

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

3

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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).

74 Population-dynamic models generally predict that harvesting can magnify population
75 fluctuations induced by environmental stochasticity, and thereby increase the risk of
76 extinction (Beddington & May 1977; Lande *et al.* 1995; Lande *et al.* 2003; Hsieh *et al.* 2006;
77 Anderson *et al.* 2008; Fryxell *et al.* 2010; Gamelon *et al.* 2019). This can occur, for instance,
78 due to lagged responses in harvest efforts to population changes (Fryxell *et al.* 2010) or
79 increased environmental sensitivity in age-truncated populations following size-selective
80 harvesting (Hsieh *et al.* 2006; Anderson *et al.* 2008). On the other hand, May and colleagues
81 (May *et al.* 1978) hypothesized that, in species with chaotic (i.e. irregular) population
82 fluctuations, reducing population density through harvesting can result in less variable
83 population trajectories by damping the density-dependent effects of environmental
84 stochasticity. Theoretical and empirical evidence across taxa now indicate that population
85 dynamics are often characterized by nonlinear amplifications of environmental stochasticity
86 caused by intrinsic processes such as density dependence (Royama 1992; Coulson *et al.*
87 2001; Barbraud & Weimerskirch 2003; Coulson *et al.* 2004; Stenseth *et al.* 2004; Hsieh *et al.*
88 2005; Lima *et al.* 2006; Anderson *et al.* 2008; Ferguson & Ponciano 2015; Gamelon *et al.*
89 2017; Hansen *et al.* 2019).

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

99 unstable dynamics and population crashes when prolonged periods of favorable conditions
100 lead to high density and high proportions of vulnerable age classes (Festa-Bianchet *et al.*
101 2003), causing amplified demographic responses to environmental perturbations, such as
102 extreme weather events (Wilmers *et al.* 2007; Ferguson & Ponciano 2015; Hansen *et al.*
103 2019). Intuitively, strong climate-density interactions would predict that harvesting – which,
104 by definition, reduces density – can weaken impacts of environmental perturbations with
105 density-dependent effects on population dynamics. Here, we use simulations from theoretical
106 and empirically parameterized, stochastic population models to show that harvesting can
107 indeed modify the climate-density interaction effects on resource limitation, leading to
108 increased population stability and resistance to environmental perturbations.

109

110 Results and discussion

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

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

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

140

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

149 population model for wild Svalbard reindeer (*Rangifer tarandus platyrhynchus*) (Fig. 4a; see
150 'Reindeer as a case-study' section in Materials and Methods for details). In this predator-free
151 reindeer population in the high Arctic, age- and density-dependent effects of winter weather
152 conditions – notably rain-on-snow (ROS) events creating ice-locked winter pastures – cause
153 large interannual variation in survival, fecundity and population size (Lee *et al.* 2015).
154 Individuals are particularly prone to starvation when ROS events occur at high population
155 density (cf. Fig. 1) and reindeer aggregate in the few feeding patches that are accessible (Fig.
156 4a). Due to the interactive effects of weather, density and age structure, the observed (Peeters
157 *et al.* 2019) and anticipated (Bintanja & Andry 2017) increase in the frequency of ROS under
158 climate warming cause counterintuitive changes in population fluctuations, with more stable
159 dynamics expected for high frequencies of extreme ROS events (Hansen *et al.* 2019).

160 As expected from our general model (Fig. 3), we found that harvesting reduced
161 fluctuations in reindeer age structure and damped the temporal variation in population growth
162 rates (Figs. 4b-d, S4a). By decreasing the population density before the onset of winter,
163 harvesting weakened the negative effect of stochastic ROS events on vital rates. These
164 demographic effects of harvesting reduced the probability of a population crash (Fig. 4e) and,
165 therefore, the risk of climate-induced quasi-extinctions (Fig. 4f). Our empirical-based
166 analysis thus confirmed our prediction that, under strong climate-density interactions,
167 harvesting can stabilize population dynamics by buffering negative effects of weather
168 conditions. While these impacts on stability were evident even at very low harvest
169 proportions (< 0.05), the effects on the long-term average population size was negligible up
170 to a harvest proportion of ca. 0.15 (Fig. S4b). Unsurprisingly, increasing harvest proportions
171 beyond this level would eventually lead to increased risk of quasi-extinction as populations
172 take longer to recover from environmental disturbances and harvesting (Beddington & May
173 1977; Lande *et al.* 1995). Overall, the sustainability of harvesting as a strategy to stabilize

