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LETTER

Harvesting can stabilise population fluctuations and buffer the impacts of extreme climatic events

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Abstract

Harvesting can magnify the destabilising effects of environmental perturbations on population dynamics and, thereby, increase extinction risk. However, population-dynamic theory predicts that impacts of harvesting depend on the type and strength of density-dependent regulation. Here, we used logistic population growth models and an empirical reindeer case study to show that low to moderate harvesting can actually buffer populations against environmental perturbations. This occurs because of density-dependent environmental stochasticity, where negative environmental impacts on vital rates are amplified at high population density due to intra-specific resource competition. Simulations from our population models show that even low levels of harvesting may prevent overabundance, thereby dampening population fluctuations and reducing the risk of population collapse and quasi-extinction following environmental perturbations. Thus, depending on the species' life history and the strength of density-dependent environmental drivers, low to moderate harvesting can improve population resistance to increased climate variability and extreme weather expected under global warming.

KEYWORDS

age structure, climate change, demographic modelling, density dependence, exploitation, extreme events, life history, population viability, resource competition, sustainability

INTRODUCTION

Overexploitation and climate change represent two of the major anthropogenic threats to biodiversity (Brook et al., 2008). While the role of environmental fluctuations in driving population dynamics is now routinely incorporated into models of harvesting and sustainability assessments (Beddington & May, 1977; Lande et al., 1995, 2003), potential interactions between harvesting and climatic drivers are still poorly understood (Gamelon et al., 2019). This is alarming, given that climate variability,

including the frequency of extreme weather events, have increased due to global warming and are forecasted to intensify further in the near future (Differbaugh et al., 2017; Fischer & Knutti, 2015).

Population-dynamic models generally predict that harvesting can magnify population fluctuations induced by environmental stochasticity and thus increase the risk of extinction (Anderson et al., 2008; Beddington & May, 1977; Fryxell et al., 2010; Gamelon et al., 2019; Hsieh et al., 2006; Lande et al., 1995, 2003). 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 (Anderson et al., 2008; Hsieh et al., 2006). On the other hand, May and colleagues (May et al., 1978) early hypothesised that, in species with chaotic (i.e. irregular) population fluctuations, reducing population density through harvesting can result in less variable population trajectories by dampening the density-dependent effects of environmental stochasticity. Since then, there has been evidence of stabilising effects of harvesting and ‘compensation’, that is an increase in natural survival and/or recruitment following a reduction in population size due to harvesting or predation, but these depended on the timing of harvesting relative to density-dependent breeding and natural mortality (Abrams, 2009; Boyce et al., 1999; Jonzén & Lundberg, 1999; Ratikainen et al., 2008; Xu et al., 2005). In cases of overcompensation, harvest or predation mortality have been predicted to lead to even higher population sizes than expected under natural population growth conditions (the so-called ‘hydra effect’, Abrams & Matsuda, 2005). However, following May et al. (1978), the implications of density-dependent environmental effects have, so far, received little attention in the context of harvesting. This is surprising given the realisation that environmental impacts on population dynamics can strongly interact with density (Coulson et al., 2004; Ferguson & Ponciano, 2015; Royama, 1992).

Both theoretical and empirical evidence across taxa now indicate that population dynamics are often characterised by nonlinear amplifications of environmental stochasticity caused by intrinsic processes such as density dependence (Anderson et al., 2008; Barbraud & Weimerskirch, 2003; Coulson et al., 2001, 2004; Ferguson & Ponciano, 2015; Gamelon et al., 2017; Hansen et al., 2019; Hsieh et al., 2005; Lima et al., 2006; Royama, 1992; Stenseth et al., 2004). 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 (Lima et al., 2006; Owen-Smith, 2000; Royama, 1992). Unfavourable conditions can therefore have multiplicative effects on individual fitness at high density, but little effect at low density (Figure 1a). Because of this, observed population growth rates of natural populations have sometimes been better explained by density-dependent environmental variance, that is, multiplicative rather than additive effects of density and climate (Ferguson & Ponciano, 2015; Gamelon et al., 2017; Hansen et al., 2019; Royama, 1992). Such ‘climate-density interactions’ may cause unstable dynamics and population crashes when prolonged periods of favourable 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 (Ferguson & Ponciano, 2015; Hansen et al., 2019; Wilmers et al., 2007). Intuitively, strong climate-density interactions would predict that harvesting—which, by definition, reduces density—can weaken the impacts of a subsequent environmental perturbation with density-dependent effects on population dynamics.

Here, we address this prediction using simulations from theoretical population models and an empirically parameterised, stochastic model of demographic rates in wild Svalbard reindeer (*Rangifer tarandus platyrhynchus*). These simulations show that harvesting can weaken the effects of climate-density interaction, leading to increased population stability and resistance to environmental perturbations.

MATERIALS AND METHODS

Theoretical models

Model properties

To evaluate consequences of harvesting on populations with density-dependent versus density-independent effects of environmental stochasticity, we considered two discrete time logistic models commonly used in population ecology: the Ricker model and Beverton–Holt model (May et al., 1978). Their deterministic analogues can be written as

$$N_{t+1} = N_t e^{\beta_0 - \beta_1 N_t}, \quad (1)$$

for the Ricker model, and

$$N_{t+1} = N_t \frac{e^{\beta_0}}{1 + \beta_1 N_t}, \quad (2)$$

for the Beverton–Holt. In both models, N_t is the population size at time t , e^{β_0} is the maximum population growth rate and $\beta_1 > 0$ describes the strength of density dependence in the population growth. The carrying capacity K (i.e. the equilibrium population size) is defined by β_0/β_1 for the Ricker model, and $(e^{\beta_0} - 1)/\beta_1$ for the Beverton–Holt model. The fundamental difference is that, when $N_t \gg K$, the Ricker model produces small N_{t+1} due to strong density dependence, whereas the Beverton–Holt model produces N_{t+1} close to e^{β_0}/β_1 and is, therefore, not characterised by population crashes (de Valpine & Hastings, 2002). Furthermore, Ricker dynamics with high values of β_0 lead to overcompensating density dependence, that is for N_t near K , decreasing values of $N_t < K$ result in exceedingly higher values of $N_{t+1} > K$. This has been described by the hydra effect in the presence of harvesting or predation (Abrams & Matsuda, 2005).

