More frequent extreme climate events stabilize reindeer population dynamics

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Extreme climate events often cause population crashes but are difficult to account for in population-dynamic studies. Especially in long-lived animals, density dependence and demography may induce lagged impacts of perturbations on population growth. In Arctic ungulates, extreme rain-on-snow and ice-locked pastures have led to severe population crashes, indicating that increasingly frequent rain-on-snow events could destabilize populations. Here, using empirically parameterized, stochastic population models for High-Arctic wild reindeer, we show that more frequent rain-on-snow events actually reduce extinction risk and stabilize population dynamics due to interactions with age structure and density dependence. Extreme rain-on-snow events mainly suppress vital rates of vulnerable ages at high population densities, resulting in a crash and a new population state with resilient ages and reduced population sensitivity to subsequent icy winters. Thus, observed responses to single extreme events are poor predictors of population dynamics and persistence because internal density-dependent feedbacks act as a buffer against more frequent events.
Extreme climate events can induce severe population crashes and destabilized population dynamics across animal taxa and biomes. For instance, El Niño years severely affect the dynamics of birds, and droughts have led to extinctions in butterflies. As accumulated evidence now suggests that global warming comes with an increase in the frequency of extreme climate events, their ecological impacts are also receiving more attention, yet mostly in plants. Given the inherent rarity of extreme events and the anecdotal approaches to study them in animals, the scientific focus has almost exclusively been on single events and their short-term effects. However, especially in long-lived species where intrinsic properties regulate population dynamics, the impact of an environmental perturbation could vary with how often it occurs. Thus, ignoring longer-term impacts, as well as anticipated changes in event frequencies under global warming, may ultimately lead to biased predictions of population persistence.

As some types of (previously extreme) events become progressively less rare—typically in climate change hotspots, such as the Arctic—novel opportunities for mechanistic insights and a predictive understanding of their ecological impacts are now emerging. In the Arctic, extreme warm spells and rain-on-snow (ROS) events in winter may cause impenetrable snow-packs and even encapsulate the entire vegetation in thick ground-ice. Such environmental perturbations on the tundra are no longer that rare, and population crashes and destabilized dynamics linked to icing events have been reported for a range of herbivore species, including muskoxen, caribou, and wild reindeer. Perturbations may have little or no impact at low density when resource competition is weak. In addition, population responses to environmental stochasticity can depend on demographic structure, with some age classes being less sensitive to environmental fluctuations than others. A change in population structure towards more resilient age classes after a population crash, i.e. a new population state, may therefore promote positive population growth rates and reduce the probability of new crashes in subsequent years. Thus, it has been suggested that high frequencies of bad years may lead to less variable population growth and, hence, stabilized rather than destabilized population dynamics. However, empirical support for this prediction is still lacking.

Here, based on demographic population modelling of empirical time-series data, we evaluate how changes in the frequency of rainy and icy winters affect wild reindeer R. t. platyrhynchus population dynamics in Svalbard, a climate change hotspot in the High Arctic. Because of the rapidly warming winter climate and the strong ROS signals in both reindeer demographic performance and abundance, this northernmost ungulate represents an excellent case study for exploring the effects of more frequent extreme events. We show that the impact of an extreme ROS and icing event on reindeer survival, fecundity, and population growth rate is strongly age- and density-dependent. A population crash causes relaxation of density dependence, more resilient age structure, and, thereby, a long-lasting reduction in the population sensitivity to subsequent extreme events. Thus, because effects of environmental stochasticity are modified by internal density-dependent feedback, frequent extreme events dampen the population dynamics and even reduce the extinction risk.

**Results and discussion**

**Exploring the climate–density interaction.** As a preliminary analysis, we first explored the impact of ROS and population density on annual reindeer population growth rates over the study period 1994–2014 (Fig. 1), obtained from the posterior means of an integrated population model (IPM) combining mark-recapture and count data. Because the trend for Arctic greening due to gradually warmer and longer summers is likely to influence the carrying capacity of the reindeer population, we accounted for variation in winter length and a linear change in carrying capacity. As expected, we found a strong negative effect of ROS on annual population growth rate (Fig. 1c).
and Supplementary Table 1). This effect was diminished at low densities, when food competition is weak or negligible (cf. ref. 33) even under icy conditions.

