

Harvesting can stabilize population fluctuations and buffer the impacts of climate change

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49 Abstract

50 Harvesting can magnify the destabilizing effects of environmental perturbations on
51 population dynamics and, thereby, increase extinction risk. However, population-dynamic
52 theory predicts that impacts of harvesting depend on the type and strength of density-
53 dependent regulation. Here, we used population models for a range of life histories and an
54 empirical reindeer case study to show that harvesting can actually buffer populations against
55 environmental perturbations. This occurs because of density-dependent environmental
56 stochasticity, where negative environmental impacts on vital rates are amplified at high
57 population density due to intra-specific resource competition. Simulations from our
58 population models show that even low levels of proportional harvesting may prevent
59 overabundance, thereby dampening population fluctuations and reducing the risk of
60 population collapse and quasi-extinction induced by environmental perturbations. Thus,
61 depending on the species' life history and the strength of density-dependent environmental
62 drivers, harvesting can improve population resistance to increased climate variability and
63 extreme weather expected under global warming.

64

65 Introduction

66 Overexploitation and climate change represent two of the major anthropogenic threats to
67 biodiversity (Brook *et al.* 2008). While the role of environmental fluctuations in driving
68 population dynamics is now routinely incorporated into models of harvesting as well as their
69 sustainability assessment (Beddington & May 1977; Lande *et al.* 1995; Lande *et al.* 2003),
70 potential interactions between harvesting and climatic drivers are still poorly understood
71 (Gamelon *et al.* 2019). This is alarming, given that climate variability and the frequency of
72 extreme weather events have increased due to global warming and are forecasted to intensify
73 in the near future (Fischer & Knutti 2015; Diffenbaugh *et al.* 2017).

Population-dynamic models generally predict that harvesting can magnify population fluctuations induced by environmental stochasticity, and thereby increase the risk of extinction (Beddington & May 1977; Lande *et al.* 1995; Lande *et al.* 2003; Hsieh *et al.* 2006; Anderson *et al.* 2008; Fryxell *et al.* 2010; Gamelon *et al.* 2019). This can occur, for instance, due to lagged responses in harvest efforts to population changes (Fryxell *et al.* 2010) or increased environmental sensitivity in age-truncated populations following size-selective harvesting (Hsieh *et al.* 2006; Anderson *et al.* 2008). On the other hand, May and colleagues (May *et al.* 1978) hypothesized that, in species with chaotic (i.e. irregular) population fluctuations, reducing population density through harvesting can result in less variable population trajectories by damping the density-dependent effects of environmental stochasticity. Theoretical and empirical evidence across taxa now indicate that population dynamics are often characterized by nonlinear amplifications of environmental stochasticity caused by intrinsic processes such as density dependence (Royama 1992; Coulson *et al.* 2001; Barbraud & Weimerskirch 2003; Coulson *et al.* 2004; Stenseth *et al.* 2004; Hsieh *et al.* 2005; Lima *et al.* 2006; Anderson *et al.* 2008; Ferguson & Ponciano 2015; Gamelon *et al.* 2017; Hansen *et al.* 2019).

Interactions between extrinsic (e.g. weather/climate variability) and intrinsic (e.g. density dependence, age structure) mechanisms are particularly expected when competition for food or space is both density-dependent and modulated by environmental conditions (Royama 1992; Owen-Smith 2000; Lima *et al.* 2006). Adverse conditions can therefore have multiplicative effects on individual fitness at high density, but little effect at low density (Fig. 1). Because of this, observed population growth rates of natural populations have sometimes been better explained by density-dependent environmental variation, i.e. interactive, rather than additive, effects of density and climate (Royama 1992; Ferguson & Ponciano 2015; Gamelon *et al.* 2017; Hansen *et al.* 2019). Such ‘climate-density interactions’ may cause

unstable dynamics and population crashes when prolonged periods of favorable conditions lead to high density and high proportions of vulnerable age classes (Festa-Bianchet *et al.* 2003), causing amplified demographic responses to environmental perturbations, such as extreme weather events (Wilmers *et al.* 2007; Ferguson & Ponciano 2015; Hansen *et al.* 2019). Intuitively, strong climate-density interactions would predict that harvesting – which, by definition, reduces density – can weaken impacts of environmental perturbations with density-dependent effects on population dynamics. Here, we use simulations from theoretical and empirically parameterized, stochastic population models to show that harvesting can indeed modify the climate-density interaction effects on resource limitation, leading to increased population stability and resistance to environmental perturbations.

Results and discussion

Harvesting can stabilize populations and reduce quasi-extinction risk. Population time series data of six wild ungulate species clearly demonstrated nonlinear responses to resource-limiting climate variables, with stronger effects at high population density (Fig. 2; see Tables S1 and S2 in Supporting Information). To assess the effects of harvesting on populations subject to such climate-density interactions, we first derived general population growth rate models with density-dependent and -independent effects of environmental stochasticity, assuming a Ricker form of density regulation (See ‘Model properties’ section in Materials and Methods for details) (Ferguson & Ponciano 2015). We then simulated population trajectories along a ‘slow-fast’ continuum of life history variation (Stearns 1992), subject to different levels of environmental stochasticity and proportional harvesting (i.e. a fixed proportion of the population is harvested each year).