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

176

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

191 The stabilizing processes outlined here will not apply to all species or under all
192 circumstances. For one, population resistance to environmental perturbations and the
193 implications of harvesting depend on the species' life history strategy (Fig. 3). Moreover,
194 density-independent stochastic mechanisms (Figs. S1, S2) (May *et al.* 1978; Lande *et al.*
195 2003), as well as ecological and evolutionary consequences of selective harvesting (Anderson
196 *et al.* 2008; Pigeon *et al.* 2016; Leclerc *et al.* 2017), can make populations more sensitive to
197 temporal variation in the environment (Gamelon *et al.* 2019). Population resistance to
198 environmental perturbations also depends on the harvesting strategy (Beddington & May

199 1977; Lande *et al.* 1995) and stochasticity in harvesting processes (Jonzén *et al.* 2002),
 200 sometimes causing lagged responses in effort and quota regulations to resource fluctuations
 201 (Fryxell *et al.* 2010). Nevertheless, stabilizing effects of harvesting under climate-density
 202 interactions likely occur in resource-limited systems with strong compensatory responses
 203 among survivors of harvesting, i.e. where the immediate reduction in resource competition
 204 due to harvesting leads to increased natural survival, fecundity, and overall fitness (Boyce *et*
 205 *al.* 1999; Jonzén & Lundberg 1999). Such buffering effects of harvesting could explain why
 206 climate-density interactions are more evident in populations with no (or very low) harvesting
 207 than in heavily harvested populations (Tveraa *et al.* 2007). Thus, our study highlights that,
 208 especially in the context of global warming, the future sustainability of wildlife resources
 209 requires a better understanding of the potential interactions of climate, internal population
 210 regulation, and harvesting strategies.

211

212 Materials and Methods

213 **Model properties**

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

$$215 \quad r_t = \beta_0 - N_t \beta_1, \quad [1]$$

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

$$219 \quad r_t = \beta_0 - N_t \beta_1 + \gamma_a Z_{a,t}, \quad [2a]$$

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

223
$$\text{Var}[r_t] = \gamma_a^2 \tag{2b}$$

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

227
$$r_t = \beta_0 - N_t \exp(\ln(\beta_1) + \gamma_m Z_{m,t}), \tag{3a}$$

228 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
 229 multiplicative environmental variation. The growth rate then has an environmental variance
 230 depending on N_t ,

231
$$\text{Var}[r_t \vee N_t] = N_t^2 \exp(2 \ln(\beta_1) + \gamma_m^2) (\exp(\gamma_m^2) - 1), \tag{3b}$$

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

234
$$r_t = \beta_0 - N_t \exp(\ln(\beta_1) + \gamma_m Z_{m,t}) + \gamma_a Z_{a,t}. \tag{4a}$$

235 The variance in growth rate then depends on the correlation ρ_Z between the random variables
 236 $Z_{a,t}$ and $Z_{m,t}$, leading to the following equation:

237
$$\text{Var}[r_t \vee N_t] = \gamma_a^2 + N_t^2 \exp(2 \ln(\beta_1) + \gamma_m^2) (\exp(\gamma_m^2) - 1) - 2 N_t \gamma_a \gamma_m \rho_Z \exp(\ln(\beta_1) + \gamma_m^2 / 2). \tag{4b}$$

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

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

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

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

$$254 \quad H_t = pN_t \quad [5]$$

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

$$256 \quad r_t = \beta_0 - (N_t - H_t) \exp(\ln(\beta_1) + \gamma_m Z_{m,t}) + \gamma_a Z_{a,t} \quad [6]$$

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

$$259 \quad N_{t+1} = (N_t - H_t) e^{r_t} \quad [7]$$

260 We simulated populations trajectories of 1,000 timesteps for β_0 ranging from 0.2 to
 261 2.0, and harvest proportions ranging from 0 to 0.25. Note that the effect of γ_m and ρ_z (Eq. 3b,
 262 4b), and therefore the variance in r_t , depended on N_t . We therefore optimized these
 263 parameters for given sets of β_0 , β_1 and $\text{Var}[r_t \vee N_t = K]_{noharvest}$, i.e. the variance in r_t for
 264 populations at their carrying capacity in the absence of harvesting. For each set of parameters,
 265 we calculated quasi-extinction probabilities as the proportion of 1,000 simulated population
 266 trajectories with $N_t < K/5$ at least once during 1,000 timesteps.