**Accounting for age-specific effects of climate and density.** Second, based on these preliminary findings, we explored the underlying demographic mechanisms by modelling annual age-specific survival and fecundity rates, obtained for 9090 posterior samples from the IPM27, as a function of weather and population size, allowing the effect of ROS to depend not only on density but also on age class20 (Supplementary Figs. 1 and 2, Supplementary Table 2). As expected in long-lived ungulates22,34, vital rates of young and old age classes were the most variable and the most strongly influenced by ROS events (Supplementary Table 2). Third, using these functions for survival and fecundity rates, together with past age structures (Supplementary Fig. 3) and weather conditions, we reconstructed fluctuations in vital rates and population sizes. Predicted population growth rates (Supplementary Fig. 4) were strongly correlated with observed growth rates (Pearson’s correlation $r = 0.89$), suggesting high predictive power of the population model (Supplementary Fig. 5).

**Population dynamics and persistence under climate change.** We evaluated the demographic consequences of a set of ROS scenarios for the reindeer population, using stochastic simulations of the population model (Fig. 3). Global circulation models suggest that mid-winter warm spells and heavy ROS events will become more frequent in the future Arctic12,14,15, including Svalbard. Therefore, we varied the frequency of extreme ROS winters (see Supplementary Fig. 6) from very low (virtually never) to low, medium (as observed in the past, i.e. 1962–2014), high, and very high (the likely future scenario). A very high frequency of extreme ROS winters (rightmost panels in Fig. 3) reduces the mean population size by only 11% (Fig. 4a, Table 1) compared to the scenario describing observed historical conditions (i.e. medium ROS winter frequency, mid panels in Fig. 3) and by 25% (Fig. 4a, Table 1) compared to the very low frequency scenario (leftmost panels in Fig. 3). However, very frequent ROS winters also result in a strong reduction in the temporal variability in population sizes and growth rates (Figs. 3 and 4, Table 1). Such a change in population variability occurs because the impact of a bad year interacts with density and age structure (Fig. 5), which, in turn, are likely to be influenced by the time since the previous bad year. This also has implications for the frequency and magnitude of population crashes under different ROS scenarios (Fig. 3). Accordingly, the probability of going extinct (population size $N = 0$) during a period of 100 years is about 15,000 times higher for the medium ROS scenario, i.e. the observed historical climate, than for the very high ROS scenario anticipated under continued global warming (Table 1). Likewise, the probability of going quasi-extinct (here arbitrarily defined as $N < 100$) is 10-fold.

**Density-dependent feedback modifies climate change effects.** To illustrate how climate-demography interactions can lead to
Fig. 3 Reindeer population fluctuations under five different rain-on-snow (ROS) scenarios. Scenarios correspond to different distributions of observed values (1962–2014), with increased frequency of extreme ROS winters. Upper panels: One randomly selected ROS simulation for each of the five scenarios, which (from the left to the right) span from a very low to very high frequency of extreme ROS winters (see Supplementary Fig. 6). Mid panels: The stochastic simulation of the population dynamics for each scenario shown in the upper panels, based on age-structured density-dependent models of vital rates. Lower panels: Stochastic simulations of the population dynamics for ten randomly chosen simulations per scenario.

Fig. 4 Reindeer population-dynamic parameters under five different rain-on-snow (ROS) scenarios. Scenarios correspond to different distributions of observed values (1962–2014), with increased frequency of extreme ROS winters. a, b Distributions of 10,000 random samples of a population sizes and b growth rates from stochastic simulations of the population dynamics for each scenario, based on age-structured density-dependent models of vital rates. White dots show the median, boxes show the lower and upper quartiles (25th and 75th percentiles), and whiskers extend to the most extreme data point which is no more than 1.5 times the interquartile range from the box.

Table 1 Reindeer population parameters under five different rain-on-snow (ROS) scenarios

| Population parameter | Frequency of extreme ROS winters |
|----------------------|----------------------------------|
|                      | Very low | Low      | Medium | High    | Very high |
| Mean, N              | 1820     | 1698     | 1546   | 1458    | 1369      |
| Variance, N          | 189,040  | 165,458  | 152,002| 102,965 | 71,090    |
| Variance, growth rate| 0.100    | 0.099    | 0.106  | 0.079   | 0.062     |
| Quasi-extinction (%) | 4.65%    | 4.59%    | 4.10%  | 1.25%   | 0.41%     |
| True extinction (%)  | 0.84%    | 0.45%    | 0.30%  | 0.02%   | 0.00002%  |

