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Understanding and forecasting population dynamics in changing arctic ecosystems

A holistic approach to study the effects of environmental changes on arctic populations of management concern

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List of papers

Paper I. Marolla, F., Henden, J.A., Fuglei, E., Pedersen, Å.Ø., Itkin, M., Ims, R.A. (MS). Iterative model predictions for a high-arctic ptarmigan population impacted by rapid climate change. In Review in Global Change Biology.

Paper II: Henden, J.A., Ims, R.A., Yoccoz, N.G., Asbjørnsen, E.J., Stien, A., Mellard, J.P., Tveraa, T., Marolla, F. and Jepsen, J.U., 2020. End-user involvement to improve predictions and management of populations with complex dynamics and multiple drivers. Ecological Applications, p.e02120. doi: 10.1002/eap.2120

Paper III: Marolla, F., Aarvak, T., Øien, I.J., Mellard, J.P., Henden, J.A., Hamel, S., Stien, A., Tveraa, T., Yoccoz, N.G. and Ims, R.A., 2019. Assessing the effect of predator control on an endangered goose population subjected to predator-mediated food web dynamics. Journal of Applied Ecology, 56(5), pp.1245-1255. doi: 10.1111/1365-2664.13346

Paper IV: Marolla, F., Aarvak, T., Hamel, S., Ims, R.A., Kéry, M., Mellard, J.P., Nater, C.R., Schaub, M., Vougioukalou, M., and Yoccoz, N.G. Life cycle analysis of an endangered migratory bird shows no evidence that predator control drove population recovery. Manuscript.

Summary

The current pace of environmental change associated to anthropogenic climate change demands that ecologists improve their understanding of climate impacts on natural systems to provide guidelines for mitigating such impacts. Long-term monitoring data are at the foundation of climate-ecological studies because they allow tracking both fast and slow ecosystem changes. They are also required information for generating forecasts of future ecosystem states, which are increasingly requested by managers and decision-makers. Among the regions of the Earth, the Arctic is one experiencing major environmental changes due to accelerated warming rate. Arctic tundra food webs exhibit complex dynamics in spite of their relatively simple structure, because of the prevalence of tight interactions between trophic levels. Climate change impacts can therefore propagate across food webs and result in non-trivial indirect effects on arctic species and populations. In this thesis, constituted by four papers, I address the general issue of how rapid climate change and other environmental stressors affect the population dynamics of arctic species of management concern. I used a combination of state-of-the-art approaches to test hypotheses on biotic and abiotic drivers of population dynamics of three target species: the Svalbard rock ptarmigan *Lagopus muta hyperborea*, the willow ptarmigan *Lagopus lagopus*, and the lesser white-fronted goose *Anser erythropus*. I based my investigation on long-term time series available for both the study populations and linked ecosystem components. I aimed to infer general ecological mechanisms driving population dynamics of arctic species facing climate change, but also provide recommendations for improved monitoring and management of the study populations. In paper I, I used state-space models to explain population dynamics of the Svalbard rock ptarmigan and generated iterative near-term forecasts of next-year population density. I found that major changes in winter climate in terms of mean temperature seem to have overruled the negative impact of other climate-change related stressors and driven the recent ptarmigan population increase. I also compared the ability of models of different complexity to predict next-year ptarmigan density and observed that more complex models seem to predict abrupt changes in density better than simpler

models. The fact that model predictions improved with more years of data supports the continuation of the ptarmigan monitoring and the forecast assessment in the coming years. I used the same approach in paper II, where I investigated population dynamics of willow ptarmigan in northern Norway. In this case, groups of different stakeholders were involved in a collaborative modelling process through a Strategic Foresight Protocol, and their views about drivers of ptarmigan dynamics were formally integrated in the statistical models. Stakeholders were also interested in having predictions of next-year ptarmigan density to adapt harvest strategies. I found evidence for stakeholders' intuition that climate change affects willow ptarmigan through intensified outbreaks of insect pests, which defoliate birch forests and consequently affect the understory vegetation causing chances in preferred ptarmigan forage. I also found evidence for an effect of delayed onset of winter, which is a key manifestation of climate change and likely leads to enhance predation on ptarmigan due to camouflage mismatch. The results regarding the near-term prediction power of the models were similar to those observed for the Svalbard rock ptarmigan. In papers III and IV, I evaluated the contribution of predator control to the recent recovery of the Fennoscandian population of lesser white-fronted goose, a highly endangered arctic-breeding population that is monitored across its entire range and safeguarded at key staging sites to improve its conservation status. In paper III, I found no evidence that culling of red foxes at the goose breeding sites in northern Norway increased goose reproductive success. The dramatic fluctuations in goose breeding success mirrored the cycles of small rodent populations, which typically drive inter-annual variability in tundra biodiversity through predator functional and numerical response. Moreover, ungulate carrion abundance had a negative impact, likely through numerical response of mesopredators. Red fox culling, however, was expected to also influence the probability that early-failed breeders embark on a long, alternative migration through Western Asia, where hunting mortality is supposed to be higher compared with the regular migration route through Eastern Europe. In paper IV, I parameterized a state-space model describing the life cycle of the goose population and found no evidence that adult survival probabilities differ between the two migration routes. The results suggest that the combination of other management interventions carried out at staging and wintering sites may have contributed to the recent population recovery more than the red fox culling program. Overall, my thesis constitutes a compelling example of how a holistic approach incorporating food web dynamics and relying on ecosystem-wide monitoring data can improve our understanding of the multifaceted impacts of environmental changes and aid the management of populations subjected to rapid climate changes.

1. Introduction

A changing planet, a changing Arctic

After the pre-industrial era, human activities have undoubtedly affected the trajectory of the Earth System, and there is enormous scientific consensus that they constitute the main cause of the environmental changes observed today (Steffen et al., 2018). Human impacts on planet Earth are so strong and pervasive that the geological epoch in which we live has been termed "Anthropocene" (Lewis & Maslin, 2015). Global warming and associated changes in climate patterns represent the unequivocal manifestation of human footprint on the planet. The global mean temperature has already increased by approximately 1°C compared to pre-industrial levels, and the increase will likely exceed 2°C by the end of the century if human greenhouse gas emissions are not dampened (IPCC, 2014).

Anthropogenic climate change affects natural systems in multiple ways and at different levels of biological organization (Bellard, Bertelsmeier, Leadley, Thuiller, & Courchamp, 2012; Parmesan, 2006; Walther et al., 2002). Climate change affects ecosystems not only through changes in average climate conditions, but also through enhanced climate variability, because frequency and intensity of extreme events is predicted to increase (Maxwell et al., 2018). Moreover, climate change interacts with other anthropogenic pressures on ecosystems, such as habitat loss, overharvesting, and introduction of exotic species (Malhi et al., 2020). Environmental changes and associated effects on biota are particularly pronounced in the polar regions (Post et al., 2009), where warming is happening faster than the rest of the world due to a phenomenon referred to as Arctic amplification (Serreze & Barry, 2011). Increasing trends in mean air temperature and precipitations, thawing permafrost, decreasing trends in sea ice extent and thickness as well as snow cover and duration, are indicators of major physical changes occurring in the Arctic (Box et al., 2019). The ecological consequences associated with arctic climate change are numerous. They involve alterations of carbon cycling, nutrient cycling, primary production (tundra greening), plant and animal phenology, frequency/intensity of insect pest outbreaks, and species distribution and dynamics (Box et al., 2019; Ims, Jepsen, Stien, & Yoccoz, 2013). Arctic ecosystems are rapidly moving into previously unseen states. Predicting these novel states requires scientists to abandon established empirical relationships between biotic and abiotic components, and instead look beyond the boundaries of historical variation of arctic ecosystems (Cook, Inayatullah, Burgman, Sutherland, & Wintle, 2014; Evans, 2012).

Population dynamics in arctic tundra food webs

Arctic tundra ecosystems host relatively simple terrestrial food webs compared to boreal and tropical ecosystems (Ims & Fuglei, 2005). Tundra ecosystems exhibit low primary productivity due to restricted plant growth and bacterial activity that ultimately leads to relatively low food web complexity (Callaghan et al., 2004; Oksanen, Fretwell, Arruda, & Niemela, 1981; Oksanen & Oksanen, 2000). Consequently, tundra food webs usually have three trophic levels – plants, herbivores, and predators (Krebs et al., 2003). In spite of this relatively low complexity, food web dynamics can be complex. Strong interspecific interactions between trophic levels dominate in tundra food webs (Ims & Fuglei, 2005). While low primary productivity imposes bottom-up limitations on higher trophic levels, both herbivores and predators can exert a certain degree of top-down control on lower trophic levels (Ims et al., 2019; Ravolainen et al., 2020). Moreover, population cycles are widespread in tundra food webs, causing high variation in species composition and abundance between years, and influencing the functioning of the whole ecosystem (Ims & Fuglei, 2005). The impressive population cycles of small rodents (lemmings and voles), usually constitute the main driving force of this inter-annual variability in tundra biodiversity. They determine dramatic changes in predation patterns by triggering functional and numerical responses in predator populations, causing reproductive success of alternative preys to fluctuate in synchrony with the rodent cycle – the so-called alternative-prey mechanism (Angerbjörn et al., 2013; Gauthier, Bêty, Giroux, & Rochefort, 2004; Ims & Fuglei, 2005; Ims, Jepsen, et al., 2013;

McKinnon, Berteaux, & Bêty, 2014; Summers & Underhill, 2009). Transient dynamics, however, are common even in cycling tundra populations (Henden, Ims, & Yoccoz, 2009). Transient dynamics are persistent dynamics regimes that can last for generations (Hastings et al., 2018) and, in tundra food webs, cause shifts in cycle occurrence, periodicity, amplitude, as well as changes in average population density (Moss & Watson, 2001). Therefore, accounting for biotic interactions and processes is important to understand population dynamics of tundra species and how they will be influenced by environmental changes.

Because environmental impacts on a given species may spread throughout the food web, understanding drivers of population dynamics means considering both direct and indirect effects of environmental changes. While direct effects usually affect species by altering their physical environment, indirect effects modify interspecific interactions within the food web (Ives, 1995; Tylianakis, Didham, Bascompte, & Wardle, 2008). For instance, advanced spring snowmelt and delayed winter onset in the Arctic, on one hand, may be beneficial for herbivores by prolonging the season with high food accessibility (Albon et al., 2017; Tveraa, Stien, Bårdsen, & Fauchald, 2013). On the other hand, it can also cause trophic mismatch with food resources (Post & Forchhammer, 2008) or enhance predation pressure on species that exhibit seasonal coat colour moult due to camouflage mismatch (Zimova et al., 2018). Similarly, extreme weather events such as heavy precipitations during winter causing formation of ground ice can negatively influence herbivores in a direct manner by impeding forage access (Hansen et al., 2014; Stien et al., 2012). However, they may also alter predation patterns by providing the predator/scavenger guild with abundant carrion resources (Eide, Stien, Prestrud, Yoccoz, & Fuglei, 2012), thereby promoting a numerical predator response and consequently higher predation on other prey species (Hansen et al., 2013; Henden et al., 2014). Climate change has also been proposed as the ultimate cause of faltering population cycles of keystone species such as lemmings and voles in some parts of the Arctic (Ims, Yoccoz, & Killengreen, 2011), which implies indirect consequences on several species.

Different life stages or life-history parameters can be influenced by direct effects of climate and environmental change, and then act as mediators of indirect effects on population dynamics. This often implies a time lag in the observed response in population dynamics. For instance, ungulate body mass is sensitive to the timing of spring onset (Tveraa et al., 2013) and affects survival and fecundity (Gaillard, Festa-Bianchet, Yoccoz, Loison, & Toigo, 2000). Therefore, changes in timing of spring onset may affect crucial vital rates at a later stage through direct effects on key life-history traits, such as body mass. Considering factors that may display delayed effects is thus fundamental when studying population dynamics.

Iterative forecasting to aid wildlife management

Under the current global environmental changes, sustainable management of wildlife populations increasingly demands ecologists to generate not only novel knowledge about target ecosystems and populations, but also predictions of future ecosystem and population states (Petchey et al., 2015). Predicting long-term effects of climate and environmental changes, however, is a challenging task (Beckage, Gross, & Kauffman, 2011; Planque, 2016). Long-term predictions are generally affected by large uncertainty (Petchey et al., 2015). The multidecadal time scale at which ecological forecasting is usually conducted does not allow assessing the accuracy of the predictions by comparison with new empirical observations (Dietze et al., 2018). In addition, long-term predictions do not match the timescale required by environmental decision-making (Dietze et al., 2018).

Generating testable predictions is not a well-established practice in ecology (Houlahan, McKinney, Anderson, & McGill, 2017). Most of the published papers in ecology are stand-alone studies grounding their conclusions on analyses that are never performed more than once (Nichols, Kendall, & Boomer, 2019). Because of the low reproducibility of results, the validity of scientific studies has already been questioned in medical sciences (Ioannidis, 2005) and psychology (Open Science Collaboration, 2015), and there is concern that the same issue may afflict ecology. For these reasons, several ecologists advocate a shift towards an iterative near-term forecasting approach (e.g.

Dietze, 2017; Dietze et al., 2018; Petchey et al., 2015; White et al., 2019). This approach implies routine generation of forecasts of an ecological target, and evaluation of the accuracy of the forecasts by comparing them with new observations as soon as new data is collected.

Testing predictions in light of new data simply reflects the hypothetico-deductive reasoning of the scientific method. The iterative near-term forecasting framework offers multiple benefits: 1) near-term predictions are practical to validate, as opposed to projections far in the future; 2) validation occurs with new data (out-of-sample) rather than the data used to make predictions (in-sample); 3) iterating the process allows more frequent hypothesis testing and thus the science to become more robust; 4) the short timescale is relevant to environmental decision-making and implementation of management policies; and 5) when management actions are involved, it allows iterative evaluation of their efficacy. Therefore, the iterative near-term forecasting framework represents a suitable platform to generate both *explanatory* predictions (to test theories) and *anticipatory* predictions (to describe future scenarios) (Maris et al., 2018). Other disciplines have already benefitted from adopting this approach. Meteorology, for instance, has remarkably improved its forecasting ability over the recent decades (Urban et al., 2016). In ecology, however, only few attempts have been made to establish automated near-term forecasting platforms. They include systems for predicting species richness (Harris, Taylor, & White, 2018), abundance (White et al., 2019), and phenology (Taylor & White, 2020).

That iterative near-term forecasting is yet not common in the context of wildlife management is somewhat surprising, because it constitutes the foundation of the concept of adaptive management (Nichols, Johnson, Williams, Boomer, & Wilson, 2015). Adaptive management was developed to frame the process of decision-making while simultaneously coping with large uncertainties of the future. The concept is not new (Walters, 1986), but it has encountered difficulties to establish in wildlife management. The case of the adaptive waterfowl harvest management in North America is one exception, where comparing >20 years of model-based predictions with observed abundances led to a significant reduction in uncertainty about processes driving mallard population dynamics. At the same time, harvesting strategies have been tuned annually based on weighted projections of population responses from competing models (see Nichols et al., 2019). The North America adaptive waterfowl management is often acknowledged as a successful story, where basic knowledge is generated while the system is actively managed.

The current pace of global environmental changes urges management practices to shift towards approaches that cope with the uncertainty of systems that are moving away from the envelope of historical variation while improving the ability to forecast on a policy-relevant timescale (Dietze et al., 2018). In the Arctic, where food webs are relatively simple but environmental changes are rapid, the iterative near-term forecasting approach may be the way to track future changes and promptly develop adaptation strategies. Because several arctic populations are currently of management or conservation concern (Ims, Ehrich, et al., 2013), developing dynamic forecasting platforms could aid disentangling increasingly complex population dynamics while adjusting management policies.

2. Thesis objectives

This thesis was carried out within the context of SUSTAIN, which was a large project funded by the Norwegian Research Council over the years 2016-2020 that involved several research institutes in Norway. Through a series of case studies across terrestrial, freshwater, and marine ecosystems, SUSTAIN aimed to address the general question of how combined anthropogenic and climatic changes affect different harvested ecosystems, and how management strategies can be improved to ensure sustainable exploitation. SUSTAIN was implemented within the framework of strategic foresight (Cook et al., 2014), a structured process where researchers work in close connection with a user panel of NGOs, decision-makers and stakeholders in the context of adaptive management.

Research questions

In this thesis, I aimed to address the general question of how rapid climate changes, in combination with other environmental drivers, affects dynamics of arctic populations of management and conservation concern. Specifically, I aimed to test hypotheses on potential biotic and abiotic drivers of population dynamics of three target species inhabiting two different ecosystems: the Svalbard rock ptarmigan *Lagopus muta hyperborea*, the willow ptarmigan *Lagopus lagopus*, and the Fennoscandian lesser white-fronted goose *Anser erythropus*. Through these case studies, presented in four papers, I intended to shed light on general ecological mechanisms that are likely to occur also in other regions of the Arctic, while providing specific recommendations for monitoring and management of the study populations.

Three overarching research questions summarize the goals of this thesis:

1. How do biotic and abiotic factors influence dynamics of managed populations in rapidly changing arctic environments?

Biotic interactions and abiotic drivers influence fluctuations in population abundance. Such influences may affect directly the population growth rate, but the effects may also travel across trophic levels and reveal themselves after a certain time lag (Gellner, McCann, & Grayson-Gaito, 2020). Therefore, disentangling drivers of population dynamics and quantifying their relative impact requires accounting for key food web interactions and their potential indirect effects (Barton & Ives, 2014; O'Connor, Emmerson, Crowe, & Donohue, 2013). This is especially important in ecosystems that are experiencing novel climates and thereby major alterations of food web interactions, such as Arctic ecosystems. I addressed this issue by investigating drivers of population dynamics of both Svalbard rock ptarmigan (paper I) and willow ptarmigan (paper II), and the determinants of reproductive success in the Fennoscandian lesser white-fronted goose (paper III). All these species/populations are subject to either harvest or management interventions.

2. How reliably can we forecast population dynamics of harvested species on a near-term temporal scale?

Generating forecasts from competing statistical models on a near-term time scale is today advocated to improve both understanding and management of natural systems (Dietze et al., 2018). The relationship between model complexity and prediction accuracy, however, is not obvious (Gerber & Kendall, 2018). Testing the accuracy of predictions on a regular basis is fundamental to improve models' predictive ability. In papers I and II, I investigated how reliably models of increasing complexity predicted next-year ptarmigan population density. I expected that the inclusion of biotic and abiotic predictors would improve the accuracy of the predictions, and that the prediction error would decrease with the length of the time series.

3. What are the impacts of management actions carried out for species of conservation

concern?

Conservation and management programs are rarely evaluated with respect to their effectiveness (Sutherland, Pullin, Dolman, & Knight, 2004). This is a challenging task especially when the target of a given intervention is a small population, because implementing proper experimental designs to assess the efficacy of the intervention is often impossible (Taylor et al., 2017). Moreover, dynamical ecosystem components may confound the effect of a management action (Angerbjörn et al., 2013). In systems dominated by strong fluctuations in weather patterns and food web interactions such as tundra ecosystems, a holistic approach is therefore required to assess the outcome of management interventions. This issue was mainly addressed in papers III and IV, where I evaluated the effectiveness of a prominent management action implemented to reverse the decline of the Fennoscandian lesser white-fronted goose population. Specifically, I quantified the contribution of 9 years of predator control – in the form of extensive red fox *Vulpes vulpes* culling – to variation in goose reproductive success, while accounting for food web interactions that were likely to constitute key drivers of reproductive success (paper III). Effective management strategies, however, should also rely on information regarding which demographic rates are more likely to be influential on population dynamics (Johnson, Mills, Stephenson, & Wehausen, 2010; Mills, 2007). I built upon the results of paper III to investigate whether the same management action affected the growth rate of the goose population through its influence on the choice of the autumn migration route, i.e. making geese avoid an alternative route where hunting mortality was expected to be high (paper IV).

3. Methods

Study systems

The study systems are located within the arctic tundra. The arctic tundra is the northernmost of earth's biomes and forms a circumpolar belt above the 10-12°C July isotherms, which represent the temperature limit for the development of forest. It appears as a vast treeless landscape that extends northward, up to the edge of the arctic oceans. The transition from continuous forest, however, is gradual, and the southern boundary is not sharp. Owing to its large extent, the tundra biome encompasses a wide range of climatic conditions, with marked latitudinal and longitudinal temperature gradients. Consequently, the arctic tundra biome shows high spatial variation in terms of ecosystem structure, especially vegetation types (Ims, Ehrich, et al., 2013). The five bioclimatic zones identified by the Circumpolar Arctic Vegetation Map (CAVM Team, 2003) can be coarsely reduced to two regions, the low- and high-arctic tundra.

The study system of paper I, the archipelago of Svalbard, belongs to the high-arctic tundra zone (Fig. 1a). The climate of Svalbard, strongly influenced by the warm North Atlantic current, is characterized by low precipitations and relatively mild winters, with average winter temperatures up to 20°C higher than elsewhere at the same latitudes (Ims, Jepsen, et al., 2013). Drier inner areas classified as polar desert give way to areas with relatively high primary production around the outer part of the western fjords, where steep altitudinal gradients are associated to steep gradients in vegetation structure. Dwarf shrubs, grasses, sedges, forbs, and mosses prevail in the deep, most productive valleys. The alpine mountains delimiting these valleys dominate the landscape and typically show sparse vegetation of the type observed in polar deserts (Ims, Jepsen, et al., 2013). The terrestrial food web of Svalbard is among the least complex arctic food webs because it lacks some typical keystone species such as small mammalian herbivores and specialist predators (Ims & Fuglei, 2005). The food web is plant-based with significant external inputs from limnic and marine ecosystems in terms of energy and nutrients (Ims, Jepsen, et al., 2013). Two herbivore species inhabit the archipelago year-round, the Svalbard reindeer *Rangifer tarandus platyrhynchus* and the Svalbard rock ptarmigan, while two herbivore bird species, the barnacle goose *Branta leucopsis* and the pink-footed goose *Anser brachyrhynchus*, are migratory and present only in the summer. The predator/scavenger guild includes the arctic fox *Vulpes lagopus* and the glaucous gull *Larus hyperboreus*, both of which are also linked to marine resources. Migrating passerine and shore bird species contribute to increase species diversity in the summer.

The study systems of papers II to IV corresponds to the northernmost part of Fennoscandia, around the lower boundary of the arctic region, and belongs to the sub- and low-arctic tundra zones (Fig. 1b). The Norwegian county of Finnmark, where the study areas lie, is a large region of approximately 45,000 km^2, with a coast indented by wide fjords. It has marked west-east and coast-inland climatic gradients, with the western and northern parts of the county being warmer and wetter due to the influence of the North Atlantic Current (Hanssen-Bauer, 1999). The steep mountain ranges and deep valleys of western Finnmark, with peaks around 800-1,200 m a.s.l., wane and become gentler towards the east, eventually plunging into the Barents Sea with sudden edges. Mild sloped hills and large plateaus typify the south-central inland part, where the landscape appears more homogenous. The sub-alpine boreal forest that constitutes the forest-tundra transition extends as narrow belts into the valleys of eastern Finnmark (Killengreen et al., 2007), while patches of mountain birch *Betula pubescens* are mostly present along a coastal belt (Bråthen et al., 2007). The low alpine zone is classified as low-shrub tundra (Walker et al., 2005) and is dominated by heath vegetation, such as *Empetrum nigrum* ssp. *hermaphroditum*, *Betula nana* and *Vaccinium* spp., interspersed by patches of mesic and wet vegetation (Bråthen et al., 2007). Grasslands typically dominate river plains (Petit Bon et al., 2020). During the long and dark winter, the tundra persists under a thick cover of ice and snow that melts between early and late June.

The plant-based food web of the sub- and low-arctic tundra of northern Fennoscandia includes emblematic trophic interactions between keystone herbivore species and specialist predators. Several species of small rodents, such as the Norwegian lemming *Lemmus lemmus*, the grey-sided vole *Myodes rufocanus*, and *Microtus* spp., inhabit the Fennoscandian tundra and influence trophic relationships across the whole food web through their population cycles. Rodent cycles in northern Fennoscandia exhibit a periodicity of 4-5 years (Ims & Fuglei, 2005), typically with a high degree of spatial and interspecific synchrony (Stenseth & Ims, 1993). Still, temporal and spatial variation in outbreak amplitude can be considerable (Kleiven, Henden, Ims, & Yoccoz, 2018). Large ungulates (semi-domesticated reindeer *Rangifer tarandus*, moose *Alces alces*) and medium-sized vertebrates (rock and willow ptarmigan, hare *Lepus timidus*) add to the herbivore guild of the Fennoscandia tundra. The semi-domesticated reindeer is the main large ungulate dwelling the region. The native Sámi people manages reindeer herds and maintain seasonal migration patterns, although with stringent spatial restrictions (Hausner, Engen, Brattland, Fauchald, & Root-Bernstein, 2020). Ptarmigan species exhibit population cycles that are linked to those of voles and lemmings (Henden, Ims, Fuglei, & Pedersen, 2017). Mammalian predators include the arctic fox *Alopex lagopus*, the ermine *Mustela ermine*, and the weasel *Mustela nivalis*, which are specialized on rodents and thus their population dynamics mirror those of rodent populations. The snowy owl *Nyctea scandiaca*, the short-eared owl *Asio flammeus*, and the rough-legged buzzard *Buteo lagopus*, also rely heavily on small rodents, while jaeger species (long-tailed jaeger *Stercorarius longicaudus*, parasitic jaeger *Stercorarius parasiticus*, pomarine jaeger *Stercorarius pomarinus*) have a more flexible diet. Several shorebird and goose species migrate up to these latitudes in the summer.

Both study systems have been exhibiting symptoms of climate change impacts in the last decades. In Svalbard, the extent of change is tangible and concerns several aspects of the climate system, including increased annual mean temperature (Nordli, Przybylak, Ogilvie, & Isaksen, 2014) and winter rain (Peeters et al., 2019), decreased snow-cover duration and depth (Descamps et al., 2017), and declined sea ice extent (Dahlke et al., 2020). This has severe effects on all trophic levels (e.g. Hansen et al., 2013; Hansen et al., 2019; Layton-Matthews, Hansen, Grotan, Fuglei, & Loonen, 2019; Ravolainen et al., 2020; Stien et al., 2012; Tombre, Oudman, Shimmings, Griffin, & Prop, 2019). In northern Fennoscandia, earlier onset of spring (Karlsen et al., 2009) and enhanced duration of geometrid moth outbreaks (Jepsen et al., 2013) represent key manifestations of climate change effects. In addition, changes in winter climate have been proposed to cause faltering lemming cycles (Ims, Henden, & Killengreen, 2008; Kausrud et al., 2008).

Fig. 1 – Study systems. a) Bjørndalen valley, Svalbard, June 2017 (©Filippo Marolla). b) Finnmark tundra (©Geir Vie).

Target species

Most of the work in this thesis is based on a food-web approach in the form of conceptual models that predict climate impacts targeted on a given species or population (Ims & Yoccoz, 2017). The target species of paper I is the Svalbard rock ptarmigan (Fig. 2a), an endemic sub-species of the rock ptarmigan inhabiting the high-arctic archipelago of Svalbard year-round. This small herbivore is able to cope with the harsh winter conditions of the Arctic thanks to exceptional morphological, physiological, and behavioural adaptations (Nord & Folkow, 2018). Novel climatic conditions in Svalbard are expected to influence the Svalbard rock ptarmigan (Henden et al., 2017). Moreover, being the most common game species in Svalbard, it is of management concern, although this population appeared to have increased in recent years contrary to other circumpolar ptarmigan populations (Fuglei et al., 2019).

The willow ptarmigan is the target species of paper II (Fig. 2b). Willow ptarmigan populations are renowned for their high-amplitude population cycles (Moss & Watson, 2001), although transient dynamics are common (Fuglei et al., 2019). The willow ptarmigan has a circumpolar distribution in the low- and sub-arctic tundra and is a popular game species across its entire range (Fuglei et al., 2019). Similar to several ptarmigan populations worldwide, willow ptarmigan populations in Norway have recently declined (Fuglei et al., 2019). Both abiotic and biotic mechanisms are thought to have caused the decline, most of which ultimately relate to climate and environmental changes (Henden et al., 2017).

Papers III and IV target a highly endangered migratory bird population, the Fennoscandian population of lesser white-fronted goose (Fig. 2c and d). This goose species is a sub- and low-arctic breeder that overwinters in temperate Eurasia. The Fennoscandian population is the smallest among the lesser white-fronted goose populations and is considered a single management unit (Ruokonen et al., 2004). The dramatic decline experienced by this population during the 20th century dragged it to the brink of extinction, with fewer than 30 individuals estimated in 2008. This resulted in the establishment of a large conservation network involving several countries across the population's range (Ekker & Bø, 2017). The extent of the international cooperation to halt the decline of the population has been remarkable so far (see Vougioukalou, Kazantzidis, & Aarvak, 2017). This has likely contributed to the recent population increase in the last decade, but the specific contributions of the different management actions, implemented both at breeding and staging sites, remains unclear.

Fig. 2 – Study species. a) Male Svalbard rock ptarmigan (paper I. ©Guro Krempig). b) Female willow ptarmigan with a chick (paper II. ©Eivind Flittie Kleiven). c) Female lesser white-fronted goose on the nest in Finnmark (paper III. ©Tomas Aarvak). d) Flying flock of lesser white-fronted geese (paper IV. ©Tomas Aarvak).

Conceptual models of climate and management impact

In all papers, we embraced the food web approach developed by COAT – Climate-ecological Observatory for Arctic Tundra (Ims, Jepsen, et al., 2013). COAT is a long-term, ecosystem-wide monitoring system that targets food webs and their dynamics rather than single species or populations to ease the detection of climate and anthropogenic changes and improve the ability to predict future changes. Based on COAT's experience, we developed case-specific conceptual models describing predicted direct and indirect pathways of climate and human impacts on the target species (Fig. 3). We did not consider food webs in their entirety, but rather targeted key state variables and interactions within food webs, those that were likely to be most affected by climate and/or management. The *a-priori* hypotheses depicted by the conceptual models were then tested with empirical data. Most of the predictors representing environmental state variables and included in the models were indicators of significant climate and ecosystem changes.

In the willow ptarmigan case study (paper II), a Strategic Foresight Protocol (Cook et al., 2014) was used to develop the conceptual food web model (Fig. 3b) while formally integrating the knowledge and needs of stakeholder groups as well as their expectations regarding potential future changes. Hunters association, governmental management authorities, and conservation groups, throughout a series of structured meetings, expressed their interest in developing a data-driven model that could both explain past dynamics of ptarmigan populations and provide near-term forecasts of ptarmigan density. Stakeholder's knowledge about the study system was important to identify potential drivers of both short-term dynamics and long-term negative trends of ptarmigan populations to include in the conceptual model. The aim of the Strategic Foresight Protocol was not only to gain consensus on the impact pathways to include in the model, but also to establish a platform for participatory modelling that could increase the trust between stakeholders and scientists and lead to better management decisions.