In accordance with previous studies (Beddington & May 1977; Lande *et al.* 1995; Lande *et al.* 2003), we found that harvesting increased the risk of quasi-extinction (i.e. a low

population size with increased extinction risk due to demographic stochasticity) when environmental variation in the population growth rate was modelled independently of density (Fig. S1). This was particularly the case towards the ‘slow’ end of the life history continuum, i.e. for species characterized by low maximum growth rates. In contrast, when environmental variation was density-dependent, low to moderate harvest proportions reduced the temporal variation in population growth and, hence, the probability of quasi-extinction (Figs. 3a-b). This occurred because harvesting reduced population density and, thereby, the effects of density-dependent environmental variation on population growth rates (Fig. 3c). Thus, harvesting can result in more stable population dynamics and decrease the magnitude of population crashes following environmental perturbations (Fig. 3d). The reduction in quasi-extinction risk by harvesting depended on the relative contributions of density-dependent vs. density-independent environmental variation, and their correlation, as well as the harvest proportion and maximum growth rate (Fig. S2). Nevertheless, under strong density-dependent environmental variation and modest harvest proportions (i.e. less than 0.2, based on our models), a substantial decline in average population size was only found for species with a long generation time (Fig. S3).

Results from a reindeer case-study. In the real world, the demographic responses of natural populations to intrinsic and extrinsic drivers (including harvesting), as well as their interactions, often depend on their age or stage structure (Caswell 2001; Coulson *et al.* 2001; Festa-Bianchet *et al.* 2003; Lande *et al.* 2003). Furthermore, the effects of weather, density and harvesting depend on the timing of harvesting as well as seasonal variation in density-dependent processes and environmental drivers of population dynamics (Boyce *et al.* 1999; Jonzén & Lundberg 1999). To evaluate the effect of proportional harvesting and assess implications under climate change, we used an empirically parameterized, stochastic

population model for wild Svalbard reindeer (*Rangifer tarandus platyrhynchus*) (Fig. 4a; see 'Reindeer as a case-study' section in Materials and Methods for details). In this predator-free reindeer population in the high Arctic, age- and density-dependent effects of winter weather conditions – notably rain-on-snow (ROS) events creating ice-locked winter pastures – cause large interannual variation in survival, fecundity and population size (Lee *et al.* 2015). Individuals are particularly prone to starvation when ROS events occur at high population density (cf. Fig. 1) and reindeer aggregate in the few feeding patches that are accessible (Fig. 4a). Due to the interactive effects of weather, density and age structure, the observed (Peeters *et al.* 2019) and anticipated (Bintanja & Andry 2017) increase in the frequency of ROS under climate warming cause counterintuitive changes in population fluctuations, with more stable dynamics expected for high frequencies of extreme ROS events (Hansen *et al.* 2019).

As expected from our general model (Fig. 3), we found that harvesting reduced fluctuations in reindeer age structure and damped the temporal variation in population growth rates (Figs. 4b-d, S4a). By decreasing the population density before the onset of winter, harvesting weakened the negative effect of stochastic ROS events on vital rates. These demographic effects of harvesting reduced the probability of a population crash (Fig. 4e) and, therefore, the risk of climate-induced quasi-extinctions (Fig. 4f). Our empirical-based analysis thus confirmed our prediction that, under strong climate-density interactions, harvesting can stabilize population dynamics by buffering negative effects of weather conditions. While these impacts on stability were evident even at very low harvest proportions (< 0.05), the effects on the long-term average population size was negligible up to a harvest proportion of ca. 0.15 (Fig. S4b). Unsurprisingly, increasing harvest proportions beyond this level would eventually lead to increased risk of quasi-extinction as populations take longer to recover from environmental disturbances and harvesting (Beddington & May 1977; Lande *et al.* 1995). Overall, the sustainability of harvesting as a strategy to stabilize

population dynamics and avoid population crashes will depend on the harvest proportions as well as the frequency and magnitude of stochastic climate events (Fig. 4f).

Harvesting can buffer climate change impacts. The combined results from simulations and realistic population models suggest that harvesting can indeed increase population stability and resistance to environmental perturbations (May *et al.* 1978). This has important general implications far beyond our case-study system. Previous studies across vertebrate species (Royama 1992; Owen-Smith 2000; Coulson *et al.* 2001; Barbraud & Weimerskirch 2003; Coulson *et al.* 2004; Stenseth *et al.* 2004; Lima *et al.* 2006; Ferguson & Ponciano 2015; Gamelon *et al.* 2017; Hansen *et al.* 2019) as well as our comparative analysis in six ungulate species (Fig. 2) clearly indicate that, in seasonal, resource-limited systems, climate-density interactions in population dynamics are far more common than previously acknowledged. Therefore, by reducing density, harvesting will often modify the effects of density-dependent environmental stochasticity on population dynamics. Accordingly, sustainable levels of harvesting can serve as a management (and even conservation) strategy to buffer negative effects of increased climate variability and extreme events (e.g. flooding, drought, storms) anticipated under global climate change (Fischer & Knutti 2015; Diffenbaugh *et al.* 2017).

