Paper V

Phase-dependent effect of conservation efforts in cyclically fluctuating populations of Arctic fox (Vulpes lagopus)

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Abstract

Predator populations with demographic cycles driven by multi-annual cycles of their key prey resource can be expected to be "cyclic phase sensitive" to management actions. We explored this by means of modelling in the case of the highly endangered Fennoscandian arctic fox population which is driven by 4-year population cycles in small rodent prey. By using a model in which the management action improved arctic fox vital rate through increased resource availability, we show that arctic fox population growth was most improved when management action was applied in the increase and decrease phase of the cycle. Except in the low phase of the cycle, the growth rate was more affected when the management action worked through improved reproduction than improved survival. There was a synergistic effect to be gained by performing management action during multiple phases during a demographic cycle. Thus we recommend that arctic fox conservation programs ought to be continuous in time, but with the highest intensities of management action in the phases of the cycle in which the target population is most prone to respond.

Key-words: demography, elasticity, synergistic effects, small rodents, red fox, arctic fox

Introduction

Tundra food webs are often characterized by pronounced multi-annual population cycles of small-sized herbivores, such as voles and lemmings (Elton, 1942). These herbivores constitute key prey for many predators restricted to the tundra (Ims and Fuglei, 2005). Due to the high degree of specialization in utilizing cyclic prey, the demography of tundra predators is dependent on the phase of the prey cycle (Angerbjörn et al., 1999; Roth, 2003). When prey availability is high, they respond instantly by increased reproductive output (in particular litter size) resulting in rapidly increasing population size. Such demographic peak years, however, are typically followed by a crash 1-2 years later due to prey density decreasing to very low levels (Tannerfeldt and Angerbjörn, 1998). As a result, these predators often exhibit pronounced cyclic population dynamics that hold the gross signature of the population cycle of their dominant prey (Pitelka et al., 1955; Batzli et al., 1980; Angerbjörn et al., 1995; Wiklund et al., 1999; Gilg et al., 2003; Roth, 2003).

The arctic is currently subject to large changes capable of disrupting the structure and functioning of tundra ecosystems (Fuglei and Ims, 2008). Global warming, with the largest impacts expected in polar areas (Hanssen-Bauer et al., 2005; Gillett et al., 2008), has been highlighted as the major component of ecosystem change in this region (Callaghan et al., 2004a, b). Predators may be particularly sensitive to such changes (Voigt et al., 2003; Ims and Fuglei, 2005; Fuglei and Ims, 2008), especially specialist predators found exclusively in tundra ecosystems where alternative prey are scarce (Fuglei and Ims, 2008). Several specialist predators (e.g. Rough-legged buzzard (*Buteo lagopus*): Kjellen and Roos, 2000; Snowy owl (*Bubo scandiacus*): Marthinsen et al., 2008; Arctic fox (*Vulpes lagopus*): SEFALO, 2004) belonging to Arctic tundra ecosystems are now declining and significant range contractions, in particular in the southern part of their distribution ranges, can be expected (Ims and Fuglei, 2005).

On the Fennoscandian peninsula, which constitutes the south-western fringe of the tundra biome in Eurasia, the arctic fox is already on the verge of extinction (Angerbjörn et al., 1995; Dalén et al., 2006). The decline and range contraction of the Fennoscandian arctic fox have, at least partly, been attributed to dampened peak abundances of cyclically fluctuating vole and lemming populations (Ims and Fuglei, 2005; Henden et al., 2008) and increased interspecific competition with the northward expanding red fox (*Vulpes vulpes*) (Hersteinsson and Macdonald, 1992; Tannerfeldt et al., 2002; Elmhagen, 2003; Ims and Fuglei, 2005; Killengreen et al., 2007). However, several other putative causes of the "Fennoscandian arctic fox problem" have been proposed (Hersteinsson et al., 1989; Hersteinsson and Macdonald, 1992). Several management actions are now being tried in an attempt to reverse the decline of the arctic fox in all of the Fennoscandian countries (Angerbjörn et al., 2007). These involve red fox culling (Norway, Sweden and Finland), supplementary feeding (Sweden) as well as captive breeding with subsequent reintroductions (Norway).

In general, management action aiming to reverse declines of endangered populations ought to explicitly take into account factors that govern demography and temporal dynamics of the population in question (Bradbury et al., 2001). For instance, potentially much can be gained by targeting management action to moments in time when the population is most responsive to any given action. Specifically, for species with pronounced multi-annual population cycles, like the arctic fox, it might be expected that the effect of a management intervention will depend on the particular phase of the demographic cycle. Hence, in this study we analyse, by means of modelling, to what extent demographic perturbations exhibit phase-dependent effects on arctic fox population growth. Based on this analysis we provide recommendations on how management actions could be temporally allocated as to be most effective.

Methods

Modelling framework

We assumed that management effort directed at arctic fox is concentrated in mountain tundra areas of Fennoscandia where population cycles with recurrent moderate to high spring densities of small rodents still prevail, as it is in such regions that the potential for arctic fox recovery would be expected to be highest (Henden et al., 2008).