In paper III, we used mathematical modelling to derive predictions of indirect food web interactions included in the conceptual model (Fig. 3c). Mathematical modelling provides a framework to explore under which conditions the hypothesized mechanisms in the conceptual model can be observed, and thus provide refined theoretical predictions. We generated theoretical predictions regarding how two resource supplies, small rodents and reindeer carcasses, may affect predation exerted by one main predator, the red fox, on one prey item, the lesser white-fronted goose. Under a set of assumptions based on available knowledge about red fox food preferences and its functional and numerical responses to the resource supplies, we observed the expected patterns, i.e. apparent facilitation by small rodents and apparent competition with reindeer carrion, in agreement with previous predictions (Abrams & Matsuda, 1996; Holt & Bonsall, 2017). Hence, we used the model assumptions and output as support to the hypothesized interactions.

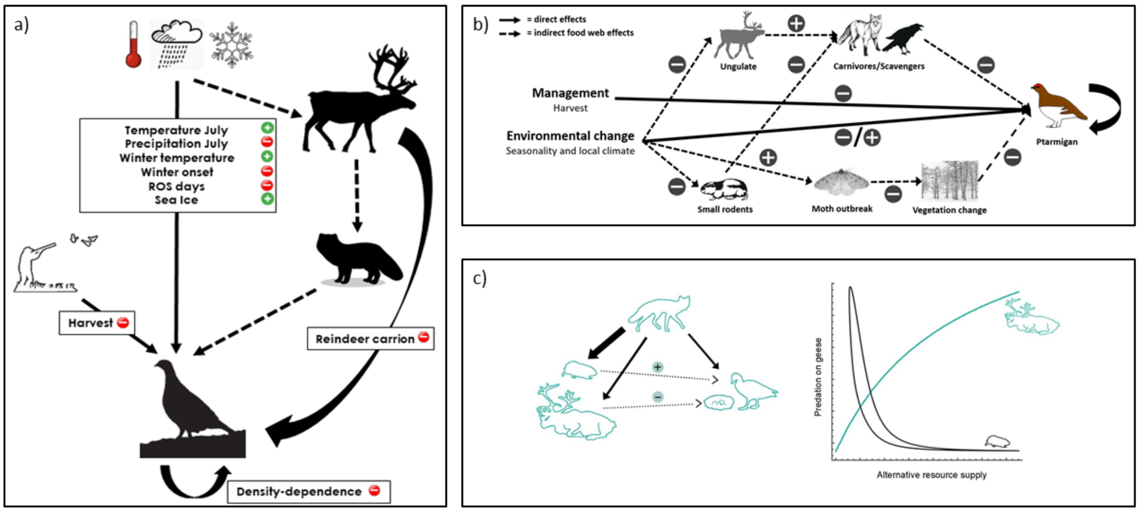

Fig. 3 – Examples of conceptual models depicting potential drivers of dynamics of the target populations; a) Svalbard rock ptarmigan, b) willow ptarmigan, c) lesser white-fronted goose. Solid arrows represent direct impacts while dashed arrows represent indirect effects or pathways. +/- denote the expected direction of the relationship. Each conceptual model was tailored on the specific study case; therefore, the interpretation of the arrows slightly differs among models. In a), expected directions of impacts are placed only on pathways that were parameterized. In b), both direct and indirect impacts were given an expected direction, even if not all the arrows were eventually parameterized. In c), indirect effects were parameterized and thus given an expected direction. The thicker arrow in c) means preference of the predator for that prey when it is abundant. The conceptual model in c) was also supported by mathematical predictions of how alternative resource supplies (rodents and ungulate carrion) influence predation on geese (graph to the right).

Data collection

The time-series data utilized in this thesis comes mostly from the COAT monitoring systems. In Svalbard, the local rock ptarmigan population is monitored by a point-transect distance-sampling design on ptarmigan males displaying territorial behaviour. As of today, the time series spans twenty years. Similarly, the willow ptarmigan in Finnmark is monitored since 2000 by line-transect distance-sampling surveys organized by one major landowner (The Finnmark Estate FeFo) and Hønsfuglportalen (http://honsefugl.nina.no/Innsyn/). State variables monitored under COAT and incorporated in the analyses of papers I and II included small-rodent abundance and moth outbreak intensity (paper I), ungulate carrion abundance (papers I and II), and a set of weather variables measured at local weather stations or generated by interpolated gridded data by the Norwegian Meteorological Institute.

For paper III, we benefitted from a long-term monitoring series on the Fennoscandian lesser white-fronted goose population, which is annually monitored by the Norwegian Ornithological Society (NOF). Individuals are counted and aged at their arrival in northern Norway in the spring. Counts are carried out before and after the breeding period, when the population gathers in a relatively small staging area. To unravel drivers of goose population dynamics, COAT data on small rodent abundance as well as ungulate carrion data were included in the analysis. The goose population is also monitored at several locations along its migration route. In paper IV, we added count data from two major stopovers in Hungary and Greece to the counts performed in northern Norway. This allowed us to describe the life cycle of the population and investigate its demographic structure and dynamics.

Analytical methods

Except for paper III, where we used standard generalized linear models to investigate drivers of breeding success in the Fennoscandian lesser white-fronted goose population, we conducted data analyses in a state-space modelling framework. Below, I briefly describe how this approach was tailored to each case study.

A typical goal of a population dynamics analysis is to estimate population growth rate and identify the environmental drivers influencing it. Typically, however, the exact size of the target population is unknown and only counts associated to a certain, unknown observation error are available. Not accounting for this error in the detection process not only makes it difficult to statistically disentangle drivers of variation in growth rate (Freckleton, Watkinson, Green, & Sutherland, 2006), it can also lead to biased estimates of abundance and growth rate (Hostetler, Sillett, & Marra, 2015). State-space models come in handy because they link the detections resulting from field surveys, i.e. the "observation process" affected by measurement error, to the latent and true state of the population, i.e. the "state process" that represents the population abundance free of observation error (Kéry & Schaub, 2011). A state-space model is a hierarchical model because the observation process is conditional to the state process and the detection error (Royle & Dorazio, 2008). The state-space modelling framework has proved extremely flexible and has been applied to several types of data to address different needs, such as estimating survival (Gimenez et al., 2007; Royle, 2008), state-transition (Lebreton, Nichols, Barker, Pradel, & Spendelow, 2009), or species occurrence and site occupancy (Kéry & Andrew Royle, 2010).

In papers I and II, we developed Hierarchical Distance Sampling models (HDS; Kéry & Royle, 2016) fitted to distance-sampling count data of ptarmigan populations in Svalbard and Finnmark. An HDS model consists of a process model that describes spatiotemporal variation in ptarmigan population density – often but not necessarily as a function of environmental predictors – and a detection model that estimates an average detection probability across survey sites based on the observed distances from the line/point transect. The skeleton of the HDS models developed for the Svalbard rock ptarmigan and the willow ptarmigan in Finnmark was the same. In both cases, the process model consists of two sub-models, one for the first year describing initial density and one for the consecutive years. The latter takes the form of a classic Gompertz population dynamics model, which on the log scale becomes a first-order auto-regressive time-series model (Dennis, Ponciano, Lele, Taper, & Staples, 2006). Hence, environmental predictors must be interpreted as affecting growth rate. The main difference between the Svalbard rock ptarmigan and the willow ptarmigan case concerns the sampling protocol, i.e. line-transect vs point-transect distance sampling, but this does not influence the calculation of the distance-sampling likelihood.

We used the state-space modelling framework also in paper IV, where we parameterized a model describing population dynamics of the Fennoscandian lesser white-fronted goose throughout its annual cycle to estimate age-specific transition probabilities and population growth rate. The modelling approach is part of a set of statistical methods developed to estimate vital rates from counts of aggregated age classes and referred to as "inverse modelling" (González, Martorell, Bolker, & McMahon, 2016). This method allows estimating survival probabilities from unmarked animals, thereby overcoming the issue of handling individuals belonging to endangered populations, which is often not advisable or feasible (Wielgus, Gonzalez-Suarez, Aurioles-Gamboa, & Gerber, 2008). We studied the life cycle of the goose population as it migrates between wintering (Greece), staging (Hungary), and breeding sites (Norway). In the state-space model, age-specific abundances at each stopover location are modelled as latent variables that generate the observed counts and that are described by stochastic processes to account for demographic stochasticity.

All state-space models were analysed in a Bayesian framework. Hierarchical models developed under a Bayesian framework have become increasingly common in ecology (Tenan, O'Hara, Hendriks, & Tavecchia, 2014). The Bayesian framework, in fact, has proved particularly convenient when the goal is estimating parameters that lie at intermediate level in a hierarchical model, or latent variables (Dorazio, 2015). The degree of complexity of a model that can be achieved by Bayesian methods is rather high. They allow, for instance, the combination of information from different types of dataset in the so-called integrated population models to improve parameter estimates (Schaub & Abadi, 2010).

A motivation behind the choice of the Bayesian framework was that it is suited for the implementation of the near-term forecasting approach. An important technical aspect of the approach is that novel knowledge about parameters should be included when analyses are iterated in light of new data. Because the Bayesian framework welcomes prior information about parameters in the form of prior distributions and starting values that initiate the MCMC chains, it constitutes an ideal environment to generate near-term anticipatory predictions that can be updated as new data are collected. We used this approach in papers I and II to test the accuracy of predictions of next-year ptarmigan population densities.

4. Results and discussion

1. How do biotic and abiotic factors influence dynamics of managed populations in rapidly changing arctic environments?

Through a series of study cases analyzed in papers I to III, we gathered evidence about effects of climate and environmental changes on three arctic populations subjected to management. In paper I, we related the recent increasing trend in the Svalbard rock ptarmigan population to major changes in winter climate, especially with respect to temperature. In the last 50 years, mean winter temperature has remarkably increased in Svalbard by 3-5°C (Hanssen-Bauer et al., 2019). To ensure thermal insulation and energy store during the inclement arctic winter, ptarmigan accumulate body fats that can exceed 30% of their body mass at the onset of winter (Grammeltvedt & Steen, 1978; Mortensen, Unander, Kolstad, & Blix, 1983). The strong positive effect of mean winter temperature on population growth rate supports the hypothesis that warmer winters reduce the energy consumption needed for thermoregulation, suggesting it improved body condition throughout winter and ultimately increased survival and recruitment. This result, however, must be interpreted with caution, owing to potential confounding between mean winter temperature and effects of harvest and density dependence. We also found support for a negative effect of rain-on-snow (ROS) events, likely through formation of ground ice that hinders access to vegetation. Although this effect is consistent with several prior studies (e.g. Hansen et al., 2013; Hansen et al., 2019; Stien et al., 2012), the most recent winters in Svalbard have been so warm that the positive temperature effect appears to have overruled the negative ROS effect. Overall, the results of paper I suggest that winter is the season when crucial changes influencing the Svalbard ptarmigan population dynamics occur.

The target species of papers II and III, the willow ptarmigan and the lesser white-fronted goose, belong to the sub/low-arctic tundra and are therefore exposed to a different environment with different food web interactions. As expected based on previous findings from several tundra ecosystems, we found that both willow ptarmigan dynamics and goose breeding success in northern Norway were positively influenced by the cyclic dynamics of sympatric rodent populations. The synchrony between rodent cycles and goose reproductive performance was exceptionally strong and temporally consistent, causing dramatic annual variation in the number of fledglings produced by each goose breeding pair. Because climate change appears to affect the temporal consistency of rodent cycles (Kausrud et al., 2008), this result suggests that the goose population may suffer from increasingly irregular cycles in the future (Nolet et al., 2013). With respect to the willow ptarmigan, we found support for previously documented effects, such as the negative impact of inclement weather conditions on early chick survival, as well as novel effects. Particularly interesting were the negative effects of insect pest outbreaks and winter onset. Outbreaks of insect pest such as geometrid moths defoliate birch forests and appear to cause shifts from shrub to grass in the understory vegetation (Jepsen et al., 2013), depriving ptarmigan of preferred forage. Moreover, increasingly late onset of snow cover in autumn appears to imply camouflage mismatch at the time of ptarmigan moulting, resulting in increased predation rates. This mechanism is supported by prior studies (Melin, Mehtatalo, Helle, Ikonen, & Packalen, 2020; Zimova, Mills, & Nowak, 2016), but there was no evidence supporting it in the case of the Svalbard rock ptarmigan (paper I). The lack of predators such as raptors that use vision to search for prey in Svalbard may explain this lack of evidence.

Eventually, in all these three papers, we were interested in investigating the potential indirect effect of abundant ungulate carrion. In northern Fennoscandia, ungulate carrion, especially reindeer, subsidizes a guild of generalist predators (Henden et al., 2014). In Svalbard, reindeer constitute a significant part of the diet of the arctic fox (Eide et al., 2012). In both systems, reindeer populations have been increasing (Le Moullec, Pedersen, Stien, Rosvold, & Hansen, 2019; Tveraa, Stien, Broseth, & Yoccoz, 2014), resulting in high availability of carcasses in some years. The numerical response of predators to increased carrion availability is predicted to have a negative effect on other prey species such as ground-breeding birds (Henden et al., 2014). We found support for this mechanism, as carrion negatively affected the reproductive success of the lesser white-fronted goose (paper III). There was also a weak indication that it affects the growth rate of the Svalbard rock ptarmigan (paper I). Nevertheless, this relationship was reversed in the case of the willow ptarmigan, indicating that more research is needed to disentangle the influence of carrion abundance on ground-breeding birds.

2. How reliably can we forecast population dynamics of harvested species on a near-term temporal scale?

In papers I and II, we used the statistical models developed to describe ptarmigan population dynamics in an iterative near-term forecasting framework to assess the accuracy of model predictions of next-year ptarmigan population density. In both cases, prediction error tended to decrease with the length of the time series. Increasing model's complexity, however, did not clearly improve predictive performances, despite the most complex models performing better in some years (paper II) or displaying greater ability to predict larger changes in next-year population density (paper I). This result was not unexpected given the relative short time series and the poor spatial resolution of some predictors, and the fact that predictions from simpler models can be as good as those from more complex models (Gerber & Kendall, 2018). We considered the models 'good enough' to perform iterative near-term forecasting on a yearly basis for the study populations, but there is certainly scope for improved predictions. With more years of data and better predictors, we could expect to be able to separate good from poor models. This will not only aid the identification of important drivers of ptarmigan dynamics, it may also constitute a tool to adapt harvesting strategies. Hunters and managers that were involved in the Strategic Foresight for the willow ptarmigan case explicitly requested to have near-term forecasts of ptarmigan dynamics to adapt their harvest strategies. The collaboration between researchers and stakeholders in this study was particularly fruitful. It demonstrated that forecasting next-future states of wildlife populations is of interest to decision-makers, and this because the time-horizon is relevant for implementing and adapting management decisions in a time of rapid change (Nichols et al., 2015).

3. What are the impacts of management actions carried out for species of conservation concern?

Papers III and IV focused on the endangered Fennoscandian population of lesser white-fronted goose. The ultimate goal of both studies was to assess the contribution of a predator control program to the recent recovery of the goose population. In paper III, we found no evidence that red fox culling improved goose breeding success. Rather, breeding success appeared to be primarily driven by indirect food web interactions in the form of apparent facilitation, through small rodent cycles, and competition, through reindeer carrion abundance. Red fox culling, however, was initiated not only to improve reproductive success, but also to minimize early breeding failure. Early failed breeders seem to leave the Norwegian breeding areas earlier in the season and embark on a long migratory journey through Western Asia, where they are supposedly exposed to higher hunting mortality than when they migrate through Eastern Europe (Jones, Whytock, & Bunnefeld, 2017; Øien, Aarvak, Ekker, & Tolvanen, 2009). In paper IV, we parameterized a population model including all migration stopovers and found no evidence that adult goose survival is lower on this allegedly riskier migration route. Therefore, we concluded that, at present, there is no evidence that predator control has influenced the goose population recovery. Still, we found indications that survival probabilities at staging and wintering sites in Hungary and Greece may have improved in the latest years. Although inconclusive due to large statistical uncertainty, this result may reflect the positive impact of a set of conservation interventions implemented in these countries approximately at the same time the red fox culling started.

The case of the Fennoscandian lesser white-fronted goose has several general implications.

First, it highlights the challenge of assessing the efficacy of management/conservation actions when proper experimental management designs are unfeasible (Taylor et al., 2017). The goose population is so small and spatially restricted that it does not allow for management interventions in a rigorous treatment/control design. Hence, we could only perform a before/after-action comparison to evaluate the effect of the red fox culling program. Secondly, it emphasizes the importance of accounting for drivers in the food web that may confound the effect of the action, and that long-term data on both the conservation target and the food web drivers are needed for a thorough evaluation. Eventually, it suggests that a conservation approach that crosses national borders is likely to be beneficial for endangered migratory populations. While most studies have so far focused on the breeding season, conditions experienced at non-breeding sites are likely non-trivial and can significantly affect population dynamics of migratory birds (Rushing et al., 2017; Wilson et al., 2018).

5. Conclusions and future perspectives

Through the work presented in this thesis, I studied the dynamics of arctic populations of management and conservation concern by applying a combination of state-of-the-art paradigms that, today, are advocated to guide management of wildlife populations in rapidly changing environments. These included (Fig. 4): focusing on food web dynamics rather than single species (Ims, Jepsen, et al., 2013); developing hypothesis-driven conceptual models to target key interactions within food webs as well as exogenous climate and human impacts and guide the scientific investigation (Ims & Yoccoz, 2017); including stakeholders in the modelling process and integrating their views to generate more nuanced hypotheses on the functioning of the system (Nichols et al., 2015); supporting hypotheses with theoretical predictions from mathematical models (Caswell, 1988); using long-term monitoring data to test hypotheses (Hughes et al., 2017); generating iterative near-term forecasts and evaluate models' predictive ability to discriminate between competing hypotheses and adapt monitoring and management (Dietze et al., 2018; Nichols et al., 2019). Although not all steps where performed in each case study, this thesis highlights that a combination of approaches is required to fully understand the impacts of current environmental changes on species and ecosystems (Turner et al., 2020).

The results presented in this thesis document the impacts on arctic species of several drivers linked to climate change. Novel climate conditions in the high-arctic Svalbard archipelago, such as milder winters, seem to offset the negative impacts of key manifestations of climate change (e.g. ROS) on resident arctic species such as ptarmigan. While these results may be transferable to other increasing rock ptarmigan populations around the Arctic (e.g. Newfoundland) or other species whose populations are increasing (e.g. Svalbard reindeer; Le Moullec et al., 2019), they may be less relevant where rock ptarmigan are declining (e.g. Greenland and Iceland; Fuglei et al., 2019). The willow ptarmigan in Fennoscandia appears to be sensitive to more intense insect pest outbreaks and late onset of winter. Both are linked to climate warming and expected to intensify in the future (Derksen, Brown, Mudryk, Luojus, & Helfrich, 2017; Jepsen et al., 2013), thus they may constitute key threats to ptarmigan populations. The general decline of ptarmigan populations goes in parallel with the decline of other alpine and arctic ground-nesting birds in Europe (Lehikoinen et al., 2019). These trends point towards common drivers of change that are related to global warming and operate at the community level, such as increased primary productivity and nest predation (Ims et al., 2019; Kubelka et al., 2018).

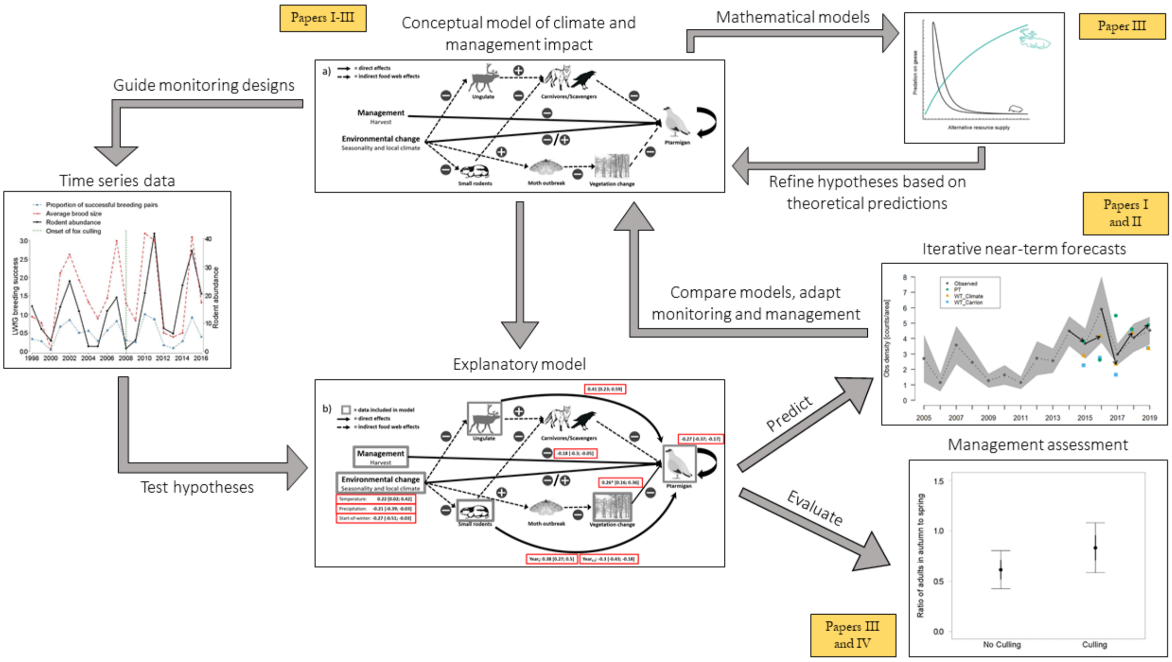

Fig. 4 – The approach I used in this thesis to study the dynamics of arctic populations of management and conservation concern. Hypothesis-driven conceptual models were develop to target key food web interactions and exogenous climate and human impacts. These models drive the ecosystem monitoring. The logic in the conceptual models could be refined by generating predictions with mathematical models. The *a-priori* hypotheses described by the conceptual models were then tested with empirical data; the conceptual model was converted into competing statistical models to quantify the relationships and thus build explanatory models. The explanatory models were used to generate short-term forecasts, which were compared to each other to evaluate models' predictive ability. The explanatory models were also used to assess the efficacy of management actions. Monitoring and management systems should be iteratively adapted according to new evidence.

Some of the effects evaluated in this thesis were very uncertain or inconsistent across ecosystems or species. For instance, carrion abundance was negatively related to the lesser white-fronted goose but positively related to the willow ptarmigan, two ground-nesting bird species that share the same environment and likely the same predator guild. Ungulate carrion constitutes an important resource for arctic predators (Ehrich et al., 2017; Eide et al., 2012; Killengreen et al., 2011). The ubiquitous occurrence of ungulate species in the Eurasian tundra and the range expansion of boreal mesocarnivores into the Arctic (Elmhagen et al., 2017) make the investigation of indirect carrion effects mediated by predators acting like facultative scavengers a crucial research topic. Eventually, other aspects of climate change that were not investigated in this thesis will deserve attention in the future. For instance, increased plant productivity (van der Wal & Stien, 2014) and a prolonged grazing season due to longer and warmer summer may benefit herbivore species (Albon et al., 2017) and have likely contributed to their increasing trends in Svalbard.

To resolve the contradictory evidence of some of the hypothesized effects, my work highlights the convenience of using a holistic approach that, through conceptual models depicting hypothesized impacts, targets key food web interactions and thus incorporate non-trivial indirect effects. This approach proved profitable also to evaluate the effect of management interventions. In the case of the lesser white-fronted goose, not accounting for food web interactions would have led to erroneous conclusions regarding the impact of predator control. This constitutes an important take-home message of my work, because conservation programs seldom include quantitative evaluations of actions (Sutherland et al., 2004). In this respect, it will be important to continue the monitoring of both the goose population and the food web drivers in the coming years. With more years of data and regular management assessment, we might be able to reduce uncertainty about the influence of the management action and identify more precisely critical stages of the goose life cycle.

The target populations of this thesis are currently of management and/or conservation interest. Managers and conservationists were concerned about how these populations will react to the climate drivers that we identified. Moreover, they were interested in quantitative evaluations of the impacts of harvest strategies for both Svalbard rock ptarmigan and willow ptarmigan, and how to adapt hunting regulations to ensure sustainable harvest. If ecology aims to have an impact on society, ecologists should commit to provide predictions of future ecosystem/population states on a management-relevant time scale and suggest mitigating actions that can be readily implemented. The collaborative platform established with the stakeholder groups to improve management of the willow ptarmigan in Finnmark represents a crucial step towards the creation of a coordinated adaptive management system. Continuing the long-term monitoring and the iterative predictions in the coming years will ease the detection of potential future climate and harvest impacts and will provide quantitative ground on which to base hunting regulations and potentially conservation actions. Within this century, in fact, it may be expected that most of Fennoscandia will be outside the climate envelope for alpine/arctic species like ptarmigan. Given the current decline of ptarmigan populations in Norway and elsewhere in alpine and arctic ecosystems, I hope that this experience will be of inspiration to establish similar collaborative monitoring systems.

6. References

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Paper I

Iterative model predictions for a high-arctic ptarmigan population impacted by rapid climate change

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Abstract

To improve understanding and management of the consequences of current rapid climate change, ecologists advocate using long-term monitoring data series to generate iterative near-term predictions of ecosystem responses. This approach allows scientific evidence to increase rapidly and management strategies to be tailored simultaneously, because the timescale of predictions is relevant to decision-making. Rapid environmental changes are currently occurring in the Arctic, which is warming twice as fast as the rest of the world. Here, we implemented the near-term forecasting approach on a population of Svalbard rock ptarmigan, an herbivore endemic to the high-Arctic archipelago of Svalbard and one of the most northerly year-round resident birds that is also subject to harvest. We aimed to 1) quantify the effect of potential drivers of ptarmigan population dynamics (*explanatory predictions*), and 2) assess the ability of different models of increasing complexity to forecast next-year population density (*anticipatory predictions*). We fitted state-space models to point-transect distance-sampling counts of ptarmigan for the period 2005-2019, when rapid climate warming occurred. Our results suggest that the recent increasing trend in the Svalbard rock ptarmigan population can be partly attributed to major changes in winter climate, especially with respect to temperature. Higher average winter temperature is likely to reduce the birds' energy consumption needed for thermoregulation, thereby improving body condition and thus survival and recruitment. Moreover, the ptarmigan population seems to compensate for current harvest levels. The predictive ability of the models improved non-linearly with the length of the time series, and the inclusion of relevant ecological predictors improved forecasts of sharp changes in next-year population density. Our study is among the firsts to use the near-term forecasting framework to improve understanding and management of climate change impacts on population dynamics. We provide recommendations for improved explanatory and anticipatory predictions in a management perspective.

1. Introduction

The climate is currently changing to the extent that ecological systems are moving away from the boundaries of historical variation and established empirical relations, experiencing previously unseen conditions (Malhi et al., 2020). Understanding how species and ecosystems will be impacted by climate change is challenging and requires a combination of different approaches (Turner et al., 2020). However, it is generally recognized that long-term monitoring represents a baseline approach for climate-ecological studies (Gauthier et al., 2013; Hughes et al., 2017; Ims & Yoccoz, 2017; Schmidt, Christensen, & Roslin, 2017). The time series data generated from appropriately designed monitoring systems serve several purposes (Likens & Lindenmayer, 2010). They allow the detection of both fast and slow changes (Hastings et al., 2018). Analyses and modelling of such data provide opportunity to generate both *explanatory predictions* (i.e. those aimed to test theories) and *anticipatory predictions* (i.e. those aimed to describe future scenarios assuming certain hypotheses to be true) (Maris et al., 2018; Mouquet et al., 2015).

Because predicting long-term effects of climate change is extremely challenging, and forecasts of future scenarios are affected by high uncertainty (Planque, 2016), ecologists advocate focusing on near-term predictions (Dietze, 2017; Dietze et al., 2018; Petchey et al., 2015; White et al., 2019). This scheme implies routine generation of forecasts of an ecological target, and evaluation of the accuracy of the forecasts by comparing them with new observations as soon as they become available. The iterative nature of the near-term forecasting approach reflects the hypothetico-deductive reasoning of the scientific method (Dietze et al., 2018; Houlahan, McKinney, Anderson, & McGill, 2017). The short timescale used for predictions allows analyses to be repeated, models to be validated, and evidence to increase rapidly (Dietze et al., 2018). The near-term forecasting approach has proved especially profitable to deal with ecosystems, species, or populations subject to management (Henden et al., 2020; Nichols, Johnson, Williams, Boomer, & Wilson, 2015), because forecasts are generated at a timescale that can be influenced by decision-making. Near-term forecasting, in fact, constitutes the foundation of adaptive management (Nichols et al., 2015). Examples of such endeavours, however, are still rare in ecology (Nichols, Kendall, & Boomer, 2019).

The Arctic is one of the regions on the Earth experiencing major environmental changes, mostly due to global warming (Ims et al., 2013a). Polar regions warm faster than the rest of the world, a phenomenon known as Arctic amplification (Serreze & Barry, 2011), which is projected to continue in the twenty-first century (Koenigk, Key, & Vihma, 2020). In the high-Arctic archipelago of Svalbard, Norway (74–81°N, 15–30°E), higher annual mean temperatures (Nordli, Przybylak, Ogilvie, & Isaksen, 2014), warmer and wetter winters (Hansen et al., 2014), decreased snow-cover duration and depth (Descamps et al., 2017), and declined sea ice extent (Dahlke et al., 2020) are indicators of ongoing changes in the climate system. Svalbard, in fact, is probably the sub-region of the Arctic that has experienced the most profound warming during the last decade (Isaksen et al., 2016; Nordli et al., 2014). Climate change impacts on the species belonging to the relatively simple terrestrial food web of Svalbard have already been detected (Descamps et al., 2017; Ims, Jepsen, Stien, & Yoccoz, 2013b). Most emphasis has been placed on the negative effect of formation of basal ice in winter following rain-on-snow (ROS) events (Rennert, Roe, Putkonen, & Bitz, 2009), which synchronizes population dynamics across mammal species (Hansen et al., 2013; Stien et al., 2012) and especially among reindeer populations (Hansen et al., 2019a) by hindering forage access. Recent studies have also dealt with climate change impacts on migratory geese in Svalbard (Layton-Matthews, Hansen, Grotan, Fuglei, & Loonen, 2019; Tombre, Oudman, Shimmings, Griffin, & Prop, 2019). Less is known about other phenomena associated with climate change and its impact on other taxa (but see Bjerke et al., 2017; Coulson, Leinaas, Ims, & Søvik, 2000)

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Our study focused on the Svalbard rock ptarmigan *Lagopus muta hyperborea*, a high-arctic sub-species of the rock ptarmigan and among the planet's most northerly year-round resident birds. These small herbivores are able to cope with the climate extremities and the low primary productivity of polar deserts as far north as 81° N. Because the Svalbard rock ptarmigan is an endemic sub-species subjected to harvesting and is predicted to be sensitive to climate change in several ways (Henden, Ims, Fuglei, & Pedersen, 2017; Ims et al., 2013b), it is rigorously monitored to both assess its status and aid its management (Pedersen, Bårdsen, Yoccoz, Lecomte, & Fuglei, 2012). However, little is known about what drives its population dynamics and how it is impacted by climate change and harvest in Svalbard (but see Pedersen, Soininen, Unander, Willebrand, & Fuglei, 2014). The time series of the Svalbard rock ptarmigan population is part of an ecosystem-wide monitoring system that encompasses the period of the most rapid recent climate warming with associated changes in the abiotic and biotic domains of the Svalbard terrestrial ecosystem, offering us the opportunity to address these knowledge gaps. Based on this long-term monitoring series and appurtenant ecosystem data, we used dynamic state-space models with the following aims: 1) in an *explanatory* framework, to identify and quantify abiotic and biotic drivers of ptarmigan population dynamics, and 2) in an *anticipatory* framework, to assess the models' ability to provide near-term (i.e. next-year) predictions of population density.