The natural-logarithm transformed version of these models is convenient for parameterising changes in population size (e.g. de Valpine & Hastings, 2002). Let the logistic population growth rate be defined as

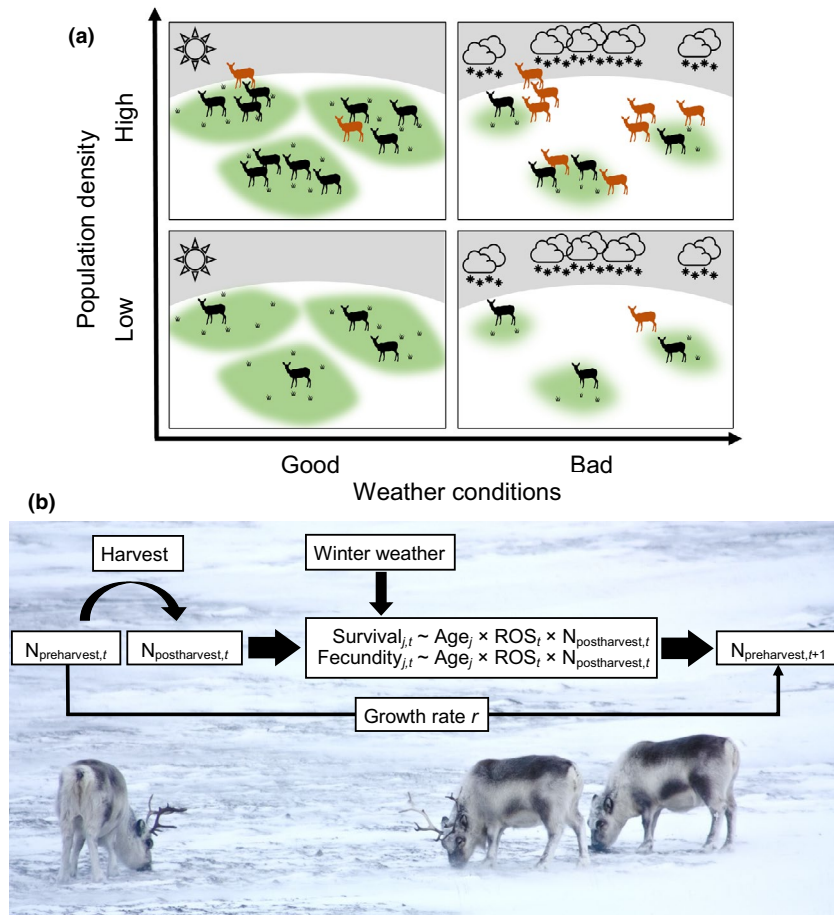


FIGURE 1 Conceptual diagram of climate-density interactions and the demographic reindeer model. (a) The *per capita* resource availability is highest when population density is low and weather conditions are good. At high population density and good weather conditions, resource competition becomes more 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 amplified by density-dependent processes at high population density. (b) In Svalbard reindeer, bad winters correspond to high amounts of rain-on-snow (ROS), causing snowpack icing and restricted access to winter forage. This leads to stronger effects of ROS on vital rates (Survival, Fecundity) at high population density (N) and for juvenile and old individuals (Age j)

$$r_t = \ln(N_{t+1}) - \ln(N_t) = \beta_0 - g(N_t), \tag{3}$$

so that

$$g(N_t) = \beta_1 N_t, \tag{4}$$

for the Ricker model, and

$$g(N_t) = \ln(1 + \beta_1 N_t), \tag{5}$$

for the Beverton–Holt model.

Environmental stochasticity is typically modelled by adding temporal noise on the maximum growth rate, β_0 , so that the environmental effect on r_t is independent of N_t (Ferguson & Ponciano, 2015; Lande et al., 2003; de Valpine & Hastings, 2002). We modelled additive environmental variance on the population growth rate as

$$r_t = \beta_0 - g(N_t) + \gamma_a Z_{a,t}. \tag{6}$$

The random variable $Z_{a,t}$ follows a normal distribution with mean 0 and variance 1, the scaling parameter $\gamma_a > 0$ describes the strength of the additive environmental noise, and the variance in the population growth rate is a constant defined by γ_a^2 .

However, the effect of environmental stochasticity on the population growth rate often depends on the population density N_t (Ferguson & Ponciano, 2015). We modelled multiplicative environmental variance (i.e. density-dependent environmental stochasticity) on the population growth rate as

$$r_t = \beta_0 - g(N_t) e^{-\gamma_m Z_{m,t}}. \tag{7}$$

Similar to $Z_{a,t}$ and γ_a in Equation 6, the random variable $Z_{m,t}$ follows a normal distribution with mean 0 and variance 1, and the scaling parameter $\gamma_m > 0$ describes the strength of the multiplicative environmental noise. The negative sign of the stochastic term ensures that negative values of $Z_{m,t}$ decrease r_t due to stronger density-dependent

environmental variance. In this case, the variance in the population growth rate depends on N_t :

$$\text{Var}[r_t|N_t] = g(N_t)^2 e^{\gamma_m^2} (e^{\gamma_m^2} - 1). \quad (8)$$

We primarily investigated models with either additive (Equation 6) or multiplicative (Equation 7) environmental variance. However, population growth rates can be modelled with both types of environmental variance and covarying $Z_{a,t}$ and $Z_{m,t}$ shaped by a correlation coefficient ρ_Z :

$$r_t = \beta_0 - g(N_t) e^{-\gamma_m Z_{m,t}} + \gamma_a Z_{a,t}, \quad (9)$$

$$\text{Var}[r_t|N_t] = \gamma_a^2 + g(N_t)^2 e^{\gamma_m^2} (e^{\gamma_m^2} - 1) - 2g(N_t) \rho_Z \gamma_a \gamma_m e^{\frac{\gamma_m^2}{2}}. \quad (10)$$