Scenarios correspond to different distributions of observed ROS values (1962–2014), with increased frequency of extreme ROS winters. True extinction risks and quasi-extinction risks are reported as the proportion of the 909,000 simulations (9090 population models [i.e. posterior samples] × 100 simulations) of population trajectories reaching population size N = 0 (during 100 years) or N < 100 (at least once during 100 years), respectively.
such differences in long-term population dynamics and persistence under contrasting ROS scenarios, we ran deterministic population simulations where we increased the time elapsed between two extreme ROS winters (Fig. 6). We modelled the extreme ROS winter as the maximum ROS amount ever recorded at the local weather station (i.e. 1996, Fig. 1b). Provided a rather high initial density characterized by a low proportion of prime-aged animals (i.e. 3–8-year olds) in year $t=0$ (i.e. representative of the population state before a known population crash in 1996), an extreme ROS winter leads to a dramatic decline in population size in year $t=1$ (Fig. 6a). In particular, many calves and old animals die (Supplementary Fig. 1) and very few new calves are born (Supplementary Fig. 2) in crash years$^{27,28}$, also resulting in a marked increase in the proportion of prime-aged animals (Supplementary Fig. 3). With no subsequent ROS winter (Fig. 6a, leftmost panel), the low density (i.e. relaxation of density dependence) and new age structure allow the population to recover towards an asymptotic population size (Fig. 6a) and stable age structure (Supplementary Fig. 7, leftmost panel). If a second ROS winter occurs immediately after the first one (Fig. 6a, second leftmost panel), the model predicts no additional decrease in population size before recovery commences. This occurs because the previous year’s crash generated a new population state, with low density as well as large proportion of prime-aged animals, showing little sensitivity to ROS. This promotes population recovery (Fig. 5). If the second ROS winter is delayed until $t=2$, the previous year’s recovery in population size induces a slight population decline due to the harsh feeding conditions. Because of these lagged effects of a population crash, it takes about 7 years before the impact of an icy winter returns to the initial level at $t=0$ (Fig. 6b). Accordingly, if there are several extreme ROS winters in a row, population size converges towards a reduced density of 1000–1500 individuals due to relaxation of density dependence (Fig. 7). These interactions between climate effects, density, and age structure explain why our study population did not recover towards its initial state as suggested by the expected growth rate in the previous year’s population state (Fig. 6b). Circles show the mean and error bars the 2.5th and 97.5th percentiles from 9090 population models (i.e. based on 9090 posterior samples). Red dashed lines the 2.5th and 97.5th percentiles from 9090 population models.

Fig. 5 Expected population growth rate as function of rain-on-snow (ROS), density, and age structure. The relationship is shown for combinations of two contrasting initial population densities ($N=1200$ and $1700$) and two initial age structures (proportion of prime-aged [3–8-year olds] = 28 and 51%), illustrating why extreme climate events do not always lead to a large population decline. Horizontal dashed line denotes population growth rate = 0.

Fig. 6 The time elapsed between two extreme rain-on-snow (ROS) winters influences reindeer population stability. a Population size ($N$) time-series from deterministic simulations with rather high initial density $N$ (1700) and low initial proportion of prime-aged (28%). The time elapsed from the first extreme ROS winter (red line) to the second one (blue line) increases from left to right. b Expected population growth rate for the second extreme ROS winter, plotted against the time elapsed since the first one. Circles show the mean and error bars the 2.5th and 97.5th percentiles from 9090 population models (i.e. based on 9090 posterior samples). Red dashed line shows the expected growth rate in the first extreme ROS winter.

Fig. 7 The effect of many consecutive extreme ROS winters on reindeer population size. Time-series of population size ($N$) are from deterministic simulations with rather high initial density $N$ (1700) and low initial proportion of prime-aged (28%), as in Fig. 6. Solid line shows the mean and dashed lines the 2.5th and 97.5th percentiles from 9090 population models (i.e. based on 9090 posterior samples)
not crash in recent icy winters (Fig. 1b). Such lagged responses to environmental stochasticity are predicted by theory\textsuperscript{11,22}, yet poorly documented (but see\textsuperscript{20}). Thus, to our knowledge, this study provides the first evidence from the wild that fluctuations in population size of long-lived species are dampened when extreme climate events become more frequent\textsuperscript{11}.