267

268 **Reindeer as a case-study**

269 **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 $RO S'_t = RO S_t \times e^{k \times N_{posthunt,t}}$, 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 (
334 $F_{0,t} = 0$) as Svalbard reindeer reach maturity during their second year of life, at the earliest.
335 Assuming a balanced sex-ratio (0.5), the total number of female calves was again modelled
336 using a binomial process. The total population size in year $t+1$ was then simply calculated by
337 taking the sum of the modelled number of individuals over all ages.

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

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

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384

385 References

386

387 1.

388 Albon, S.D., Irvine, R.J., Halvorsen, O., Langvatn, R., Loe, L.E., Ropstad, E. *et al.* (2017).
389 Contrasting effects of summer and winter warming on body mass explain population
390 dynamics in a food-limited Arctic herbivore. *Glob. Change Biol.*, 23, 1374-1389.

391 2.

392 Albon, S.D., Stien, A., Irvine, R.J., Langvatn, R., Ropstad, E. & Halvorsen, O. (2002). The
393 role of parasites in the dynamics of a reindeer population. *Proc. R. Soc. B*, 269, 1625-
394 1632.

395 3.

396 Anderson, C.N.K., Hsieh, C.-H., Sandin, S.A., Hewitt, R., Hollowed, A., Beddington, J. *et al.*
397 (2008). Why fishing magnifies fluctuations in fish abundance. *Nature*, 452, 835-839.

398 4.

399 Barbraud, C. & Weimerskirch, H. (2003). Climate and density shape population dynamics of
400 a marine top predator. *Proc. R. Soc. B*, 270, 2111-2116.

401 5.

402 Beddington, J.R. & May, R.M. (1977). Harvesting natural populations in a randomly
403 fluctuating environment. *Science*, 197, 463-465.

- 404 6.
405 Bintanja, R. & Andry, O. (2017). Towards a rain-dominated Arctic. *Nat. Clim. Change*, 7,
406 263-267.
- 407 7.
408 Bjørkvoll, E., Lee, A.M., Grøtan, V., Sæther, B.E., Stien, A., Engen, S. *et al.* (2016).
409 Demographic buffering of life histories? Implications of the choice of measurement
410 scale. *Ecology*, 97, 40-47.
- 411 8.
412 Boyce, M.S., Sinclair, A.R.E. & White, G.C. (1999). Seasonal compensation of predation and
413 harvesting. *Oikos*, 87, 419-426.
- 414 9.
415 Brook, B.W., Sodhi, N.S. & Bradshaw, C.J.A. (2008). Synergies among extinction drivers
416 under global change. *Trends in Ecology & Evolution*, 23, 453-460.
- 417 10.
418 Caswell, H. (2001). *Matrix population models: construction, analysis, and interpretation*.
419 Sinauer Associates, Sunderland, Massachusetts.
- 420 11.
421 Coulson, T., Catchpole, E.A., Albon, S.D., Morgan, B.J.T., Pemberton, J.M., Clutton-Brock,
422 T.H. *et al.* (2001). Age, sex, density, winter weather, and population crashes in Soay
423 sheep. *Science*, 292, 1528-1531.
- 424 12.
425 Coulson, T., Rohani, P. & Pascual, M. (2004). Skeletons, noise and population growth: the
426 end of an old debate? *Trends Ecol. Evol.*, 19, 359-364.
- 427 13.
428 Diffenbaugh, N.S., Singh, D., Mankin, J.S., Horton, D.E., Swain, D.L., Touma, D. *et al.*
429 (2017). Quantifying the influence of global warming on unprecedented extreme
430 climate events. *PNAS*, 114, 4881-4886.
- 431 14.
432 Ferguson, J.M. & Ponciano, J.M. (2015). Evidence and implications of higher-order scaling
433 in the environmental variation of animal population growth. *PNAS*, 112, 2782-2787.
- 434 15.
435 Festa-Bianchet, M., Gaillard, J.-M. & Côté, S.D. (2003). Variable age structure and apparent
436 density dependence in survival of adult ungulates. *J. Anim. Ecol.*, 72, 640-649.
- 437 16.
438 Fischer, E.M. & Knutti, R. (2015). Anthropogenic contribution to global occurrence of
439 heavy-precipitation and high-temperature extremes. *Nat. Clim. Change*, 5, 560-564.
- 440 17.
441 Fryxell, J.M., Packer, C., McCann, K., Solberg, E.J. & Sæther, B.-E. (2010). Resource
442 management cycles and the sustainability of harvested wildlife populations. *Science*,
443 328, 903-906.
- 444 18.
445 Gamelon, M., Grøtan, V., Nilsson, A.L.K., Engen, S., Hurrell, J.W., Jerstad, K. *et al.* (2017).
446 Interactions between demography and environmental effects are important
447 determinants of population dynamics. *Sci. Adv.*, 3, e1602298.
- 448 19.
449 Gamelon, M., Sandercock, B.K. & Sæther, B.-E. (2019). Does harvesting amplify
450 environmentally induced population fluctuations over time in marine and terrestrial
451 species? *J. Appl. Ecol.*, 56, 2186– 2194.
- 452 20.

