatic signals are particularly strong in our model system, causing large annual fluctuations in vital rates (Lee et al. 2015) that are unaffected by complicating factors such as predation, interspecific competition, harvest, anthropogenic landscape change, and insect harassment. In many other ungulate systems, where the climatic signals are typically less strong and potentially masked by sex-biased harvest, population count data alone are likely insufficient to detect such sex-specific effects, if present. We encourage future studies, both in similar and in contrasting systems, testing the general relevance of these results using long-term and high-quality individual-based data from both sexes. In particular, while our results on the climate part find indirect support in the sex-specific climate effects reported in, for example, Alpine chamois (*Rupicapra rupicapra*, Willisch et al. 2013) and Soay sheep (Coulson et al. 2001), the generality and mechanisms behind the observed sex-specific density dependence need to be tested.

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