In contrast to our study area (a hotspot for winter climate change\textsuperscript{3,14}), heavy ROS is still an uncommon phenomenon in many parts of the Arctic\textsuperscript{3,13}, where the anticipated near-future winter warming\textsuperscript{2,15} may first imply moving from very low to low frequency of extreme ROS winters (Fig. 3). When ROS is still that rare, ungulate populations are more likely to be in the kind of state (in terms of density, as well as demographic structure) that may lead to a crash when an extreme event occurs. Recent observations of occasional population crashes across the circum-polar Arctic\textsuperscript{3,14,17,18} support this, with potentially large socio-economic and ecosystem implications\textsuperscript{3,18}. However, one important message from our simulations, supported by observed population dynamics (Fig. 1b), is that the impact of an extreme ROS winter on the population growth rate is far less dramatic if it occurs soon after each annual reproduction (i.e. moving towards very high ROS frequencies, Fig. 3). This is likely characteristic of the near-future winter climate in many coastal Arctic regions\textsuperscript{3,14,15}, including Svalbard.

Extreme environmental perturbations can have unexpected ecological impacts\textsuperscript{36}, and therefore represent one of the major challenges in future predictions of ecosystem change\textsuperscript{13,17}. Because extreme climate events are by definition rare, studies based on empirical data from the wild are also typically of anecdotal nature\textsuperscript{10}. Our case study clearly demonstrates that population-dynamic inference based solely on single events and their short-term impacts—ignoring potential long-term impacts, as well as the consequences of multiple events—may lead to erroneous conclusions. In particular, our results emphasize how internal density-dependent feedback processes can modify the effects of environmental stochasticity and, hence, buffer populations of long-lived species if extreme events become the norm due to global warming.

Methods

Study area and species. Our study population of wild Svalbard reindeer is located in the Reindalen, Semmeldalen, and Colesdalen valley system in central Spitsbergen (78°N, 15°E), Svalbard, Norway. The area is characterized by U-shaped coastal valleys with High Arctic tundra vegetation of low stature, dominated by mussels, graminoids, dwarf shrubs, and forbs. Because of semi-isolation by the sea, steep mountains, and glaciers, as well as a stationary weather, there is very little exchange of animals with other nearby reindeer populations\textsuperscript{38}. The reindeer occur alone or in small groups and are not subject to significant levels of predation (polar bear attacks are very rare\textsuperscript{39}, inter-specific competition, or insect harassment. Each fall, there is a very low level of harvest\textsuperscript{10}, and some reindeer have been culled for scientific purposes\textsuperscript{41}. Both hunted and cull animals are reported and their age is determined\textsuperscript{42}.

ROS has previously been reported as the main climatic driver of vital rates and population growth in Svalbard reindeer\textsuperscript{19,29,40}. The proximate mechanism behind this is that ROS causes icing, which restricts food availability, in turn affecting body mass and reproduction\textsuperscript{28}. Although during the study period reindeer have been known to suffer increased plant productivity\textsuperscript{23,43,44}, representing the most plausible explanation for positive trends in autumn body mass and population size (Fig. 1b) in our study population\textsuperscript{29}.

Data. The reindeer data used in this study originate from a mark-recapture study, which protocol applies with and is approved by the Norwegian Animal Research Authorities and the Governor of Svalbard. The reindeer are captured as calves (and recaptured in later years) in a net between two snow mobiles during April each year, and a post-breeding resighting survey is performed in early August\textsuperscript{40}. A posterior sample of 9090 estimates of annual survival (Supplementary Fig. 1) and fecundity (Supplementary Fig. 2), as well as population size \(N\), for six female age classes during 1994–2014, were obtained from an IPM\textsuperscript{27,30} (Fig. 2). The posterior means of each age-specific demographic parameter were hereafter referred to as observed values or observations. The six age classes considered are 0 (calves), 1, 2, 3, 4, and ≥5 year olds, corresponding to age classes 1–6 in Supplementary Figs. 1 and 2, Supplementary Table 2. The model combines individual mark-recapture data with population counts within a Bayesian state-space modelling framework, accounting for potential error and demographic stochasticity. The small and controlled level of harvest and scientific culling was also accounted for. Detailed modelling and data methodology are described in ref. 27, with further model updates in ref. 30.