2. Materials and methods

2.1 Sampling design and ptarmigan monitoring protocol

The study area is located in Spitsbergen, Nordenskiöld Land (78°15' N, 17°20' E), within the middle Arctic tundra zone and is centered on the large, glacial valleys of Adventdalen and Sassendalen. These valleys are characterized by wetland, ridge, and heath vegetation communities and surrounded by peaks reaching 1,200 m a.s.l. (Pedersen et al., 2012; Soininen, Fuglei, & Pedersen, 2016). In April, ptarmigan males establish territories and display territorial behavior (Unander & Steen, 1985). To estimate the pre-breeding population density (males/km^2), we used a long-term annual monitoring time series obtained from point-transect distance sampling conducted by the Norwegian Polar Institute on calling territorial males during four weeks in April (Pedersen et al., 2012). We used data from 2005-2019, when a sampling design based on 148 survey points in a study area of ca. 1,200 km^2 was established and systematically perpetuated (Fig. S1). Of the 148 survey points, 101 were non-randomly selected based on altitude and terrain characteristics that are known to be preferred ptarmigan habitats (henceforth "non-random points"). The remaining 47 points were randomly assigned and included in the sampling design to sample also sub-optimal ptarmigan habitats (henceforth "random points") (Pedersen et al., 2012). To reduce observer bias during the surveys, each survey point is visited two or three times per season, each time by a different trained observer. Each visit lasts 15 minutes and the radial distance to birds observed on ground is measured using a laser distance binocular. For details regarding the sampling protocol see Pedersen et al. (2012).

2.2 Expectations and predictor variables

Expectations regarding potential drivers of the dynamics of Svalbard rock ptarmigan populations were derived from Ims et al. (2013b) and Henden et al. (2017) and are summarized in Fig. 1. Because the knowledge about the response of Svalbard rock ptarmigan to environmental fluctuations is limited, expectations are partly based on current evidence from other arctic and alpine ptarmigan populations.

Abiotic variables

Inclement weather conditions are likely to affect early chick survival, which is regarded as a critical demographic component of several grouse species (Hannon & Martin, 2006; Ludwig, Aebischer, Bubb, Roos, & Baines, 2018). A combination of low temperatures (Ludwig, Alatalo, Helle, & Siitari, 2010) and heavy rainfall (Kobayashi & Nakamura, 2013; Novoa, Astruc, Desmet, & Besnard, 2016) is expected to be particularly detrimental by preventing food intake and hindering thermoregulation (Erikstad & Andersen, 1983; Erikstad & Spidsø, 1982). We obtained local weather data from the Svalbard airport weather station in Longyearbyen (78°14′46’N, 015°27′56’E) collected by the Norwegian Meteorological Institute (available at http://seklima.met.no). We extracted data on daily mean temperature and daily maximum precipitation for the first week of July to cover the critical period for early ptarmigan chick survival, and calculated mean temperature (°C) and cumulative precipitation (mm).

Based on the extreme physiological adaptation in terms of fat deposition of this subspecies (body fat normally exceeds 30% of the bird body mass at the onset of winter; Grammeltvedt & Steen, 1978; Mortensen, Unander, Kolstad, & Blix, 1983; Steen & Unander, 1985), it is evident that winter weather is critical in the life cycle of the Svalbard rock ptarmigan. Accordingly, we had strong expectations regarding the influence of changes in winter climate on ptarmigan survival. With increasingly warmer winters (Hanssen-Bauer et al., 2019), ptarmigan are expected to reduce their need for energy consumption, i.e. consume less body reserves, thereby improving their winter survival. Changes in winter climate concern also snow duration, which is now shorter than in the past, due to late snow arrival and early snowmelt (Descamps et al., 2017; Liston & Hiemstra, 2011). Late onset of winter has been shown to hamper survival of colour moulting species including ptarmigan (Henden et al., 2020; Melin, Mehtatalo, Helle, Ikonen, & Packalen, 2020), likely due to camouflage mismatch resulting in elevated predation rates (Zimova, Mills, & Nowak, 2016). We used daily temperature data to calculate mean temperature (°C) in the core winter season (December$_{t-1}$ –March$_{t}$) and onset of winter (Julian day). The latter is defined as the day when the average of a 10-day forward-moving window was below 0°C for the first time in autumn and remained below 0°C for ≥10 days (Le Moullec et al., 2018).

Rain-on-snow (ROS) events can cause basal ice formation, which encapsulates ground vegetation and affects ptarmigan by preventing forage access during winter (Hansen et al., 2013; Hansen et al., 2014). Following Hansen et al. (2013), we used daily temperature and precipitation to calculate an index of ROS, i.e. the number of rainy days (with rain ≥ 1 mm and temperature ≥ 1 C°) in the core winter season ($December_{t-1}$ – $March_t$).

In Svalbard, marine resources dominate the diet of the arctic fox *Vulpes lagopus* (Ehrich et al., 2015; Eide, Eid, Prestrud, & Swenson, 2005; Prestrud & Nilssen, 1992), the only year-round predator of Svalbard rock ptarmigan. This indicates that sea ice is an important hunting platform for the arctic fox in winter. As sea ice cover in the fjords declines due to global warming (Dahlke et al., 2020), arctic foxes may be forced to rely more on terrestrial prey resources like ptarmigan. Time series of average sea ice extent in the fjords of Svalbard were calculated using ice charts issued by the Norwegian Ice Service (NIS) since 1969 (Dahlke et al., 2020) and used as a proxy for accessibility of marine resources to arctic fox during winter. We calculated the mean of the monthly average sea ice extent (km^2) in the core winter season ($December_{t-1}$ – $March_t$) for the period 2005-2019 (see Appendix S1 for details).

Biotic variables

Reindeer carrion constitute an important winter food resource for the arctic fox (Eide et al., 2005; Fuglei, Øritsland, & Prestrud, 2003). High reindeer mortality can occur following heavy ROS events (Hansen et al., 2013; Hansen et al., 2019a). Abundant reindeer carrion during winter may cause arctic foxes to respond numerically through increased survival and reproduction, eventually leading to higher predation pressure on ground-breeding birds like ptarmigan (Eide, Stien, Prestrud, Yoccoz, & Fuglei, 2012; Hansen et al., 2013; Marolla et al., 2019). Counts of reindeer carcasses are carried out every summer (June-July) in the valley of Adventdalen since 1979. Five to six observers walk pre-defined routes located less than 1 km apart to monitor the whole study area within a week. They scan the area with 10x42 mm binoculars and record the position of each spotted reindeer carcass on a map. Reindeer carcasses are easily detected as large, white spots on the treeless tundra. Given the low decomposition rate of organic matter in the Arctic, we assumed that the amount of carcasses found in the summer is representative of carrion abundance during winter. We also assumed that the temporal variation in the number of reindeer carcasses in Adventdalen is representative of the variation in the neighbouring valley of Sassendalen. This is supported by the high correlation between annual number of carcasses in two adjacent monitoring areas, Adventdalen and Reindalen (r [95% CI] = 0.93 [0.83; 0.97]).

The population dynamics of Svalbard rock ptarmigan is also likely to be subject to density-dependent processes (e.g. in the form of saturated breeding habitats, Pedersen et al., 2014), and negatively influenced by human harvesting that is regulated by the local government. Harvesting has been regulated since 1998 and today occurs between September 10th and December 23rd. While hunters must obtain a hunting license from the Governor of Svalbard, there is no limit to the number of issued licenses (Soininen et al., 2016). Hunters – mostly residents – report the number of birds harvested, while hunting effort is not systematically reported. Hence, bag limits are not based on an assessment of sustainable harvest. For our analysis, we used the number of birds harvested from 2005 to 2018 in the study area. We excluded birds harvested by trappers, who tend to live in remote places far from the study area. Hunting statistics are available at the website of MOSJ (Environmental Monitoring of Svalbard and Jan Mayen, http://www.mosj.npolar.no).

Time series data for all the predictors are showed in Fig. S2.

2.3 Data analysis

Model structure

We applied a modified version of the Hierarchical Distance Sampling model described by Kéry and Royle (2016) to model point-transect distance-sampling counts of ptarmigan performed in 2005-2019 over the 148 survey points. This state-space model allows explicit modelling of the spatiotemporal variation in ptarmigan abundance while accounting for detection errors. It consists of two parts, a detection model that estimates detection probability, and a dynamic process model that models spatiotemporal variation in population growth rate. The detection process is based on the distance-sampling likelihood for point transect data (Buckland, 2001). We used a half-normal detection function to describe the decline of detection probability p of an observed bird with the radial distance d from the observer,

$$\log(p) = \frac{d^2}{2\sigma_s^2} \tag{1}$$

where σ is the half-normal scale parameter at point s. We modelled σ as a log link function of site-specific terrain covariates (terrain ruggedness, aspect, and slope; data obtained from a 20×20 m digital elevation model of the study area) to account for their influence on detection probability. To reduce the effect of potential inaccurate distance estimations and movements of birds reacting to observer's presence, we grouped data into eight 50-m distance classes, up to a maximum distance of 400 m from the centre of the survey point based on the frequency distribution of detection distances (Kéry & Royle, 2016). The site-specific detection probability $pcap_s$ is then calculated as the integral of the distance function over the distance classes (Kéry & Royle, 2016). The process model consists of a sub-model for the first year (i.e. initial density) and a Gompertz population dynamics model for the consecutive years. In the dynamic part of the model, we used the average detection probability $pcap_s$ to link the sum of observed counts of ptarmigan males y across repeated visits $Nrep$ at each point s in year t to the average latent abundance $N_{s,t}$:

$$y_{s,t} \sim binom(N_{s,t} * Nrep_{s,t}, pcap_s) \tag{2}$$

where $N_{s,t}$ is assumed to be a Poisson random variable with $E[N_{s,t}] = \lambda_{s,t}$ and $\lambda_{s,t}$ is modelled as the product of ptarmigan density $D_{s,t}$ and the observable size of the surveyed area. The latter was estimated specifically for each survey point by a viewshed analysis that accounted for different terrain morphology affecting the observer's view (Appendix S2). Finally, we assumed log density to be a normal random variable with mean $\mu_{s,t}$ and process error variance σ^2_{proc}

$$\log(D_{s,t}) \sim norm(\mu_{s,t}, \sigma^2_{proc}) \tag{3}$$

and modelled $\mu_{s,t}$ as function of a set of *a priori*-selected predictors

$$\mu_{s,t} = \beta 0_{areas} + rCl + \beta_{DD}\mu_{s,t-1} + \beta_x X_t \tag{4}$$

where $\beta 0_{areas}$ is a fixed covariate with three levels (i.e. Adventdalen random, Adventdalen non-random, and Sassendalen) accounting for differences between macro-valleys and different survey point selection strategies, rCl is a random cluster effect (i.e. $rCl \sim Norm(0, \sigma^2_{Cl})$) accounting for potential non-independence of observations at points located close to each other (with the number of cluster estimated by a hierarchical clustering algorithm), $\beta_{DD}\mu_{s,t-1}$ is the density-dependence parameter based on the log density the year before, and $\beta_x X_t$ is a set of *a priori*-selected predictors. The low annual number of random points surveyed in Sassendalen did not allow us to model random and non-random points in this valley separately. On the log scale, the classic Gompertz model, becomes a linear autoregressive time-series model of order 1 (Dennis, Ponciano, Lele, Taper, & Staples, 2006), thus effects of predictors are modelled on the growth rate. This model structure was applied to all years except the first (i.e. initial density, t=1), which had a similar but simpler structure,

$$\mu_{s,1} = \beta 1_{areas} + rCl_1 \tag{5}$$

where $\beta 1_{areas}$ and rCl_1 ($rCl_1 \sim Norm(0, \sigma^2_{Cl1})$) have the same signification as in the dynamics model (i.e. t > 1).

Explanatory predictions

To evaluate the effect of the selected predictors on ptarmigan growth rate, we developed a suite of models including different combinations of predictors, and assessed the consistency of effect size estimates across models (Table 1). We considered the following predictors: mean temperature and maximum precipitation in the first week of July, mean winter temperature, day of winter onset, number of winter days with ROS, sea ice extent, number of reindeer carcasses, and number of ptarmigan harvested. We also included a trend parameter to account for any excess trend in the data that was not explained by the predictors. Except for ROS, winter temperature, and sea ice extent – predicted to influence winter survival and recruitment and thus modelled at time t – all the other variables were modelled at time $t-1$, because they were expected to influence reproduction and survival during summer and autumn. We point out that, although ROS events can cause high mortality in reindeer, here there is no conflict between the variables accounting for ROS and reindeer carrion effects, because the former tests for a direct impact of ROS through inaccessible vegetation, while the latter tests for a delayed, indirect effect of carrion abundance that may be due to ROS events and/or other phenomena (e.g. density-dependent processes, Hansen et al., 2019b).

Because winter temperature and sea ice extent were highly correlated (r [95% CI] = -0.74

[-0.91; -0.34]), we modelled their effect in two separate "climate-impact" models containing all the other climate variables (WT_Climate and SI_Climate models in Table 1). Moreover, we extended the two climate-impact models by the inclusion of the effect of reindeer carrion abundance (WT_Carrion and SI_Carrion models in Table 1). However, because the number of reindeer carcasses was somewhat correlated with winter temperature, sea ice extent, and ROS, we also run WT_Carrion and SI_Carrion without ROS (WT_Carrion2 and SI_Carrion2 models in Table 1) to evaluate the consistency of estimates. We scaled all variables to ease interpretation of coefficients and model convergence. We fitted the models using Markov Chain Monte Carlo methods implemented in JAGS (Plummer, 2003) through the R package jagsUI (Kellner, 2015), assigning vague priors to the parameters. We run 400,000 iterations on four chains at a thinning rate of 50, burn-in of 4,000, and adaptation phase of 80,000, yielding 31,680 samples. Convergence of parameter estimates was evaluated by ensuring that the Gelman-Rubin convergence statistics R-hat was below 1.1 (Brooks & Gelman, 1998). We provide the JAGS code in Appendix S3.

Anticipatory predictions

We implemented the near-term forecasting approach by using our model to predict next-year ptarmigan density, following Henden et al. (2020). We sequentially fitted the models to the time series of ptarmigan counts spanning t = 10 to t = 14 years of prior data. For each time step, we predicted next-year point-specific density (*t+1*) using the estimated model parameters from previous years of data (Appendix S4). We assessed whether the addition of abiotic and biotic predictors improved model's forecasting ability by comparing a climate-impact model (WT_Climate) and its extension including reindeer carrion abundance (WT_Carrion) to a simpler model containing only ptarmigan data (i.e. density-dependence and harvest; PT). We then compared predicted densities to observed densities for each survey-point by calculating the symmetric mean absolute percentage error (sMAPE, Makridakis, Spiliotis, & Assimakopoulos, 2018; Appendix S4). A fundamental aspect of iterative near-term forecasting is the opportunity to update the models not only with new data, but also with incoming evidence about model parameters. At each model run, therefore, we used the parameter estimates generated from the previous model run to initiate the MCMC chains, thereby providing the model with an indication of plausible parameter values. To address the contribution of measurement error to the predictive performances of the models, we compared each sMAPE to a theoretical minimum prediction error expected from a "perfect" Poisson process model (Appendix S4). Finally, we assessed whether the WT_Climate and WT_Carrion models were better than the PT model at forecasting next-year mean density, which is a measure of practical management value. It was not possible to perform this whole analysis for the SI_Climate and SI_Carrion models because parameters of the latter failed to reach convergence when it was fitted to reduced time series.

3. Results

3.1 Density and detection probability

Estimated average model-based densities of territorial ptarmigan males ranged between 0.4 and 6.1 individuals/km^2 (Fig. 2a). As could be expected, non-random points in Adventdalen exhibited the highest densities. However, both Adventdalen and Sassendalen showed an overall increasing trend in density from 2014, regardless of the point selection strategy, but with substantial between-year variation especially towards the end of the series. A small decrease in density from 2018 to 2019 estimated by the WT_ models (Fig. 2a, Fig. S3) contrasted with a small increase in observed density (Fig. 2b) and in density estimated by the SI_ models (Fig. S3). However, this decrease was consistent with the observed decrease in winter temperature from 2018 to 2019 (Fig. 2c).

Detection probability was generally low and did not vary substantially across survey points (mean = 0.34; SD = 0.02; range = [0.29 – 0.39]). There was no evidence of terrain covariates influencing detection probability, except for a small negative effect of terrain aspect (mean [95% CI] = -0.032 [-0.063; -0.002]).

3.2 Explanatory predictions

Most of the estimates of predictor effects on ptarmigan growth rate pointed in the expected directions. However, due to large uncertainty in effect sizes across models, the evidence was far from conclusive for most of them (Fig. 3, Table S1). Mean winter temperature consistently showed the strongest effect on ptarmigan growth rate, with highly coherent positive estimates across models. Sea ice extent, as could be expected from the high negative correlation with winter temperature, had a strong negative effect. Among the other predictors, the negative effects of ROS and reindeer carrion abundance were the most consistent, despite large uncertainty. The effect of mean temperature in the first week of July was always positive and the effect of cumulative precipitation in the same week mostly negative, but effect sizes varied across models and credible intervals tended to overlap zero. Similarly, the effect of winter onset was always negative but with low consistency of estimates. While there was no evidence for an influence of harvest on ptarmigan growth rate, there was evidence of negative density-dependence, albeit large credible intervals limited the inference about the strength of the effect. Finally, a small excess temporal trend in the growth rate suggests that the predictors in the model and/or the model structure did not account for all the variation in population growth rate.

3.3 Anticipatory predictions

The near-term predictive performances of the three candidate models used for anticipatory predictions (i.e. PT, WT_Climate, and WT_Carrion; Table 1) tended to increase with more years of data (i.e. the length of the time series, Fig. 4). On average, the sMAPE of our models was approximately 30% higher than that expected from a "perfect" Poisson process model (Fig. 4). However, there was a small trend towards lower prediction error with more years of data. At the end of the time series, the discrepancy between models' prediction error and minimum prediction error was approximately 20%. While, in the end, the PT model displayed the lowest sMAPE, the WT_Carrion model showed the largest improvement from 2015 to 2019 ($\Delta sMAPE_{PT} \approx 12\%$; $\Delta sMAPE_{WT\_Climate} \approx 12\%$; $\Delta sMAPE_{WT\_Carrion} \approx 16\%$).

In general, the models predicted next year's density fairly well, at least in the sense of anticipating population increase and decrease (Fig. 5). Overall, the WT_Climate model performed slightly better compared to the PT and the WT_Carrion model. Although predictions from the PT model were closer to the observed density in some years (i.e. 2015 and 2019), the WT_Climate model displayed greater ability to predict larger changes in ptarmigan density in consecutive years (i.e. 2016 and 2017).

4. Discussion

In this study, we aimed to 1) identify drivers of population dynamics of the Svalbard rock ptarmigan and 2) develop a tool for iterative near-term forecasting of the population state of this high-arctic endemic species in an era of rapid climate warming. Benefitting from a spatially extensive and statistically rigorous monitoring design, we were able to parameterize state-space models to meet these purposes. While many ptarmigan populations in the circumpolar arctic have recently declined, the ptarmigan population in Svalbard shows an increasing trend in the latest years (Fuglei et al., 2019). Here we relate this increase to the rapidly changing winter climate in this part of the high Arctic.

Explanatory predictions

Among the four seasons, winter temperature shows the largest increase in Svalbard, alongside spring temperature. In the period 1971-2017, the increase in winter temperature ranged between 3 and 5 °C (Hanssen-Bauer et al., 2019), with at least six of the ten warmest winters occurring after 2000 (Isaksen et al., 2016; Nordli et al., 2014). In the years following 2012, ptarmigan density fluctuated in remarkable synchrony with winter temperature (Fig. 2). Svalbard rock ptarmigan's adaptations to the harsh conditions of the arctic winter are exceptional, and involve behavioural, morphological, and physiological adjustments (Nord & Folkow, 2018), among which deposition of fat stores plays a fundamental role in terms of energy store and thermal insulation (Mortensen & Blix, 1986; Stokkan, Harvey, Klandorf, Unander, & Blix, 1985). Our results add support to the notion that warmer winters contribute to reduce the total energy consumption of ptarmigan, i.e. lower the need for thermoregulation, thereby sustaining their body conditions and improving survival throughout the winter. The body condition of hens is regarded as the most important factor for chick production in this species (Steen & Unander, 1985). Winter temperature in the Svalbard archipelago is also influenced by the sea ice-ocean atmosphere system (Benestad, 2002). Sea ice shrinkage (Dahlke et al., 2020) is a direct consequence of Arctic warming, and it likely promotes a positive feedback due to more open water that can cause temperatures on land to be even higher (Isaksen, Benestad, Harris, & Sollid, 2007). Our analysis suggests that increased winter temperature may constitute the aspect of changing arctic climate that contributed the most to the positive ptarmigan population trend, while hypothesized indirect effects of sea ice loss through modifications of predation patterns have likely no effect on ptarmigan. However, we caution against strong inference about these relationships. The relatively short time series and the high covariance between ptarmigan density and winter temperature in the last part of the time series may have confounded other effects, e.g. density-dependent processes and/or harvest effects. Therefore, more years of data are needed to confirm the observed patterns.

The drastic increase in winter temperature has resulted also in increased frequency of ROS events (Hansen et al., 2014; Peeters et al., 2019). Despite considerable uncertainty, the average negative effect of number of ROS days we found here is consistent with Hansen et al. (2013). They showed that, if ROS events are associated with ice-crust formation at the ground level that hinders access to vegetation, they might cause sudden population crashes in resident herbivore species. Our result is relevant because their analysis did not include data from the most recent warming period. The influence of ROS on ptarmigan population dynamics may be partly mediated by high reindeer mortality following heavy ROS events (Hansen et al., 2019a). Reindeer carrion constitutes an important resource for arctic foxes (Eide et al., 2012; Fuglei et al., 2003), which may respond numerically and thereby exert higher predation pressure on ground-breeding birds like ptarmigan (Eide et al., 2012; Henden et al., 2014; Killengreen et al., 2011; Marolla et al., 2019). The average negative effect of carrion abundance suggests that this may affect the Svalbard rock ptarmigan (but see Henden et al., 2020 for a contrasting example). Importantly, because the negative effect of ROS is reliant on formation of basal ice, we acknowledge the possibility that increasingly frequent warm spells during winter may prevent basal ice formation in the future, leading to improved forage accessibility through rain opening up winter foraging grounds and thus a positive effect on ptarmigan growth (Tyler, Forchhammer, & Øritsland, 2008).

Although the estimates tended to be in the expected directions, large uncertainty and poor consistency of estimates characterised most of the other predictors in our model. Making strong inference about their effects, therefore, is difficult. Given the relatively short time series available for the Svalbard rock ptarmigan, it is possible that the strong winter temperature effect overrode other effects. Notably, we could not detect any impact of harvest on the breeding component of the ptarmigan population. Combined with evidence of relatively strong density-dependence, this result suggests that the population may be able to compensate for the harvest, likely due to higher survival in recent years as compared to estimated survival from the 1980s (Unander et al., 2016) and the existence of a surplus of floater birds that occupy vacant breeding territories (Pedersen et al., 2014).

It is also important to acknowledge other aspects of climate that have changed in the recent decades, but were not included in the analysis. For instance, not only winters, but also summers are becoming warmer, and longer. This may benefit ptarmigan through increased plant productivity (van der Wal & Stien, 2014) and a prolonged grazing season, as observed for the larger herbivore in Svalbard, the Svalbard reindeer (Albon et al., 2017; Le Moullec, Pedersen, Stien, Rosvold, & Hansen, 2019). A hint of this effect may be the small excess positive population trend that we detected in our study. Climate warming-induced changes that show trends but happen at a slow pace, like summer lengthening and prolonged grazing seasons, will deserve attention in the imminent future in terms of their potential effects on ptarmigan population dynamics.

Anticipatory predictions

Assessing the predictive ability of ecological models of different complexity is not only a strategy to validate models and gather evidence efficiently, but also to align management of populations, species, and communities to current environmental change (Nichols et al., 2019). The Svalbard rock ptarmigan is the most popular recreational game species in Svalbard (Soininen et al., 2016), and there is concern that harvest may affect the populations at least at the local level. The Svalbard Environmental Protection Act and harvesting regulations for Svalbard allow harvest on the condition that the total offtake does not have an appreciable impact on the population. Hence, tools capable of accurately forecasting next-year population density and providing insights on the effect of harvest would be useful to adapt harvesting strategies in the face of current and future climate change (Nichols et al., 2015).

The difference between the prediction error of our models and a theoretical minimum expected under a “perfect” Poisson process was similar to that found by Henden et al. (2020), who used the same metric for the same purpose. Although none of our models outperformed the others with respect to forecasting next-year mean population density, the inclusion of local climate and food web predictors was important for predicting large changes between years (e.g. 2016 and 2017). A more complex model, therefore, may be better suited for the Svalbard rock ptarmigan population, although simpler models can perform as well in some cases (cf. Gerber & Kendall, 2018). A noticeable exception was 2019, when the more complex models (i.e. WT_Climate and WT_Carrion) underestimated densities, likely due to the strong influence of the winter temperature predictor that showed a low value in 2019 (i.e. average temperature from December 2018 to March 2019; Fig. 2c). Overall, we deem the predictive ability of our models sufficient for iterative forecasting on a yearly basis. There is, however, scope for improved predictions, which will be possible with better spatial matching of predictor variables and ptarmigan monitoring (i.e. accounting for spatial variation), and a longer time series.

Although our study area in Svalbard is relative small compared to the size of the Svalbard archipelago, the geomorphology of the glacial valleys and the fact that some parts are considerably distant from the coast can cause substantial variation in local temperatures and precipitations (Isaksen et al., 2016). Because the sMAPE is the mean of the per-survey site prediction error, not accounting for spatial variation in weather covariates may have influenced the predictive performance of the models. The current installation of new weather stations throughout the study area, combined with the development of modelling systems that reconstruct spatial weather by interpolation techniques, provides scope for more accurate gridded data of local climate variables. With more data and better predictors, we expect confidence to rise in models that perform well and decrease in those that perform poorly. This will likely lead to more precise and useful predictions with respect to which drivers of population dynamics are most important. Iterating the forecasting process in the next years will elucidate whether some of the strong effects we found are real or occurred by chance (e.g. the effect of winter temperature). Moreover, as our models do not account for potential interaction effects between some of the drivers (e.g. between population density and ROS as shown for Svalbard reindeer, Hansen et al., 2019a and b), more sophisticated, hypothesis-specific models could be developed. Generating predictions from several hypothesis-specific models to evaluate potential interactions could improve the understanding of the mechanisms governing the population dynamics of the Svalbard rock ptarmigan.

Conclusions

We provided a first assessment of the impacts of different manifestations of climate change on the Svalbard rock ptarmigan, a year-round resident, endemic species inhabiting an archipelago where the temperature increase is among the highest on Earth. Our study highlights the importance of winter conditions in determining the population state at the time of breeding, but also the challenge of disentangling the effect of drivers that are interlinked and can act both directly and indirectly on ptarmigan population dynamics. In a situation of limited knowledge, such as for the Svalbard rock ptarmigan population, committing to validate predictions from hypothesis-driven models against new data will allow more frequent hypothesis testing and thus more robust explanatory science about the impact of climate change. Prediction, in the end, is the ability to demonstrate understanding (Houlahan et al., 2017). With respect to the management of the Svalbard rock ptarmigan population, although no influence of current harvest levels was detected, continuing the ongoing long-term time series and the iterative predictions will likely increase the probability to detect potential future harvest effects. The ongoing, rapid climate change may have yet unknown effects on ptarmigan's ability to tolerate harvesting. In addition, we suggest that the formal integration of stakeholders' views (e.g. the hunters and the Governor of Svalbard) in the modelling process through standardised protocols (cf. Henden et al., 2020) could help generating more nuanced hypotheses about drivers of change (e.g. how they affect demographic structure). The management may also benefit from the iterative-forecast framework we developed as a tool to evaluate and adjust hunting quotas based on model predictions. Because hunting takes place in the autumn, winter predictors will need to be assigned average values from the most recent warming period (e.g. average over the last 6-7 years) or evaluated under scenario assessment (e.g. high winter temperature versus low winter temperature).

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Author contributions statement: F. Marolla, J-A. Henden, E. Fuglei, and Å. Ø. Pedersen conceived the idea; F. Marolla and J-A. Henden designed methodology; E. Fuglei and Å. Ø. Pedersen provided ptarmigan data, Å. Ø. Pedersen provided reindeer carrion data, M. Itkin made calculation of sea ice coverage; F. Marolla and J-A. Henden prepared and organized the ptarmigan data; F. Marolla analyzed the data; F. Marolla led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication. None of the

authors has conflict of interest to declare.