The stabilizing processes outlined here will not apply to all species or under all circumstances. For one, population resistance to environmental perturbations and the implications of harvesting depend on the species' life history strategy (Fig. 3). Moreover, density-independent stochastic mechanisms (Figs. S1, S2) (May *et al.* 1978; Lande *et al.* 2003), as well as ecological and evolutionary consequences of selective harvesting (Anderson *et al.* 2008; Pigeon *et al.* 2016; Leclerc *et al.* 2017), can make populations more sensitive to temporal variation in the environment (Gamelon *et al.* 2019). Population resistance to environmental perturbations also depends on the harvesting strategy (Beddington & May

1977; Lande *et al.* 1995) and stochasticity in harvesting processes (Jonzén *et al.* 2002), sometimes causing lagged responses in effort and quota regulations to resource fluctuations (Fryxell *et al.* 2010). Nevertheless, stabilizing effects of harvesting under climate-density interactions likely occur in resource-limited systems with strong compensatory responses among survivors of harvesting, i.e. where the immediate reduction in resource competition due to harvesting leads to increased natural survival, fecundity, and overall fitness (Boyce *et al.* 1999; Jonzén & Lundberg 1999). Such buffering effects of harvesting could explain why climate-density interactions are more evident in populations with no (or very low) harvesting than in heavily harvested populations (Tveraa *et al.* 2007). Thus, our study highlights that, especially in the context of global warming, the future sustainability of wildlife resources requires a better understanding of the potential interactions of climate, internal population regulation, and harvesting strategies.

Materials and Methods

Model properties

The Ricker model of growth rate r_t (Ricker 1954) can be written as

$$r_t = \beta_0 - N_t \beta_1, \quad [1]$$

where N_t is population size at time t , β_0 is the maximum growth rate, and an increase in β_1 reduces the carrying capacity K , which is $K = \beta_0 / \beta_1$. Environmental stochasticity can be included as an additive term on the maximum growth rate:

$$r_t = \beta_0 - N_t \beta_1 + \gamma_a Z_{a,t}, \quad [2a]$$

where $Z_{a,t}$ is a random variable with a normal distribution $N(0,1)$ and γ_a is the effect of additive environmental variation on the growth rate. The growth rate in Eq. 2a has the following constant environmental variance:

$$\text{Var}[r_t] = \gamma_a^2, \quad [2b]$$

We modified Eq. 1 to represent the case in which the effect of environmental variation on r_t depends on N_t , which is referred to as multiplicative environmental variance (Ferguson & Ponciano 2015):

$$r_t = \beta_0 - N_t \exp(\ln(\beta_1) + \gamma_m Z_{m,t}), \quad [3a]$$

where $Z_{m,t}$ is a random variable with a normal distribution $Z_{m,t} \sim N(0,1)$ and γ_m is the effect of multiplicative environmental variation. The growth rate then has an environmental variance depending on N_t ,

$$\text{Var}[r_t \vee N_t] = N_t^2 \exp(2 \ln(\beta_1) + \gamma_m^2) (\exp(\gamma_m^2) - 1), \quad [3b]$$

A general model including both additive and multiplicative environmental variance can be written as

$$r_t = \beta_0 - N_t \exp(\ln(\beta_1) + \gamma_m Z_{m,t}) + \gamma_a Z_{a,t}. \quad [4a]$$

The variance in growth rate then depends on the correlation ρ_Z between the random variables $Z_{a,t}$ and $Z_{m,t}$, leading to the following equation:

$$\text{Var}[r_t \vee N_t] = \gamma_a^2 + N_t^2 \exp(2 \ln(\beta_1) + \gamma_m^2) (\exp(\gamma_m^2) - 1) - 2 N_t \gamma_a \gamma_m \rho_Z \exp(\ln(\beta_1) + \gamma_m^2 / 2). \quad [4b]$$

A special case of Eq. 4b is where $\rho_Z = 0$ and the variance in growth rate simply becomes the sum of Eq. 2b and 3b.

We validated that the Ricker model with multiplicative environmental variance is a realistic model by testing the above three models (Eq. 2-4) on published time series from ungulate species with observed or expected density-dependent effects of climatic drivers (Table S1). Parameters were estimated using an optimization function developed with the R-package TMB (Kristensen *et al.* 2016) which allowed the estimation of $Z_{a,t}$ and $Z_{m,t}$ as random effects, and minimized the log likelihood. Model selection was then performed using

the corrected Akaike's Information Criterion (AIC_c). Note that the model with both additive and multiplicative environmental variance (Eq. 4b) required two extra parameters to be estimated, i.e. one extra noise term and ρ_z . We also tested these models for the same species with the reported climate variable as an additive or multiplicative covariate, or both, in Eq. 2-4. Results from these models are shown in Fig. 2 and Table S2.