We obtained daily historical weather data for Longyearbyen airport, ca 25 km from our study population, from the Norwegian Meteorological Institute (freely available at http://eklima.met.no). Based on daily temperature and precipitation during 1962–2014, we first calculated annual winter rain amount by summing the amount of precipitation recorded at temperatures ≥1 °C during November–April\textsuperscript{3,14,20}. We added 1 to this value and log-transformed it to get the variable ROS. The ice/winter–ROS interaction was estimated using the length of the winter based on a 10-day running mean of daily temperatures. We considered the onset of winter as the first day in autumn when the running mean was <0 °C and then stayed <0 °C for a minimum of 10 consecutive days. Likewise, end of winter was estimated as the first day (after the winter period November–April) when the running mean was ≥0 °C and then stayed ≥0 °C for a minimum of 10 consecutive days.

Population growth rate as a function of density and climate. Based on the observed total population sizes \(N_t\) (where \(t\) is time) from the IPM\textsuperscript{27,30}, we first explored climate–density interactions by fitting a linear regression of annual population growth rate (\(log(N_{t+1}/N_t)\)) against log(\(N_t\)), linearly detrended and climate covariates, namely ROS and length of the winter (Fig. 2). We found a negative effect of length of the winter (\(t\) to \(t + 1\)) and a negative interaction effect between the amount of ROS (\(t\) to \(t + 1\)) and population size (Supplementary Table 1), suggesting a density-dependent ROS effect and supporting the assumption that increased plant abundance due to warmer summers\textsuperscript{2,15} has a gradual effect on the carrying capacity \(K\) (thereby, the detrended \(N_t\)). To visually illustrate the ROS-density interaction effect (Fig. 1c), we divided population sizes into high, medium, and low \(N\) (detrended). The respective linear regression model replacing the covariate \(N\) with these population size classes (as factor) provided qualitatively similar results as the model described above (Supplementary Table 1).

Survival and fecundity as functions of density and climate. We obtained 9090 posterior samples from the IPM\textsuperscript{27,30} of each of them consisting of annual age-class-specific demographic rates (i.e. survival and fecundity) and population sizes from 1994 to 2014. For each of these posterior samples, we investigated the effects of weather and population density on survival and fecundity, generating in total 9090 population models. First, the effects of weather and population density on survival \(S\) of each age class \(i\) at year \(t\) were estimated separately for each posterior sample (Fig. 2, Supplementary Fig. 1), using linear mixed-effects models (function \texttt{lme} in \texttt{R} package \texttt{nlme}). As survival might be negatively affected by an increase in population size \(N_{\text{posthunt}}\) (i.e. number of calves + adult females at the end of the hunting season), we tested for an effect of (scaled) population size in year \(t\) on survival. We fitted a density-dependent ROS effect\textsuperscript{29} (cf. Fig. 1c) using the form \(\text{ROS} = R_{\text{ROS}} \times N_{\text{posthunt}}\) (see ref. 21 for a similar approach). This form of the interaction effect ensures that the effect of ROS is strictly negative or positive (depending on the fitted coefficient of \(\text{ROS}\)) for all values of \(N_{\text{posthunt}}\) (Supplementary Figs. 8 and 9). In contrast, the simpler and more common specification of an interaction effect, such as \(\times \text{ROS} \times N_{\text{posthunt}}\), would implicitly lead to a switch in sign of the effect of ROS at some level of \(N\), and the stronger the interaction effect, the more likely it is that the change of sign is well within the data range. Notably, this can result in an optimization function aiming at minimizing Akaike’s Information Criteria. Moreover, mean survival is likely to differ among age classes, and the effect of climate may also differ among age classes (e.g. ref. 39), thus we included an interaction between age and the density-dependent ROS effect. Finally, year was added as a fixed (numeric) effect to account for trends. Year was also added as a random (intercept) effect to account for non-independence among age classes, leading to a survival model with the following form:

\[
\logit(S_{it}) = a_i + N_{\text{posthunt}} + \text{year} + \text{ROS} + a_t + \text{length winter} + \text{random(year)} + \epsilon_{it}
\]

where \(a_i\) is the age class \(i\), \(N_{\text{posthunt}}\) is population size just at the end of the hunting season, and \(\epsilon_{it}\) is the residuals of the regression. The posterior distributions of the parameters of Eq. (1) shown in Supplementary Table 2 represent a combination of uncertainty due to finite time series, uncertainty stemming from stochasticity, and uncertainty in the IPM. Likewise, we ran a model of similar structure for fecundity \(F\) of each age class \(j\) at year \(t\), as females produce at most one calf per year (Supplementary Fig. 2). Note that there is one age class less than in the survival analysis, as calves do not get pregnant:

\[
\logit(F_{ij}) = a_j + N_{\text{posthunt}} + \text{year} + \text{ROS} + a_t + \text{length winter} + \text{random(year)} + \epsilon_{ij}
\]