6. Figures

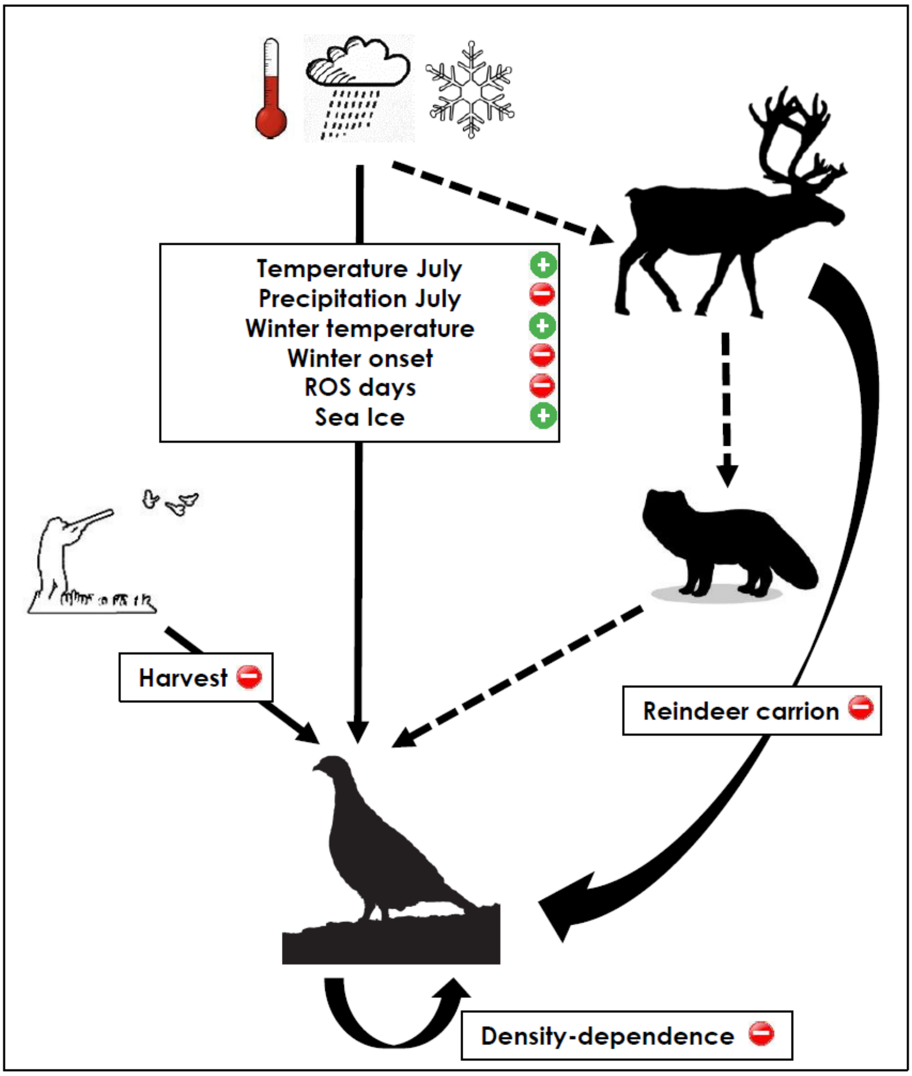

Fig. 1 – Conceptual model depicting potential drivers of Svalbard rock ptarmigan population dynamics. Solid arrows represent direct paths that were included in the models and parameterized, dashed arrows represent the hypothesized mechanisms behind indirect effects. +/- denote the expected direction of the relationship. Predictors and units of measurement are described in section 2.2 in the main text.

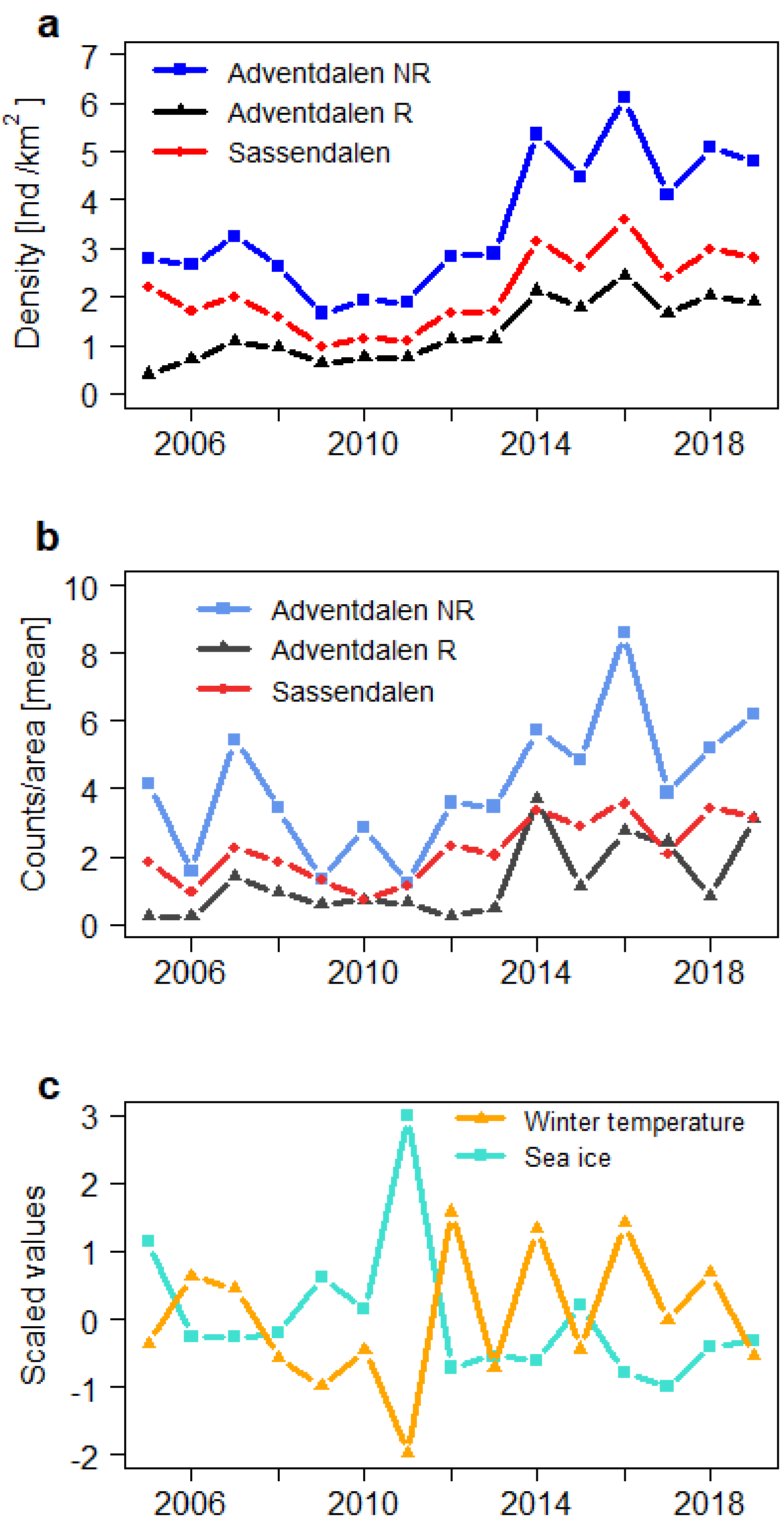

Fig. 2 – a) Average area-specific model-based estimates of Svalbard rock ptarmigan male population density (males/km^2) for the period 2005-2019 from the WT_Climate model ("climate-impact" model including Winter Temperature). NR = Non-Random survey points; R

= Random survey points. Sassendalen includes random and non-random points together. b) Average area-specific observed density for the period 2005-2019. Legend abbreviations as in panel a. Note the scale on the y-axis differs between panel a and b. c) Time series of winter temperature and sea ice extent in the study area. Values are scaled to ease comparison.

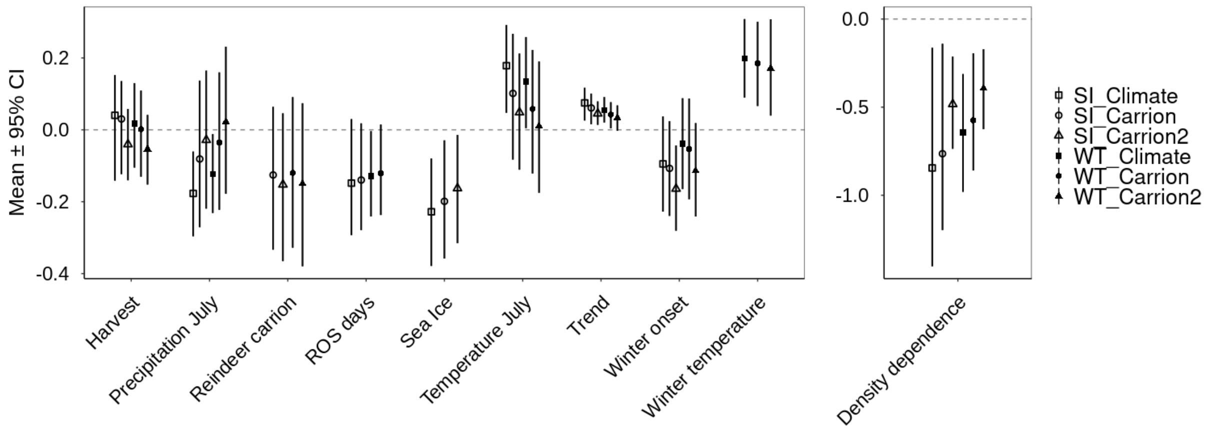

Fig. 3 – Mean ± 95% Credible Intervals of estimated posterior distributions of scaled predictors. Abiotic and biotic effects and density dependence are reported separately for graphical purposes. Note the scale on the y-axis differs between a and b. Effects should be interpreted as change in ptarmigan population growth rate for an increase of 1 standard deviation in the predictor. The number of bars differs among predictors because not all predictors were included in each model. SI_Climate = “climate-impact” model including Sea Ice; SI_Carrion = SI_Climate with the addition of Reindeer Carrion; SI_Carrion2 = SI_Carrion without ROS days; WT_Climate = “climate-impact” model including Winter Temperature; WT_Carrion = WT_Climate with the addition of Reindeer Carrion; WT_Carrion2 = WT_Carrion without ROS days.

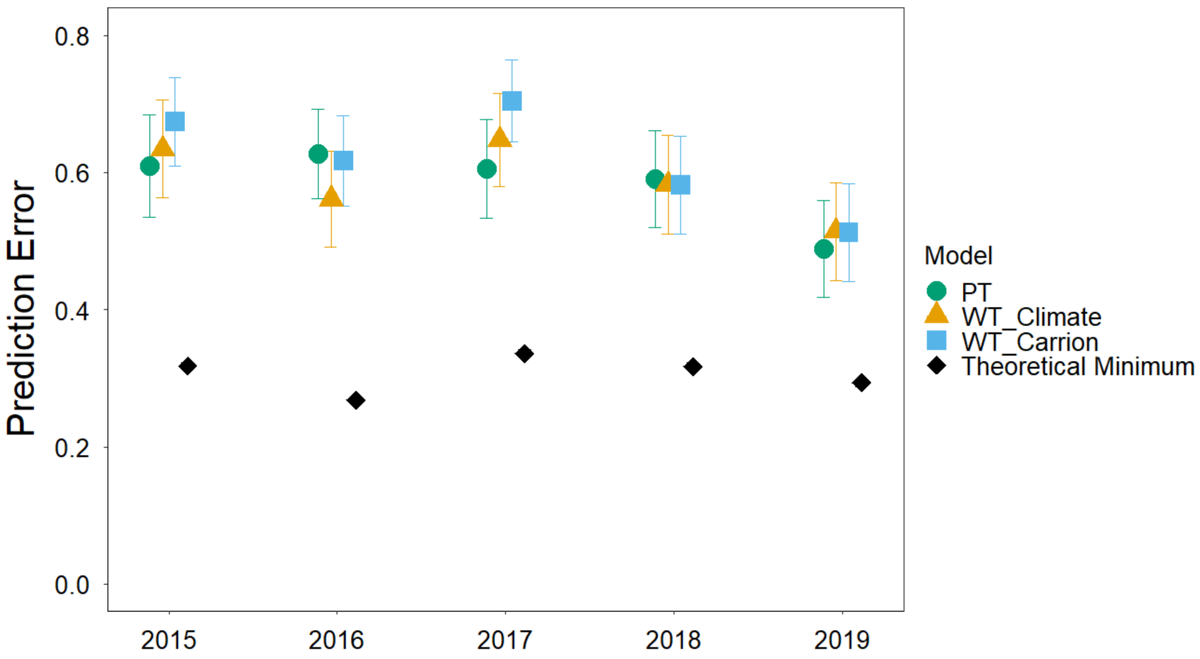

Fig. 4 – Prediction error (sMAPE) for the three candidate models used for anticipatory predictions. PT = Ptarmigan model; WT_Climate = “climate-impact” model including Winter Temperature; WT_Carrion = WT_Climate with the addition of Reindeer Carrion. Theoretical Minimum is the expected prediction error under a Poisson process model.

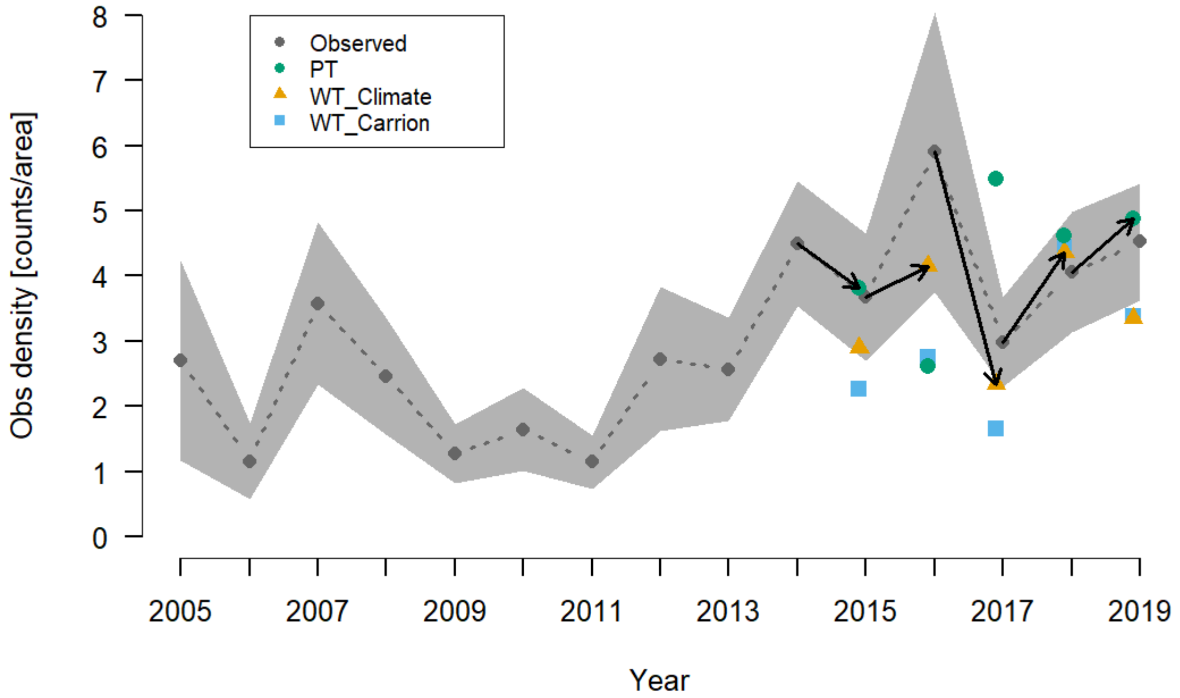

Fig. 5 – Ability of candidate models to predict next-year mean population density of the Svalbard rock ptarmigan in the study area. Predicted next-year mean densities are compared to actually observed densities. Arrows point at the model that provided the best prediction. PT = Ptarmigan model; WT_Climate = "climate-impact" model including Winter Temperature; WT_Carrion = WT_Climate with the addition of Reindeer Carrion.

7. Tables

Table 1 – Combination of predictors in the candidate models. The table indicates also whether a given model was used for explanatory predictions or anticipatory predictions, or both. WT_Climate = “climate-impact” model including Winter Temperature; WT_Carrion = WT_Climate with the addition of Reindeer Carrion; WT_Carrion2 = WT_Carrion without ROS days; SI_Climate = “climate-impact” model including Sea Ice; SI_Carrion = SI_Climate with the addition of Reindeer Carrion; SI_Carrion2 = SI_Carrion without ROS days; PT = Ptarmigan model.

Variable	WT_Climate	WT_Carrion	WT_Carrion2	SI_Climate	SI_Carrion	SI_Carrion2	PT
Temperature July	X	X	X	X	X	X	-
Precipitation July	X	X	X	X	X	X	-
Winter temperature	X	X	X	-	-	-	-
Winter onset	X	X	X	X	X	X	-
ROS days	X	X	-	X	X	-	-
Sea Ice	-	-	-	X	X	X	-
Reindeer carrion	-	X	X	-	X	X	-
Harvest	X	X	X	X	X	X	X
Density dependence	X	X	X	X	X	X	X
Trend	X	X	X	X	X	X	-
Explanatory predictions	Yes	Yes	Yes	Yes	Yes	Yes	No
Anticipatory predictions	Yes	Yes	No	No	No	No	Yes

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Supplementary Material

Appendix S1

Time series of sea ice extent

Data on sea ice extent in the fjords of Svalbard (km^2) have been calculated using ice charts, which are based on satellite information issued by the Norwegian Ice Service (NIS) since 1969 (Dahlke et al., 2020). Ice charts are produced manually based on the best available satellite information. After the observations are collected, they are classified into six classes based on sea ice concentration, ranging from open water (0 to 10 % ice concentration) to the very close drift ice (90 to 100 %) and fast ice (100%). Prior to 1997, ice charts have been produced on a weekly basis using cloud free measurements by optical and thermal infrared sensors like Television and Infrared Observation Satellite cameras and Advanced Very High Resolution Radiometer (AVHRR) on board meteorological satellites. Spatial resolution of the images was 1 to 4 kilometers. From 1997, ice charts have been generated digitally on a daily basis. Passive microwave observations (PMW) have been added to the sources as well as the optical and thermal infrared sensors like Moderate Resolution Imaging Spectroradiometer (MODIS) and Visible Infrared Imaging Radiometer Suite (VIIRS) that obtain imagery at higher spatial resolution of 250 - 500 meters per pixel. From 2008, NIS has been using near daily RADARSAT-2 (Scheuchl, Flett, Caves, & Cumming, 2004) synthetic aperture radar (SAR) observations resampled to 100 meters per pixel. In 2014, the addition of daily Sentinel-1 measurements (Torres et al., 2012) allowed near complete coverage of the Svalbard area with SAR observations. Passive microwave imaging and SAR technology allow observing sea ice year round independently from cloud and light conditions, improving the quality of sea ice mapping. Because various data sources have been used throughout the time series, it is likely that the quality of observations at the beginning of the time series is lower compared to the later periods when SAR, PMW and high resolution optical and thermal infrared measurements were added.

Our study area is limited to the Isfjorden system that consists of several fjord arms in central Spitsbergen. We used sea ice charts for the winter and spring period (December to June) from 2005 to 2019. In this study, the extent statistics (km^2) include only very close drift ice and fast ice classes. These ice features, filtered by time and area, have been aggregated to compute minimum, maximum and average values for each month using PostgreSQL/POSTGIS software.

Appendix S2

Viewshed analysis

The viewshed analysis was performed using the viewshed-analysis plugin in QGIS (QGIS_Development_Team, 2018). The viewshed analysis uses the elevation value of each cell of the digital elevation model (DEM) of Svalbard (Norwegian Polar Institute, 2014) to determine visibility from the centre of each ptarmigan survey point and compute the observable area (in km^2). We estimated point-specific observable area within a buffer of 400 m in radius from the observer, based on the frequency distribution of detection distances. For the analyses, we assumed the average height of an observer equal to 1.6 m and the height of ptarmigan equal to 0 m (i.e. the entire ptarmigan would be seen). Moreover, we discarded areas within the 400 m radius consisting of open water.

Appendix S3

JAGS code for the state-space model

```
#------------#
# JAGS model #
#------------#
cat("
model{
  # Prior distributions
  # potential Regression parameters
  alpha0 ~ dunif(-10,10)  # intercept detection prob on sigma (shape parameter)
  rugd ~ dunif(-10,10)
  asp ~ dunif(-10,10)
  slp ~ dunif(-10,10)

  for(j in 1:Nlev){         #3 levels fixed effect!
    beta0[j] ~ dunif(-10,10)  # intercept initial density/Abundance
    betat0[j] ~ dunif(-10,10) # intercept density dynamic model
  }

  taubtDD <- pow(2,-2)
  btDD ~ dnorm(0,taubtDD)I(-2,2) # DD parameter
  btTREND  ~ dnorm(0,100)  # excess trend in growth
  btPrect ~ dunif(-10,10)   # cumulative precipitation effect
  btROSt ~ dunif(-10,10)    # ROS effect
  btTempt ~ dunif(-10,10)   # temperature effect
```

```
  btWiOnt ~ dunif(-10,10)    # Winter Onset effect
  btWiTemp ~ dunif(-10,10)    # Winter Temperature effect
  #btCarct ~ dunif(-10,10)    # temporal carcass effect
  btHarvt ~ dunif(-10,10)    # Harvest effect
  #btSeaIcet ~ dunif(-10,10)    # Sea ice effect

## Specification of precision via inverse gamma distribution
  PrOc ~ dgamma(alphaProc, betaProc) # approximates inv.gamma with vague priors, alpha and beta = 0.01
  PrEc ~ dgamma(alphaPrec, betaPrec)
  sdproctau <- 1/sqrt(PrOc)
  sdprectau <- 1/sqrt(PrEc)

  ##Definition of random transect cluster effect
  for (j in 1:NClust) # NClust = number of clusters (areas)
  {rCl1[j]~ dnorm(0,rtau)
    rCl[j]~ dnorm(0,rtau2)}
  rtau ~ dgamma(alphaTau, betaTau)
  rtau2 ~ dgamma(alphaTau2, betaTau2)
  sdrtau <- 1/sqrt(rtau)
  sdrtau2 <- 1/sqrt(rtau2)

  # 'Likelihood'
  for (s in 1:nsites){
    # Linear model for detection function scale
```

```
    log(sigma[s]) <- alpha0 + rugd*vrm_d[s] + asp*aspect_d[s] + slp*slope_d[s]
    # Compute detection probability
    for(k in 1:nD){
      log(p[s,k]) <- -midpt[k]*midpt[k]/(2*sigma[s]*sigma[s]) # Half-normal detection function
      f[s,k] <- p[s,k]*pi[s,k]
      fc[s,k] <- f[s,k]/pcap[s]
      fct[s,k] <- fc[s,k]/sum(fc[s,1:nD])
      pi[s,k] <- (2*midpt[k]*delta )/(B*B)
    }
    pcap[s]<-sum(f[s,1:nD])  # Overall detection probability, i.e. sum over all bins!

    # Process model
    # Abundance/density model for Yr1 as in Sillett et al 2012
    y[s,1] ~ dbin(pcap[s], (N[s,1]*Nrep[s,1]))  # measurement error
    N[s,1] ~ dpois( lambda[s,1] )   # poisson variation       # N is poisson with expected value
#lambda
    lambda[s,1] <-  D[s,1] * areadet[s]
    logD[s,1] ~ dnorm( mu[s,1], PrEc )
    mu[s,1] <- beta0[ThreeLev[s]] + rCl1[Clust[s]]
    # model on density
    D[s,1] <- exp(logD[s,1])

    # Population dynamics model for subsequent years
    for (t in 2:T){
      y[s,t] ~ dbin(pcap[s], (N[s,t]*Nrep[s,t]))
```

```
      N[s,t] ~ dpois(lambda[s,t])  ## poisson variation
      lambda[s,t] <- D[s,t] * areadet[s]
      logD[s,t] ~ dnorm( mu[s,t] , PrOc ) # precision Process
      # Autoregressive model: mu is the latent state to be estimated!!
      mu[s,t] <- betat0[ThreeLev[s]] + rCl[Clust[s]] + btDD * mu[s,t-1] +
      btHarvt*Harvt[t-1] +
      btTempt*Temp1Julyt[t-1] +
      btPrect*Prec1Julyt[t-1] +
      btWiOnt*WiOnt[t-1] +
      btROSt*ROS_days[t] +
      btWiTemp*WiTemp[t] +
      btTREND * (t-1)
      # model on growth rates because of delayed effect (btDD), i.e. effect estimates are on the
growth rate
      D[s,t] <- exp(logD[s,t])
     }
   }

  # Distance sampling observation model for observed (binned) distance data
  for(i in 1:nobs){
    dclass[i] ~ dcat(fct[site[i],]+0.01)  # 1:nD, add a small (0.01) value to obtain pos descrete
#values
  }

  for(s in 1:nsites){
```

```
    for(t in 1:T){
      PredY[s,t] <- ((exp(mu[s,t]+ 0.5*(sdproctau*sdproctau))*areadet[s])*Nrep[s,t]) * pcap[s]
# See Bled et al. PlosOne 2013
    }    } # prediction

  # Derived quantities:
  for(t in 1:T){
    Ntot[t] <- sum(N[,t])
    Dest[t] <- Ntot[t] / sum(areadet) # 400m point = 0.5026548 km2
  }
}
", file="DynDensSvalbardPt.txt")
```

Appendix S4

Details on the method to generate anticipatory predictions

Following Henden et al. 2020, we used the coefficients estimated by the model from year t and covariate (scaled) values for the next year (t+1) to predict next year's log density (pred*mu*) for each surveyed point. Next year's counts were predicted as

$$P_{s,t+1} = (\exp(predmu_{s,t+1} + 0.5 * \sigma^2_{proc}) * area_{s,t+1}) * pcap_s \quad , \qquad \text{(S1)}$$

where σ^2_{proc} is the estimated sd of the process variance, *area* is the surveyed area (km^2) around each point, and *pcap* is the estimated site-specific detection probability. This operation was applied iteratively to the ptarmigan count times series spanning t = 10 years to t = 14 years of prior data.

To compare the predicted counts (P_s) to the observed counts (O_s), we used the symmetric mean absolute percentage error (sMAPE), a commonly used measure to assess forecast accuracy

$$sMAPE = \frac{1}{n}\sum_{S=1}^{sites} \frac{|P_s - O_s|}{(|O_s|+|P_s|)} \quad . \qquad \text{(S2)}$$

The potential theoretical minimum prediction error that we calculated for each year to assess the contribution of measurement error to the models' predictive ability, was based on a model with no process error but only Poisson variability (so called «perfect model», see R-code below). We first generated a vector with length equal to the number of sites surveyed (N) and within the range of observed log counts for year t (y_{vec}). We then performed 1000 simulation where we extracted the predicted values ($ypred_t$) from a Poisson GLM of a random Poisson variable (y_t), with size = N and expected values = y_{vec}, regressed against y_{vec}. We then calculated sMAPE values for each simulation, with $O_s = y_t$ and $P_s = ypred_t$. We finally calculated the mean and standard deviation over the 1000 simulations as a measure of theoretical minimum prediction error (see R-code below for more detail).

############ Theoretical minimum prediction error (R-code): #################

```
Nsites = SDp.err.P = VARp.err.P = MEANp.err.P = numeric(dim(YmaxNx_updt2005)[2])
Pred.errorP <- numeric(1000)
for(j in 1:dim(YmaxN)[2]) { # years
  minN = min(YmaxN[,j], na.rm=T) # minimum count
  maxN = max(YmaxN[,j], na.rm=T) # maximum count
  N = length(na.omit(YmaxN[,j]) ) # number of sites surveyed
  l.max = log(maxN) # log of max count
  l.min = log(minN+1) # log of min count
  (Y.vec <- seq(l.min,l.max,length=N)) # predictor
  for (i in 1:1000) {
    Y = rpois(n=N,lambda=exp(Y.vec)) # response
    Y.pred = predict(glm(Y~Y.vec,family=poisson),type="response")
    Pred.errorP[i] = (1/N)*sum(abs(Y.pred - Y)/(abs(Y) + abs(Y.pred)))
  }

  MEANp.err.P[j] <- mean(Pred.errorP)
  VARp.err.P[j] <- var(Pred.errorP)
  SDp.err.P[j] <- sd(Pred.errorP)
  Nsites[j] <- N
}

StdErrp.err.P = SDp.err.P/sqrt(Nsites)
```

Appendix S5

Supporting figures and tables

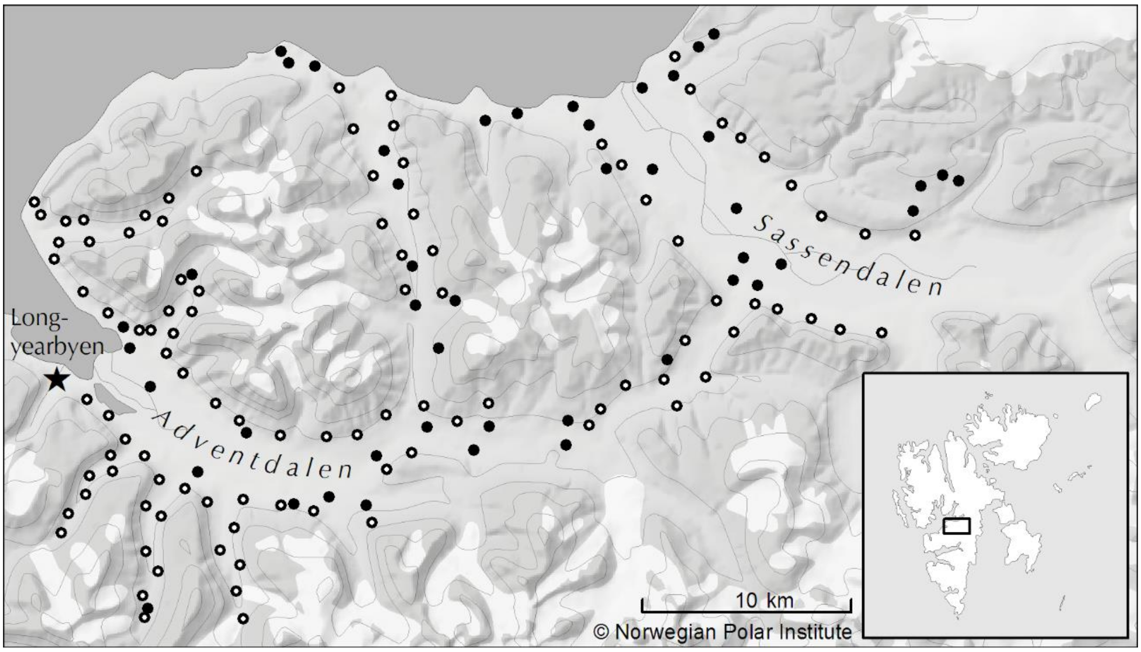

Fig. S1 – Map showing the study area for annual abundance surveys of territorial Svalbard rock ptarmigan males and its location in the Svalbard archipelago. Open circles represent non-random survey points, solid circles represent random survey points. Borrowed from Pedersen et al. (2012).