To investigate the effect of harvesting on the stochastic growth rate with additive and multiplicative environmental variance, we included a proportional harvest function in Eq. 4a:

$$H_t = pN_t \quad [5]$$

where p is the harvest proportion. The Ricker growth rate function from Eq. 4a then becomes,

$$r_t = \beta_0 - (N_t - H_t) \exp(\ln(\beta_1) + \gamma_m Z_{m,t}) + \gamma_a Z_{a,t} \quad [6]$$

Similarly, the variance in growth rate can be found by substituting N_t with $(N_t - H_t)$ in Eq. 4b. Note that the population size at time $t+1$ is now given as,

$$N_{t+1} = (N_t - H_t) e^{r_t} \quad [7]$$

We simulated populations trajectories of 1,000 timesteps for β_0 ranging from 0.2 to 2.0, and harvest proportions ranging from 0 to 0.25. Note that the effect of γ_m and ρ_z (Eq. 3b, 4b), and therefore the variance in r_t , depended on N_t . We therefore optimized these parameters for given sets of β_0 , β_1 and $\text{Var}[r_t \vee N_t = K]_{\text{noharvest}}$, i.e. the variance in r_t for populations at their carrying capacity in the absence of harvesting. For each set of parameters, we calculated quasi-extinction probabilities as the proportion of 1,000 simulated population trajectories with $N_t < K/5$ at least once during 1,000 timesteps.

Reindeer as a case-study

Climate-density interaction

270 Arctic ungulates, like Svalbard reindeer, can experience dramatic declines in population size
271 when extreme rain-on-snow (ROS) events occur (Miller & Gunn 2003; Kohler & Aanes
272 2004; Hansen *et al.* 2011). The tundra vegetation becomes encased in ice as rain- and
273 snowmelt-water freezes on the ground (Kohler & Aanes 2004; Peeters *et al.* 2019), thus
274 restricting access to food (Albon *et al.* 2017). The strength of ROS effects on the age-specific
275 vital rates depends on the population density at the time of the event, such that a ROS event
276 strongly affects demographic performances mainly at high density (Hansen *et al.* 2019).
277 Recently, Hansen *et al.* (2019) developed an empirically parameterized stochastic population
278 model where this ROS-density interaction was modelled on vital rates for six age-classes of
279 female Svalbard reindeer. From this population model and simulated ROS-scenarios, they
280 found that increased frequency in extreme ROS events could stabilize population dynamics
281 and reduce extinction risk. The studied population, situated in the Reindalen-Semmeldalen-
282 Colesdalen valley system in central Spitsbergen (78°N, 16°E), is lightly hunted during
283 autumn and some reindeer have been culled for scientific purposes (Albon *et al.* 2002),
284 resulting in annual offtake < 5% of the female population. However, only the effects of ROS
285 and density on reindeer population dynamics have been modelled so far, and potential
286 harvesting effects have been neglected.

287 Here, we investigated the combined effects of weather, density and harvesting on
288 reindeer population dynamics by extending previously developed models (Hansen *et al.*
289 2019). We simulated the reindeer population dynamics for different climate scenarios with
290 varying frequencies and intensities (i.e. amount) of ROS events. In addition, we simulated
291 different rates of proportional harvesting and evaluated their effects on climate-induced
292 variation in the reindeer population dynamics.

293

294 **Reindeer demographic population model**

295 We adopted the demographic population model developed by Hansen *et al.* (2019). Briefly,
 296 annual population size (N) and annual vital rates (i.e. survival S and fecundity F) for six age
 297 classes was estimated between 1994 and 2014 with an integrated population model (IPM)
 298 (Lee *et al.* 2015; Bjørkvoll *et al.* 2016). The six age classes consisted of calves (0 years),
 299 yearlings (1 year), and adults of 2, 3-8, 9-11, and ≥ 12 -years. Hansen *et al.* (2019) modelled
 300 the effects of postharvest population density (N_{posthunt}), winter length, and a three-way
 301 interaction between age-class, N_{posthunt} , and ROS on age-specific vital rates using linear
 302 mixed-effects models. To ensure that the effect of ROS was strictly negative (or positive) for
 303 all values of N_{posthunt} , the ROS-density interaction was included using the form
 304 $ROS'_t = ROS_t \times e^{k \times N_{\text{posthunt},t}}$, where the constant k was estimated using an optimization function
 305 aiming at minimizing Akaike's Information Criterion (AIC). Year was included as a random
 306 effect to account for environmental noise not accounted for by the fixed parameters, and as a
 307 fixed effect to correct for a positive trend in population size during the study period. These
 308 models were run for a posterior sample of 9,090 estimates of age-class-specific annual
 309 survival, fecundity and population sizes from the IPM (see Table S2 in Hansen *et al.* (2019)
 310 for model coefficients).

311 In this study, we simulated population trajectories of 100 years using these models of
 312 vital rates with the parameter estimates from 1,000 posterior models. The fixed variable year
 313 was set to 2014 and the average observed winter length during 1994-2014 was used for the
 314 entire trajectory. Importantly, to account for sources of environmental stochasticity due to
 315 processes other than covariates included in the model, we incorporated a covariance matrix of
 316 the different vital rates for all age classes. From this covariance matrix, we generated 100
 317 new residuals from a multivariate normal distribution, i.e. one for each year of the simulated
 318 trajectory. These vital rate models then allowed us to estimate the population size at time $t+1$
 319 from the population size of each age at time t , and simulated ROS and harvest levels.