Again, the posterior distributions of the parameters of Eq. 2 shown in Supplementary Table 2 represent a combination of uncertainties (see above for confidence intervals), respectively\textsuperscript{30}.
Reconstructing past vital rates and population growth rates. Based on the above models of vital rates, for each posterior sample we estimated age-specific survival and fecundity rates for past conditions of population density, winter harshness (i.e. ROS amount), and winter length (Fig 2, Supplementary Table 2). Importantly, to account for sources of environmental stochasticity due to processes other than covariates included in the model, we estimated a covariance matrix $\Sigma$ of the different vital rates (fecundity, survival) for all age classes based on the random year effects and the residuals $e_{t}$, $a_{t}$ of Eqs 1 and 2. From this covariance matrix $\Sigma$, we generated 100 new residuals from a multivariate normal distribution. These rates then allowed the population size at time $t + 1$ to be estimated from the population size of each age at time $t$. The population size just before the hunting season at time $t + 1$, $N_{\text{sim};t+1}$, corresponds to the sum of females of different ages:

$$N_{\text{sim};t+1} = \sum_{i} N_{\text{sim},i; t+1} + \sum_{j} N_{\text{sim},j; t+1}$$

(3)

Each of these terms can be estimated based on the vital rates. The number of calves produced, $N_{\text{sim},c; t+1}$ (first term on right side of Eq 3), consists of calves produced by females of each age (except yearlings). $N_{\text{sim},c; t+1}$ was modelled using a binomial process to allow for demographic stochasticity (i.e. chance events that affect individuals independently):

$$N_{\text{sim},c; t+1} \sim \text{Bin}(N_{\text{sim},i+1; t+1} + N_{\text{sim},j; t+1} + \cdots + N_{\text{sim},13; t+1})$$

(4)

where $F_{i,j}$ is the estimated fecundity rate for females of age $i$ at time $t$, resulting in calves at time $t + 1$. For instance, $F_{i,2}$ is the probability of a 2-year-old female at time $t$ having a calf at time $t + 1$ (individual and population size at time $t$, see Eq 2). The number of female calves was then drawn from a binomial distribution with a probability 0.5 (i.e. we assumed a balanced sex ratio). $N_{\text{sim},y; t+1}$ (second term on right side of Eq 3) corresponds to the number of female calves that have survived from time $t$ to time $t + 1$ and was also modelled using a binomial process to include demographic stochasticity. Moreover, a few female calves are removed from the population by hunting (H) or scientific culling (C). Thus the number of female yearlings is modelled as follows:

$$N_{\text{sim},y; t+1} \sim \text{Bin}(N_{\text{sim},i+1; t+1} + N_{\text{sim},j; t+1} + \cdots + N_{\text{sim},13; t+1})$$

(5)

where $S_{i,j}$ is the estimated survival probability of females of age $i$ at time $t$. Similarly, $N_{\text{sim},5; t+1}$, $\ldots$, and $N_{\text{sim},14; t+1}$ (all other terms in Eq 3) correspond to the population size in the previous age that have survived from time $t$ to time $t + 1$. Thus, for age $j \in [2, 13]$

$$N_{\text{sim};j+1; t+1} \sim \text{Bin}(N_{\text{sim};j+1; t+1} + H_{\text{sim};j+1} - C_{\text{sim};j+1})$$

(6)

Note that summer mortality in calves (as well as for other age classes) is considered to be close to zero. Thus $N_{\text{sim};i+1}$ can be estimated from observed values of ROS, length of the winter, and population size, estimating $S$ and $F$ from the models presented above.

Using the models described above, we estimated age-specific survival rates (from 1995 to 2014), density-dependent ROS (from 1995 to 2014), and the population size (from 1995 to 2014) through a step-by-step approach. Each year was estimated based on observations of age-specific population sizes (provided by the IPM; Supplementary Fig 3) and observed ROS and winter length the previous year. Thus, in Eqs 5 and 6, $N_{\text{sim},c; t+1}$ was replaced with $N_{\text{obs},c; t+1}$ and $N_{\text{sim},y; t+1}$ was replaced with $N_{\text{obs},y; t+1}$. The estimated population size $N_{\text{sim};t+1}$ may then be calculated step by step (Eq 3) and compared with the observed population size.