For a given environmental noise $Z_{a,t}$ and $Z_{m,t}$ at time t , the population size \widehat{N}_t that gives $r_t = 0$, sometimes referred to as the stochastic or seasonal carrying capacity K_t (Lande et al., 2003; Xu et al., 2005), can be expressed as

$$\widehat{N}_t = \frac{\beta_0 + \gamma_a Z_{a,t}}{\beta_1 e^{-\gamma_m Z_{m,t}}}, \quad (11)$$

for the Ricker model, and

$$\widehat{N}_t = \frac{e^{\frac{\beta_0 + \gamma_a Z_{a,t}}{\beta_1}} - 1}{\beta_1}, \quad (12)$$

for the Beverton–Holt model.

Model validation

We validated the Ricker and Beverton–Holt models on population growth rates of six ungulate species: ibex (*Capra ibex*, Mignatti et al., 2012), Soay sheep (*Ovis aries*, Coulson et al., 2001), red deer (*Cervus elaphus*, Bonardi et al., 2017), Svalbard reindeer (Hansen et al., 2019), mule deer (*Odocoileus hemionus*, Monteith et al., 2014) and muskox (*Ovibos moschatus*, Asbjørnsen et al., 2005). We selected these population time series as they have previously been shown or suggested to experience density-dependent effects of climatic drivers (Table S1). We first fitted models of observed logistic growth rates with Ricker or Beverton–Holt models and additive (Equation 6), multiplicative (Equation 7), or both (Equation 9) types of environmental variance. We then also analysed growth rate models with the reported climate variable as an additive or multiplicative covariate after standardisation. Because models with residuals from both additive and multiplicative environmental variance required two extra parameters (i.e. two noise terms and their correlation, Equations 9 and 10), we only considered models with either additive or multiplicative residual variance when

including the climate covariate. Models were developed with the R-package TMB (Kristensen et al., 2016) using the nlminb optimisation function to allow the estimation of $Z_{a,t}$ and $Z_{m,t}$ as random effects and minimise the log likelihood between the observed and predicted population growth rates. Model selection was performed using the corrected Akaike's information criterion (AICc).

Harvest simulations

We investigated consequences of harvesting on population growth rates with additive versus multiplicative environmental variance. For simplicity, we considered only proportional harvesting for the theoretical models (see ‘Reindeer as a case study’ below for simulations of constant yield harvesting). Proportional harvesting of magnitude $(1 - p)$ was applied to population density at the beginning of each time interval:

$$h(N_t) = N_t (1 - p), \quad (13)$$

Density-dependent processes and environmental stochasticity were then applied to the postharvest population:

$$r_t = \ln(h(N_t) e^{\beta_0 - g(h(N_t))}) - \ln(N_t). \quad (14)$$

This formulation is realistic for many species, such as most Holarctic ungulates, where harvest happens in autumn, mortality rates are highest during winter and recruitment occurs as birth pulses in spring.

We simulated populations trajectories of 1000 time-steps for different sets of parameters. Note that the variance in r_t depended on N_t for the models with multiplicative environmental variance (Equation 8). Therefore, to make models with different types of density dependence and environmental variance more comparable, we optimised γ_m for given sets of β_0 and β_1 so that $\text{Var}[r_t|N_t = K]_{\text{noharvest}}$ (i.e. the variance in r_t for populations at their carrying capacity in the absence of harvesting) equalled γ_a^2 (i.e. the variance in the population growth rate for models with only additive environmental variance). We calculated the risk of quasi-extinction (i.e. increased extinction risk due to demographic stochasticity when the population size is small) as the proportion of 1000 simulated population trajectories that experienced $N < K/5$ at least once during 1000 timesteps.

Reindeer as a case study

Study population

Arctic ungulates, like Svalbard reindeer, can experience dramatic declines in population size when extreme rain-on-snow (ROS) events occur (Forbes et al., 2016; Hansen et al., 2011; Miller & Gunn, 2003). The tundra vegetation

becomes encased in ice as rain- and snowmelt-water freezes on the ground (Peeters et al., 2019), thus restricting access to food (Albon et al., 2017). The strength of ROS effects on the age-specific vital rates depends on the population density at the time of the event, such that a ROS event strongly affects demographic performances at high density (Hansen et al., 2019). Recently, Hansen et al. (2019) developed an empirically parameterised stochastic population model where this ROS-density interaction was modelled on vital rates for six age-classes of female Svalbard reindeer. From this population model and simulated ROS scenarios, they found that increased frequency in extreme ROS events could stabilise population dynamics and reduce extinction risk. The study population, situated in central Spitsbergen (78°N, 16°E), is lightly hunted during autumn, and some reindeer have been culled for scientific purposes (Albon et al., 2002), resulting in annual offtakes <5% of the female population. However, potential harvesting effects accounting for this interaction between ROS and density on reindeer population dynamics have so far remained unclear.

Demographic population model

We adopted the demographic population model developed by Hansen et al. (2019) to simulate effects of harvesting on the reindeer population dynamics, accounting for age-specific, density-dependent effects of ROS (Figure 1b). In short, annual population size (N) and vital rates (i.e. survival S and fecundity F) were estimated for six age classes for the period 1994 to 2014 with an integrated population model (IPM) (Bjørkvoll et al., 2016; Lee et al., 2015). The six age classes consisted of calves (0 years), yearlings (1 year) and adults of 2, 3–8, 9–11 and ≥ 12 years. Hansen et al. (2019) modelled the effects of postharvest population density ($N_{\text{postharvest}}$), winter length and a three-way interaction between age-class, $N_{\text{postharvest}}$, and ROS on age-specific survival and fecundity using linear mixed-effects models (Figure 1b). To ensure that the effect of ROS was strictly negative (or positive) for all values of $N_{\text{postharvest}}$, the ROS-density interaction was included using the form $ROS'_i = ROS_i \times e^{k \times N_{\text{postharvest},i}}$ where the constant k was estimated using an optimisation function aiming at minimising Akaike's information criterion (AIC). Year was included as a random effect to account for environmental noise not captured by the fixed parameters, and as a fixed effect to correct for a positive trend in population size during the study period. These models were run for a posterior sample of 9090 estimates of age-class-specific annual survival, fecundity and population sizes from the IPM (see table S2 in Hansen et al. (2019) for model coefficients).