- 453 Hansen, B.B., Aanes, R., Herfindal, I., Kohler, J. & Sæther, B.-E. (2011). Climate, icing, and
454 wild arctic reindeer: past relationships and future prospects. *Ecology*, 92, 1917-1923.
455 21.
- 456 Hansen, B.B., Gamelon, M., Albon, S.D., Lee, A.M., Stien, A., Irvine, R.J. *et al.* (2019).
457 More frequent extreme climate events stabilize reindeer population dynamics. *Nat.*
458 *Commun.*, 10, 1616.
459 22.
- 460 Hsieh, C.-H., Glaser, S.M., Lucas, A.J. & Sugihara, G. (2005). Distinguishing random
461 environmental fluctuations from ecological catastrophes for the North Pacific Ocean.
462 *Nature*, 435, 336-340.
463 23.
- 464 Hsieh, C.-H., Reiss, C.S., Hunter, J.R., Beddington, J.R., May, R.M. & Sugihara, G. (2006).
465 Fishing elevates variability in the abundance of exploited species. *Nature*, 443, 859-
466 862.
467 24.
- 468 Jonzén, N. & Lundberg, P. (1999). Temporally structured density-dependence and population
469 management. *Ann. Zool. Fennici*, 36, 39-44.
470 25.
- 471 Jonzén, N., Ripa, J. & Lundberg, P. (2002). A theory of stochastic harvesting in stochastic
472 environments. *Am. Nat.*, 159, 427-437.
473 26.
- 474 Kohler, J. & Aanes, R. (2004). Effect of winter snow and ground-icing on a Svalbard reindeer
475 population: results of a simple snowpack model. *Arct. Antarct. Alp. Res.*, 36, 333-341.
476 27.
- 477 Kristensen, K., Nielsen, A., Berg, C.W., Skaug, H. & Bell, B.M. (2016). TMB: Automatic
478 differentiation and Laplace approximation. *J. Stat. Softw.*, 70, 1-21.
479 28.
- 480 Lande, R., Engen, S. & Sæther, B.-E. (1995). Optimal harvesting of fluctuating populations
481 with a risk of extinction. *Am. Nat.*, 145, 728-745.
482 29.
- 483 Lande, R., Sæther, B.-E. & Engen, S. (2003). *Stochastic population dynamics in ecology and*
484 *conservation*. Oxford University Press, Oxford.
485 30.
- 486 Leclerc, M., Zedrosser, A. & Pelletier, F. (2017). Harvesting as a potential selective pressure
487 on behavioural traits. *J. Appl. Ecol.*, 54, 1941-1945.
488 31.
- 489 Lee, A.M., Bjørkvoll, E.M., Hansen, B.B., Albon, S.D., Stien, A., Sæther, B.-E. *et al.* (2015).
490 An integrated population model for a long-lived ungulate: more efficient data use with
491 Bayesian methods. *Oikos*, 124, 806-816.
492 32.
- 493 Lima, M., Previtali, M.A. & Meserve, P.L. (2006). Climate and small rodent dynamics in
494 semi-arid Chile: the role of lateral and vertical perturbations and intra-specific
495 processes. *Clim. Res.*, 30, 125-132.
496 33.
- 497 May, R.M., Beddington, J.R., Horwood, J.W. & Shepherd, J.G. (1978). Exploiting natural
498 populations in an uncertain world. *Math. Biosci.*, 42, 219-252.
499 34.
- 500 Miller, F.L. & Gunn, A. (2003). Catastrophic die-off of Peary caribou on the western queen
501 Elizabeth Islands, Canadian High Arctic. *Arctic*, 56, 381-390.
502 35.

503 Nowosad, R.F. (1973). Twinning in reindeer. *J. Mammal.*, 54, 781.
504 36.

505 Owen-Smith, N. (2000). Modeling the population dynamics of a subtropical ungulate in a
506 variable environment: Rain, cold and predators. *Nat. Resour. Model.*, 13, 57-87.
507 37.