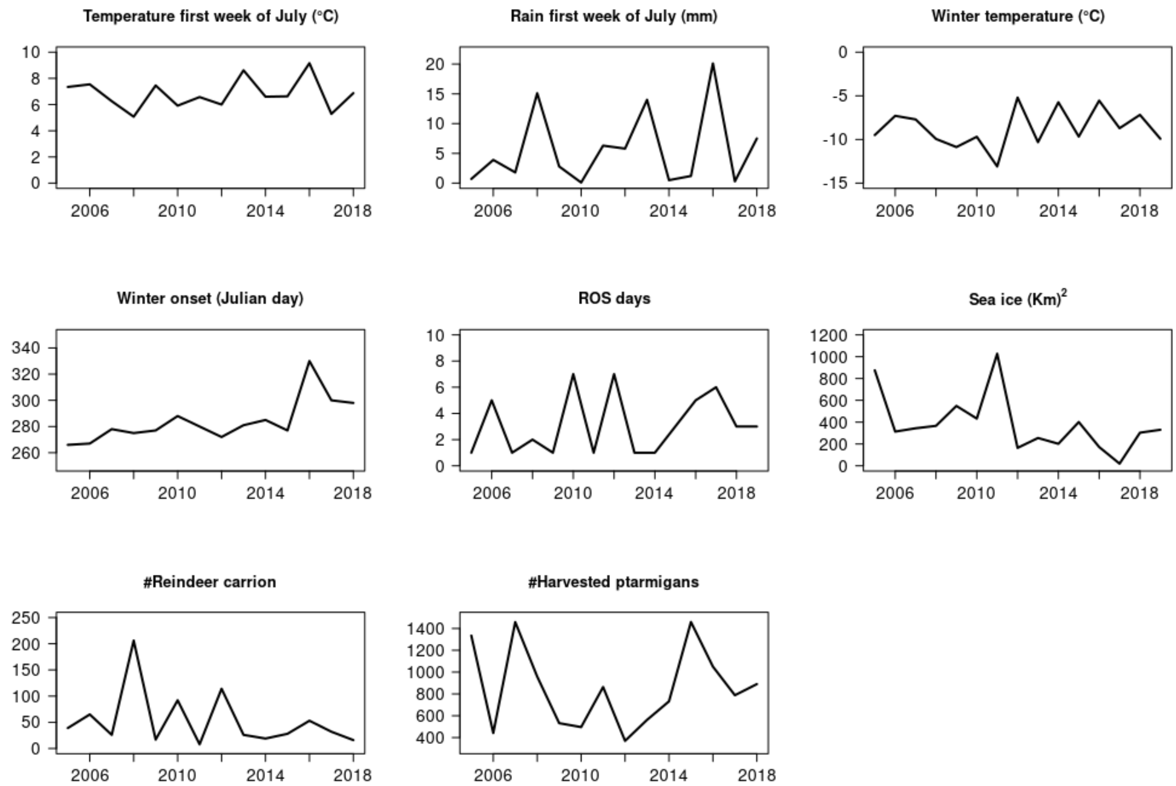

Fig. S2 – Time series data for the different predictors in the models for both explanatory and anticipatory predictions. Data for predictors expected to influence winter survival and recruitment, and thus modelled at time *t*, are shown for the period 2005-2019. Data for predictors expected to influence reproduction and survival during summer and autumn, and thus modelled at time *t-1*, are shown for the period 2005-2018.

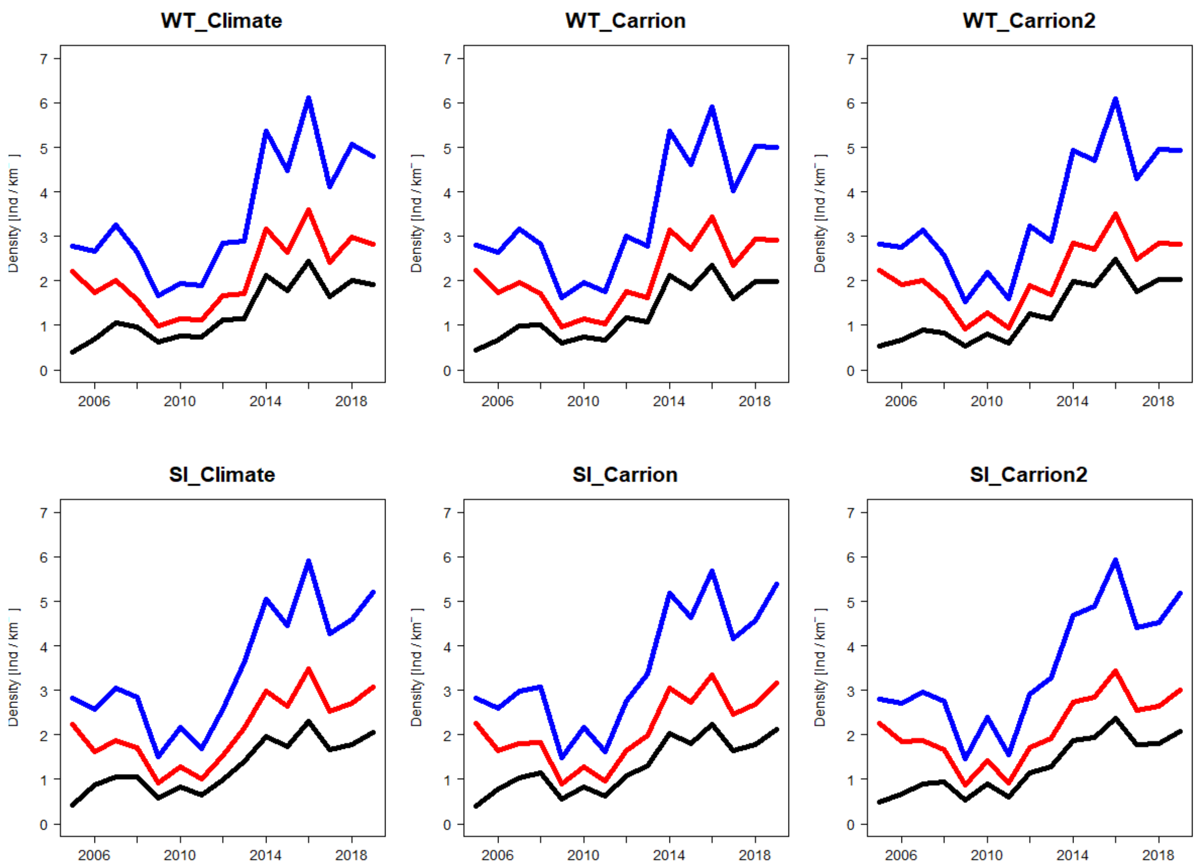

Fig. S3 - Average area-specific model-based estimates of Svalbard ptarmigan population density for the period 2005-2019 from all the models used to generate explanatory predictions. Blue line = Adventdalen non-random points; black line = Adventdalen random points; red line = Sassendalen (it includes random and non-random points pooled). WT_Climate = "climate-impact" model including Winter Temperature; WT_Carrion = WT_Climate with the addition of Reindeer Carrion; WT_Carrion2 = WT_Carrion without ROS days; SI_Climate = "climate-impact" model including Sea Ice; SI_Carrion = SI_Climate with the addition of Reindeer Carrion; SI_Carrion2 = SI_Carrion without ROS days.

Table S1 – Estimates of effects and 95% credible intervals for predictors from all the models used to generate explanatory predictions. Effects should be interpreted as change in ptarmigan population growth rate for an increase of 1 standard deviation in the predictor. Temperature July = average temperature in the first week of July (°C). Precipitation July = cumulative precipitation in the first week of July (mm). Winter temperature = average temperature in the core winter season (December-March). Winter onset = day of winter onset (Julian day) defined as the day when the average of a 10-day forward moving window was below 0°C for the first time in autumn and remained below 0°C for ≥10 days. ROS days = number of rainy days (with rain ≥ 1 mm and temperature ≥ 1 C°) in the core winter season (December – March). Sea ice = mean of the monthly average sea ice extent (km^2) in the core winter season (December – March). Reindeer carrion = number of reindeer carcasses found in the Adventdalen during the annual census. Harvest = yearly number of ptarmigan harvested in the study area.

Variable	WT_Climate	WT_Carrion	WT_Carrion2	SI_Climate	SI_Carrion	SI_Carrion2
Temperature July	0.134 (0.005; 0.258)	0.058 (-0.122; 0.222)	0.010 (-0.175; 0.190)	0.178 (0.047; 0.291)	0.101 (-0.083; 0.267)	0.048 (-0.111; 0.212)
Precipitation July	-0.123 (-0.231; -0.012)	-0.035 (-0.223; 0.160)	0.022 (-0.178; 0.231)	-0.177 (-0.296; -0.060)	-0.081 (-0.271; 0.137)	-0.028 (-0.219; 0.164)
Winter temperature	0.199 (0.090; 0.308)	0.185 (0.066; 0.301)	0.171 (0.039; 0.308)	-	-	-
Winter onset	-0.039 (-0.165; 0.088)	-0.053 (-0.193; 0.087)	-0.114 (-0.241; 0.019)	-0.095 (-0.228; 0.037)	-0.107 (-0.240; 0.024)	-0.164 (-0.281; -0.044)
ROS days	-0.129 (-0.241; -0.004)	-0.121 (-0.237; 0.015)	-	-0.148 (-0.293; 0.030)	-0.140 (-0.280; 0.018)	-
Sea ice	-	-	-	-0.228 (-0.379; -0.080)	-0.199 (-0.358; -0.029)	-0.163 (-0.315; -0.014)
Reindeer carrion	-	-0.120 (-0.328; 0.091)	-0.150 (-0.380; 0.074)	-	-0.126 (-0.334; 0.064)	-0.152 (-0.365; 0.046)
Harvest	0.017 (-0.105; 0.130)	0.002 (-0.130; 0.109)	-0.054 (-0.152; 0.041)	0.040 (-0.141; 0.152)	0.030 (-0.123; 0.136)	-0.040 (-0.140; 0.058)
Density dep.	-0.642 (-0.981; -0.312)	-0.574 (-0.860; -0.194)	-0.394 (-0.625; -0.171)	-0.845 (-1.403; -0.163)	-0.764 (-1.198; -0.140)	-0.483 (-0.736; -0.213)
Trend	0.055 (0.021; 0.091)	0.042 (0.004; 0.077)	0.033 (0.002; 0.069)	0.075 (0.026; 0.117)	0.061 (0.016; 0.101)	0.045 (0.014; 0.079)

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Paper II

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End-user involvement to improve predictions and management of populations with complex dynamics and multiple drivers

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Abstract. Sustainable management of wildlife populations can be aided by building models that both identify current drivers of natural dynamics and provide near-term predictions of future states. We employed a Strategic Foresight Protocol (SFP) involving stakeholders to decide the purpose and structure of a dynamic state-space model for the population dynamics of the Willow Ptarmigan, a popular game species in Norway. Based on local knowledge of stakeholders, it was decided that the model should include food web interactions and climatic drivers to provide explanatory predictions. Modeling confirmed observations from stakeholders that climate change impacts Ptarmigan populations negatively through intensified outbreaks of insect defoliators and later onset of winter. Stakeholders also decided that the model should provide anticipatory predictions. The ability to forecast population density ahead of the harvest season was valued by the stakeholders as it provides the management extra time to consider appropriate harvest regulations and communicate with hunters prior to the hunting season. Overall, exploring potential drivers and predicting short-term future states, facilitate collaborative learning and refined data collection, monitoring designs, and management priorities. Our experience from adapting a SFP to a management target with inherently complex dynamics and drivers of environmental change, is that an open, flexible, and iterative process, rather than a rigid step-wise protocol, facilitates rapid learning, trust, and legitimacy.

Key words: climate change; decision-making; food web; harvesting; near-term forecasting; population cycles; stakeholders; strategic foresight.

Introduction

Sustainable management of wildlife populations can be facilitated by building models that both identify current drivers of natural dynamics and anthropogenic-induced change (Caughley 1994), and provide near-term predictions of future states (Mouquet et al. 2015, Urban et al. 2016, Bradford et al. 2018, Dietze et al. 2018). This is especially relevant in light of the pace of current and future climate change (Mouquet et al. 2015, Urban et al. 2016, Dietze et al. 2018). While ecologists often aim to devise models that can aid environmental decision-making and lead to changes in policy, they often fail to achieve this goal (Dietze et al. 2018). If ecology aims to contribute to policy and management, there is a need to build models and make ecological predictions directly relevant and at a time horizon corresponding to environmental decision-making (Nichols et al. 2007, Pouyat et al. 2010, Hobbs et al. 2015, Hobday et al. 2016, Dietze et al. 2018). This can be achieved through an integrated approach in which scientists and stakeholders collaborate in the process of deciding on objectives, data, models, and analyses (Nichols et al. 2007, Cook et al. 2014*a*, Parrott 2017) as well as identifying forthcoming problems, opportunities, and surprises (Sutherland et al. 2014). Such participatory or collaborative modeling approaches that involve stakeholders have been forwarded as a way of ensuring direct relevance and uptake of modeling outcomes by end users (Parrott 2017, Reiter et al. 2018, Reiter et al. 2019). This involves all aspects of the research process from simple information and data sharing to development of model structure or interpretation of its output (Parrott 2017, Reiter et al. 2018, Reiter et al. 2019).

A food web consists of directly and indirectly connected species (Wootton 1994). Environmental impact on one species has the potential to propagate through the food web, affecting other species indirectly through multiple pathways (Barton and Ives 2014). Hence, understanding the consequences of environmental

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change and harvesting in complex, natural systems warrants the inclusion of biotic interactions and processes across several trophic levels (O'Connor et al. 2013, Barton and Ives 2014, Urban et al. 2016, Kadin et al. 2019). This is particularly important for harvested species, which are often situated at intermediate trophic levels in food webs, and therefore affected by both lower and higher trophic levels. Harvested species are increasingly recognized to exhibit complex population dynamics (Krebs et al. 2001, Moss and Watson 2001, Glaser et al. 2014), including population cycles, synchrony/travelling waves (Krebs et al. 2018), and transient dynamics (Hastings et al. 2018), expressed as shifts between alternative stable states. Such complex population dynamics may result from high dimensionality in the underlying ecological interactions in combination with strong exogenous environmental drivers (Hastings et al. 2018). Further complications are expected as ecosystems are increasingly subjected to novel climates and food web interactions (Ims et al. 2008). Many harvested populations have been declining in recent decades (Free et al. 2019, Fuglei et al. 2019) and developing predictive models is therefore a more challenging and pressing task than ever.

Case study

The Willow Ptarmigan (*Lagopus lagopus*) is a species known to have complex dynamics. The Willow Ptarmigan has sparked fascination and debate among hunters, managers, and scientists for more than a century (Nansen 1915, Elton 1924, Elton and Nicholson 1942, Moss and Watson 2001), likely due in part to their high-amplitude population cycles (Krebs et al. 2001, Moss and Watson 2001). However, transient dynamics (Hastings et al. 2018), expressed as shifts in cycle period and amplitude, alternation between cyclic and non-cyclic dynamics, or changes in average population density, is also pervasive in most Ptarmigan populations (Moss and Watson 2001). With its circumpolar distribution in mainly sub-Arctic and low-Arctic biomes, the Willow Ptarmigan is also one of the world's most abundant and popular small game species (Potapov and Sale 2013).

Like many other Alpine and Arctic bird species in Europe (Lehikoinen et al. 2014, Lehikoinen et al. 2019), Ptarmigan populations have recently been declining (Fuglei et al. 2019). In Norway, both Rock (*Lagopus muta*) and Willow Ptarmigan were placed on the Norwegian Red List in 2015 as "near threatened" (Henriksen and Hilmo 2015). While climate change has been proposed as the ultimate cause of this decline (Kausrud et al. 2008), the ecological mechanisms involved and consequently how management should respond, remain unresolved both for Ptarmigan and most other Arctic-Alpine bird species that currently are declining (Lehikoinen et al. 2019). The Willow Ptarmigan is preyed upon by different predator guilds and is affected by other herbivores in the ecosystem, some that have recently experienced changed dynamics (see Henden et al. 2017 for an overview). Moreover, several Ptarmigan life cycle stages are thought to be sensitive to climate (Erikstad and Spidsø 1982, Erikstad and Andersen 1983, Wilson and Martin 2012, Henden et al. 2017). Because of the potential multitude of climatic drivers and biotic mechanisms that may be involved, an ecosystem-based approach to data capture, modeling, and forecasting is warranted (Ims and Yoccoz 2017).

We develop a dynamic state-space model of Willow Ptarmigan population dynamics tailored to a spatially extensive population monitoring data set, spanning 17 yr and covering the largest management area for Ptarmigan in Norway. Different tools and approaches exist to facilitate model use by management (Gregory et al. 2012, Scheele et al. 2018, Schwartz et al. 2018). However, involvement of end users at the development and research stage, as well as in ongoing engagement and communication, are considered important (Reiter et al. 2018, Reiter et al. 2019). We used a Strategic Foresight Protocol (Cook et al. 2014*a*, Ims and Yoccoz 2017) to incorporate the knowledge, views and needs of major stakeholders in joint decisions on what should be the structure and purpose of the model.

Material and Methods

Target system

The Finnmark Estate (~45,000 km^2) is the largest game management unit for Willow Ptarmigan in Norway. The estate spans sub- and low-Arctic bioclimatic zones (Walker et al. 2005), with steep gradients from the western part, which is relatively mild and wet, to the eastern costal and southern inland parts, which are relatively colder and drier (Hanssen-Bauer 1999). Western Finnmark is topographically most diverse with large islands, steep mountain ranges, deep valleys and fjords (Appendix S1: Fig. S2). The eastern part also contains fjords and large peninsulas, but the relief is gentler. The south-central inland part is topographically the most homogenous with moderately sloped hills and plateaus. Good Willow Ptarmigan habitats. i.e., open sub-alpine/sub-Arctic birch forest and low sub-Arctic/low-Arctic shrub tundra, are well represented across Finnmark (Pedersen et al. 2012), although they are most fragmented in the western part and more continuous in the south-central part.

One major landowner (The Finnmark Estate; FeFo) is responsible for both the management (i.e., hunting regulations) and monitoring (line-transect surveys) of the Willow Ptarmigan in Finnmark. The most extensive land-use in Finnmark is, however, reindeer husbandry, which has profound effects on structure and dynamics of the food web (Ims et al. 2007, Ims and Henden 2012, Henden et al. 2014).

Strategic foresight protocol (SFP)

Stakeholders included in the SFP were the major landowner (FeFo), representatives from the hunters association, governmental management authorities, and conservation bodies (Appendix S1: Section S1). A first heuristic step in the process was to decide on the purpose. The purpose was primarily to develop a data-driven model that could explain past dynamics (i.e., provide explanatory predictions). Later in the process, the stakeholders also expressed a need for using the model for providing near-term forecasts (anticipatory predictions). The key data source stemmed from FeFo's spatially extensive line-transect survey of Willow Ptarmigan across Finnmark.

The opinions of the stakeholder group constituted an integral part of the iterative process of model development (Appendix S1: Section S1: Fig. S1). In this process, the model was updated with predictors to potentially explain both short-term dynamics and more long-term negative trends, as well as pose future threats to Ptarmigan populations (Fig. 2a). Many stakeholders are well acquainted with previous research on Willow Ptarmigan from Scandinavia. Hence, several of the proposed predictors could also have been included on a purely scientific basis. Stakeholders decided that the modeling should be based on a food web approach because of the complexity of the suggested impacts of different drivers on Willow Ptarmigan (Henden et al. 2017, Ims and Yoccoz 2017). A conceptual food web model was built to highlight biotic interactions suspected to affect both short-term population dynamics and long-term trends. Predation on Ptarmigan was considered potentially very important and thought to be driven indirectly by two links involving other herbivores in the food web. One link is due to the cyclic population dynamics of small rodents driving a synchronized alternative prey mechanism (Steen et al. 1988, Ims et al. 2013*b*). The second link is due to increasing amount of reindeer carcasses subsidizing a guild of generalist predators (Henden et al. 2014). Impact of a recent large-scale geometrid moth outbreak, thought to negatively affect all browsing herbivores (Vindstad et al. 2019) was also included among the biotic predictors. Among abiotic factors, we included the potential effect of severe weather conditions (temperature and precipitation) around hatching, previously shown to be important for Ptarmigan chick survival (Erikstad and Spidsø 1982, Erikstad and Andersen 1983). Moreover, we included the potential negative effect of late onset of winter, due to the camouflage-mismatch effect found for other species that shift to a white plumage in the autumn (Zimova et al. 2016). Finally, we included terms for density dependence and effect of harvest on Ptarmigan population growth (Pedersen et al. 2004). Fig. 1 provides an overview of the annual life cycle of Willow Ptarmigan together with information on when the different drivers have been recorded. Because of a lack of data on some intermediate components of indirect links in the conceptual model (Fig. 2a, e.g., generalist predators in the reindeer carcass–predators–Ptarmigan path), some of the indirect effects are modeled as direct effects in the statistical model (Fig. 2b). However, these effects (e.g., carcass abundance) are interpreted and referred to according to the expectation from the conceptual indirect effect in the conceptual model (Fig. 2a).

The spatial scale of the model was also discussed in the SFP process. FeFo operates with an eastern, western, and interior Ptarmigan management area (Appendix S1: Fig. S2) based on the contrasts in climate and topography described above (Target system), and their knowledge about gross spatial differences in Willow Ptarmigan dynamics across Finnmark. Hence, it was decided to derive model predictions at this scale, but also to consider higher spatial resolution to the extent that data sources, model specifications, and technical aspects of analyses allowed.

Data sources and variables

Ptarmigan data for modeling population growth rates (response variable) were obtained from transect lines surveyed yearly between 5 and 20 August by trained personnel with pointing dogs according to a distance sampling protocol (Buckland et al. 2001). From 2000 to 2016, a total of 315 lines were surveyed (Appendix S1: Fig. S2). However, the number surveyed ranged from 67 to 229 lines (122 ± 54, mean $\pm$ SD) between years. A large part of this variation is due to an intensive study on the effect of hunting conducted in 2008–2010, when extra lines where included in the interior and western part of Finnmark (E. J. Asbjørnsen, *personal communication*). As vegetation structure is likely to influence detection probability, we extracted vegetation data by using a vegetation map for Norway based on Landsat TM/ETM + data (Johansen 2009). From this digital map, we estimated the proportion of vegetation classes reflecting forest and erect woody vegetation within the sampled area (sampled area [km^2] = length [km] $\times$ 2width [km]) of each line transect. This proportion entered the modeling of the detection probability.

We now provide a brief overview of the different predictor variables. Detailed descriptions of the different predictor variables can be found in the Appendix S1 (Section S2). Generally, we strove to obtain as high a spatial resolution of the predictor variables as the underlying data allowed.

Harvest statistics for the entire period were available for each municipality that contained transect lines. For the harvest predictor we used the number of shot Ptarmigan per municipality divided by the areas of the municipality since the different municipalities vary greatly in size. Hence, transect lines within the same municipality were given the same value of the predictor. Note that the scale of the harvest predictor (number of

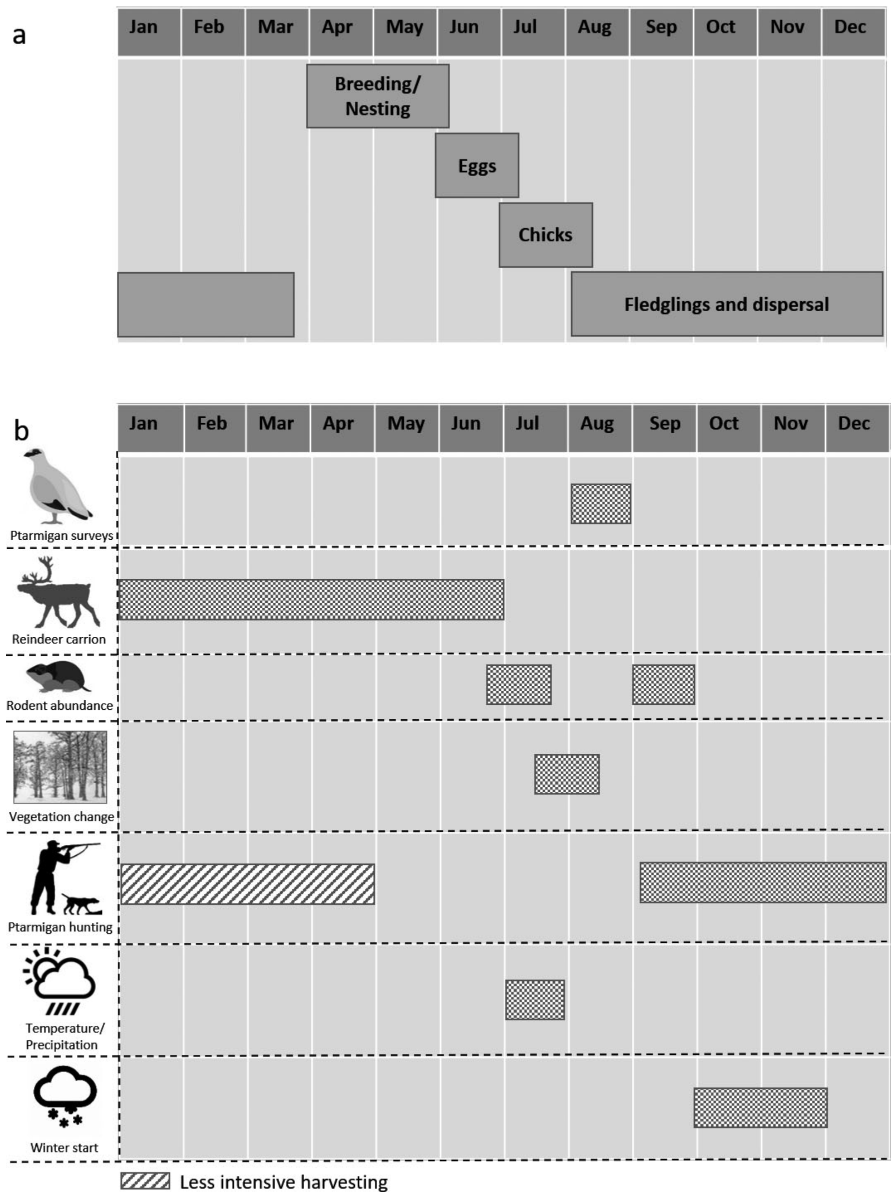

FIG. 1. (a) Annual life cycle of Willow Ptarmigan in Finnmark, denoting the breeding/nesting, egg, chick, and fledgling and dispersal phases. (b) Annual life cycle of data collection for the different drivers included in the model. Note that, while hunting may proceed well into late winter, the majority of hunting is performed in the autumn.

Ptarmigan harvested/km^2) corresponds to the scale of the response variable (change in the Ptarmigan density/km^2).

The two predictors linking Ptarmigans indirectly to predators (Fig. 2a) have different spatial scales. The spatial resolution of the rodent data is at the scale of the three main regions of Finnmark (western, interior, and eastern), while for reindeer carrion the scale is the entire county of Finnmark. Annual rodent density indices from each of the three regions were obtained from two ongoing monitoring programs (Yoccoz and Ims 2004, Ims et al. 2011), with constant effort across years and areas. We used the number of small rodents trapped in standardized programs conducted in each of the three regions as the predictor. Annual counts of reindeer carcasses were retrieved from a national database at the scale of Finnmark (database *available online*).[5] We used the sum of the number of reindeer found dead across municipalities in Finnmark during winter (January–June) every year as an index of the carcass abundance.

Moth outbreak intensity was estimated using a cumulative defoliation score based on NDVI data from

[5] www.rovbase.no

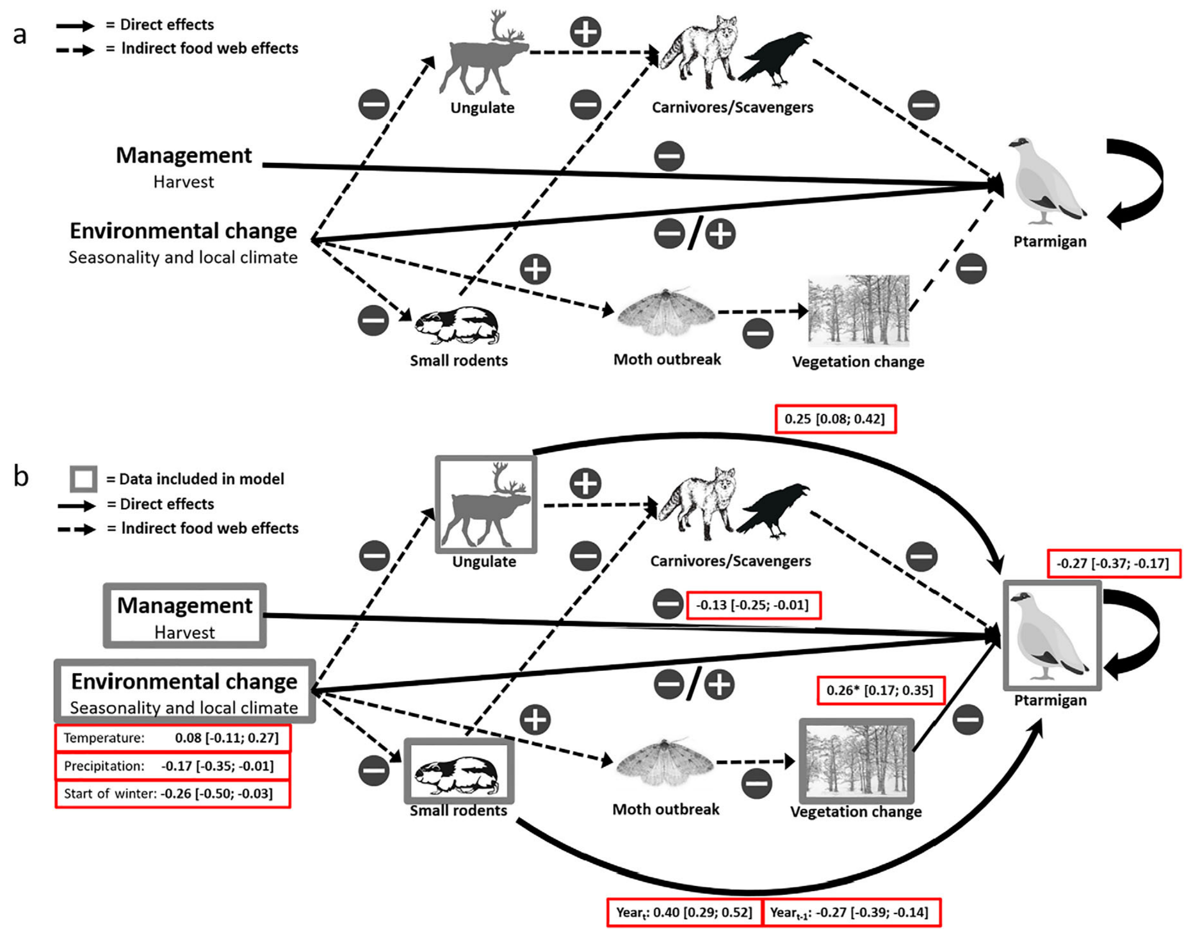

FIG. 2. (a) Conceptual model denoting the main mechanism and drivers of Willow Ptarmigan dynamics coming out from the Foresight process. Solid lines denote direct effects, while stippled lines denote indirect effects of different drivers on Ptarmigan population growth and density. Boxes with gray perimeter lines denote predictor and response data included in the model. (b) Conceptual model denoting the main mechanism and drivers modeled in the state-space model. Values with red perimeter lines denote estimated coefficients with 95% credible intervals of specific paths of the conceptual model. Note that as we used an inverse measure of moth outbreak intensity, the model estimate represents a negative effect. Note also that the moth effect shown is the residual effect, which mostly represents a temporal effect.