The current model held essentially the same characteristics as the model framework developed by Henden et al. (2008) for linking arctic fox demography to small rodent population dynamics. Arctic fox was modeled as a resident specialist with temporal variation in vital rates driven by the amount of available rodent prey (Angerbjörn et al., 1999). Cyclic small rodent dynamics was generated from a stochastic second order autoregressive model (i.e. AR[2] model) (Bjørnstad et al., 1995; Stenseth, 1999). In the present analysis we selected AR-coefficients that provided small rodent dynamics with a typical 4-year cycle period. It is important to note that the periodicity in our model is statistical (Henden et al., 2008) and not strictly mathematical. Because of this and the fact we use stochastic small rodent dynamics as the driver of arctic fox demography, we have chosen a numerical as opposed to a strictly periodic matrix model (cf. Caswell and Kaye, 2001; Caswell, 2005). The resultant arctic fox dynamics was obtained from an age-structured demographic model in which yearly matrices of demographic parameters are made dependent on the prevailing rodent density (for more details see Henden et al., 2008). The simulated small rodent dynamics in the present analysis yielded a long-term stochastic growth rate log λ = -0.0096 (i.e. $\log \lambda = \frac{1}{T} \sum_{t=0}^{T-1} r_t$, where T = time span, $r_t = \log(N_{t+1}/N_t)$ (cf. Caswell, 2001)) for the arctic fox (10 000-year realization), when no management action was implemented in the model.

Relationship between management action and arctic fox vital rates

It is well known that vital rates in arctic fox populations are highly dependent on the amount of available natural resources such as small rodents (Tannerfeldt and Angerbjörn, 1998). On the other hand there is still a scarcity of quantitative information in the literature about demographic responses of arctic fox to management perturbation. Here we generally assumed that management action affected population growth rate through increasing the amount of resources available to the arctic fox. Resources in this context may constitute supplementary food or access to resources or habitat that would otherwise be monopolized by the competitively dominant red fox.

Due to the lack of knowledge about how management actions actually work to improve arctic fox vital rates we investigated two contrasting scenarios of increased resource availability resulting from management action (see Figure 1). In a *constant scenario* the amount of resources was set to increase by a constant proportion of the prevailing resource level in the ecosystem (i.e. as determined by the small rodent dynamics). In the other scenario we assumed that management action was most effective at low natural resource levels and that the proportional increase due to the action decreased with increased natural resource levels. This *diminishing return scenario* could, for instance, either result from higher exploitation of artificially supplied food when more preferential natural food sources are scarce or from more effective culling when red fox are attracted to hunters' baits at low natural resource levels. Moreover, to assess the possibility that the magnitude (i.e. proportional increase) of the management induced increase in resource availability may have a disproportional effect on arctic fox growth rate, we simulated and compared three levels of the magnitude of change in the response scenarios (i.e. *diminishing return scenario* (maximum levels): 20%, 50% and 100% , *constant scenario*: 10%, 25% and 50%). Finally,

146 due to uncertainty about which vital rates are most affected by management action we ran the
147 simulations assuming that (1) only reproductive parameters were affected; (2) only survival
148 rates were affected and (3) all vital rates were affected by the management action.
149 A very important feature of the arctic fox model is the logistic functions relating
150 prevailing resource levels (i.e. small rodent density) to arctic fox vital rates (see Henden et
151 al., 2008 for more details). These functions cause the vital rates to respond non-linearly to
152 increased resource availability (Figure 2). Specifically, on the background of low resource
153 levels (and consequently low demographic rates) a given proportional increase in resource
154 availability will result in a larger demographic response than the same proportional increase
155 at high natural resource levels (and higher baseline demographic rate) (see Figure 2).
156
157 **Defining cyclic phases**
158 To be able to pinpoint the management actions to a specific phase of the small rodent cycle
159 (and thus the demographic cycle of the arctic fox), we used a simple, practical rule to predict
160 the next phase (t+1) based on the previous 3-4 years of the dynamics (see Table 1 and S1 in
161 the appendix for more details). Owing to the stochastic nature of the AR[2] model used to
162 generate small rodent dynamics the rule employed for predicting cyclic phases led to a certain
163 frequency of misclassification. Even in empirical time series of small rodent dynamics there
164 is usually a considerable variation around the mean periodicity and amplitude of the cycles
165 (Hanski et al., 1993). In our simulations there was a tendency to over-estimate the frequency
166 of increase and decrease phases (i.e. ~ 0.27) in the underlying small rodent time series as
167 compared to the expected equal frequency of 0.25 for each phase in the 4-year cycle. The
168 effect of management action over 10 000 years is confounded by the number of years in each
169 phase. For instance, if a phase consists of more years, the effect on log λ will be higher and
170 vice versa. In order to correct for this bias we scaled all log λ values according to

$$\log \lambda = \frac{\log \lambda_u}{Freq_{emp}} * Freq_{the} \quad , \quad \text{eqn 1}$$

where *log* λ_u denotes the unscaled growth rates, $Freq_{emp}$ denotes the realized frequency of a specific phase in the small rodent time series and $Freq_{the}$ denotes the expected frequency (i.e. 0.25).