In this study, we simulated population trajectories of 100 years using these models of vital rates with the parameter estimates from 1000 posterior models. The

fixed variable year was set to 2014 and the average observed winter length during 1994–2014 was used for the entire trajectory. Importantly, to account for sources of environmental stochasticity due to processes other than covariates included in the model, we incorporated a covariance matrix of the different vital rates for all age classes. From this covariance matrix, we generated 100 new residuals from a multivariate normal distribution, that is one for each year of the simulated trajectory. These vital rate models then allowed us to estimate the population size at time $t + 1$ from the population size of each age at time t , and simulated ROS and harvest levels.

Changes in the number of females were simulated for ages 0–12, while the number of females ≥ 13 years old were pooled in one (senescent) age class. Vital rates in the IPM were estimated for six age classes, meaning that the numbers of 12- and ≥ 13 -year-old females were simulated from the vital rates of 9–11 and ≥ 12 years old respectively. Using a similar approach to Hansen et al. (2019), annual survival and fecundity rates were estimated based on the population size after harvesting $N_{\text{postharvest}}$ and stochastic simulations of ROS (Figure 1b; see 'climate-harvesting scenarios' below). Summer mortality for all age classes is considered to be close to zero due to virtual lack of predation (Reimers, 1983). The number of individuals of age j in year t surviving to age $j + 1$ was modelled using a binomial process with probability $S_{j,t}$ and $n = N_{j,t}$ random draws to allow for demographic stochasticity (i.e. chance events that affect individuals independently). Similarly, the number of calves born in year $t + 1$ from the surviving individuals, now age $j + 1$, was modelled using a binomial process with probability $F_{j,t}$ and $n = N_{j+1,t+1}$ random draws. Svalbard reindeer do not reach maturity before their second year of life, thus fecundity of calves $F_{0,t} = 0$, and produce maximum one calf per year (Nowosad, 1973). Assuming a balanced sex-ratio (0.5), the total number of female calves was again modelled using a binomial process. The total population size in year $t + 1$ was then simply calculated by taking the sum of the modelled number of individuals over all ages.

Population trajectories were initiated using the age distribution and population size in year 2014 ($N_0 = 1747$; i.e. the last published population estimate from the IPM) (Bjørkvoll et al., 2016). Since the IPM estimated population sizes for the six age classes, we estimated the number of females in 2014 for ages 3–12, and ≥ 13 years, using simple cohort analysis (Solberg et al., 1999). This resulted in the following initial age structure from 0 to ≥ 13 years: 335, 258, 152, 172, 121, 116, 22, 49, 69, 122, 109, 114, 23 and 85 individuals. Nevertheless, the outcome of the 100-year-long trajectories was insensitive to the initial age structure.

Climate-harvesting scenarios

We simulated population trajectories for different harvest intensities and three climate scenarios: low, medium

and high frequencies of extreme ROS events (note that these correspond to the very low, medium and very high-frequency scenarios in Hansen et al. (2019)). The medium climate scenario reflects the historical state between 1962 and 2014, and simulated realisations of ROS in all three climate scenarios fell within the range of observed values of ROS during this period (see Hansen et al. (2019) for further details).

We compared the effects of proportional versus constant yield harvesting on reindeer population dynamics. A proportional harvest strategy involves a constant effort where, each year, a fixed proportion of the population is harvested (Beddington & May, 1977; Lande et al., 1995). With a constant harvesting strategy, the same number of individuals are harvested each year. We used fixed harvest proportions ranging from 0 to 0.3 and constant yields of 0 to 300 individuals per year. For simplicity, annual harvest yields were evenly distributed across age classes, that is simulating the same age distribution in the harvest offtake as in the preharvest population. This is a rather realistic simplification as it reflects the overall management aim to ‘shoot through’ the population (Peeters et al., 2021). For each climate scenario and fixed harvest proportion or constant, we simulated 100-year-long population trajectories based on 10 simulated ROS trajectories for each parameter set of 1000 posterior models of S and F , that is 10,000 population trajectories. These were used to calculate population properties, such as average population size, variability in the *per capita* growth rate and probabilities of a population crash and quasi-extinction. We defined the probability of a population crash within 100 years as a reduction of the pre-harvest population size by half from one year to the next. The probability of a quasi-extinction within 100 years we defined as a reduction below 20% of the initial population size ($N_0 = 1747$, so $N_{\text{quasi-extinct}} < 350$). All analyses were performed using the statistical software R (R Core Team, 2019).

RESULTS

Theoretical models

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 (Figure 2; see model selection in Table S2 and parameter estimates in Table S3). The form of density dependence was only of significance for Soay sheep, which showed stronger support for Ricker than Beverton–Holt types of growth rates. When no climate covariate was included, models performed clearly better with multiplicative environmental variance, except for muskoxen, which tended to show stronger support for a model with additive environmental variance than

a model with both additive and multiplicative variance. Nevertheless, model fitting improved with climate covariates included as a multiplicative term, that is interacting with β_1 and N_t . Only for mule deer, a model with an additive climate effect performed marginally better (Table S2), yet with much stronger uncertainty in the estimation of β_0 and β_1 than when the climate covariate was included as a multiplicative term (Table S3).