MODIS v6 (Jepsen et al. 2009). The cumulative defoliation score estimates the degree to which the annual peak plant productivity in an area is lower than the maximum across the time period 2000–2017. We used the mean cumulative defoliation score for each line-transect survey area, including a 6-km buffer zone, as a measure of local outbreak intensity. Larger negative values of the cumulative defoliation score denote more intense moth outbreaks and hence increased negative impacts on Willow Ptarmigan habitats.

Climate-related predictors were all quantified as the mean at the scale of the line-transect survey area using interpolated gridded data (1-km^2 pixel size) from the Norwegian meteorological institute (MET Norway; see Lussana et al. 2016). Mean temperature and max precipitation during the first week of July were used as predictors for the conditions affecting chick survival. The seasonality predictor (onset of winter), related to the camouflage-mismatch hypothesis, was obtained from remote sensing data (Appendix S1: Section S2.3).

Statistical model

To assess the effect of different predictors of Willow Ptarmigan growth rate, we used a modified version of the Hierarchical Distance Sampling (HDS) model from Kéry and Royle (2016). This model consists of a detection model, which estimates an average detection probability based on the observed distances from each transect line, and a process model, which models the spatial-temporal variation in population density as a function of a set of predictors. The process model consists of a sub-model for the first year (i.e., initial density) and a Gompertz population dynamics model for the consecutive years. All covariates (except year) were scaled (over all locations and time points) to mean = 0 and SD = 1 to ease convergence and interpretation of effect sizes. Note that since small rodent data where acquired using different sampling methods, the data from different regions were scaled separately. The temperature, precipitation, start of winter, and moth outbreak intensity data were all split into three components in the analyses: a temporal component that captured the overall average between-year variation, a spatial component that captured the overall average between-sites variation, and a residual component that represented the interaction between the temporal and spatial components (Oedekoven et al. 2017). Consequently, the three management-area-specific intercepts denote the growth rate at average values of the covariates. Our models were fitted using Markov Chain Monte Carlo (MCMC) methods as implemented in JAGS (Plummer 2003). A detailed description of the state-space model as well as the JAGS code is given in Appendix S1 (Section S2.5) and Data S1.

Near-term forecasting

According to the stakeholders' desire to obtain anticipatory predictions (i.e., forecasts), we used the full food web model to forecast a given year's survey counts (P_s) by using the estimated model coefficients based on data sources from previous years and predictors available in early summer the same year. In order to see to what extent the forecasts improved with more years of data, we ran the model with t = 10 to t = 16 yr of prior data. We then compared the predicted (P_s) and observed (O_s) survey counts by calculating the symmetric mean absolute percentage error (sMAPE; Makridakis 1993, Makridakis et al. 2018).

In order to assess the contribution of measurement error to our models' predictive ability, we calculated the potential "theoretical" minimum prediction error based on a "perfect" Poisson process model (see Appendix S1: Section S2.6, for details and Data S1 for the R code). We assessed the contribution of a potential hunting ban as a management action, by comparing predictions of observed counts of the full model (hereafter FoodWeb model) with and without harvest for 2016.

Finally, we assessed the importance of the food web approach by comparing predictive ability of the FoodWeb model with a model containing only Ptarmigan data (including direct density dependence [DD] and harvest, hereafter called PtarmiganOnly) and a model containing Ptarmigan and local climate data (DD, harvest, temperature, precipitation and time of winter, hereafter called PtarmiganClimate). We did this to assess the value of collecting additional extensive and potentially costly food web and local climate data for the management of Ptarmigan. To assess whether predictive ability was different between management regions, we also decomposed predictive ability of the three alternative models into management-area-specific predictive ability.

Results

The SFP process produced two major purposes (i.e., deliveries) of the modeling: (1) explanatory predictions to yield a more comprehensive (i.e., ecosystem-based) understanding of the main mechanisms and drivers of Willow Ptarmigan dynamics as a basis for devising efficient monitoring and management strategies and (2) anticipatory predictions to inform stakeholders about the near future state of the population as a basis for adaptive annual management decisions with respect to the Ptarmigan hunt.

Explanatory predictions: Drivers of Ptarmigan population dynamics

The coefficients of the temporal predictors of the full FoodWeb model are given in Fig. 2b (see Appendix S1: Section S3, for more details about less central covariates and parameters).

Most of the temporal climatic predictors significantly influenced Ptarmigan population growth. Increased precipitation around the time of hatching (i.e., first week of July) had a negative effect, while the effect of temperature at the same time had a positive, but non-significant effect. Consistent with the expectation from the camouflage-mismatch hypothesis, there was reduced population growth associated with a later start of winter.

All the predictors reflecting food web interactions were significant. Both a high reindeer carcass abundance and a high rodent abundance the same year had a positive effect on Ptarmigan population growth, while high rodent abundance the previous year had a negative effect. Intensive moth outbreak had a strong negative effect on Ptarmigan population growth.

As expected, harvest had a negative effect on population growth, albeit with a small estimated coefficient relative to the coefficients of the food web predictors and the negative density dependence in Ptarmigan population growth. There was a small negative temporal trend in population growth not accounted for by the covariates in the model.

Annual density estimates were highest in the western part of Finnmark (except for initial density), while the density estimates for inner and eastern part were lower (Fig. 3). There was large variation among transects within each region (Appendix S1: Section S3), and several of the spatial predictors contributed significantly to this variation (see Appendix S1: Section S3, for estimates of the spatial predictors). Despite the significant spatial and residual effects (interaction between spatial and temporal predictors), there was a high degree of synchrony in Willow Ptarmigan population dynamics between the three parts of Finnmark (Fig. 3). As indicated by the coefficients of the direct and delayed rodent predictors (Fig. 2b), there was also some synchrony between Ptarmigan and rodents (Appendix S1: Fig. S5), in particular during the peaks and crashes in 2011–2012 and 2015–2016. The link between Ptarmigan and rodents was not at all clear during 2002–2008, when there was a strong and steady decline in the Ptarmigan populations across Finnmark. This period coincided with an extensive moth outbreak in Finnmark (Jepsen et al. 2013).

Regarding the detection part of the state-space model, average transect level detection probability varied little between transect lines and was generally low (mean = 0.171, SD = 0.019, range = [0.134, 0.195]). As expected, there was a negative relationship between detection probability and the proportion of erect woody vegetation in the surveyed area of the transect lines.

Anticipatory predictions: Near-term forecasting

Short-term predictive performance of the FoodWeb model generally increased (i.e., improved iterative short-term predictive performance) with increasing length of the time series used to parameterize the model (Fig. 4a). This trend was also apparent for the two alternative models. Moreover, predictive performance was on average higher (i.e., lower prediction error) for the FoodWeb model compared to both the PtarmiganOnly and PtarmiganClimate models, even though there were some exceptions in single years (Fig. 4a). After 2014, the prediction error of most candidate models was only 10–25% greater than the theoretical minimum prediction error. While all candidate models predicted next years observed density fairly well (Fig. 4b), the predictions from the FoodWeb model were on average as close or closer to the observed (compared to the two other models). There was, however, one big exception (year 2014), in which both the FoodWeb and PtarmiganClimate models performed poorly. This poor performance is most likely due to extreme values of three predictors (Start of winter 2013, Carcass 2014, and Rodents 2013 and 2014) leading to greatly overestimated predicted densities in 2014, compared to the observed data.

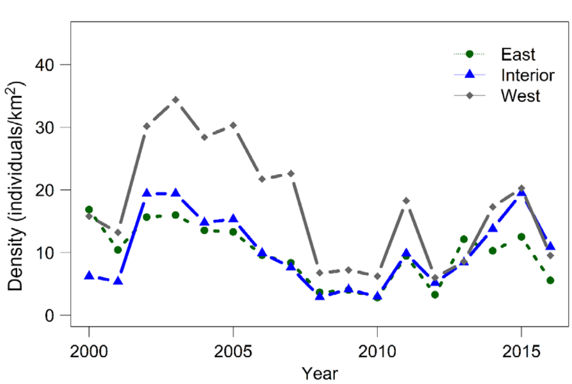

Fig. 3. Willow Ptarmigan population dynamics given as the average model-based density estimates from the FoodWeb model for each of the three parts of Finnmark (east, west, and the interior part).

The contribution of harvest to predictive performance of the FoodWeb model was marginal, accounting for only a 5% (~1.2 individuals/km^2) difference in observed density in 2016 (with harvest 22.56, without harvest 23.77).

Discussion

In an era of rapid and extensive changes in ecosystems worldwide, ecology is increasingly challenged by policy-makers, managers, and everyday citizens with questions about the future state of species and ecosystems. We cannot rely on our understanding of dynamics based on historic variability alone for forecasting future ecosystem change (Groffman et al. 2006, Jackson and Hobbs 2009), as the current pace of environmental change results in increasing novelty of ecological drivers. Hence, decision-makers will need data and predictions, at a time horizon relevant for environmental decision-making, to support and adapt effective mitigating management decisions for the benefit of both wildlife and users. Without adequate models to foresee future impacts of environmental change and guide decisions, we may risk that changes accumulate without a proper understanding of their effects (Halpern and Fujita 2013). Exploring potential impacts and predicting short-term future states, such as in our case study of game populations in a rapidly changing Arctic, provides the basis for collaborative learning, refined data collection, monitoring designs, and management priorities. Coupled with a quantitative objective function, this approach is a required step for building adaptive management programs in a time of rapid and uncertain change (Nichols et al. 2011, Williams and Brown 2016).

Strategic foresight protocol (SFP)

Although it has for decades been advocated for the great value of involving stakeholders in the ecological research process has been advocated for decades, a core ingredient in adaptive management (Walters and Holling 1990) and monitoring (Lindenmayer and Likens 2010), there are not many examples of applying structured protocols for doing so. Here we adopted the Strategic Foresight Protocol (SFP) that has been proposed for tackling rapidly emerging problems in applied ecology (Cook et al. 2014*a*). The SFP is very similar to other stakeholder-oriented processes, such as group model building (Otto and Struben 2004), collaborative modeling for decision support (Langsdale et al. 2013), participatory modeling (Beall and Zeoli 2008), and mediated modeling (Van den Belt 2004), although they use slightly different methods for structured involvement of stakeholders. In the case of the recently red-listed, but still harvested, population of Willow Ptarmigan in Northern Norway,

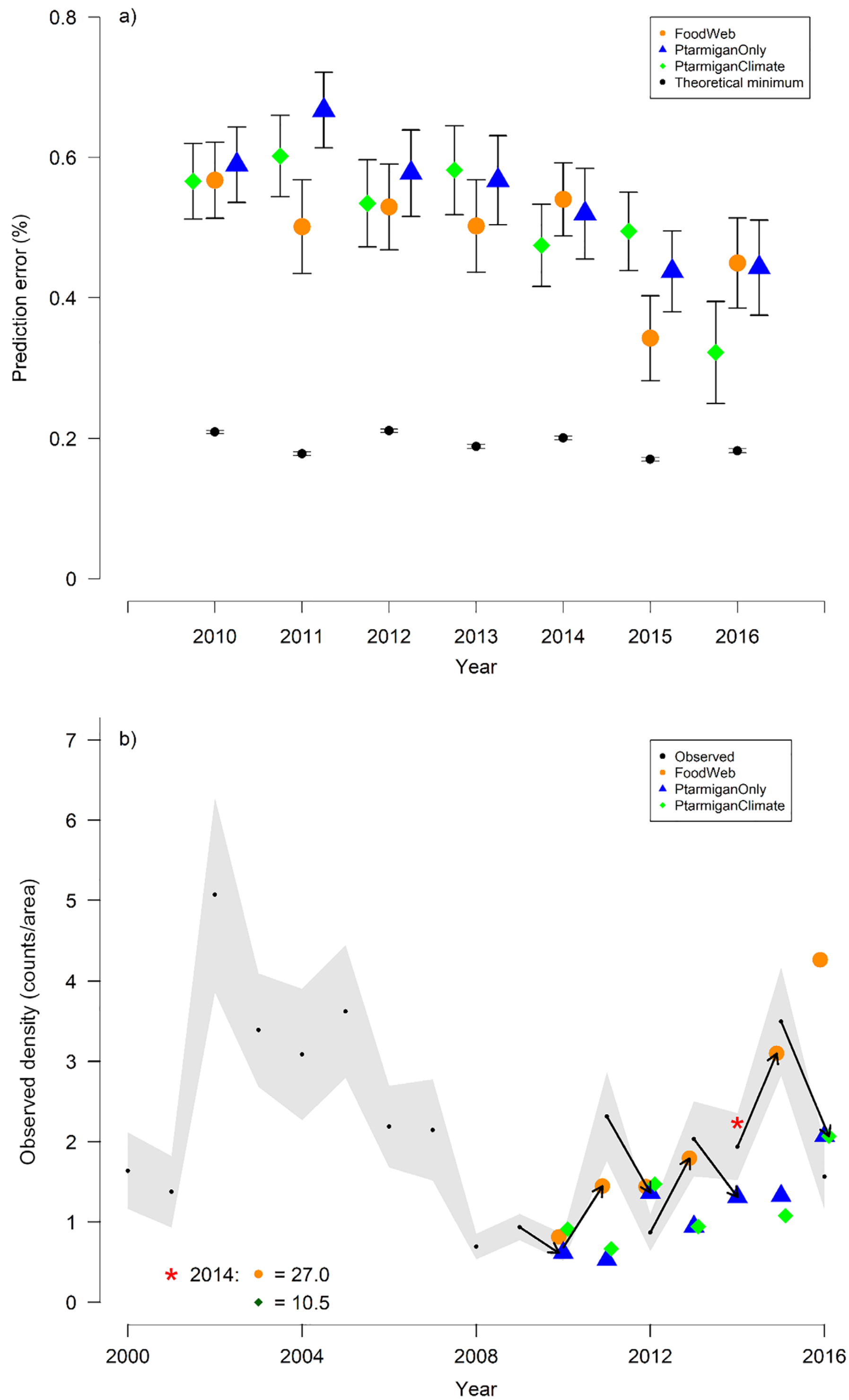

FIG. 4. Prediction error and near-term prediction of line-transect survey counts at the scale of Finnmark. (a) Show iterative percent (percent/100) prediction error (sMAPE) for the three candidate models. (b) Show the three candidate models' ability to predict next year's mean observed density (counts/sampling area). Note (inset) the poor ability of the FoodWeb and the PtarmiganClimate model to predict observed density in 2014. Arrows point to the model that each year predicts next years observed density best. Equivalent graphs for each of the three parts of Finnmark separately (west, interior, and east) is provided in Appendix S1: Fig. S4.1 and S4.2.

we experienced that the SFP constituted a highly functioning framework for involving stakeholders in modeling efforts for the purpose of identifying drivers of past and current dynamics as well as for deriving prediction of the near future state of the population. Our positive experience may have been aided by the traditionally high interest in Ptarmigan as a game species in Norway and the enhanced attention created by the recent red-listing. The SFP also likely benefitted from stakeholders that were well acquainted with previous research on Willow Ptarmigan from Scandinavia.

Implementing the SFP was more time intensive (>3.5 yr) than we expected, even for the first four of six stages of the SFP (Appendix S1: Fig. S1), as they required the commitment of much time from both managers, stakeholders, and researchers. The SFP can appear as a rigid linear stage-by-stage process (Cook et al. 2014*a*), where each stage is completed before moving to the next. However, we decided to adopt a more dynamic approach whereby new views and hypotheses could be implemented in the modeling at every meeting in the stakeholder group. While the process has not yet reached the stage of decision-making on management actions, consensus has been reached about what the likely drivers of Ptarmigan dynamics are, which data sets are to be used, and how models should be used to explore the near future. Several positive and useful experiences have come from the collaborative process. Early involvement of all major stakeholders was decisive in providing legitimacy and trust in the objectives of the process and thereby for the focus and progress of the work. An informal kick-off meeting, governed by an external moderator, enabled stakeholders the opportunity to voice their needs, views, and opinions, as well as take active part in setting the scope of the work, discussing lack of data, data needs, and suitability of available data sources. This increased the understanding of the basis for different stakeholders' viewpoints and counteracted potential conflicts (Redpath et al. 2015). The adopted flexibility in the process, i.e., flexible in the sense that we moved back and forth between stages 2, 3, and 4 of the SFP (see Appendix S1: Section S1), reduced the potential for missed opportunities, and increased the likelihood that stakeholders' views were incorporated as collaborative learning evolved. In summary, the SFP has increased the trust and understanding of different viewpoints among stakeholders as well as between stakeholders and scientists, and thereby increased the likelihood for a positive future outcome with regard to management decisions and actions.

Explanatory predictions: Drivers of Ptarmigan population dynamics

Our model highlights several environmental drivers, acting directly and indirectly, that are important in explaining Ptarmigan population growth and thereby the recent decline of Norwegian Ptarmigan populations (i.e., later winter start, increased precipitation around hatching, intensified moth outbreaks, and potentially a weaker link to small rodent peak years). Some of the effects have been documented in previous studies based on other data sources and time periods. Those include the classic link between Ptarmigan dynamics and the population cycles of sympatric rodents (Myrberget 1984, Steen et al. 1988), the negative impact of severe weather conditions for early chick survival (Erikstad and Spidsø 1982, Erikstad and Andersen 1983) and the weak compensation of harvest despite strong density-dependent growth (Pedersen et al. 2004, Sandercock et al. 2011). However, several of the food web effects documented here have not been previously documented for Ptarmigan, such as the indirect effects of carrion abundance, moth outbreak intensity, and the potential effect of increased camouflage-mismatch on Ptarmigan population growth.

It has been argued that increased abundance of carrion could lead to a resource-driven mesopredator release (Killengreen et al. 2011), negatively impacting tundra-breeding birds (Henden et al. 2014, Henden et al. 2017). A recent study on Lesser White-fronted Goose in Finnmark (Marolla et al. 2019) found a negative impact of carrion abundance on Goose reproductive performance. Hence, the positive effect of carrion abundance on Willow Ptarmigan growth found in this study was unexpected. Future studies should aim to uncover whether and how an increase in carrion abundance may affect Willow Ptarmigan growth rate positively. The timing of a resource pulse relative to the timing of predation-sensitive life-stages of alternative prey might tip such relationships from apparent competition to apparent mutualism (Abrams and Matsuda 1996, 2004).

The duration and severity of outbreaks by geometrid moths in northern Fennoscandian mountain birch forests have intensified due to climate warming (Jepsen et al. 2013). The most recent moth outbreak in Finnmark (2002–2008) resulted in large-scale defoliation of birch trees and shrubs as well as a region-wide state shift of the understory vegetation from shrubs to grass (Jepsen et al. 2013). Interestingly, Jepsen et al. (2013) showed that these effects cascaded to affect the abundance of both rodents and ungulates. Since Willow Ptarmigan diet consists mainly of shrubs (*Salix* and *Vaccinium* spp.) (Weeden 1969, Williams et al. 1980), the large-scale defoliation of these preferred forage plants has likely resulted in less forage for Ptarmigan in areas of intense outbreaks. Insect outbreaks in northern-boreal forests are expected to intensify due to climate warming (Jepsen et al. 2013) and may even extend into the shrub tundra (Karlsen et al. 2013). Therefore, this may constitute a future threat to low- and sub-Arctic Ptarmigan populations.

One of the key manifestations of climate change in Arctic and alpine regions is the increasingly later onset of snow cover in autumn and an advanced spring with earlier snowmelt (Ims et al. 2013*a*, Derksen et al. 2017).

For Ptarmigan, this implies longer periods with white plumage against dark bare ground, and thereby likely increased predation risk as has been documented for boreal hares (Zimova et al. 2016). Considering that predation constitutes the main form of juvenile and adult mortality in most Ptarmigan populations (Smith and Willebrand 1999, Martin 2001, Munkebye et al. 2003) and the autumn season is when Ptarmigan mortality is the highest (Smith and Willebrand 1999), the impact of a mismatch between molt and onset of winter snow cover can be high. The strong negative effect of late onset of winter on population growth is in accordance with the proposed mechanism of increased predation in years of larger mismatch between plumage color and snow cover in autumn (Henden et al. 2017). Hence, in the absence of an adaptive response, such mortality costs could result in strong population-level declines of Ptarmigan populations as snow cover in autumn is predicted to be further delayed due to climate change (Derksen et al. 2017).

Finally, it should be noted that Ptarmigan (both Rock Ptarmigan and Willow Ptarmigan) are presently declining together with a host of other ground-nesting bird species in alpine and Arctic ecosystems (Lehikoinen et al. 2014, Lehikoinen et al. 2019). This trend points toward drivers of change that are not exclusively linked to species-specific traits or management, but rather to general changes in the ecosystem such a climate-warming-induced increased primary productivity (greening) and increased nest predation rates (Kubelka et al. 2018, Ims et al. 2019). This may also explain the declining trend in the Willow Ptarmigan population that was not accounted for by any of the predictors included in our model.

Anticipatory predictions: Near-term forecasting

One of the main needs arising from the foresight process was to assess the performance of models in making *anticipatory predictions* (Bradford et al. 2018, White et al. 2019); i.e., based on the desire of managers and hunters to have near-term forecast of Ptarmigan dynamics prior to the line transect census in late summer. Predictive performance was fairly good compared to what can be theoretically expected given a “perfect” Poisson model, even though predictions in some years were not as good as might be desired (cf. Nichols et al. 2015). There was no clear difference among the different candidate models with regard to predicting next year’s survey counts or improving iterative predictive performance, although the FoodWeb model performed better in most years. Hence, there is currently no strong support for including biotic interactions and thereby embarking on large-scale sampling of food web interactions to aid prediction and management decisions. However, this is not unexpected, given the relatively short time series and low quality and/or resolution of those variables that represented some of the indirect food web interactions such as carcass dynamics, moth outbreak intensity, and small rodent dynamics. However, it may also reflect that simpler models might be preferred to complex models for making decisions (Gerber and Kendall 2018). With more and better data from coming years, our expectation is that confidence will rise in models that perform well and decrease in those that perform poorly. This process will allow us to attain more precise and useful predictions with respect to which drivers of population dynamics are most important (Nichols et al. 2015).

If ecology is to become more relevant for society, we need to be willing to contribute to anticipating and mitigating expected environmental changes, i.e., ecology needs to be more predictive (Evans et al. 2012, Mouquet et al. 2015). Hence, there has recently been an increasing focus on conducting near-term ecological forecasts that operate on timescales relevant to decision-makers (cf. Dietze et al. 2018; Ecological Forecasting Initiative [EFI], *available online*).[6] To our knowledge, we are among the first (Mäntyniemi et al. 2013) to adopt this approach to harvested species while simultaneously addressing the effect of alternative model complexity on short-term forecast ability. In the long run, we think a food web approach to modeling will be most suited for species with complex population dynamics such as many small game populations. This is because more mechanistic models will better accommodate shifting dynamical regimes due to ecological interactions that change over time than simpler phenomenological models (Urban et al. 2016).

Scopes for improved predictions

Although the overall outcome of the SFP has been satisfactory with respect to its purpose, there remains scope for improving on predictive ability. For example, there are limitations regarding what time series of annual population density estimates can explain in terms of mechanisms affecting population growth rates. Demographic data can provide better insights about such mechanisms.

While few studies on harvested species have been able to assess the effect of environmental change by means of demographic models, such approaches will likely provide a richer understanding of the complex effects of climate change (Jenouvrier 2013). Indeed, it has been argued that such understanding is key for the development of more mechanistic models to promote robust predictions (Evans et al. 2012, Urban et al. 2016). However, acquiring individual-based demographic data from Arctic-alpine Ptarmigan populations are logistically and methodologically challenging, and hardly achievable on the temporal and spatial scales relevant for management. However, there is scope for future studies that are able to combine intensive demographic studies

[6] http://ecoforecast.org/

conducted on a relatively small scale with survey-type population monitoring data acquired on a large scale.

Another scope for improving predictions is in data quality. More transect lines and a spatially extended effort to survey Ptarmigan populations could yield more spatially resolved predictions, for instance, at the scale of local municipalities in a management region. Also, higher precision could be gained by better spatial matching of response and predictor variables. In particular, some of the predictor variables that entered our state-space model were spatially interpolated proxies with unknown measurement errors. Increasing sampling efforts to reduce the extent of interpolation and conducting trials to assess measurement errors would likely contribute improved predictive ability.

Conclusion

We used a Strategic Foresight Protocol (Cook et al. 2014*a*, Schwartz et al. 2018), that included several interest groups, to integrate the views and needs of stakeholders. Importantly, drivers that proved to be influential in the modeling were taken into account because of stakeholder involvement, drivers that would not have been included in a purely researcher-driven process. Interestingly, some of these drivers were related to outcomes of recent climate change (e.g., novel pest insect outbreaks and Ptarmigan plumage color mismatch) observed by local stakeholders. Hence, the SFP facilitated the inclusion of recently acquired local knowledge about rapid environmental change. The incentive for conducting near-term forecasting was due to the management's need to have time to prepare, organize, and inform about upcoming harvest regulations. Thus, the ability of the dynamical state-space model to predict population increases and decreases will provide the landowner extra time to consider appropriate harvest regulations as well as early communication of hunting expectations for both local and visiting hunters. The feedback from the landowner indicated that such predictions would be desired and valuable. In general, the modeling approach and access to extensive population and ecosystem data, offer a suitable framework for implementing the views of stakeholders as alternative hypotheses that can be confronted with data. Moreover, the approach forms a structured basis for making short-term predictions that can be iteratively updated and improved as more and new data become available.

Our collaborative modeling approach widens the scope for potential mitigating actions, by highlighting several novel and manageable drivers of Ptarmigan population dynamics and changes. While our results indicate that protection against hunting or reduced hunting quotas would have a positive effect, it appears that the current harvest quotas are not among the key drivers of Ptarmigan population dynamics in the management region and time period considered in the present study. One should be aware that the effect of harvest could to some extent be confounded with the strong negative effect of winter onset, as late snowfall may lead to a longer hunting season compared with years of early snowfall. However, our results suggest that other management actions could be more effective, such as forest management after moth outbreaks. Given that multiple drivers impact the population dynamics, potential management actions are diverse and complicated by the uncertainty in how the drivers act in concert, especially if acted upon by management. Considerations are further complicated by uncertainty about whether the population is in a transient state or at its natural attractor (Hastings et al. 2018), that itself may be moving due to climate change. Furthermore, the community and continent-wide decline in ground-nesting birds (Lehikoinen et al. 2014, Lehikoinen et al. 2019) also urge for consideration of general drivers of change in alpine-Arctic ecosystems (Ims et al. 2019).

Our experience supports the growing evidence of the potential for SFP to aid ecological decision-making (Cook et al. 2014*a*, *b*, Schwartz et al. 2018). However, our experience also emphasizes the need for appropriate time and funding in order to be successful, as well as long-term ongoing involvement from all involved (Reiter et al. 2018). It is difficult to assess the potential benefit of SFP in leading to positive biodiversity change in the long term (Young et al. 2013). Our experience is that an open and flexible process, where all stakeholders' views and opinions are included and treated as "alternative" hypotheses confronted with data, will promote social learning, trust and legitimacy of conservation programs (Young et al. 2013, Sterling et al. 2017). This will increase the likelihood of positive future biodiversity outcomes, which is especially important in light of the current and rapid changes to the natural world (Young et al. 2013, Sterling et al. 2017).

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Supporting Information

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.2120/full

Data Availability

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.hqbzkh1cb

Appendix S1:

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End-user involvement to improve predictions and management of populations with complex dynamics and multiple drivers.

Ecological Applications

Section S1. Strategic foresight process

Table S1. Stakeholders involved in the process:

Affiliation	Representative
Norwegian Biodiversity Information Center	Senior Advisor
FEFO (Landowner Finnmark)	Managers and Head of wilderness division
Ministry of Climate and Environment	Adviser
Environmental Agency	Senior adviser
NOF-BirdLife Norway	Head of Conservation Science Department
The Norwegian Forest Owners Federation	Manager
The Norwegian Association of Hunters and Anglers (NJFF)	Senior Advisor
The Norwegian Association of Hunters and Anglers (NJFF) - Finnmark chapter	Leader, division for small game
The Norwegian state-owned land and forest enterprise	Senior Adviser for Hunting and Fishing
Local pointing dog club – Lakselv, Finnmark	Deputy board members

Section S1.1. Decision on focus and drivers

Stakeholders agreed that the modelling should be based on a food web approach because of the complexity of the suggested impacts of different drivers on willow ptarmigan (Henden et al. 2017, Ims and Yoccoz 2017), such as small rodents and carcass abundance working through predation, and moth insect outbreaks working through vegetation change. However, the willow ptarmigan case study was also a part of larger research project (SUSTAIN) that was mandated by the Research Council of Norway to take an ecosystem-based approach. This also provided an incentive for addressing combined effects of climate and harvesting in a food web context.

The opinions of the stakeholder group constituted an integral part of the iterative process of model development. The inclusion of several of the drivers was largely driven by stakeholders' opinions. For example, the inclusion of carcass abundance, even though the quality of these data are uncertain, and the potential impact of moth insect outbreaks, which mostly impacts sub-optimal willow ptarmigan habitat, was to a large degree initiated by stakeholders' persistent views and opinions. Moreover, it was argued that changes in onset of spring is likely not as important as weather conditions in the time around hatching of mismatch in late autumn, and therefor onset of spring was not included in the model (partly also because of onset of spring was correlated with early July temperature predictor).