320 Changes in the number of females were simulated for ages 0-12, while the number of
 321 females ≥ 13 years old were pooled in one (senescent) age class. Note that vital rates in the
 322 IPM were estimated for six age classes, meaning that the numbers of 12 and ≥ 13 years old
 323 females were simulated from the vital rates of 9-11 and ≥ 12 years old, respectively. Using a
 324 similar approach to Hansen *et al.* (2019), annual survival and fecundity rates were estimated
 325 based on the simulated ROS and population size after harvesting $N_{posthunt}$ (see “climate-
 326 harvesting scenarios” below). Note that summer mortality for all age classes is considered to
 327 be close to zero (Reimers 1983). The number of individuals of age j in year t surviving to age
 328 $j+1$ was then modelled using a binomial process with probability $S_{j,t}$ and $n = N_{j,t}$ random
 329 draws to allow for demographic stochasticity (i.e., chance events that affect individuals
 330 independently). Similarly, the number of calves born in year $t+1$ from the surviving
 331 individuals, now age $j+1$, was modelled using a binomial process with probability $F_{j,t}$ and n
 332 $= N_{j+1,t+1}$ random draws. Note that twinning is very rare comparative to other Rangifer
 333 (Nowosad 1973) and that individuals becoming one year old in $t+1$ do not produce calves ($F_{0,t} = 0$) as Svalbard reindeer reach maturity during their second year of life, at the earliest.
 334 Assuming a balanced sex-ratio (0.5), the total number of female calves was again modelled
 335 using a binomial process. The total population size in year $t+1$ was then simply calculated by
 336 taking the sum of the modelled number of individuals over all ages.
 337

338 Trajectories were initiated using the age distribution and population size in year 2014
 339 ($N_0 = 1,747$; i.e. the last published population estimate from the IPM) (Bjørkvoll *et al.* 2016).
 340 Since the IPM estimated population sizes for the six age classes, we estimated the number of
 341 females in 2014 for ages 3-12, and ≥ 13 years, using simple cohort analysis (Solberg *et al.*
 342 1999). This resulted in the following initial age structure from 0 to ≥ 13 years: 335, 258, 152,
 343 172, 121, 116, 22, 49, 69, 122, 109, 114, 23, and 85 individuals. Nevertheless, the outcome of
 344 the 100-year-long trajectories was insensitive to the original age structure.

345

346 **Climate-harvesting scenarios**

347 We simulated population size trajectories for different harvest intensities and three climate
348 scenarios (i.e. low, medium, and high frequencies of extreme ROS events; note that these
349 correspond to the very low, medium, and very high frequency scenarios in Hansen *et al.*
350 (2019)). The medium climate scenario reflects the historical state between 1962 and 2014,
351 and simulated realizations of ROS in all three climate scenarios fell within the range of
352 observed values of ROS during this period (see Hansen *et al.* (2019) for further details).

353 We considered the effect of proportional harvesting on reindeer population dynamics,
354 which is a classical harvesting strategy commonly applied in fisheries and hunted
355 populations. This strategy involves a constant effort where, each year, a fixed proportion of
356 the population is harvested (Beddington & May 1977; Lande *et al.* 1995). We used fixed
357 harvest proportions ranging from 0 to 0.3 with increments of 0.01, which, for simplicity, were
358 the same across ages. For each climate scenario and fixed harvest proportion, we simulated
359 100-year-long population trajectories based on 10 simulated ROS trajectories for each
360 parameter set of 1,000 posterior models of S and F , i.e. 10,000 population simulations. These
361 were used to calculate population properties, such as average population size, variability in
362 the per-capita growth rate, and probabilities of a population crash and quasi-extinction (see
363 below).

364 Simulated population trajectories indicated significant reductions in the long-run
365 average population size from the unharvested scenario when harvest proportions exceeded
366 approximately 0.16, 0.15, and 0.13 in the low, medium, and high frequency scenario,
367 respectively (Fig. S4a). Harvest proportions above 0.27 reduced long-run average population
368 sizes well below 500 individuals. We therefore only considered harvest proportions ranging
369 from 0 to 0.2 as sustainable levels to investigate how harvesting can modify weather effects

on population dynamics of Svalbard reindeer. We estimated the probability of a population crash within 100 years defined as a reduction by half of the pre-harvest population size from one year to the next, and the probability of a quasi-extinction within 100 years defined as a reduction below 20% of the initial population size ($N_0 = 1,747$). Both probabilities were estimated based on 1,000 simulated trajectories for each climate scenario and harvest proportions ranging from 0 to 0.2. All analyses were performed using the statistical software R (R Core Team 2019).