Quantifying the effect of management action: Elasticity analyses

In order to evaluate the effect of management action on the population growth rate of arctic fox, we calculated the phase-dependent empirical elasticity of log λ to management action (referred to hereafter as E_{tot}) following Nichols and Hines (2002, equations 27 and 28):

$$E_{tot} = \frac{\Delta \log \lambda}{\Delta\, Action} = \log \lambda_{managed} - \log \lambda_{non-managed} \quad , \quad \text{eqn. 2}$$

where Δ log λ is the difference in log λ between a managed and a non-managed population. Δ *Action* was here taken as one (i.e. 1 (action) vs. 0 (no action)), but could equally represent the effort of managers in rising resources to a specific level (e.g. a 20% increase) or the unit cost attributed to a specific increase in resource availability (cf. Nichols and Hines, 2002). As mentioned above, the total elasticity of log λ to management action was mediated through increased resources. However, the corresponding effect on the population growth rate was dependent on the ability of arctic fox to convert increased resource availability into increased demographic rates. Thus, E_{tot} could be decomposed into two components:

$$E_{tot} = \frac{\Delta \log \lambda}{\Delta\, Action} = \frac{\Delta \log \lambda}{\Delta\, Res} * \frac{\Delta\, Res}{\Delta\, Action} = E_1 * E_2 \quad , \quad \text{eqn. 3}$$

where Δ *Res* denotes the phase-specific difference in mean resource availability between the managed and non-managed population. Thus, the second component (referred to hereafter as E_2) reflected the ability of management action to raise resources available to arctic fox in a specific phase of the cycle, whereas the first component (referred to hereafter as E_1) represented the phase-specific ability of arctic fox to convert this increase in resource availability into a demographic response (i.e. increased vital rates). Finally, we assessed to what extent management actions in more than one phase per cycle would yield synergistic effects on log λ. Thus, we simulated actions in all combinations of two phases and compared the resulting values of log λ (i.e. synergistic effect) with the sum of Δ log(λ) from the two respective phases as obtained from the single phase simulations (i.e. additive effect).

All simulations were based on a 10 000 year time series to obtain robust measures of the long term stochastic growth rate (cf. Caswell, 2001) of arctic fox.

Results

The elasticity of the growth rate to management action (E_{tot}) was, as expected, highly dependent on the phase of implementation (Figure 3). In general the patterns of phase-specific elasticities were very similar for the two response scenarios; the highest impact of management action was obtained in the increase phase, closely followed by the decrease phase. The main difference in the patterns between the two response scenarios was in the low and peak phase due to a somewhat higher elasticity in low compared to peak phase for the *diminishing return scenario* compared to the *constant scenario*, where the opposite was the case (Figure 3i). In both scenarios the elasticity to management action (E_{tot}) was mainly driven by the phase-specific elasticity of λ to increased resource availability (E_1; Figure 3ii).

219 Simulations quantifying the effect of management actions on reproduction and survival
220 separately showed (for both scenarios) that reproductive output had higher impact on arctic
221 fox growth rate than survival in all phases except in the low phase (Figure 3).

222 Increasing the magnitude of change in resource availability from management action
223 increased, as expected, the elasticity of the growth rate (Table 2), but without changing the
224 phase-specific pattern. The increase in E_{tot} was mainly ruled by the increased resource
225 availability as derived from management action (i.e. E_2). However, at the largest magnitude
226 of increase (i.e. 100% and 50%, respectively) this pattern was slightly counteracted by the
227 reduced ability of increased resource availability to mount a further increase in demographic
228 rates (E_1, Table 2, see also Figure 2), especially in the peak and increase phases of the
229 demographic cycle.

230 There was, generally, a substantial synergistic effect of implementing management
231 action in combinations of two phases per cycle as compared to simply adding the effects over
232 the same two phases as derived from single-phase perturbations (Table 3). There was not
233 much difference in the magnitude of the synergistic effect between the different combinations
234 of phases.

235

236 ## Discussion

237 Although several management actions presently are conducted to reverse the regional decline
238 of the arctic fox in Fennoscandia, no attempt has yet been made to evaluate how these actions
239 could be temporally allocated so as to maximize their impact. Such an evaluation appears to
240 be particularly relevant for populations with pronounced resource driven multi-annual
241 demographic cycles. In such cases the effect of management action could be expected to be
242 "cyclic phase-dependent". Indeed, using a modelling approach we confirmed this
243 expectation. Generally, management action appeared to be most effective when applied in the

244 increase and decrease phase of the cycle. In these phases (and in particular in the increase
245 phase) it was possible through management action to realize some of the intrinsically large
246 reproductive potential possessed by the arctic fox.

