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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.

1. Introduction

Tundra food webs are often characterized by pronounced multiannual 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 (Wiklund et al., 1999; 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 rapidly 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 mimic 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 the Arctic (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 belonging to Arctic tundra ecosystems are now declining (e.g. Rough-legged buzzard (*Buteo lagopus*): Kjellen and Roos, 2000; Snowy owl (*Bubo scandiacus*): Marthinsen et al., 2008; arctic fox (*Vulpes lagopus*): Hersteinsson et al., 1989) 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 southwestern 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

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et al., 1989; Hersteinsson and Macdonald, 1992). Three types of management actions are now run in an attempt to reverse the decline of the arctic fox in all of the Fennoscandian countries (Angerbjörn et al., 2007). These are red fox culling (Norway, Sweden and Finland), supplementary feeding (Sweden) and captive breeding with subsequent reintroductions (Norway).

While preliminary empirical results suggests that especially red fox culling and supplementary feeding (which are the two actions that has been run for some time) seem to give positive responses in arctic fox populations (Angerbjörn et al., 2007), there is scope for exploring how the implementation of such actions could be optimized. 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 (Bradbury et al., 2001). For instance, 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.

2. Methods

2.1. 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 and explore how various characteristics of small rodent cycles (such as cycle period, amplitude and mean small rodent abundance) affects arctic fox population growth rate. 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 (Supplementary material). It is important to note that the periodicity in our small rodent model is statistical (Henden et al., 2008) in the sense that a 4-year period is an expectation with variance. Because of the fact that 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 Supplementary material and Henden et al., 2008). The simulated small rodent dynamics in the present analysis yielded a long-term stochastic growth rate $\log \lambda = -0.0096$ (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.

2.2. 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 (Macpherson, 1969; Englund, 1970; Lindström, 1989; Tannerfeldt et al., 1994; Angerbjörn et al., 1995; Tannerfeldt and Angerbjörn, 1998). However, there is still a scarcity of quantitative information in the literature about demographic responses of arctic fox to management action. Here we 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 Fig. 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, due to uncertainty about which vital rates are most affected by management action we ran the simulations assuming that (1) only reproductive parameters were affected;

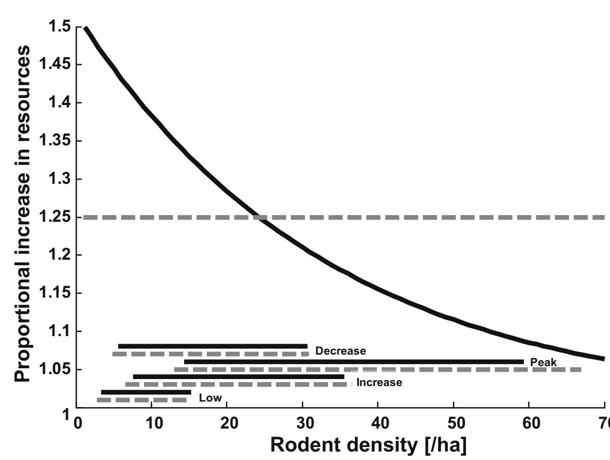

Fig. 1. Two scenarios applied in the analysis linking management action to an increase in resource availability to the arctic fox, depending on the prevailing rodent density. Gray stippled line (i.e. at 1.25) denotes the constant scenario, whereas the black solid line denotes the diminishing return scenario. 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.