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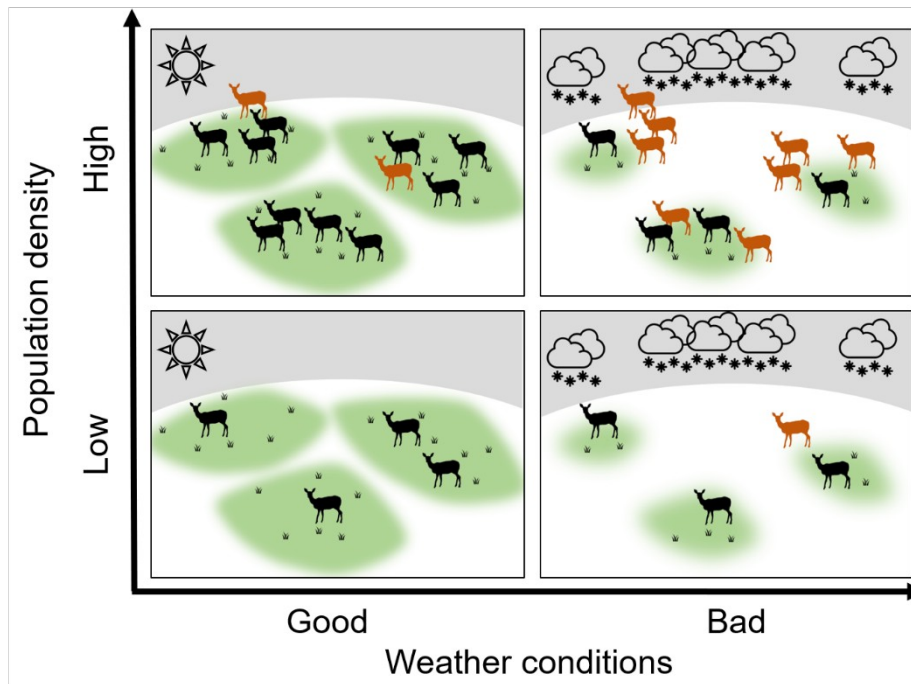


Fig. 1| Increasing impacts of weather conditions at high population densities. The per-capita resource availability is highest when population density is low and weather conditions are good. At high population density and good weather conditions, resource competition becomes more influenced by density-dependent processes, but not weather. However, when bad weather conditions restrict the per-capita resource availability, the effects of weather on demographic rates (red animals indicate individual mortality) are limited at low population density, but multiplicatively amplified by density-dependent processes at high population density.