Both Ricker and Beverton–Holt models with only additive environmental variance showed that increasing harvest proportions increased the variance in (log-) population size (Figure 3). However, the opposite result was found for models with multiplicative environmental variance; proportional harvesting reduced the variance in population growth rates (Figure 4a), leading to stabilised population fluctuations (Figures 3 and 4b) and reduced quasi-extinction risk (Figure 4c). Particularly for the Ricker model, ‘moderate’ harvest proportions relative to β_0 buffered population crashes when poor environmental conditions with multiplicative effects occurred at high population density.

Population dynamics from the Beverton–Holt model were not as strongly characterised by population crashes and compensatory dynamics as from the Ricker model, but nevertheless showed that population declines were buffered by harvesting when environmental stochasticity was multiplicative rather than additive to density-dependent population growth (Figures S1–S3). The clearest difference between the Ricker and Beverton–Holt models was the effect of harvesting on the average population size for different maximum growth rates. Ricker dynamics with high values of β_0 displayed compensation of harvesting, that is increased average population size, but average population size decreased with harvesting for low values of β_0 and for population trajectories with Beverton–Holt dynamics regardless of β_0 (Figure 3). However, this was caused by the formulation of density dependence *per se* (Equations 4 and 5) and not by how environmental stochasticity entered the models.

Reindeer as a case study

Simulated population trajectories from our demographic model of Svalbard reindeer (Figure 1b) showed stabilising effects of both proportional and constant harvesting on climate-driven fluctuations in population size and age structure (Figure 5a–c, Figure S4). The risk of population crashes and, consequently, quasi-extinction was highest in the climate scenario with medium (i.e. historical) frequency of ROS events (cf. Hansen et al., 2019) but was in all ROS scenarios strongly reduced by annually harvesting a low proportion (<0.10) of the population (Figure 5d–e, Figure S4). Moreover, the variance in both population growth rate and log-population size decreased markedly for low to moderate harvest

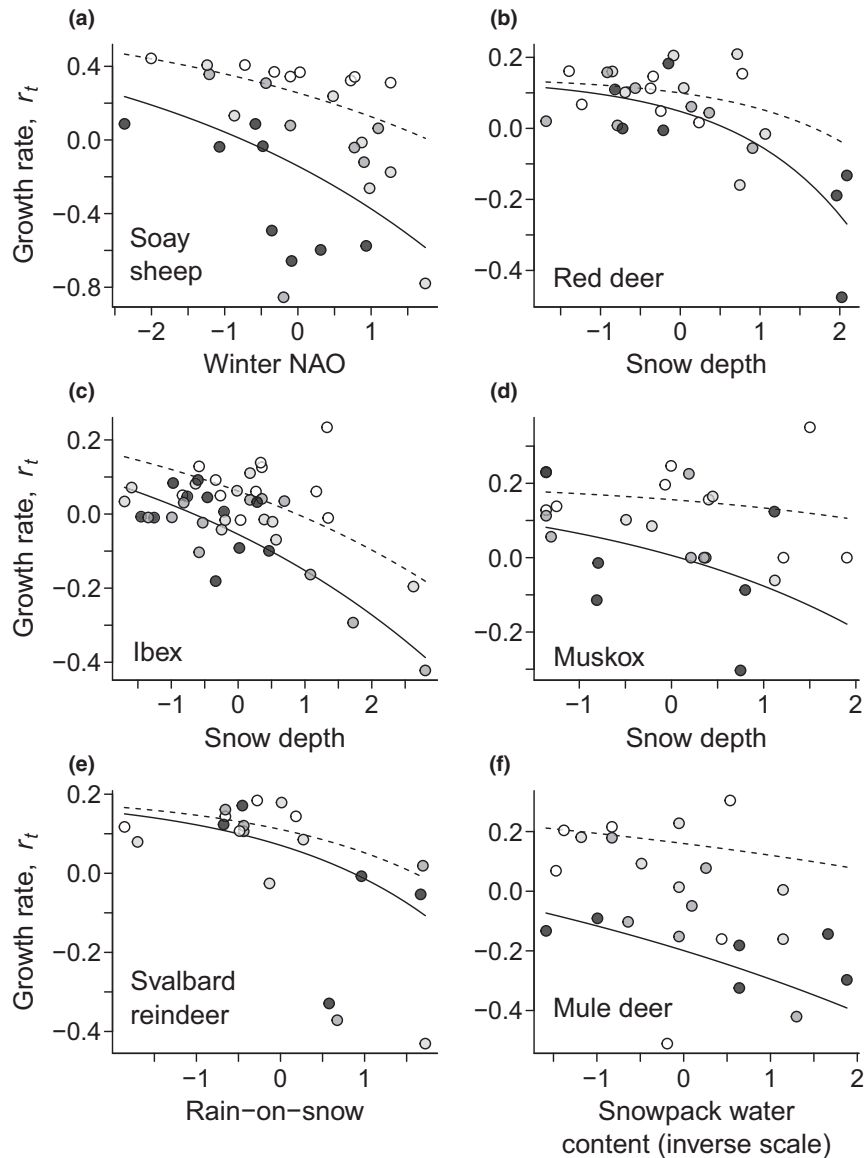


FIGURE 2 Climate-density interactions in six ungulate populations. Nonlinear, density-dependent effects of weather conditions on population growth rate (r_t) are found in (a) Soay sheep, (b) red deer, (c) ibex, (d) muskox, (e) Svalbard reindeer and (f) mule deer. Weather variables were standardised. Dot colours indicate low (white), medium (grey) and high (black) observed population sizes. Predicted responses of density-dependent population growth rate are shown for low (mean -1 SD; dashed lines) and high (mean $+1$ SD; solid lines) population sizes

proportions (up to ca. 0.13 and 0.16 for high and low ROS frequencies, respectively, Figure S4). However, the long-run average population size remained approximately unchanged up to these levels of harvesting.

Similarly, for constant harvesting, the variance in population growth rate and log-population size decreased with low to moderate yields (up to ca. 150 and 250 individuals for high and low ROS frequencies respectively). Constant harvesting reduced the quasi-extinction risk at low harvest yields but not as strongly as comparable levels of proportional harvesting. Also, critical harvest yields, that is, beyond which the mean population size dropped and quasi-extinction risk sharply increased, varied little between ROS scenarios for proportional harvesting, but strongly for constant harvesting.