508 Peeters, B., Pedersen, Å.Ø., Loe, L.E., Isaksen, K., Veiberg, V., Stien, A. *et al.* (2019).
509 Spatiotemporal patterns of rain-on-snow and basal ice in high Arctic Svalbard:
510 detection of a climate-cryosphere regime shift. *Environ. Res. Lett.*, 14, 015002.
511 38.

512 Pigeon, G., Festa-Bianchet, M., Coltman, D.W. & Pelletier, F. (2016). Intense selective
513 hunting leads to artificial evolution in horn size. *Evol. Appl.*, 9, 521-530.
514 39.

515 R Core Team (2019). R: A language and environment for statistical computing. R Foundation
516 for Statistical Computing Vienna, Austria.
517 40.

518 Reimers, E. (1983). Mortality in Svalbard reindeer. *Holarctic Ecol*, 6, 141-149.
519 41.

520 Ricker, W.E. (1954). Stock and recruitment. *J. Fish. Res. Board Can.*, 11, 559-623.
521 42.

522 Royama, T. (1992). *Analytical population dynamics*. Chapman & Hall, London.
523 43.

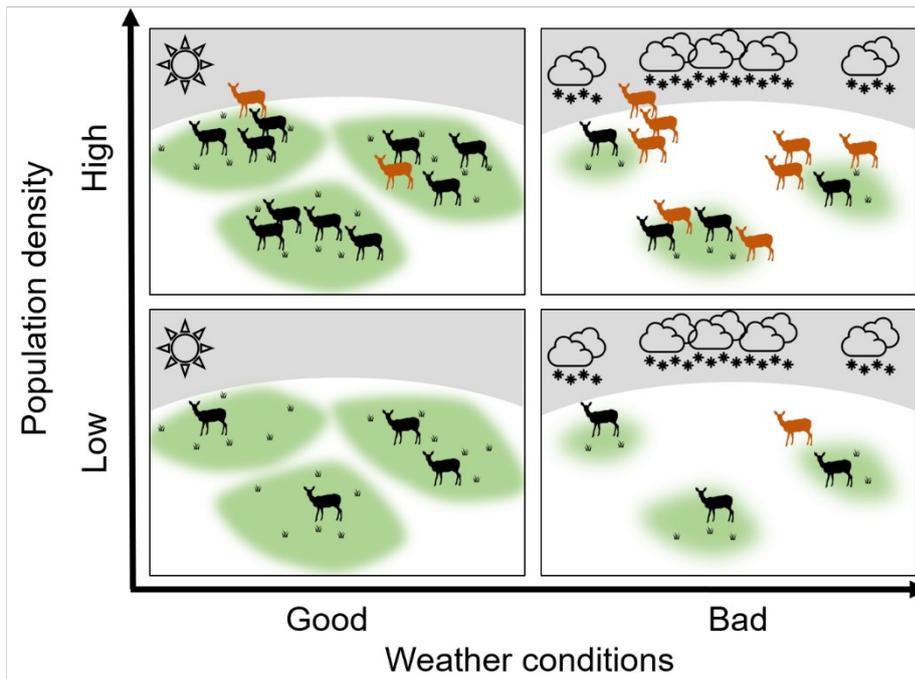
524 Solberg, E.J., Sæther, B.-E., Strand, O. & Loison, A. (1999). Dynamics of a harvested moose
525 population in a variable environment. *J. Anim. Ecol.*, 68, 186-204.
526 44.

527 Stearns, S.C. (1992). *The evolution of life histories*. Oxford University Press, Oxford, UK.
528 45.

529 Stenseth, N.C., Chan, K.S., Tavecchia, G., Coulson, T., Mysterud, A., Clutton-Brock, T. *et*
530 *al.* (2004). Modelling non-additive and nonlinear signals from climatic noise in
531 ecological time series: Soay sheep as an example. *Proc. R. Soc. B*, 271, 1985-1993.
532 46.