The annual age-specific survival rates (Supplementary Fig 1) and fecundity rates (Supplementary Fig 2) estimated within this framework were closely correlated to the ones observed (i.e. obtained from the IPM). Pearson’s correlations ranged from $r = 0.72$–0.89 for survival rates and $r = 0.65$–0.84 for fecundity rates. Accordingly, our model was able to reconstruct annual fluctuations in total population size well (Supplementary Fig 4), with a strong correlation ($r = 0.89$) between estimated and observed population growth rates (Supplementary Fig 5).

Reindeer population projections with different ROS scenarios. Finally, we analysed how increasing frequency of rainy winters affects the population growth rate ($r_{c}$). To simulate realizations of ROS (Supplementary Fig 6), we used the observed ROS data from 1962 to 2014 and an inverse transformation method. Given a continuous uniform variable $U$ in $[0,1]$ and a cumulative distribution function $D$, the random variable $X = D^{-1}(U)$ has distribution $D$. We can change the distribution (i.e. different scenarios of ROS) by using a non-uniform distribution of $D$. Thus, because the cumulative ROS distribution is bounded between 0 and 1, we used a beta distribution $f(U) \propto U^{\alpha_{1}}(1-U)^{\alpha_{2}}$, where $\alpha_{1}$ and $\alpha_{2}$ are shape parameters to simulate different ROS scenarios. We used the following parameters to obtain different ROS scenarios (Supplementary Fig 6): very high frequency of extreme ROS winters ($\alpha_{1} = 4$, $\alpha_{2} = 1$), high frequency ($\alpha_{1} = 2$, $\alpha_{2} = 1$), low frequency ($\alpha_{1} = 1$, $\alpha_{2} = 2$), and very low frequency ($\alpha_{1} = 1$, $\alpha_{2} = 4$), respectively. In addition, the median frequency ($\alpha_{1} = 2$, $\alpha_{2} = 2$) was kept at its mean observed value (1994–2014) to keep the real ROS data’s frequency and variation. The beta distribution was then used to simulate different ROS scenarios (as described above) for various years from 1995 to 2014. We used the stochastic version of our population model, keeping winter length constant at its mean observed value. We simulated a 1996 crash. We fed our population model with the eight different sequences of ROS and estimated the expected population growth rate for each ROS value.

We explored how increasing amount of ROS affects the population growth rate, under different age structures and population densities. To do so, we considered two initial age structures (low prime-aged [3–8–year olds] proportion $= 28\%$, high prime-aged proportion $= 51\%$). Note that the two age structures reflect the observed demography before and after the 1996 population crash. We used the deterministic version of our population model, keeping winter length constant at its mean observed value (1994–2014). From these population projections, the expected population growth rate for each ROS value was determined for each combination of density/age structure (see Fig 5).

Finally, we examined how the time elapsed since the previous extreme ROS winter affects the population growth rate during a second extreme ROS winter. An extreme ROS winter reflects the conditions in 1996 (i.e. 1995/96), with the highest ROS value recorded (log ROS = 4.2). We simulated different ROS sequences where ROS was kept at its mean recorded value (1994–2014) except for a first extreme ROS winter always occurring at $t = 0$, and a second extreme ROS winter occurring at $t = 1$, then at $t = 2$, and so on until $t = 7$. We also included a ROS sequence with no second extreme ROS winter and a sequence with many consecutive extreme ROS winters (keeping winter length constant at its mean observed value), we then used the deterministic version of our population model to calculate time-series of population sizes (Figs 6a and 7) and age structures (Supplementary Fig 7) following a rather high initial population density (N = 1700) and a low initial proportion of prime-aged individuals (28%), reflecting the population state prior to the 1996 crash. We fed our population model with the eight different sequences of ROS and estimated the expected population growth rate for the second extreme ROS winter (Fig 6b). All analyses were performed with the statistical software R.
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Author contributions
S.D.A., R.J.I., E.R., A.S., L.E.L. and V.V. collected reindeer data. B.B.H. initiated the study. S.D.A., R.J.I., E.R., A.S., L.E.L. and V.V. conducted the field work, and UNIS for logistics support.

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