247 In lack of specific information about how different management actions specifically
248 affect arctic fox vital rates we assumed a rather generalized demographic response acting
249 through improved resource availability. This assumption seems reasonable since lower
250 resource availability, either owing to dampened small rodent cycles or displacement from
251 high quality habitats by red fox, has been suggested to underlie the most recent decline of the
252 arctic fox in Fennoscandia (Tannerfeldt et al., 2002; Ims and Fuglei, 2005; Henden et al.,
253 2008). Moreover, the fact that the general pattern of the phase-dependent elasticities was
254 relatively unaffected by both the magnitude and the functional aspects of the resource
255 availability released by management action, indicates that the predictions from our model are
256 relatively robust. What appears to be among the most critical aspect of management action,
257 and which is in need of empirical information, is whether any given action acts to improve
258 arctic fox survival and/or reproductive parameters. Our analysis suggests that actions that
259 improve reproductive output usually have the largest effect on arctic fox growth rate. Only in
260 the low phase of the cycle the elasticity of the growth rate was more impacted by improved
261 survival than reproduction. The overall importance of reproductive parameters in the arctic
262 fox capacity for growth is also reflected by the exceptionally high variance in such
263 parameters observed in natural populations (Tannerfeldt and Angerbjörn, 1998; Angerbjörn
264 et al., 2004). Survival rate, in particular in adult age classes, appears to be much less variable
265 (cf. Meijer et al., 2008).

266 Although we have here identified specific phases in the demographic cycle of arctic
267 fox populations in which management efforts are likely to be most effective, we have also
268 highlighted the importance of allocating the efforts over multiple phases. Indeed, as evident

269 from the synergistic effect resulting from combined actions over two phases per cycle there is
270 an extra gain to be obtained by spreading the effort in time. Thus, a general recommendation
271 to be derived from the present study is that management programs should be run as
272 continuously as possible, but with the highest intensity allocated to phases of the
273 demographic cycle in which the arctic fox population is most prone to respond positively to
274 management action. Accordingly, we advise that under low phase actions directed towards
275 increased survival should be prioritized, whereas actions during increase and decrease phases
276 should be directed towards reproduction. More explicit, we suggest that actions aimed at
277 reproductive rates could be focused on the breeding territories during late winter/spring and
278 summer such as supplemental feeding and red fox control, whereas actions aimed at
279 promoting survival should be spread out over time and space. Such a phase-sensitive
280 management strategy should be feasible to implement in most conservation programs. The
281 simple empirical rule we applied for identifying cyclic phases worked well in the framework
282 of the simulated rodent dynamics with a great deal of stochastic variation (Appendix, S1).
283 This was also the case when tested on an empirical time series (Appendix, S1) derived from
284 vole trapping in Kilpisjävri, northern Finland (Henttonen and Wallgren, 2001). Thus,
285 adequately monitored natural rodent populations are likely to provide an equally good basis
286 for identifying phases. Moreover, since arctic fox population dynamics tightly mirrors that of
287 their small rodent prey even monitoring data on the arctic fox population itself could serve as
288 an adequate predictor of the next phase of the demographic cycle. In addition, monitoring
289 arctic fox activity on dens during winter and early spring may provide important updated
290 information on the likely state of the next phase than that derived solely from predictions
291 based on the previous year(s) of small rodent/arctic fox dynamics.
292
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Table 1. Practical rule to predict the next phase of small rodent dynamics from knowledge of the dynamics in the past 4 years. This rule comprises a set of logical statements that in sum will yield the likely next phase of the small rodent dynamics.

Table 2. Phase dependent elasticity of log λ to management action for A) the **Diminishing return scenario** and B) the **Constant scenario**. **Elasticity of λ to resource availability** (E_1) denotes the demographic response of arctic fox to the increase in resource level. **Elasticity of resource availability to management action** (E_2) denotes the ability of management action to raise resource availability for the arctic fox. **Elasticity of λ to management action** (E_{tot}) denotes the overall effect of management perturbation on the population growth rate of arctic fox, where E_{tot} is the product of E_1 and E_2. **Vital rates** denote which set of vital rates are affected by the management perturbation and **Impact** denotes the maximum possible increase in resource availability possible from management perturbation. **Low** denotes the low phase, **Increase** denotes the increase phase, **Peak** denotes the peak phase and **Decrease** denotes the decrease phase of small rodent dynamics when management perturbations are implemented, respectively.

Table 3. The effect on **log(λ)** of management actions implemented in two phases simultaneously during the demographic cycle of arctic fox compared to the additive effect of summing the respective phases from single phase simulations for A) The **Diminishing return scenario** and B) the **Constant scenario**. **Vital rates** denote which set of vital rates are affected by management action. **Effect** denotes the synergistic or additive effect of two phase implementation and **Impact** denotes the magnitude of change in resource availability achievable from management action. The different **Phase** compositions denote which phases are perturbed simultaneously in each simulation.

Figure 1. Two scenarios applied in the analysis linking management action to an increase in resource availability to the arctic fox, depending on the prevailing rodent density. Gray stippled line (i.e. at 1.25) denotes the constant scenario, whereas the black solid line denotes the diminishing return scenario. Horizontal lines at the bottom of the figure depict the range (i.e. 95% of values, between the 0.025 and 0.975 quantiles) of resource density after management action in the respective phases of the demographic cycle of arctic fox for the two response scenarios. The figure represents a simulation with a maximum magnitude of change equal to 50% (i.e. proportional increase of 1.5) for the decreasing scenario and a constant magnitude of 25% for the constant scenario.