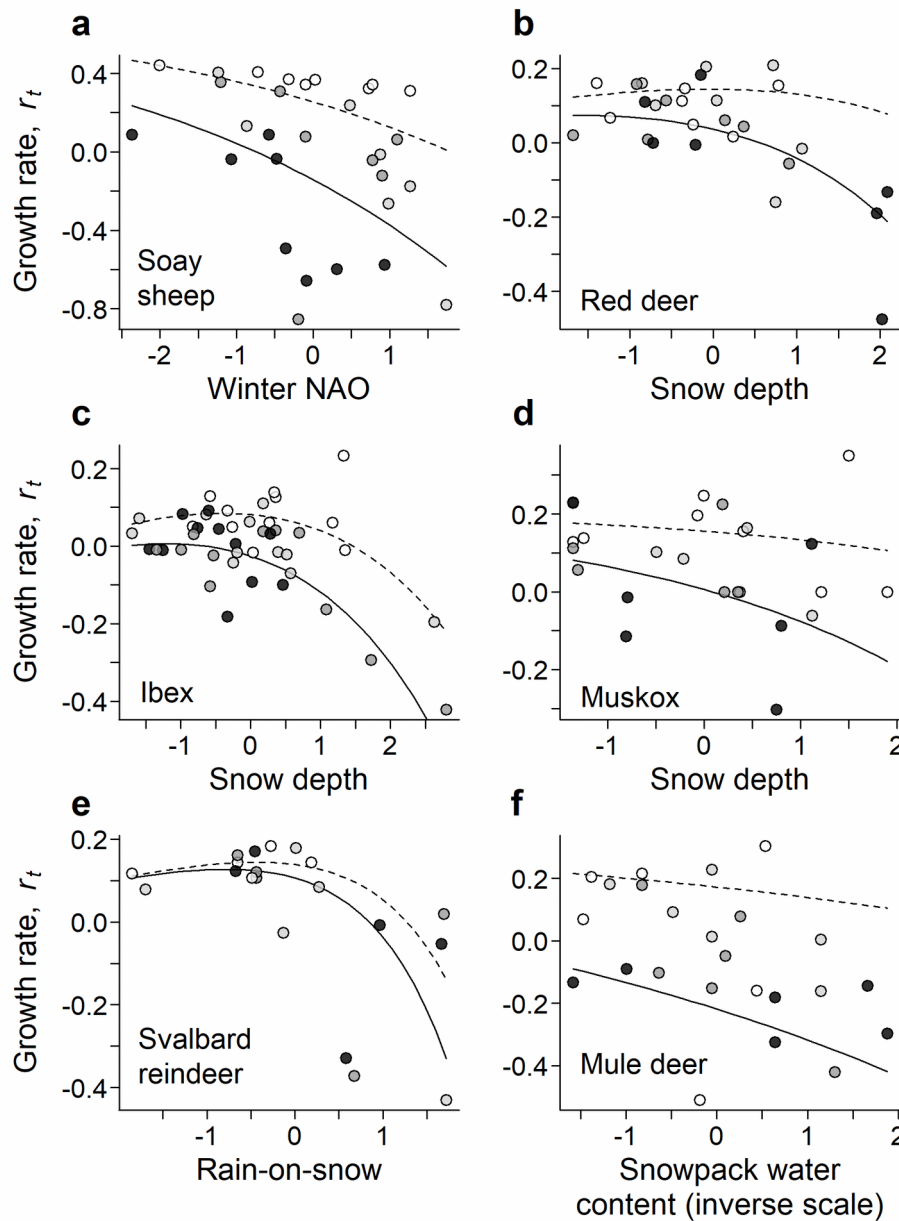


Fig. 2| Climate-density interactions in ungulate populations. Nonlinear, density-dependent effects of weather on population growth rate (r_t) are found in (a) Soay sheep *Ovis aries*, (b) red deer *Cervus elaphus*, (c) Alpine ibex *Capra ibex*, (d) muskox *Ovibos moschatus*, (e) Svalbard reindeer *Rangifer tarandus platyrhynchus*, and (f) mule deer *Odocoileus hemionus* (Tables S1, S2). Weather variables were standardized. White to black color gradient of dots indicate low to high observed population sizes, respectively. Predicted responses from a Ricker model of density-dependent population growth are shown for low (mean - 1SD; dashed lines) and high (mean + 1SD; solid lines) population sizes.

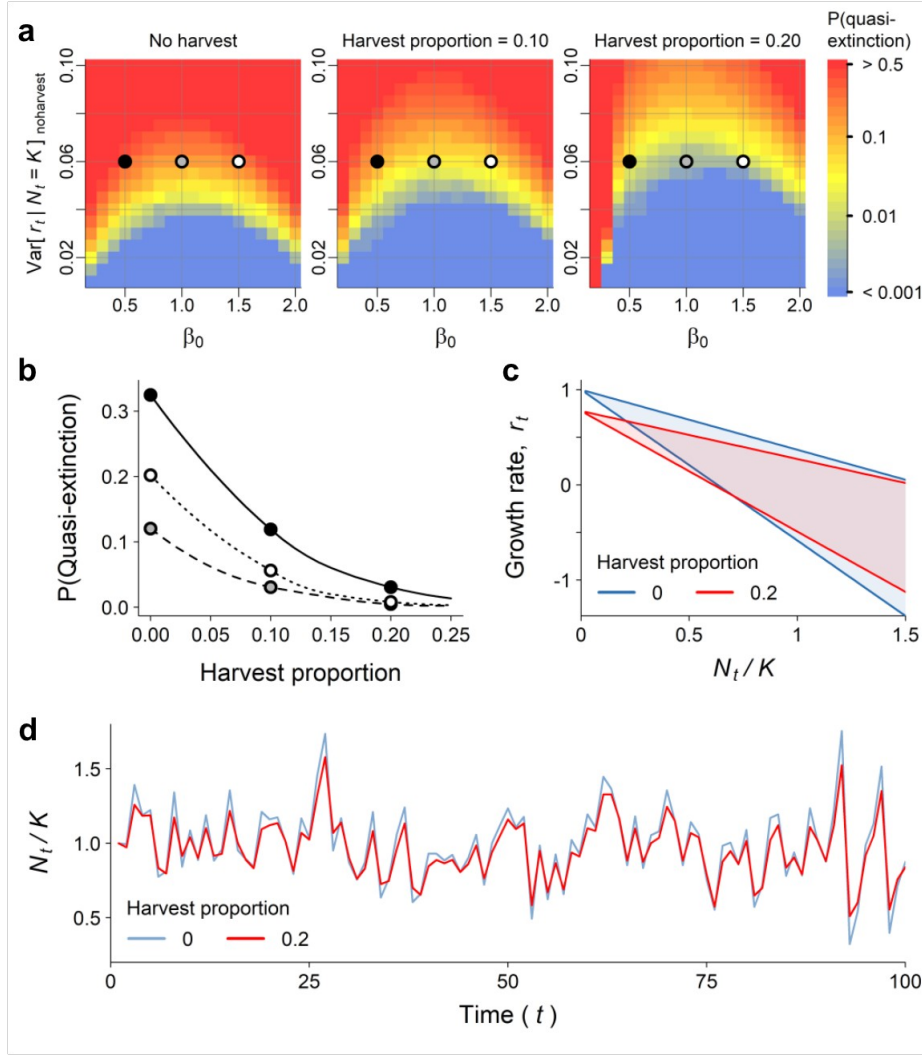


Fig. 3| Proportional harvesting reduces the density-dependent effect of environmental variation. (a) Quasi-extinction probability for different harvest proportions, maximum growth rates (β_0 , cf. (b) for symbols) and variance in growth rate (shown for populations at their carrying capacity (K) in the absence of harvesting, $\text{Var}[r_t \vee N_t = K]_{\text{noharvest}}$; see ‘Model properties’ section in the Methods). (b) Effect of proportional harvesting on quasi-extinction probability for $\beta_0 = 0.5$ (black dots, solid line), 1.0 (grey dots, dashed line) and 1.5 (white dots, dotted line), at $\text{Var}[r_t \vee N_t = K]_{\text{noharvest}} = 0.06$. (c) Change in the distribution of r_t ($\beta_0 = 1.0$) as a function of population density (N_t/K) and proportional harvesting (blue = 0, red = 0.2). (d) Simulated population trajectories using the same parameters as in (c).