DISCUSSION

In this study, we have shown how harvesting can weaken effects of density-dependent environmental stochasticity, leading to stabilised population fluctuations and lower quasi-extinction risks. Depending on the timing of harvesting, this can be expected for systems where bad weather conditions restrict the access to resources and, thereby, increase resource competition nonlinearly with increased population density (Figure 1) (Royama, 1992). Population analyses of six ungulate species (Figure 2), together with previous findings in the literature (e.g. Barbraud & Weimerskirch, 2003; Coulson et al., 2001; Ferguson & Ponciano, 2015; Gamelon et al., 2017), indicated that such climate-density interactions

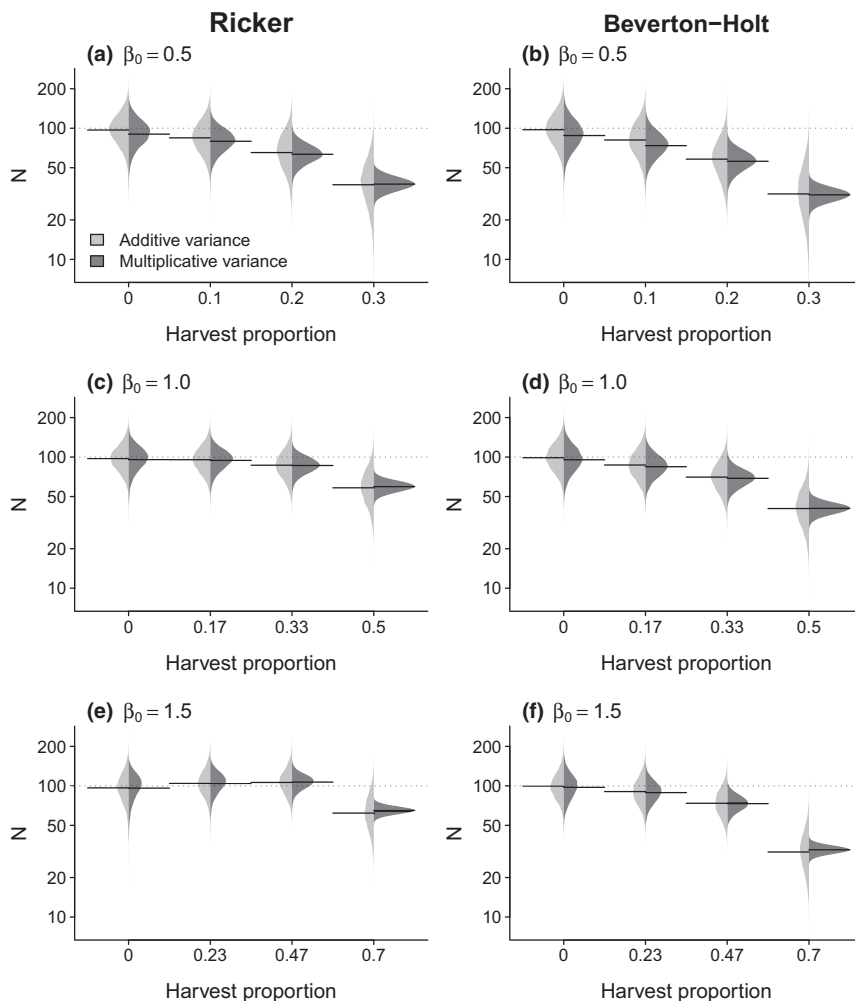


FIGURE 3 Effects of proportional harvesting on the distribution of population sizes for Ricker (left panels) and Beverton–Holt (right panels) models with additive (grey distributions) versus multiplicative (black distributions) environmental variance, and maximum growth rates (a, b) $\beta_0 = 0.5$, (c, d) $\beta_0 = 1.0$ and (e, f) $\beta_0 = 1.5$. Average population sizes are indicated by black horizontal lines. Note that x-axes are on different scales for the different values of β_0 and y-axes are on log-scale. Chosen parameters were $K = 100$ (grey horizontal lines), $\gamma_a = 0.224$, and for γ_m we used the resultant values when the variance of $r = 0.05$ for $N = K$ in the absence of harvesting (i.e. $\text{Var}[r_t | N_t = K]_{\text{noharvest}}$); (a, b) $\gamma_m = 0.397$, (c, d) $\gamma_m = 0.216$, (e, f) $\gamma_m = 0.147$

are more common than previously acknowledged, that is high population density generally amplified negative effects of overwintering climatic conditions on population growth rates. Both Ricker and Beverton–Holt models with such multiplicative environmental variance revealed stabilising effects of proportional harvesting on population fluctuations as harvesting reduced the density-dependent effects of environmental stochasticity on the logistic growth rate (Figures 3 and 4). Simulations from an age-structured, stochastic model of demographic rates in Svalbard reindeer provided empirically based support for these theoretical findings; low to moderate levels of both proportional and constant yield harvesting can stabilise population dynamics by mitigating climate-density interactions and, thereby, the risk of climate-induced population crashes (Figure 5).

In accordance with previous studies (Beddington & May, 1977; Lande et al., 1995, 2003), we found that

harvesting increased the variance in log-population size for our theoretical models with only additive environmental variance, making populations more vulnerable to extinction. In contrast, when environmental stochasticity was density-dependent low to moderate harvest proportions reduced the temporal variation in population size and, hence, the probability of quasi-extinction. This occurred because harvesting reduced population density and, thereby, the effects of subsequent density-dependent environmental stochasticity in population growth rates. The reduction in quasi-extinction risk by harvesting thus depends on the relative contributions of density-dependent versus density-independent environmental variation, and their correlation, as well as the harvest level and maximum population growth rate (Figures S5 and S6).