Figure 2. Diagram demonstrating how increased resource availability translates nonlinearly to arctic fox vital rates relative to the baseline demographic rates as determined by the prevailing small rodent density. Black solid line denotes the logistic functional relationship linking prevailing small rodent density to arctic fox vital rates. Black filled circles denote two baseline small rodent densities and the gray filled circles denote the corresponding baseline demographic rates. Black arrows denote the same proportional (i.e. 50%) management induced increase in resource availability for the two baseline small rodent densities. Gray arrows denote how this increase in resource availability transfers nonlinearly to increased vital rates of the arctic fox through the logistic curve.

Figure 3. Phase-specific elasticity for panels A) the Diminishing return scenario and B) the Constant scenario. Subplots denote i) Elasticity of λ to management action (i.e. E_{tot}), ii), Elasticity of λ to increased resource availability (i.e. E_1) and iii) Elasticity of increased resource availability to management action (i.e. E_2). The partial contribution from survival and reproductive parameters make up the bars, except for iii) where the elasticity of resource increase to management action is the same irrespective of the set of vital rates simulated. Note that the scale of the y-axis is different between the three plots in each panel, and that elasticities represent simulations with a maximum magnitude of change of 20% (Table 2). Also, the sum of the elasticity of survival and reproductive rates is not exactly equal to the elasticity of all rates, due to the use of numerical versus theoretical elasticities.

Appendix:

S1. Performance of the rule for predicting the next phase of the cycle (see Table 1). A) Simulated (i.e. AR[2]-model generated) time series and B) Kilpisjävri small rodent time series (Henttonen and Wallgren, 2001). Left y-axes and the corresponding black lines denote the prediction of the different phases, whereas the right y-axes and the corresponding red lines denotes the respective time series to be predicted. Filled squares denote the prediction of the specific phases, where red squares denote low, blue denote increase, green denotes peak and black denote decrease phase, respectively.

Table 1.

The set of statements that form the classification rule		
No.	**Statement**	**Next Phase**
1.	If previous year was a peak, and density declines	Decrease phase
2.	If previous year was a peak, and density increases	new Peak phase
3.	If density is declining this year and declined the year before	Low phase
4.	If density increase this year, but decreased the year before	Increase phase
5.	If density increase this year as well as the year before	Peak phase
6.	If density decreases this year, but increased the year before	Decrease phase
7.	If none of the above	Low phase, by default

Table 2.

		Elasticity of λ to resource availability, E_1				Elasticity of resource availability to management action, E_2				Elasticity of λ to management action, E_{tot}			
Vital rates	**Impact**	**Low**	**Increase**	**Peak**	**Decrease**	**Low**	**Increase**	**Peak**	**Decrease**	**Low**	**Increase**	**Peak**	**Decrease**
A) Diminishing return scenario													
All	20%	0.1579	0.2687	0.1991	0.2171	0.1591	0.1319	0.1009	0.1391	0.0251	0.0354	0.0201	0.0302
	50%	0.1763	0.2700	0.1745	0.2287	0.3584	0.3014	0.2346	0.3166	0.0632	0.0814	0.0409	0.0724
	100%	0.2024	0.2576	0.1354	0.2360	0.6214	0.5317	0.4226	0.5560	0.1258	0.1370	0.0572	0.1312
Survival	20%	0.1109	0.0710	0.0146	0.0794	0.1591	0.1319	0.1009	0.1391	0.0176	0.0094	0.0015	0.0110
	50%	0.1065	0.0567	0.0140	0.0657	0.3584	0.3014	0.2346	0.3166	0.0382	0.0171	0.0033	0.0208
	100%	0.0951	0.0431	0.0102	0.0518	0.6214	0.5317	0.4226	0.5560	0.0591	0.0229	0.0043	0.0288
Reproduction	20%	0.0383	0.1974	0.1727	0.1382	0.1591	0.1319	0.1009	0.1391	0.0061	0.0260	0.0174	0.0192
	50%	0.0592	0.2016	0.1521	0.1529	0.3584	0.3014	0.2346	0.3166	0.0212	0.0608	0.0357	0.0484
	100%	0.0875	0.1942	0.1182	0.1640	0.6214	0.5317	0.4226	0.5560	0.0544	0.1032	0.0500	0.0912
B) Constant scenario													
All	10%	0.1537	0.2640	0.1674	0.2190	0.0953	0.0953	0.0953	0.0953	0.0146	0.0252	0.016	0.0209
	25%	0.1685	0.2594	0.1518	0.2225	0.2231	0.2231	0.2231	0.2231	0.0376	0.0579	0.0339	0.0496
	50%	0.1856	0.2507	0.1250	0.2277	0.4055	0.4055	0.4055	0.4055	0.0753	0.1016	0.0507	0.0923
Survival	10%	0.1072	0.0704	0.0104	0.0797	0.0953	0.0953	0.0953	0.0953	0.0102	0.0067	0.0010	0.0076
	25%	0.1083	0.0582	0.0120	0.0678	0.2231	0.2231	0.2231	0.2231	0.0242	0.0130	0.0027	0.0151
	50%	0.1025	0.0472	0.0097	0.0568	0.4055	0.4055	0.4055	0.4055	0.0415	0.0191	0.0039	0.0230
Reproduction	10%	0.0347	0.1976	0.1457	0.1441	0.0953	0.0953	0.0953	0.0953	0.0033	0.0188	0.0139	0.0137
	25%	0.0511	0.1952	0.1327	0.1498	0.2231	0.2231	0.2231	0.2231	0.0114	0.0436	0.0296	0.0334
	50%	0.0703	0.1898	0.1094	0.1578	0.4055	0.4055	0.4055	0.4055	0.0285	0.0770	0.0444	0.0640

Table 3.