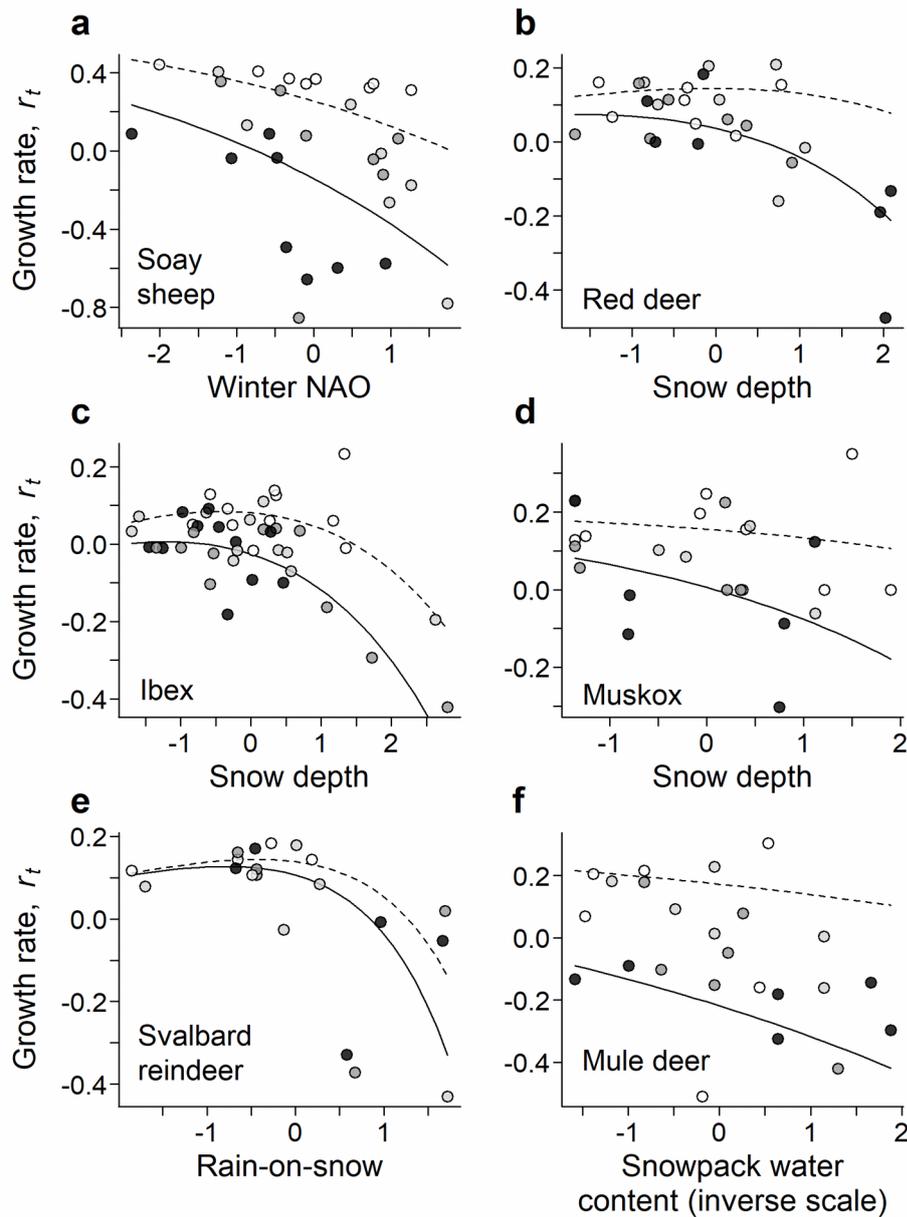
533 Tveraa, T., Fauchald, P., Yoccoz, N.G., Ims, R.A., Aanes, R. & Hogda, K.A. (2007). What
534 regulate and limit reindeer populations in Norway? *Oikos*, 116, 706-715.
535 47.

536 Wilmers, C.C., Post, E. & Hastings, A. (2007). A perfect storm: the combined effects on
537 population fluctuations of autocorrelated environmental noise, age structure, and
538 density dependence. *Am. Nat.*, 169, 673-683.
539



540

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



549

550 **Fig. 2| Climate-density interactions in ungulate populations.** Nonlinear, density-dependent

551 effects of weather on population growth rate (r_t) are found in (a) Soay sheep *Ovis aries*, (b)

552 red deer *Cervus elaphus*, (c) Alpine ibex *Capra ibex*, (d) muskox *Ovibos moschatus*, (e)