In the real world, the demographic responses of natural populations to intrinsic and extrinsic drivers (including

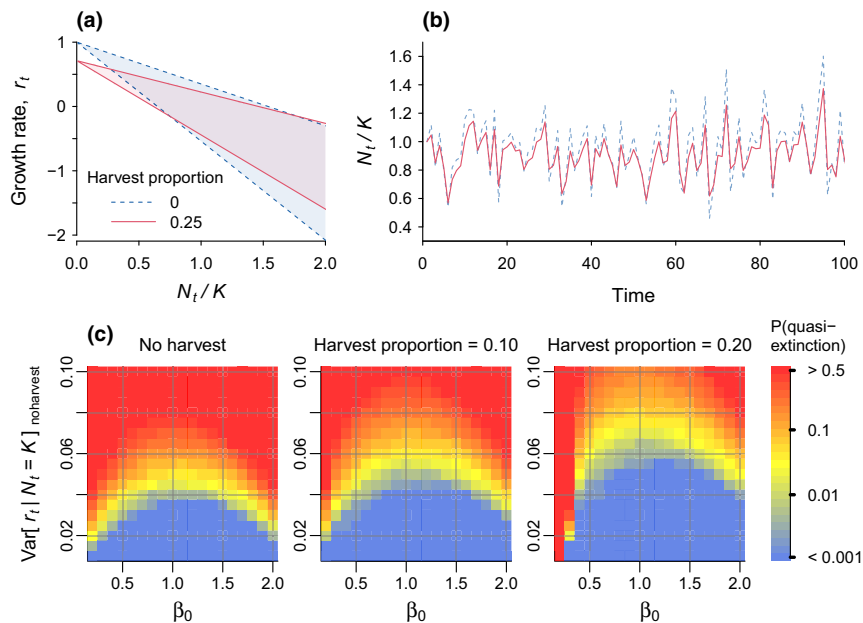


FIGURE 4 Proportional harvesting reduces population fluctuations and quasi-extinction risk. Effects of proportional harvesting in the Ricker logistic growth rate model with multiplicative environmental variance. (a) Distribution in population growth rate (r_t) as a function of population density (N_t/K) and harvest proportions 0 (blue shade and dashed lines) and 0.25 (red shade and solid lines) and (b) simulated population trajectories. Chosen parameters are $\beta_0 = 1.0$, $K = 100$, $\gamma_m = 0.22$. (c) Probabilities of quasi-extinction (increasing $P(N < K/5)$) indicated by the blue-to-red gradient) for increasing harvest proportions (left = 0, centre = 0.1, right = 0.2), maximum growth rates (β_0 , x-axis) and variance in growth rate (y-axis, shown for populations at their carrying capacity (K) in the absence of harvesting, $\text{Var}[r_t | N_t = K]_{\text{noharvest}}$)

harvesting), and 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; Xu et al., 2005). The empirically parameterised, stochastic population model for wild Svalbard reindeer (Bjørkvoll et al., 2016; Hansen et al., 2019; Lee et al., 2015) provided a heuristic framework to investigate how harvesting can influence population dynamics by modifying density-dependent effects of climatic conditions. Hansen et al. (2019) showed how more frequent extreme ROS events reduced the quasi-extinction risk as populations become less likely to exceed their carrying capacity. Overabundant populations are at high risk of collapsing when extreme climate events restrict the *per capita* resource availability.

As expected from our theoretical models, we found that harvesting dampened the temporal variation in population growth rates and reduced fluctuations in reindeer abundance and age structure. This happened because harvesting weakened the negative, density-dependent effect of stochastic ROS events on vital rates by decreasing the population density before the onset of winter. Consequently, harvesting reduced the probability of a population crash and, therefore, the risk of climate-induced quasi-extinctions. This empirically based analysis thus confirmed our prediction that, under strong climate-density

interactions, harvesting can stabilise population dynamics by buffering negative, density-dependent effects of weather conditions (May et al., 1978). While these impacts on stability were already evident at very low harvest proportions (<0.05), the effects on the long-term average population size were negligible up to a harvest proportion of ca. 0.15 (Figure S4). Unsurprisingly, increasing harvest proportions further, notably beyond 0.20, increased the risk of quasi-extinction as populations take longer to recover from environmental disturbances and harvest mortality (Beddington & May, 1977; Lande et al., 1995).

In practice, managers often implement a quota harvesting strategy. Proportional, threshold and proportional threshold harvesting are generally recommended as more sustainable harvest strategies, but these require estimates of abundance which typically are unavailable or come with large uncertainties (Engen et al., 1997; Lande et al., 1995). Interestingly, though, low constant harvest yields in our reindeer model also reduced population fluctuations without affecting the long-term average population size. Nevertheless, the stabilising effect and reduction in quasi-extinction risk were less prominent than for harvest proportions with similar impacts. Also, the critical constant harvest yield beyond which the quasi-extinction risk increased steeply was very sensitive to the frequency of ROS events (Figure S4), indicating that constant harvesting is a less sustainable strategy for populations subject to such climate change.

The combined results from simulations and realistic population models suggest that harvesting can