A) Diminishing return scenario								
			log (λ)					
Vital rates	**Effect**	**Impact**	**Phase 1& 2**	**Phase 1 & 3**	**Phase 1 & 4**	**Phase 2 & 3**	**Phase 2 & 4**	**Phase 3 & 4**
All	**Synergistic**	20 %	0.0516	0.0366	0.0456	0.0466	0.0548	0.0409
	Additive	20 %	0.0413	0.0260	0.0361	0.0363	0.0464	0.0311
Survival	**Synergistic**	20 %	0.0166	0.0104	0.0185	0.0019	0.0100	0.0037
	Additive	20 %	0.0077	-0.0001	0.0094	-0.0084	0.0011	-0.0067
Reproduction	**Synergistic**	20 %	0.0241	0.0149	0.0165	0.0341	0.0345	0.0267
	Additive	20 %	0.0129	0.0043	0.0061	0.0242	0.0260	0.0174
B) Constant scenario								
All	**Synergistic**	10 %	0.0310	0.0220	0.0263	0.0320	0.0354	0.0273
	Additive	10 %	0.0205	0.0113	0.0163	0.0218	0.0268	0.0176
Survival	**Synergistic**	10 %	0.0070	0.0025	0.0080	-0.0014	0.0039	-0.0005
	Additive	10 %	-0.0023	-0.0854	-0.0014	-0.0115	-0.0049	-0.0106
Reproduction	**Synergistic**	10 %	0.0139	0.0086	0.0082	0.0233	0.0220	0.0177
	Additive	10 %	0.0029	-0.0020	-0.0022	0.0135	0.0133	0.0084

Figure 1.

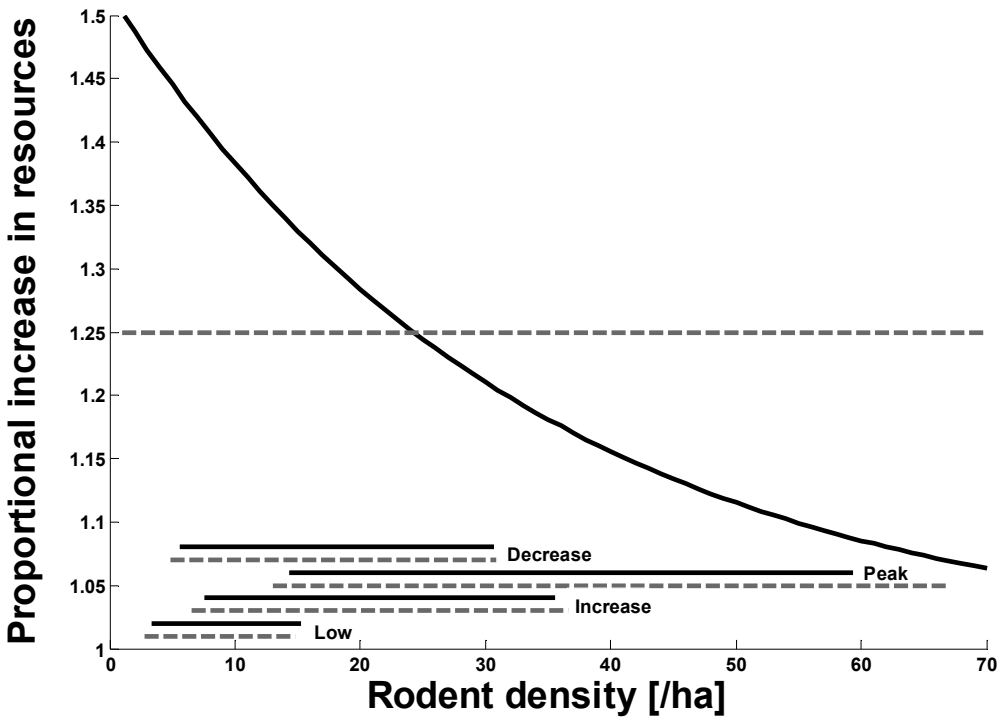

Proportional increase in resources
1.5
1.45
1.4
1.35
1.3
1.25
1.2
1.15
1.1
1.05
1
0
10
20
30
40
50
60
70
Rodent density [/ha]
Decrease
Peak
Increase
Low

Figure 2.