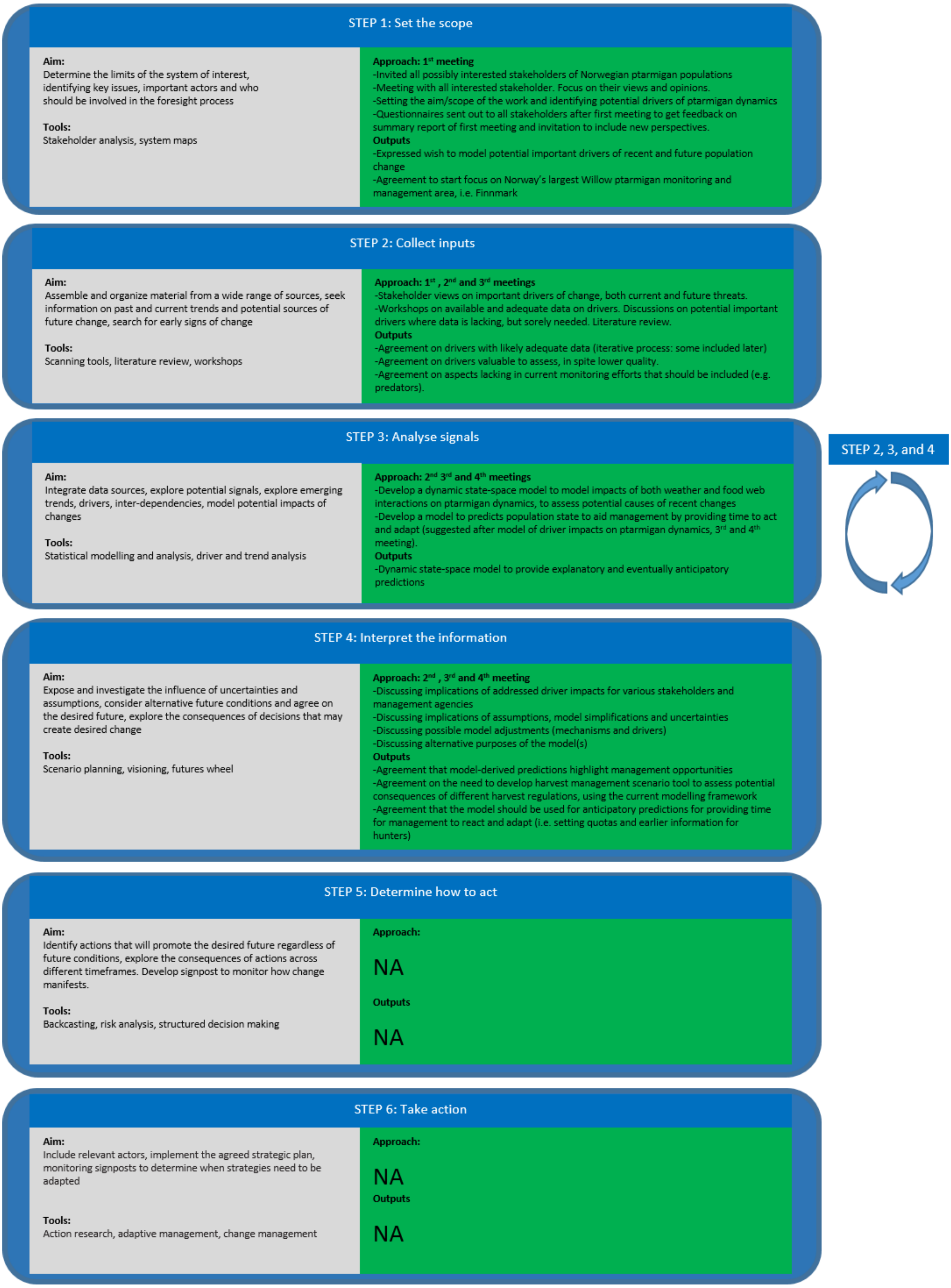

FIG. S1. The six stages of the strategic foresight process with the aims and potential tools (Cook et al., 2014; gray shaded area) and the approach that we have used and the outputs that came out at each stage of the process (green shaded areas). Note that the present paper includes the first four of the suggested six steps in Cook et al. (2014). Figure outline adapted from Adams et al. (2018).

Section S2. Extended material and methods section

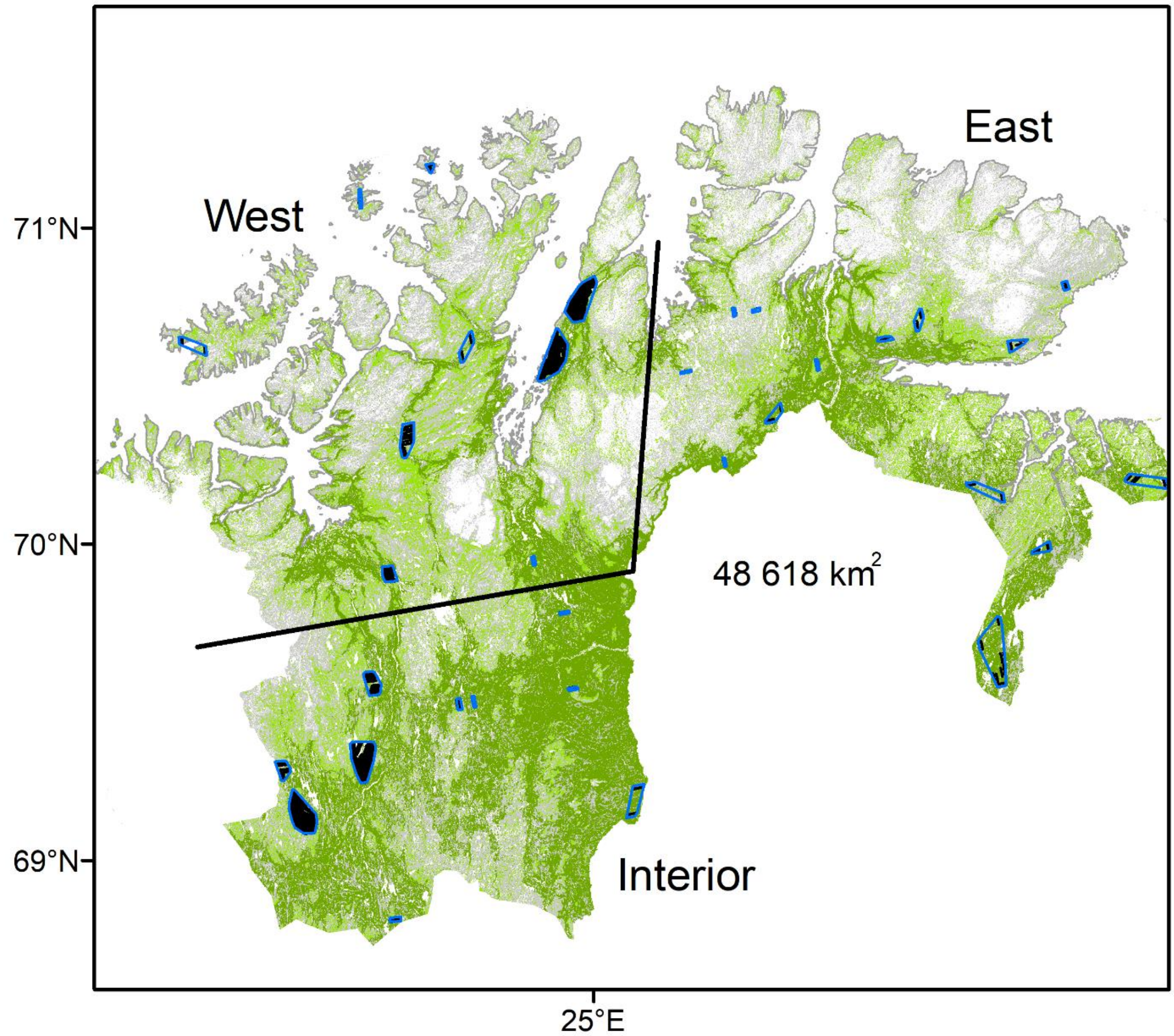

Fig. S2. Finnmark map showing the three management regions (divided by black lines), line-transect areas (blue polygons) and woody vegetation (Dark green: forest, Light green: shrub, Grey: non-woody vegetated, White: other (non-vegetated, water, agriculture, build-up areas)).

Section S2.1. Harvest statistics

FEFO operate with an eastern, western and interior ptarmigan management area (Figure 1), defined based on contrasts in climate, different reindeer herding pastures and estimated ptarmigan densities (Asbjørnsen pers. com.). Harvest regulations were few to none from 2000 – 2010 in Finnmark. However, from 2010 onwards, Finnmark was divided up in 138 hunting terrains and hunting regulations were gradually implemented based on estimated densities from line-transect surveys in August and partly adjusted at the hunting terrain level based on a habitat model (Pedersen et al. 2012). Harvest statistics for each municipality in Finnmark exist for the entire period. However, because of low reporting by hunters up until 2010 (as low as 16%), the local landowner (i.e. management authorities) has adjusted the harvest statistics based on the proportion of hunters reporting each year (e.g. number reported shot / proportion of hunters reporting harvest). From 2010, reporting frequency has gradually increased and is currently high (>90%), due to both better reporting procedures and potential restrictions on hunting if harvest is not reported by the hunter. In the model we used the number of shot ptarmigan per municipality divided by the areas of the municipality, since the different municipalities vary greatly in size. Hence, transect lines within the same municipality were given the same value of the predictor.

Section S2.2. Small rodent and reindeer carrion abundance

Since spring 2004, we have used a large-scale, permanent system for monitoring rodent populations in the tundra of eastern Finnmark, Norway (70°N to 71°N) (Ims et al. 2011), by means of the small quadrat method (Myllymäki et al. 1971). The monitoring system encompasses 109 permanent census sites distributed in treeless tundra easily accessible from roads. At each site, a trapping unit (a 15-m × 15-m small quadrate) with 12 snap traps is activated for 2 d shortly after snow melt in late June (spring) and in mid-September (fall) every year. In the western and interior part of Finnmark small rodent monitoring has been conducted since 2000 (Yoccoz and Ims 2004), by means of live trapping (i.e. capture-mark-recapture), along a transect from the Porsanger fjord (69°N 24°E) along the coast to Karasjok (69°N 25°E) in the interior of Finnmark (Fig. 1). This monitoring system encompasses 12 permanent census sites distributed along valleys in birch forest. At each site, a trapping unit (60x60 m grid) with 16 live traps (Yoccoz & Ims 2004). Trapping is conducted for two days shortly after snowmelt in mid-June (spring) and mid-September (autumn) ever year. Here this transect has been split into the 8 northernmost sites (Porsanger fjord), representing small rodent dynamics in the western part, and the 4 sites around Karasjok, representing small rodent dynamics in the interior part of Finnmark. For the abundance of small rodents, we calculated the mean number of small rodents trapped across trapping grids and days in each region.

We retrieved data on reindeer carcasses from the national database on livestock found dead by reindeer herders (www.rovbase.no). Because of varying effort in searching and documenting reindeer carcasses between different herding districts in Finnmark, the absolute number of reindeer found dead in different areas in Finnmark might not be directly comparable. Therefore, we used the sum of the number of reindeer found dead in Finnmark during winter (January-June) every year as an index of relative carcass abundance at the scale of the entire county.

Section S2.3. Local climate variables

To represent weather conditions during early chick life for willow ptarmigan we acquired data on temperature and precipitation from the Norwegian meteorological institute (MET Norway). This weather data is a collection of observational gridded datasets for temperature and precipitation that covers the Norwegian mainland (Lussana et al. 2016). The gridded datasets are based on the observations from the MET Norway's Climate database and the observations are interpolated on a high-resolution regular grid (1 by 1 km, see Lussana et al. 2016). We used gridded datasets of 1-week average temperature and 1-week total precipitation, respectively. From the gridded datasets we extracted values per transect line (i.e. nearest cells, n=315) per year.

To represent changes in seasonality, we acquired MODIS vegetation indices from USGS (Didan 2015). It has been shown that vegetation index-derived phenology to a large extent agrees with the end-of-snowmelt for the start of the growing season and the start-of-snowing for the end of the growing season (Jin et al. 2017). We chose the enhanced vegetation index (EVI; 16-day L3 Global 250m) which is derived from atmospherically-corrected reflectance in the red, near-infrared, and blue spectrum (Huete et al. 2002). From these data, we estimated the onset of spring and onset of winter as average values for each transect-line area in Finnmark (n=32 line areas), using a double logistic function (Tveraa et al. 2013).

Section S2.4. Moth outbreak intensity

To calculate moth outbreak intensity (i.e. cumulative defoliation score) we followed the procedure used in Jepsen et al. (2009), using MODIS v6. We calculated a NDVI-anomaly score reflecting the degree to which the productivity in an area is lower than the potential, observed across the entire time period (2000-2017). For every pixel, we calculated a reference value as the 95% quantile of max NDVI during the summer (day of year 193-217). For every 8-day period during the summer we calculated the anomaly compared to the reference value. The median over all periods constitutes the anomaly for any given pixel for a given year (see Jepsen et al. 2009 for more details of the method). We used the mean calculated within a 6 km buffer (113 km^2) around each line-transect survey area as the measure of outbreak intensity to get estimates that are more robust for small survey areas. Since these are anomalies, larger negative values denote larger/more intense moth outbreaks.

Section S2.5. State-space model description and JAGS-model code

Statistical analyses

To assess the effect of different covariates on willow ptarmigan growth rate we used a modified version of the Hierarchical Distance Sampling (HDS) model from Kéry & Royle (2016) (see JAGS model code below). When conducting line transect-based distance sampling, the perpendicular distance of each observation to the transect line is recorded (Buckland et al. 2001). The detection probability on the transect line is assumed to be perfect (i.e. p=1), and the detection probability *p* of an observation is defined by a declining function of its distance, *d*, to the transect line. In the current model, we use a half-normal detection function. Then the natural logarithm of the detection probability is:

$$\log(p) = -\frac{d^2}{2\sigma^2} \qquad \text{(S1)}$$

where σ denote the scale parameter of the detection function. Using all the distance data from 2000-2016, we grouped observations into 24 distance bins (max distance = 600 m, bin width = 25 m). This binning smooths inaccuracies in distance estimation and reduces effects of smaller movements of animals in response to observers and dogs (Kéry and Royle 2016, Sollmann et al. 2016). Then, detection probability (i.e. *pcap*) is the integral of the distance function over the distance bins (Kéry & Royle 2016), providing an average detection probability for each transect line (i.e. length*(2*width*)) across years. Note that using a bin-width of 50m did not change the estimates of average detection probability. Because of potential differences in the dogs' search image to dens erect woody vegetation, we modeled the scale parameter σ as a function of a site-specific variable (Marques and Buckland 2003, Sillett et al. 2012). We used a variable denoting the proportion of forest and erect woody vegetation within the sampled area of each line (sampled area (km^2) = length * (2*width)), of each line transect:

$$\log(\sigma_s) = \alpha_o + \alpha_1 * PropForest_s \qquad \text{(S2)}$$

where α_o is the intercept and α_1 is the coefficient related to the site-specific habitat covariate.

Then, for the first year (t=1) we linked the observed counts of ptarmigans (y) for each transect line (s) to the latent abundance N in a strip using the average detection probability, pcap:

$$y_{s,t=1} \sim binom(N_{s,t=1}\ ,\ pcap_s) \tag{S3}$$

Further, we assumed $N_{s,t=1}$ to be a Poisson random variable with expected value $\lambda_{s,t=1}$:

$$N_{s,t=1} \sim poisson(\lambda_{s,t=1}) \tag{S4}$$

Because of variability in the length of line transects and thereby the area covered, the expected value $\lambda_{s,t=1}$ is modelled as the product of density (D) and the surveyed area (i.e. length*(2*width), km^2) covered for each transect:

$$\lambda_{s,t=1} = D_{s,t=1} * area_{s,t=1} \tag{S5}$$

We assumed log density to be normally distributed with mean, mu, and variance σ_1^2, where mu was modelled as a function of covariates:

$$\log\left(D_{s,t=1}\right) \sim norm(mu_{s,t=1},\ \sigma_1^2) \tag{S6}$$

$$mu_{s,t=1} = \beta1_{0,reg} + rCl_1 + \beta1_{x1} * X1_{s,1}\ , \tag{S7}$$

where $\beta1_{0,reg}$ is a regional fixed effect (the three management regions used by FEFO), $\beta1_x$ is a vector of coefficients associated with covariates $X1_{s,1}$. Due to the potential non-independence of transect lines very close together we included a random cluster effect (i.e. rCl_1, ~ Norm(0, σ_{Cl1})). The number of unique clusters was estimated by means of cluster analysis based on the distances between transect lines, using the function *hclust* (method = single) in package *stats* in R. Based on a cutoff distance of 20 km between transect lines, the cluster analysis estimated 25 unique clusters.

For the other years (t > 1) we used the same model structure as above, except that we used the stochastic Gompertz model on $mu_{s,t}$. On the logarithmic scale, the Gompertz model becomes a linear, autoregressive time series model of order 1 [AR(1) process] (Dennis et al. 2006):

$$\log\left(D_{s,t}\right) \sim norm(mu_{s,t},\ \sigma_{proc}^2) \tag{S8}$$

$$mu_{s,t} = \beta_{0,reg} + rCl + \beta_{DD} * \mu_{s,t-1} + \beta_x * X_{s,t} + \beta_{Trend} * (t-1)\ \ , \tag{S9}$$

where $\beta_{0,reg}$ is a regional fixed effect, β_{DD} is the density dependence parameter based on the log density the year before (i.e. $mu_{s,t-1}$), β_x is a vector of coefficients associated with covariates $X_{s,t}$, β_{Trend} is a trend parameter to assess any excess trend across years, not explained by the covariates in the model, and where σ^2_{proc} constitute the variance of the process error. Again we included a random cluster effect (i.e. rCl, ~ Norm(0, σ_{Cl})). It is important to note that because of the trend parameter (i.e. Year), the intercept will increase or decrease as the years increase, depending on the sign of β_{Trend}. Hence, the estimated intercepts in the model (i.e. $\beta_{0,reg}$) corresponds to the first year. Also, $\beta_{DD} < 1$ implies negative density-dependence.

We included the following covariates in the model: average temperature and total precipitation during the first week of July the same year (t), onset of winter the year before (t-1), small rodent abundance both the same year (t) and the year before (t-1) (to represent both the functional and numerical response of predators to rodent abundance, respectively), carcass abundance the same year (t), moth outbreak the year before (t-1) and harvest rate the autumn before (t-1). Moreover, since many covariates consist of a mix of spatial (between sites within year) and temporal (between years within sites) effects, we modelled all the covariates, except small rodent and carcass abundance (which only has a temporal component), with an average spatial (X_s) and temporal effect (X_t), in addition to the "residual" covariate effect ($X_{s,t}$). The average spatial effect is then the average of a covariate across years per site and the average temporal effect is the average value of a covariate across sites per year. For initial log density (t=1), we used small rodent abundance the same year as well as average temperature and total precipitation the first week of July the same year (t) as covariates. Our analysis was performed using JAGS (Plummer 2003), which uses Markov Chain Monte Carlo (MCMC) simulations to estimate posterior probability distributions. All covariates (except year) were scaled (over all locations and time points), with mean = 0 and variance = 1 sd, to ease convergence and interpretation of effect sizes. Note that since small rodent data where acquired using different sampling methods, the data from different regions where scales separately. Consequently, the regional intercepts denote the growth rate at average values of the covariates. All effect sizes from the analysis are given by the mean of the posterior distribution and the 95% Credible Interval (CI), if not otherwise stated.

Section S2.6. - Near-term forecasting

To assess the models ability to predict next year's survey counts (P_s, i.e. predicted observed counts from distance sampling) and more importantly, whether this ability improved with increasing amount of data, we ran the model with t=10 to t=16 years of data. From each run of the model we predicted next year's log density (pred*mu*) for each surveyed line by using the model coefficients from year t and covariate values for the next year (t+1) (which are all measured prior to population surveys in the autumn). Note that we used the covariates scaled across all years and sites for each prediction of pred$mu_{s,t+1}$. While this will influence the estimated parameters (since the mean and sd of any covariate would change with additional years), it will not affect the predictive ability as long the standardization is exactly equal to that of the fitted model (Eager 2017). We then predicted next year's counts by:

$$P_{s,t+1} = (\exp(predmu_{s,t+1} + 0.5 * \sigma^2_{proc}) * area_{s,t+1}) * pcap_s \quad , \qquad \text{(S10)}$$

where σ^2_{proc} is the estimated sd of the process variance, *area* denote the surveyed area (km^2) around each line (i.e. length * (2*width)) and *pcap* is the estimated site-specific detection probability.

The predicted counts (P_s) were compared to the observed counts (O_s) by calculating the symmetric mean absolute percentage error (sMAPE (Makridakis 1993, Makridakis et al. 2018)):

$$sMAPE = \frac{1}{n}\sum_{S=1}^{sites} \frac{|P_S - O_S|}{(|O_S| + |P_S|)} \qquad \text{(S11)}$$

This measure is a frequently used measure of forecast accuracy in the forecast literature. In order to assess the contribution of measurement error to the models' predictive ability we calculated the potential "theoretical" minimum prediction error each year based on a model with no process error but only Poisson variability (so called «perfect model», see R-code below). First, we generated a vector with length equal to the number of lines walked (N) and within the range of observed log counts for year t (y_{vec}, See below for more details). We then performed 1000 simulation where we extracted the predicted values ($ypred_t$) from a Poisson GLM of a random Poisson variable (y_t), with size = N and expected values = y_{vec}, regressed against y_{vec}. We then calculated sMAPE (eq. 2 above) values for each simulation, with $O_s = y_t$ and $P_s = ypred_t$. Finally, we calculated the mean and standard deviation over the 1000 simulations as a measure of theoretical minimum prediction error (see R-code below for more detail).

Finally, we assessed the importance of the food web approach by comparing predictive ability of the full food web model (FoodWeb model) with a model containing only ptarmigan data (intraspecific DD and harvest, hereafter called PtarmiganOnly) and a model containing only ptarmigan and local climate data (intraspecific DD, harvest, temperature, precipitation and time of winter, hereafter called PtarmiganClimate). We did this to assess the importance for the management of ptarmigan in collecting additional extensive and potentially costly food web data. To assess whether predictive ability was different between management regions, we also decomposed predictive ability of the three alternative models into region-specific predictive ability. Note that we performed the procedure of assessing predictive ability in the same manner as for the FoodWeb model, only varying model structure complexity.

Section S3. Model coefficients and effect sizes on realized scale

Table S2. Posterior mean and 95% credible interval of effects on ptarmigan initial density (upper part) and population growth (lower part) in Finnmark. In the lower table, negative parameter estimate indicate a negative effect on population growth, while positive estimates indicate a positive effect on population growth. However, for moth outbreak effects, this is reversed as outbreak intensity is measured as the deviance from a normal year (see material and methods section). Estimates in bold (*) indicate significant effects (i.e. CI not including zero).

Initial density	**Posterior mean**	**95% Credible Interval**	
Region East	1.5	[-0.28 ; 3.26]	
Region Inner	0.96	[-6.36 ; 7.97]	
Region West	0.66	[-8.98 ; 9.61]	
Rodent abundance	-0.67	[-9.39 ; 7.53]	
Temperature	0.06	[-1.18 ; 1.33]	
Precipitation	-0.41	[-1.53 ; 0.69]	
	Posterior mean	**95% Credible Interval**	
Region East	0.71	[0.39 ; 1.04]	
Region Inner	0.61	[0.27 ; 0.96]	
Region West	0.95	[0.63 ; 1.29]	
Density dependence	**-0.27**	[-0.37 ; -0.17]	*
Start of winter - residual	-0.04	[-0.11 ; 0.02]	
Start of winter - spatial	0.09	[-0.02 ; 0.21]	
Start of winter - temporal	**-0.26**	[-0.5 ; -0.03]	*
Temperature - residual	0.12	[-0.02 ; 0.25]	
Temperature - spatial	**-0.41**	[-0.62 ; -0.2]	*
Temperature - temporal	0.08	[-0.11 ; 0.27]	
Precipitation - residual	**-0.15**	[-0.24 ; -0.05]	*
Precipitation - spatial	0.1	[-0.39 ; 0.58]	
Precipitation - temporal	**-0.17**	[-0.35 ; -0.01]	*
Rodent abundance	**0.4**	[0.29 ; 0.52]	*
Rodent abundance (t-1)	**-0.27**	[-0.39 : -0.14]	*
Carcass abundance	**0.25**	[0.08 ; 0.42]	*
Moth outbreak - residual	**0.26**	[0.17 ; 0.35]	*
Moth outbreak - spatial	**-0.37**	[-0.51 ; -0.24]	*
Moth outbreak - temporal	0.38	[-0.31 ; 0.94]	
Harvest - residual	-0.03	[-0.1 ; 0.04]	
Harvest - spatial	**0.24**	[0.09 ; 0.42]	*
Harvest - temporal	**-0.13**	[-0.25 ; -0.01]	*
Trend	-0.03	[-0.07 ; 0]	

Effect sizes on realized scale

Precipitation (temporal effect):

for an increase in maximum precipitation of 1 sd. (~ 9.39 mm), ptarmigan population growth rate decreases by 0.17, on the log scale.

Onset of winter (temporal effect):

for a delay in the onset of winter of 1 sd. (~ 6.48 days) ptarmigan population growth rate decreases by 0.26, on the log scale.

Small rodents (temporal effect):

for an increase in concurrent small rodent abundance 1 sd. (~ 3.43 rodents) result in a 0.40 increase in ptarmigan growth rate, on the log scale, while a similar increase in the preceding year leads to a decrease of 0.27 in ptarmigan growth rate. Note that the number of rodents for a 1 sd. change is slightly different for the three management regions, as they are scaled individually, due to different sampling methods. The value of 3.43 denote the Western and interior parts of Finnmark.

Moth outbreaks (residual and temporal effect):

for a decrease in defoliation anomaly of 1 sd. (~ 6.95), ptarmigan population growth rate increases by 0.26 and 0.38, on the log scale, for the residual and temporal effect, respectively. Note that moth outbreaks is measured as the anomaly in NDVI and hence larger outbreaks leads to larger negative values.

Carcass effect (temporal effect):

for an increase in number of carcasses of 1 sd. (~ 417 carcasses), ptarmigan population growth rate increases by 0.25, on the log scale.

Harvest (temporal effect):

for an average increase in harvest rate of 1 sd. (~ 1.23 individuals / km^2), ptarmigan population growth rate decreases by 0.13, on the log scale.

Average spatial effects:

Temperature: A negative spatial effect implies that in areas of Finnmark with generally higher temperatures, ptarmigan population growth is generally lower. In the beginning of July, this constitutes the interior and eastern interior parts of the county.

Moth outbreaks: A positive spatial effect (note the inverse effect) implies that in areas of generally more intense outbreaks, ptarmigan population growth is generally lower. This effect likely relates to areas of more birch forests in the interior and eastern interior parts of Finnmark, where the outbreaks where most intense (See Jepsen et al. 2009) and where there is less optimal ptarmigan habitats.

Harvest: A positive spatial effect implies that in areas of generally higher harvest outtake, ptarmigan population growth is higher. These areas are in traditionally attractive hunting areas in the interior and western parts of the county.

Variation in density among transects

Table S3. Variation in density among transects within each region and year

Region	Metric	2000.0	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016
East	mean	16.9	10.4	15.6	16.0	13.5	13.3	9.6	8.4	3.6	4.0	2.8	9.5	3.3	12.1	10.3	12.5	5.5
	sd	9.9	9.6	20.7	15.1	13.1	11.3	11.5	11.7	3.4	4.2	3.5	10.7	4.0	17.9	12.4	14.7	6.4
	range	[1.9, 37.4]	[1.6, 57.7]	[1.5, 114.2]	[1.8, 77.8]	[1.5, 54.5]	[1.4, 43.6]	[1.0, 53.1]	[0.8, 65.8]	[0.6, 16.4]	[0.9, 17.3]	[0.4, 16.1]	[1.0, 55.4]	[0.5, 21.1]	[0.7, 81.6]	[1.1, 71.1]	[1.3, 75.2]	[0.8, 37.3]
Interior	mean	6.3	5.4	19.4	19.4	14.8	15.3	9.9	7.7	2.9	4.1	3.0	9.9	5.2	8.4	13.8	19.5	10.9
	sd	5.5	3.6	15.8	12.4	10.2	12.0	10.7	6.7	2.8	3.6	2.5	7.4	2.9	5.1	6.0	10.0	6.2
	range	[1.8, 27.0]	[1.3, 23.3]	[2.0, 99.3]	[3.2, 84.4]	[3.2, 60.2]	[2.6, 72.4]	[1.5, 76.0]	[0.7, 42.0]	[0.4, 18.5]	[0.5, 18.3]	[0.3, 23.3]	[0.7, 60.1]	[0.4, 23.1]	[0.6, 37.7]	[0.9, 44.9]	[0.9, 78.3]	[0.6, 58.7]
West	mean	15.8	13.2	30.2	34.4	28.4	30.3	21.7	22.6	6.8	7.2	6.2	18.3	6.0	8.6	17.3	20.3	9.5
	sd	11.8	7.3	14.7	13.7	13.2	12.2	8.2	13.4	7.1	6.3	7.2	19.1	6.9	8.0	10.4	17.6	10.3
	range	[0.4, 88.3]	[0.7, 44.2]	[1.2, 105.1]	[1.6, 63.6]	[1.4, 109.6]	[1.5, 79.7]	[1.4, 48.6]	[1.5, 94.4]	[0.9, 47.9]	[0.9, 34.1]	[1, 46.0]	[1.4, 122.9]	[1, 58.6]	[1.3, 54.5]	[1.9, 73.1]	[2, 148.5]	[1.6, 109.0]

Section S4. Additional figures and tables

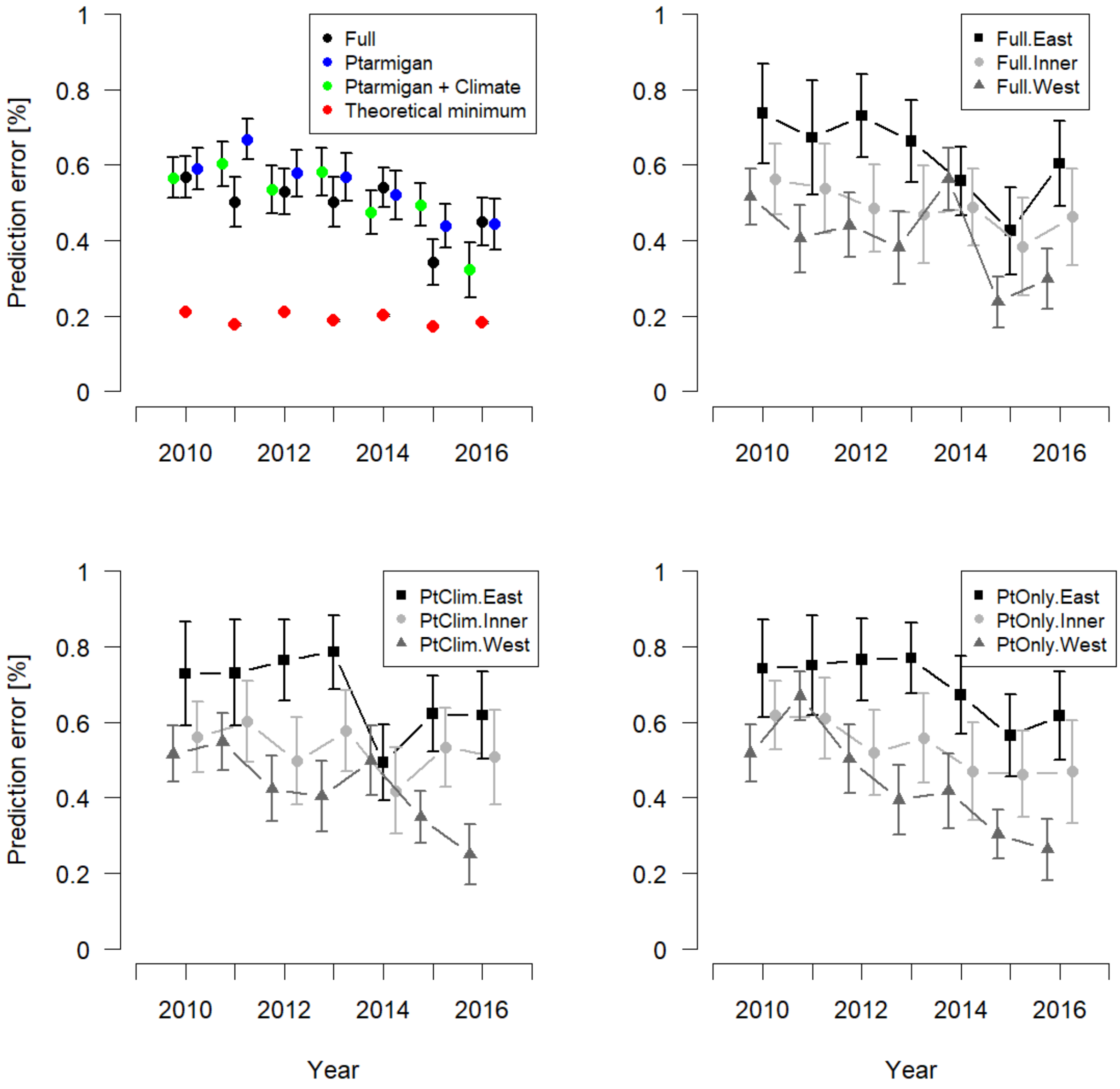

Fig. S3. One-year ahead prediction error as estimated by sMAPE for the years 2010-2016. Upper left panel denote prediction error of the three candidate models and prediction error expected from a perfect poisson process model. Upper right panel denote contrasts in prediction error for the FoodWeb in the three management regions. The two lower panels denote contrasts in prediction error in the three management regions for the PtarmiganClimate and PtarmiganOnly model, respectively.