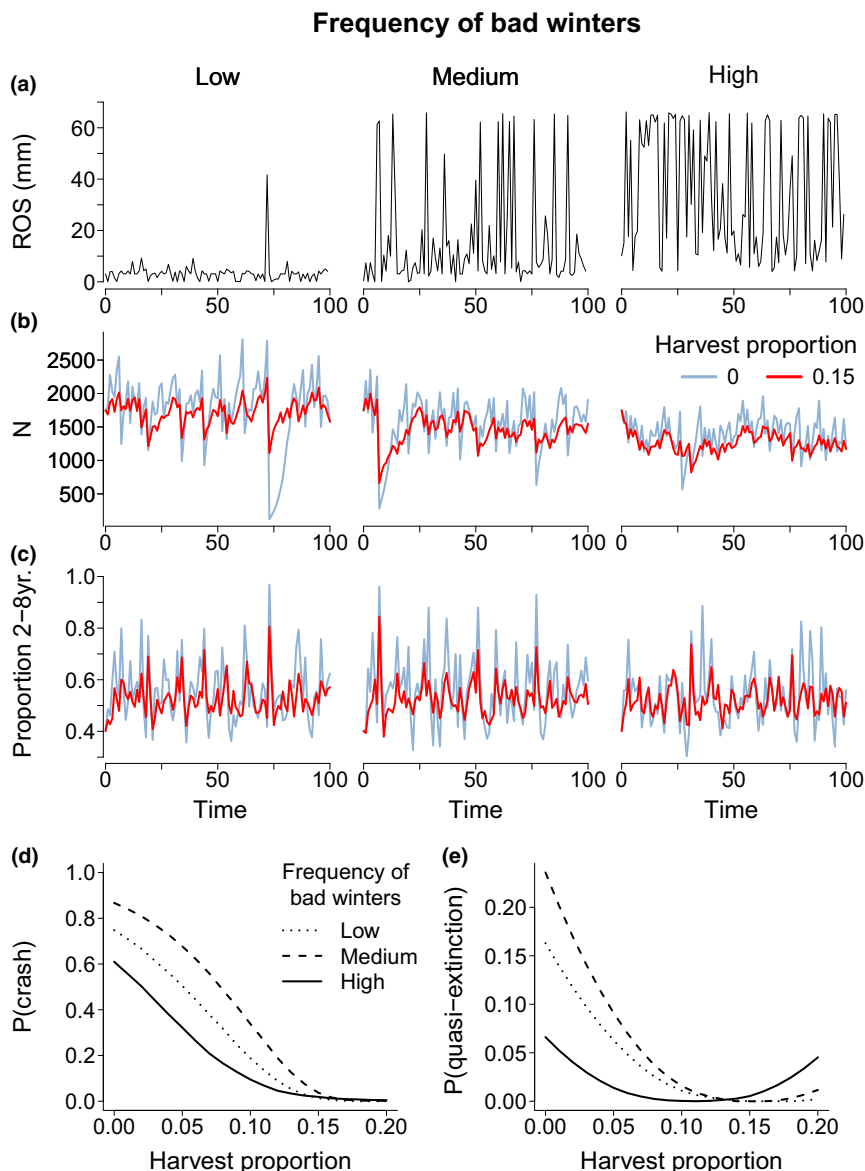


FIGURE 5 Stabilising effects of harvesting in a climate-driven population of high Arctic reindeer. (a) Simulated trajectories with low to high frequencies of ROS events and consequent responses in (b) female population size and (c) the proportion of prime-aged (2–8 years old) females, indicating stabilising effects of proportional harvesting (red lines = 0.15, blue lines = no harvesting). (d) Probability of population crashes and (e) probability of quasi-extinction in response to proportional harvesting for low (dotted lines), medium (dashed lines) and high (solid lines) frequencies of bad winters

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 (Barbraud & Weimerskirch, 2003; Coulson et al., 2001, 2004; Ferguson & Ponciano, 2015; Gamelon et al., 2017; Hansen et al., 2019; Lima et al., 2006; Owen-Smith, 2000; Royama, 1992; Stenseth et al., 2004) as well as our comparative analysis in six ungulate species (Figure 3) clearly indicate that, in seasonal, resource-limited systems, climate-density interactions in population dynamics are far more common than previously acknowledged. Therefore, harvesting will often modify the effects

of density-dependent environmental stochasticity on population dynamics. By avoiding overabundant populations, managers could even buffer population crashes induced by stochastic extreme events that affect individual fitness through resource competition. Accordingly, sustainable levels of harvesting can serve as a management (and even conservation) strategy to weaken negative effects of increased climate variability and extreme events (e.g. flooding, drought, storms) anticipated under global climate change (Diffenbaugh et al., 2017; Fischer & Knutti, 2015). The sustainability of implementing harvesting as a strategy to stabilise population dynamics and avoid population crashes will, however, depend on,

for example the strength of density-dependent versus density-independent environmental effects, the implemented harvest strategy and the frequency and magnitude of stochastic climate perturbations.

Thus, the stabilising effect of harvesting outlined here will not apply to all species or under all circumstances. For one thing, population resistance to environmental perturbations and implications of harvesting depend on the species' life-history strategy. Moreover, density-independent stochastic mechanisms (Lande et al., 2003; May et al., 1978), as well as ecological and evolutionary consequences of selective harvesting (Anderson et al., 2008; Leclerc et al., 2017; Pigeon et al., 2016), 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). Autocorrelation and seasonal variation in the strengths of density-dependent versus density-independent environmental variance may also complicate the stabilising effects of harvesting. Nevertheless, our discrete-time logistic models are approximate for systems, such as many ungulate populations, where harvesting reduces population density just before natural population changes are driven by density dependence and environmental stochasticity. Stabilising effects of harvesting under climate-density interactions likely occur in resource-limited systems with strong compensatory responses among survivors of harvesting (Boyce et al., 1999; Jonzén & Lundberg, 1999). Such buffering effects of harvesting could explain why climate-density interactions seem to be 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 resource exploitation requires a better understanding of the potential interactions of climate, internal population regulation and harvesting strategies.

COMPETING INTERESTS

The authors declare no competing interests.

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AUTHORSHIP

B.P., B.B.H. and V.G. designed the study and developed the conceptual ideas with contributions from M.G., V.V., B.-E.S. and J.M.F.; V.G., B.P., A.M.L. and S.E. developed the theoretical models. B.P. and V.G. tested the theoretical models on empirical population data and harvest simulations. B.P. and M.G. performed analyses on the demographic model of Svalbard reindeer with significant contributions of B.B.H., V.G., V.V. and A.M.L.; S.A., L.E.L. and V.V. collected the Svalbard reindeer data. B.P. created visual presentations of the results and wrote the original manuscript. All co-authors reviewed the final manuscript.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The code and data used to produce the results are archived and available on <https://doi.org/10.5281/zenodo.5803067>.

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