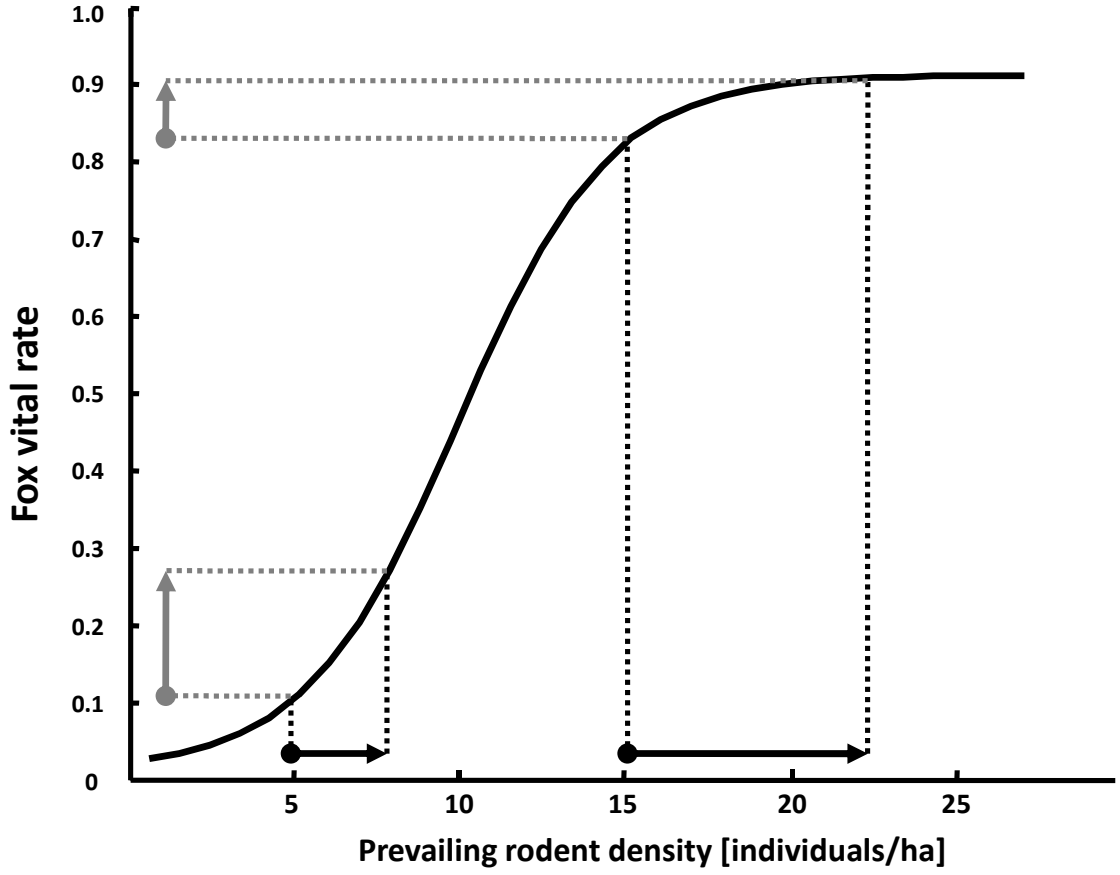
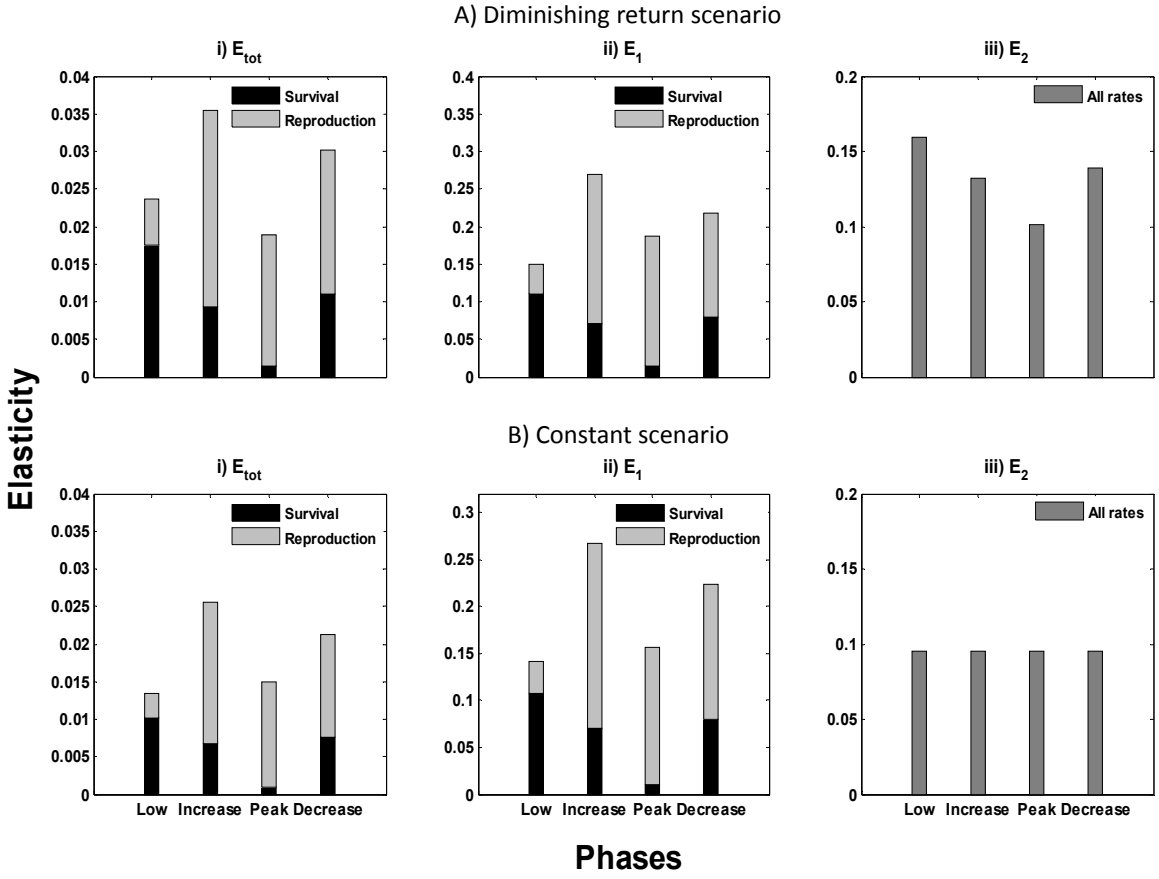
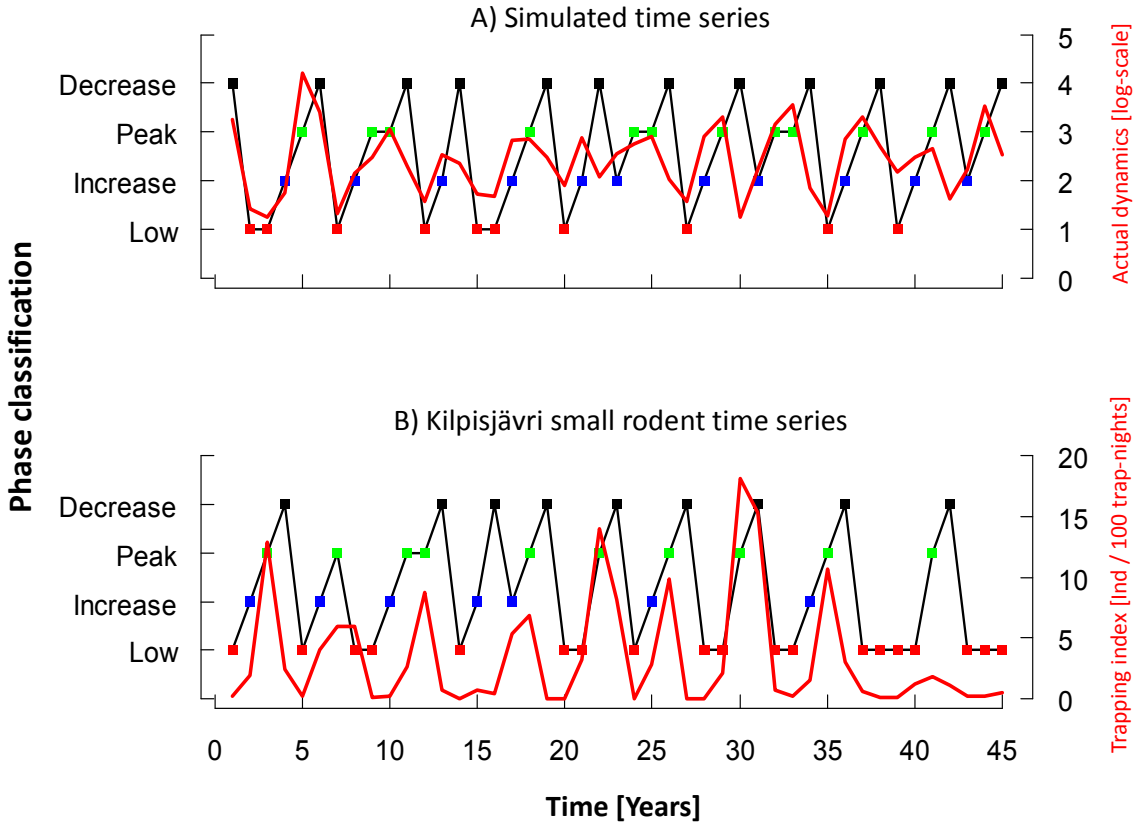

1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Fox vital rate
5
10
15
20
25
Prevailing rodent density [individuals/ha]

Figure 3.


A) Diminishing return scenario
i) E_{tot}
ii) E_1
iii) E_2
Survival
Reproduction
All rates
B) Constant scenario
Elasticity
Low Increase Peak Decrease
Phases

Appendix

S1.


A) Simulated time series
Decrease
Peak
Increase
Low
Actual dynamics [log-scale]
B) Kilpisjävri small rodent time series
Phase classification
Trapping index [Ind / 100 trap-nights]
Time [Years]