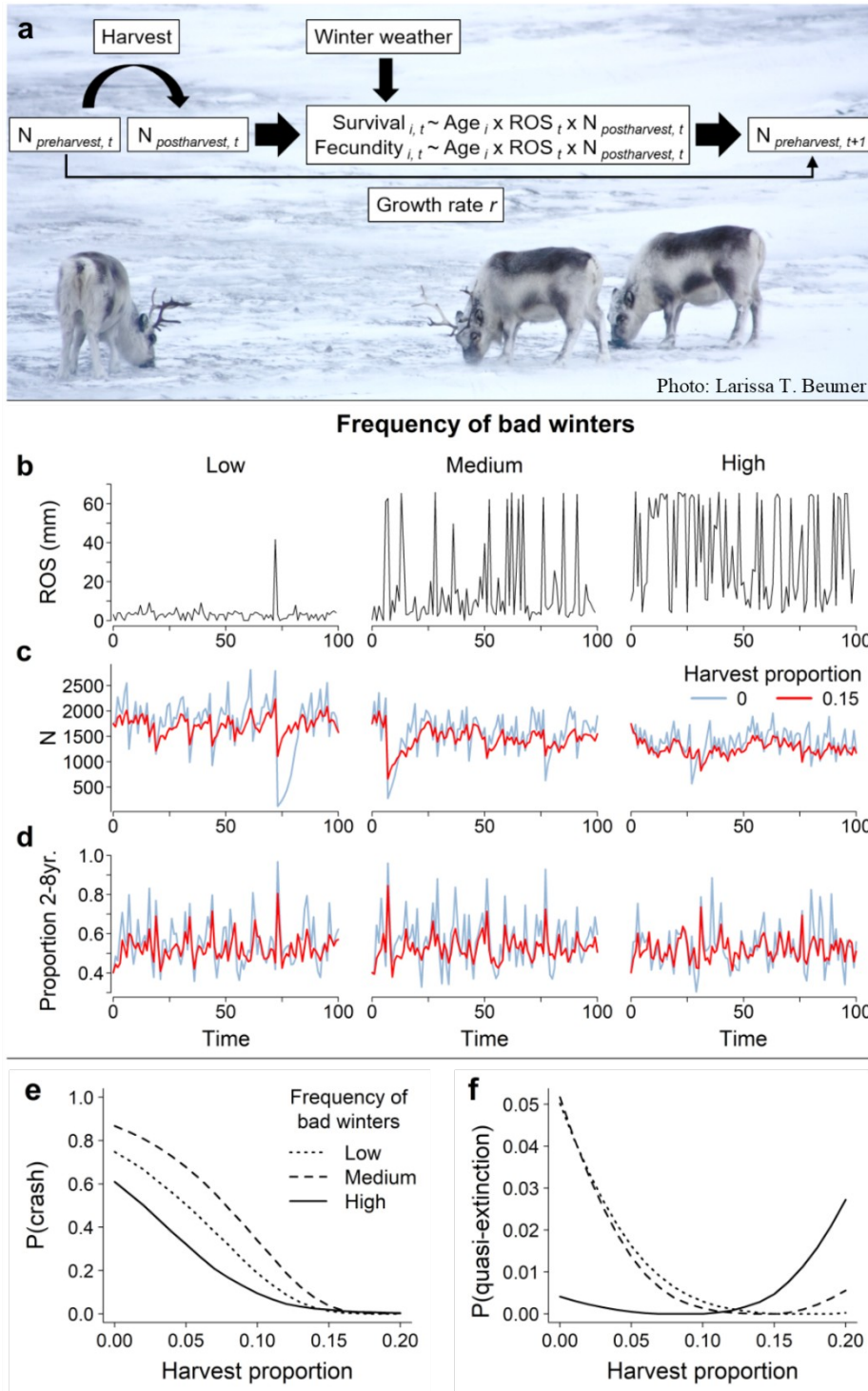


Fig. 4| Stabilizing effects of harvesting in a climate-driven population of high Arctic reindeer. (a) Schematic view of the population model in Svalbard reindeer. Bad winters correspond to high amounts of rain-on-snow (ROS), causing snowpack icing and restricted access to winter forage. (b) Simulated trajectories with low to high frequencies of ROS events and consequent responses in (c) female population size and (d) the proportion of

574 prime-aged (2-8 yr. old) females indicating stabilizing effects of proportional harvesting (red
575 lines = 0.15, blue lines = no harvesting). (**e**, **f**) Effects of proportional harvesting and low
576 (dotted lines), medium (dashed lines), and high (solid lines) frequency of bad winters on the
577 probability of (**e**) population crash and (**f**) quasi-extinction.