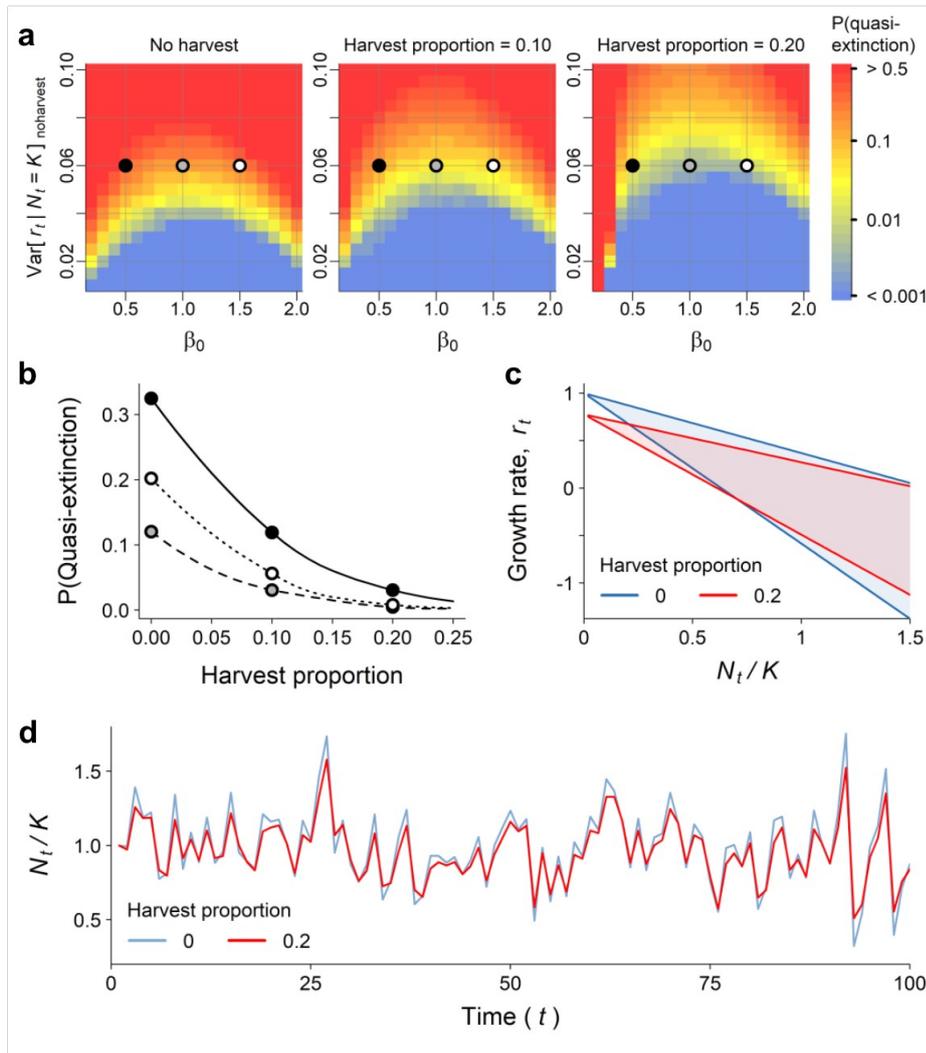
553 Svalbard reindeer *Rangifer tarandus platyrhynchus*, and (f) mule deer *Odocoileus hemionus*

554 (Tables S1, S2). Weather variables were standardized. White to black color gradient of dots

555 indicate low to high observed population sizes, respectively. Predicted responses from a

556 Ricker model of density-dependent population growth are shown for low (mean - 1SD;

557 dashed lines) and high (mean + 1SD; solid lines) population sizes.



558

559 **Fig. 3| Proportional harvesting reduces the density-dependent effect of environmental**

560 **variation. (a)** Quasi-extinction probability for different harvest proportions, maximum

561 growth rates (β_0 , cf. (b) for symbols) and variance in growth rate (shown for populations at

562 their carrying capacity (K) in the absence of harvesting, $\text{Var}[r_t \vee N_t = K]_{\text{noharvest}}$; see ‘Model

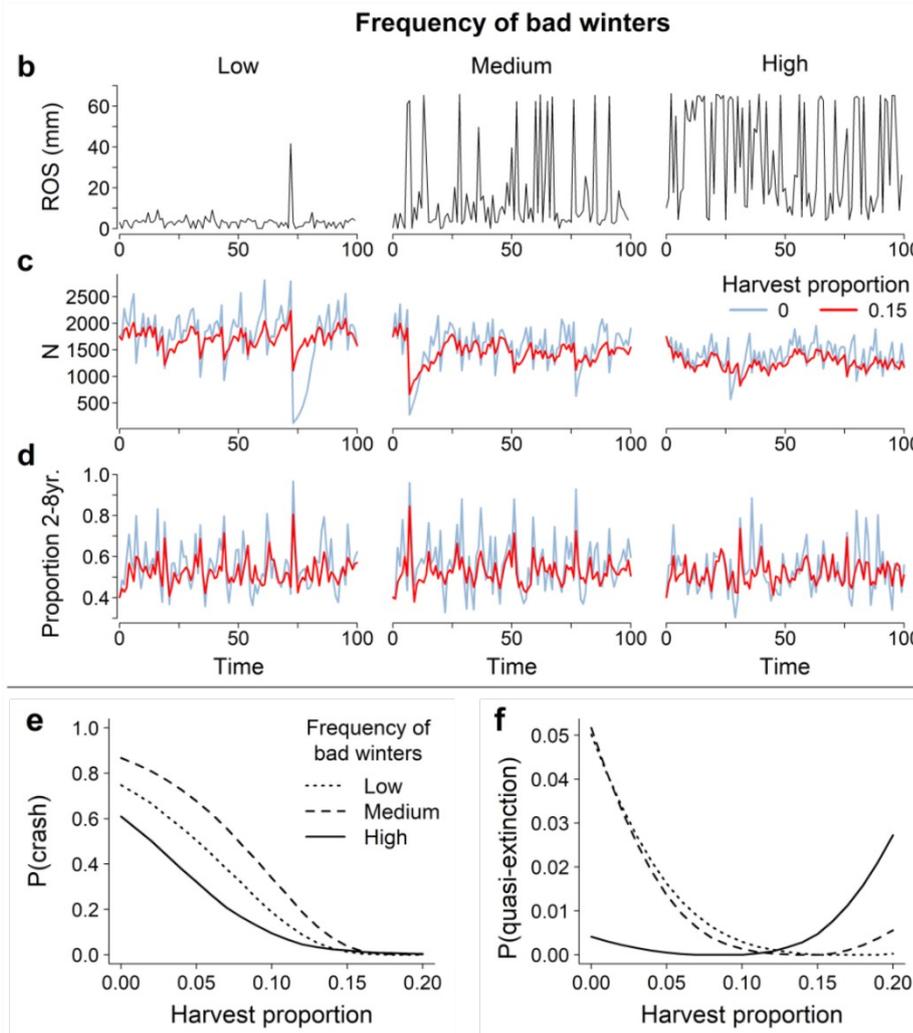
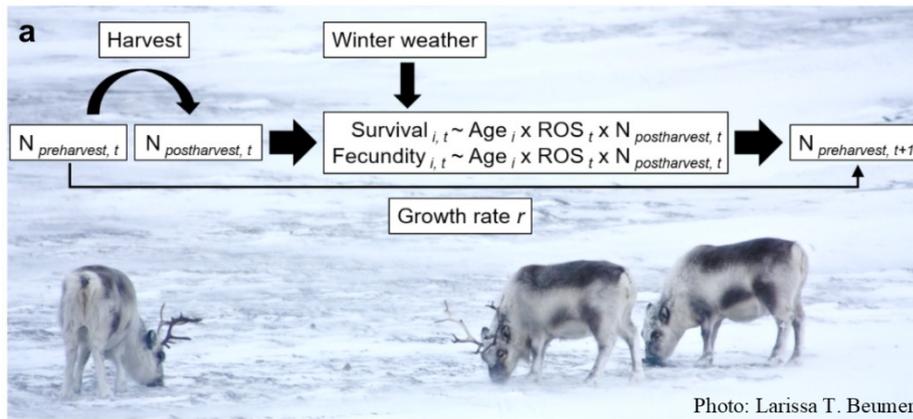
563 properties’ section in the Methods). **(b)** Effect of proportional harvesting on quasi-extinction

564 probability for $\beta_0 = 0.5$ (black dots, solid line), 1.0 (grey dots, dashed line) and 1.5 (white

565 dots, dotted line), at $\text{Var}[r_t \vee N_t = K]_{\text{noharvest}} = 0.06$. **(c)** Change in the distribution of r_t ($\beta_0 =$

566 1.0) as a function of population density (N_t/K) and proportional harvesting (blue = 0, red =

567 0.2). **(d)** Simulated population trajectories using the same parameters as in (c).



568

569 **Fig. 4| Stabilizing effects of harvesting in a climate-driven population of high Arctic**

570 **reindeer. (a)** Schematic view of the population model in Svalbard reindeer. Bad winters

571 correspond to high amounts of rain-on-snow (ROS), causing snowpack icing and restricted

572 access to winter forage. **(b)** Simulated trajectories with low to high frequencies of ROS

573 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.