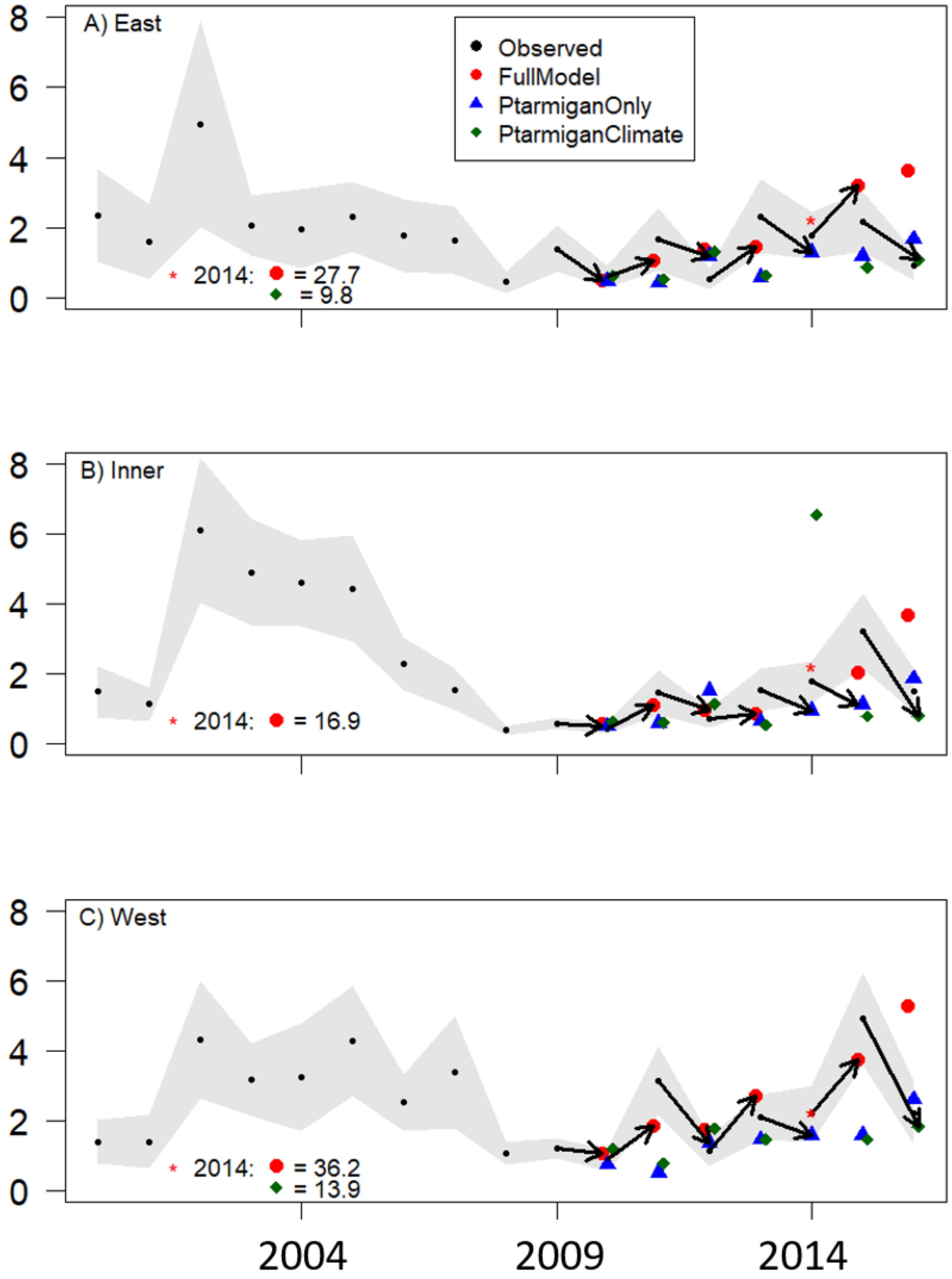

Fig. S4. Regional short-term prediction ability. A-C) show the three candidate model's ability to predict next year's mean observed density (counts/sampling area) for the eastern, Inner and western part of Finnmark, respectively. Arrows point to the model that each year predicts next years observed density best.

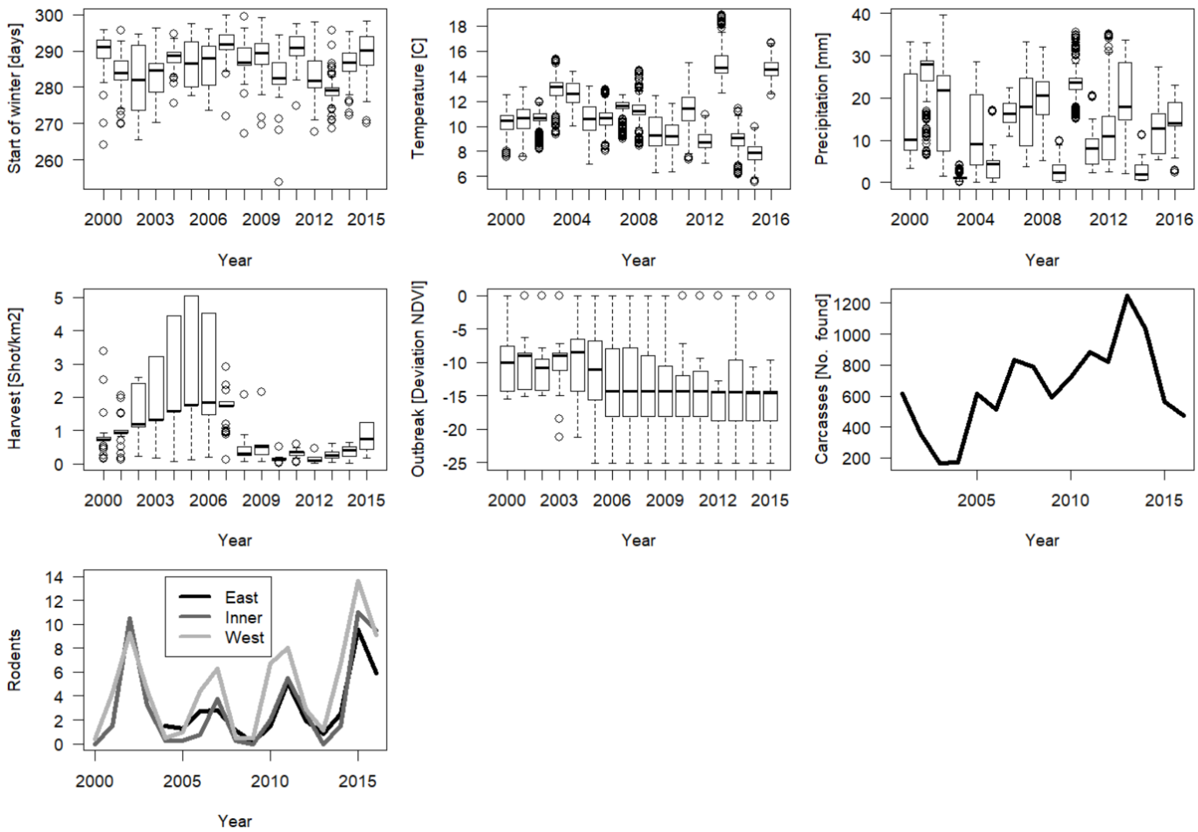

Fig. S5. The time series data for the different predictors in the model. For those predictors where we have adequate spatial replication, we show data as box plots.

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Paper III

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RESEARCH ARTICLE

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Assessing the effect of predator control on an endangered goose population subjected to predator-mediated food web dynamics

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Abstract

1. Assessing the effectiveness of conservation actions to halt population declines is challenging when confounded by other factors. We assessed whether culling of red fox, a predator currently increasing in number in the sub-Arctic, contributed to recent recovery of the critically endangered Fennoscandian population of Lesser White-fronted Goose *Anser erythropus*, while controlling for potentially confounding food web dynamics.
2. Using 19 years of data, 10 before and 9 after the implementation of annual red fox culling, we estimated the effect of this action on annual performance of the goose population. We corrected for the potentially confounding effects of cyclic rodent dynamics and semi-domestic reindeer carrion abundance, both of which are expected to trigger predator functional and numerical responses, as well as for annual variation in spring phenology.
3. Goose reproductive success fluctuated in synchrony with the rodent cycle and was negatively related to abundant carrion. When accounting for these aspects of food web dynamics, there was no evidence for an effect of red fox culling on reproductive success. There was, however, a tendency for fox culling to increase adult survival.
4. Our analysis suggests that goose performance in their breeding area is influenced by fluctuating offspring predation, mediated by mainly natural (rodents) and partly anthropogenic (semi-domestic reindeer) dynamic components of the food web.
5. *Synthesis and applications*. The effect of a decade-long red fox culling on goose reproductive success and survival is currently uncertain, despite predation driving reproductive success through changes in rodent and reindeer carrion abundance. New management actions may consist of regulation of reindeer herd sizes and/or removal of carcasses to reduce the subsidizing effect of reindeer carrion on meso-predators. Getting robust evidence regarding the impact of red fox culling on population recovery depends on continuing research to disentangle food web dynamics and efficiency of management actions.

KEYWORDS
carrion, culling, Lesser White-fronted goose, management evaluation, red fox, reindeer, rodents, tundra food web

1 | INTRODUCTION

Conservation programmes for endangered populations often lack a strategy for evaluating their effectiveness (Sutherland, Pullin, Dolman, & Knight, 2004). Making such evaluations is challenging, especially when the cause of the population decline is uncertain (Caughley, 1994) and when populations have become so small that proper experimental designs underpinning the evaluation of actions are not feasible (Taylor et al., 2017). Therefore, management decisions and their evaluations are often based on ecological intuition rather than scientific evidence (Sutherland et al., 2004).

Conservation actions are typically considered successful when the size of the target population increases (Taylor et al., 2017). Population dynamics, however, is governed by biotic and abiotic interactions. Therefore, attributing a population recovery to a given management action requires considering potential confounding factors (Angerbjörn et al., 2013). Here, we evaluated the effectiveness of a management action implemented to reverse the negative trend of the critically endangered Fennoscandian population of Lesser White-fronted Goose *Anser erythropus*.

This goose species is a long-distance migrant that breeds in sub-Arctic tundra and overwinters in temperate Eurasia. Three distinct populations exist, of which the Fennoscandian population is considered a single management unit (Ruokonen et al., 2004), despite the occurrence of immigration of males from the neighbouring West Russian population (Ruokonen, Aarvak, Chesser, Lundqvist, & Merila, 2010). The Fennoscandian population was breeding in large numbers in northern Fennoscandia until 1920, but in the 1970s, small population sizes started to cause concern (Norderhaug & Norderhaug, 1982). In 2008, the population was estimated to be less than 20 breeding pairs (Aarvak, Leinonen, Øien, & Tolvanen, 2009) and conservation actions were deemed necessary to prevent it from extinction. Actions including habitat restoration, surveillance of stopover sites and attempts to reduce poaching have been implemented through two EU Life projects (Vougioukalou, Kazantzidis, & Aarvak, 2017). The most prominent action is culling of red foxes *Vulpes vulpes* in the goose breeding area. This action is motivated by two hypothesized impacts of red fox predation: (a) that it is a key determinant of goose reproductive success (Aarvak, Øien, & Karvonen, 2017), and (b) that it causes early reproductive failure and the subsequent choice of an alternative moult migration route associated with reduced adult survival (Øien, Aarvak, Ekker, & Tolvanen, 2009; Figure 1a). Both hypotheses are based on the long-term increase of red fox abundance in the Arctic (Elmhagen et al., 2017), while the second posits on the potential risk of adult birds being illegally shot at moulting and staging areas in Russia and, especially, north-western Kazakhstan (Jones, Martin, Barov, & Szabolcs, 2008). There, hundreds of hunters may be unaware of species protection and unknowingly illegally hunt Lesser White-fronted geese (Jones, Whytock, & Bunnefeld, 2017). No estimates of hunting effects on survival rates are available. However, 7 out of 10 transmitter-equipped failed breeders took the alternative route between 1995 and 2006, of which two were later reported shot and three had the signal ceasing abruptly in the supposedly risky areas (Aarvak & Øien, 2003; Lorentsen et al., 1999; Øien et al., 2009). Additionally, four ringed geese were recovered shot-to-death in those areas (Lorentsen et al., 1999). Although this is not a strong evidence for a higher risk along this migratory route, these observations are consistent with this hypothesis. The fact that this goose population was decreasing by 4.4% annually before the onset of the red fox culling programme and increased approximately by 15% annually after (Aarvak et al., 2017; Figure 1b), may suggest a positive effect of this management action. This interpretation, however, may be confounded by other dynamical components of the sub-Arctic food web that have also changed in recent decades.

First, population cycles of small rodents are important drivers of tundra food web dynamics (Ims & Fuglei, 2005) exerting an indirect impact on bird breeding success through the alternative prey mechanism (e.g. Ims, Henden, Thingnes, & Killengreen, 2013; McKinnon, Berteaux, & Bêty, 2014). Numerical and functional responses of fox populations to rodent cycles are key components of this mechanism, which typically causes breeding success of many bird species (the alternative prey) to fluctuate in synchrony with the rodent cycle. While long-term declines in rodent cycle amplitude may have contributed to population declines in northern bird species (Elmhagen, Kindberg, Hellström, & Angerbjörn, 2015; Kausrud et al., 2008), the fact that recent rodent peak densities in northern Fennoscandia have been relatively high (Angerbjörn et al., 2013; Ims et al., 2017) could have had a positive effect.

Secondly, reindeer *Rangifer tarandus* are a key component of tundra food webs (Ims et al., 2007). Fennoscandian semi-domesticated reindeer are maintained at high population densities and often subjected to high mortality rates (Tveraa et al., 2007). Reindeer carcasses constitute a significant part of the winter diet of red foxes in the low phase of the rodent cycle (Killengreen et al., 2011). The increase in red fox abundance has been partly attributed to increased availability of reindeer carrion (Elmhagen et al., 2017; Henden, Stien, Bårdsen, Yoccoz, & Ims, 2014; Ims et al., 2017), resulting from increased herd sizes and changed winter climate (Tveraa, Stien, Brøseth, & Yoccoz, 2014). The numerical response of the red fox to increased carrion availability is expected to have a negative effect on other prey species (Henden, Ims, & Yoccoz, 2009), including the Lesser White-fronted Goose (Lee, Cranswick, Hilton, & Jarrett, 2010).

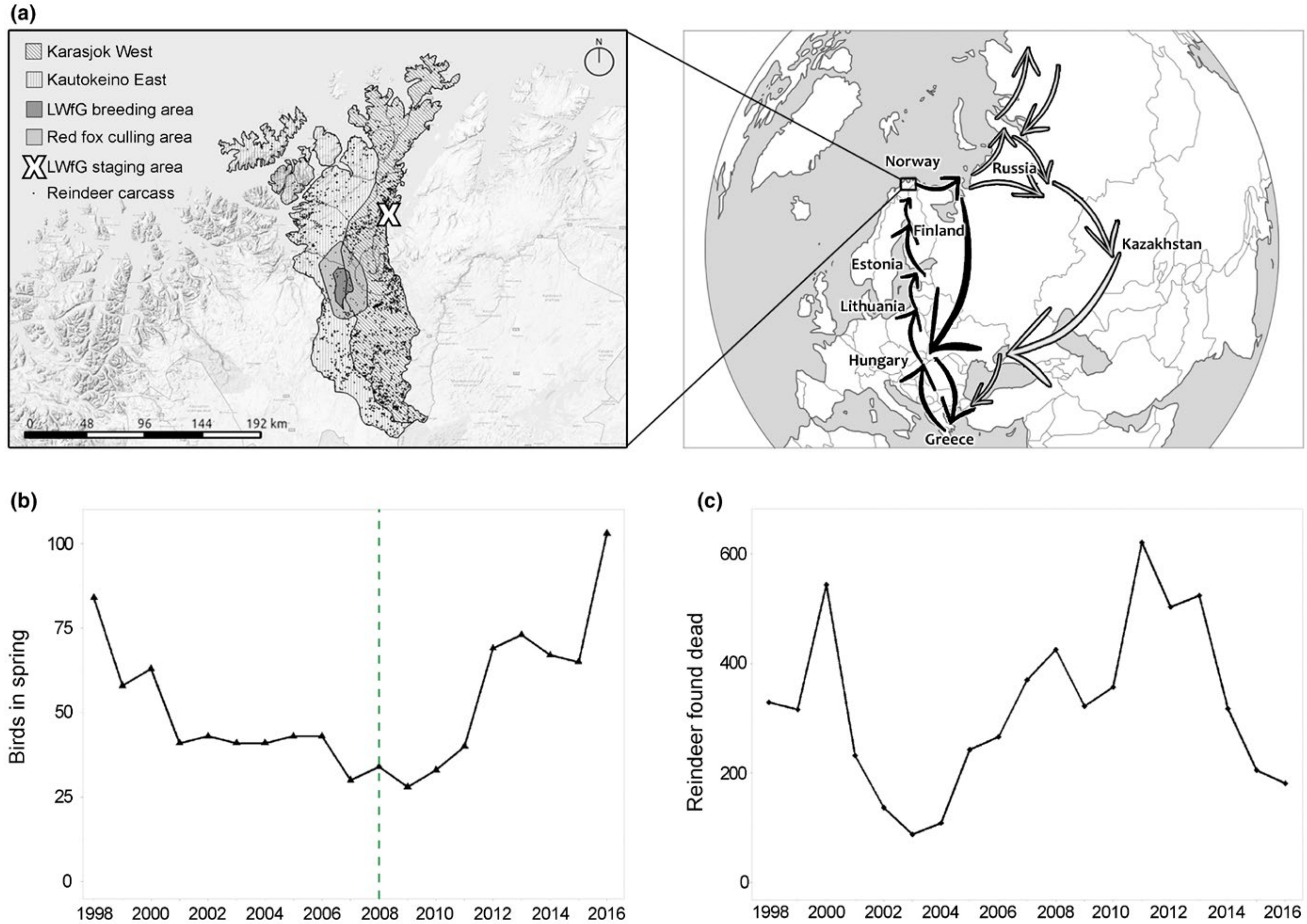

FIGURE 1 (a) Map showing the study area and the migration routes of the Fennoscandian Lesser White-fronted Goose. In the autumn, successful breeders and fledglings migrate over Europe to the wintering sites in Greece (black arrows). Breeders failing at an early stage and non-breeders tend to migrate to moulting tundra areas in western Russia, from the Kanin to the Taymyr Peninsula (Aarvak & Øien, 2003). From there, the autumn migration route takes them through Central Asia with Kazakhstan as a major staging ground, before turning west to the same wintering areas in Greece as the successful breeders (grey arrows). Due to hunting, geese may experience high mortality on this route. (b) Annual goose population size counted during the spring monitoring. The vertical dotted line indicates the onset of the red fox culling programme. (c) Annual number of reindeer found dead in the study area

A third important component is spring phenology. In the Arctic, spring onset typically exhibits large variability between years (Tveraa, Stien, Bårdsen, & Fauchald, 2013), with a trend towards earlier springs during the last decades in Fennoscandia (Karlsen et al., 2009). Spring phenology is expected to affect reproductive success in birds (Visser, Holleman, & Gienapp, 2006), for example, by reducing nesting performance in geese in response to extensive snow cover at onset of breeding (e.g. Madsen et al., 2007; Reed, Gauthier, & Giroux, 2004).

We evaluated whether red fox culling had the expected positive effect on Fennoscandian Lesser White-fronted Goose reproductive success and avoidance by adult birds of the alternative, supposedly riskier migration route, while accounting for rodent population dynamics, amount of reindeer carrion and spring phenology. We based our analysis on a 19-year time series on goose demography that included 10 years before and 9 years after the onset of the management action. We predicted goose breeding success, as well as the number of adults not embarking on the alternative migration route: (a) to fluctuate in synchrony with the rodent cycle due to the alternative prey mechanism, and (b) to respond negatively to increases in reindeer carcasses, because these would enhance fox survival during the winter, leading to higher spring fox abundance and thereby greater predation risk (Figure 2; Appendix S1). We predicted the association between goose population dynamics, rodent population dynamics and reindeer carrion abundance to be weaker after the implementation of the fox culling programme, since the mediation role of red fox would come undone if foxes are effectively removed. Finally, we expected early snowmelt to improve access to nesting sites and thus increase goose-nesting performance.

2 | MATERIALS AND METHODS

2.1 | Monitoring of the goose population

Approximately 90% of the Fennoscandian Lesser White-fronted Goose population breeds in Finnmark County, Norway (69°N–71°N,

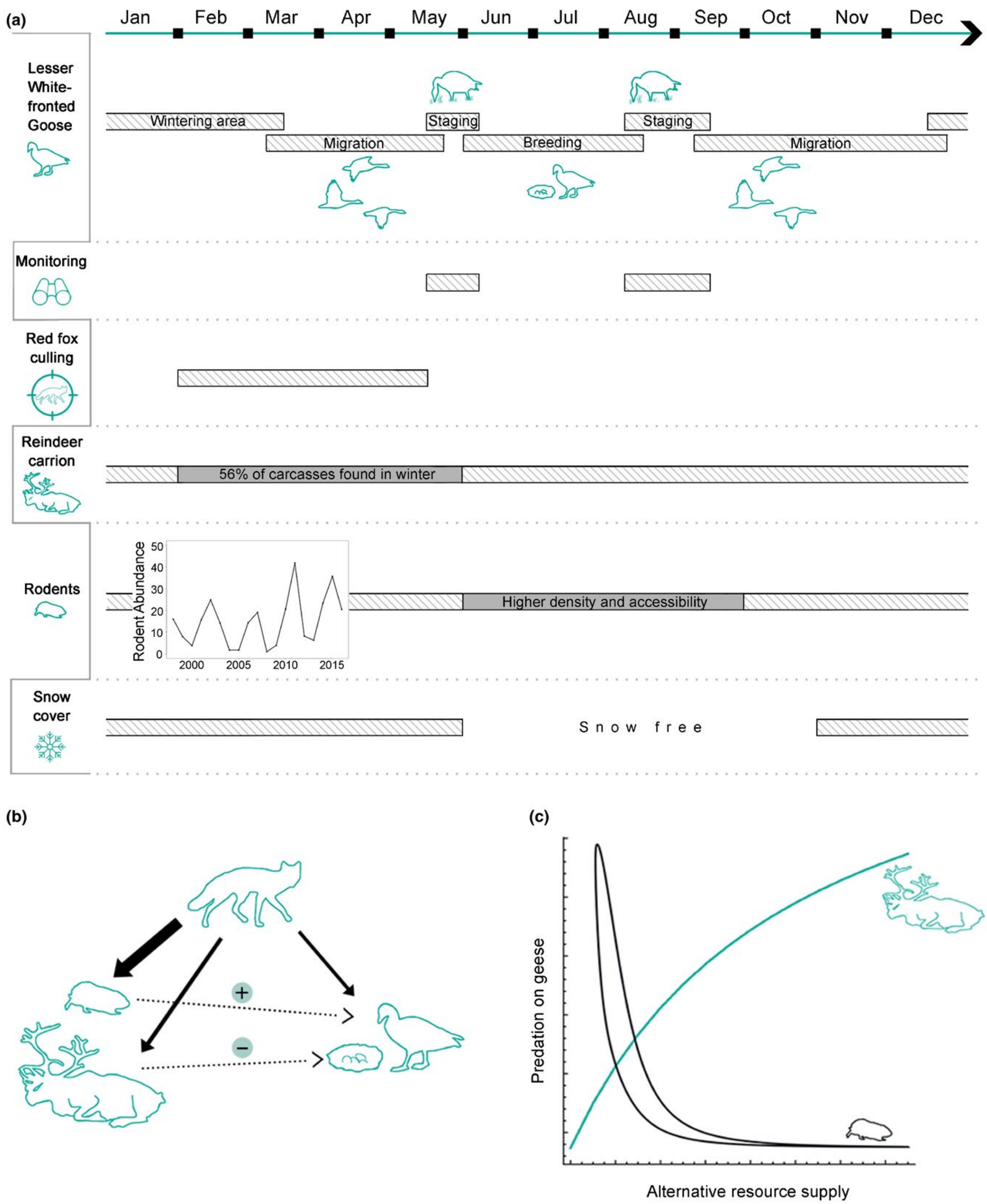

FIGURE 2 (a) Diagram showing the annual cycle of the Fennoscandian Lesser White-fronted Goose population, food web dynamics, monitoring and predator control. Darkest bars mean higher availability and accessibility of the prey item for red foxes. In the study area, rodents show 3–5-year population cycles. (b) Conceptual model depicting a priori interactions between the main species. Full arrows show predation by the main predator, the red fox, on the different prey items. Dashed arrows depict expected indirect predator-mediated relationships. Thicker arrows mean preference for that prey when it is abundant. (c) Model-based predictions (see Appendix S1) showing the effect of alternative resource supplies (small rodents and reindeer carcasses) on predation pressure exerted by red foxes on goose offspring (eggs and chicks). The model predicts that small rodents should show apparent facilitation to geese, while reindeer carrions should show apparent competition with geese

Figure 1a, Aarvak et al., 2009). Geese typically arrive at the staging site at the coastal Valdak Marshes, Stabbursnes (70°10′N 24°40′E) in mid-May, and move to the core inland breeding area by Lake Iešjávri after a staging period of about 1 week (Øien et al., 2009). Eggs hatch at the end of June, and successful pairs start moulting and become flightless. In mid-August, adults and fledglings return to the staging area and stay there for 3 weeks before embarking on the autumn migration. Breeding and staging sites are likely to be exclusively utilized by Fennoscandian breeding pairs, because immigration of birds from Russia is restricted to males and follows pair formation during the non-breeding season (Ruokonen et al., 2010). Immigration is therefore unlikely to occur between the two staging periods. We monitored the goose population annually at the staging site, in spring (since 1990) and autumn (since 1994, Figure 2a). In spring, we recorded the total number of individuals and potential breeding pairs. We identified individuals based on unique patterns in the black belly patch by means of telescopes and digital videos. In autumn, we recorded the total number of adults, juveniles, broods and brood sizes. These counts provided a minimum number of birds that is probably close to the number of birds that utilized the breeding area, under the assumption that most birds also used the staging site. Because the belly patch pattern changes slightly each year, individuals could not be identified across years. See Øien, Aarvak, Lorentsen, and Bangjord (1996) and Aarvak et al. (2009).

2.2 | Red fox culling

Field inspectors from the Norwegian Environment Agency culled red foxes in February–May during 2008–2016 in an area of 1,242 km^2 encompassing the goose breeding grounds (Figure 1a). Culling was aided by means of snowmobiles and snow conditions that allow detection of fresh fox tracks, and finished when snow conditions made the search for fox tracks ineffective. The number of foxes culled varied considerably between years (mean [range] = 101 [10, 360]), owing to both variation in snow conditions and fox numerical response to rodent cycles (Figure S1). By means of a removal model fitted to the number of red foxes culled every year, we estimated the reduction in fox population size due to culling as varying between 22% and 43% among years (Appendix S2; Figure S2).

2.3 | Dynamical and environmental components

Data on small rodent population dynamics come from a monitoring programme conducted in the coastal birch forest along the Porsanger Fiord, approximately 50 km from the goose breeding area. The numerically dominant rodent species in the study region, the grey-sided vole *Myodes rufocanus*, was live-trapped on eight 60 × 60 m grids each year in June and September between 1998 and 2016. The rodent index was derived from capture–mark–recapture data as described in Ehrich, Yoccoz, and Ims (2009). We used the average number of individuals per trapping grid and year as a measure of rodent abundance (Figure S3).

Data on reindeer carrion come from the national database on livestock found dead by reindeer herders (www.rovbase.no). As an index of carrion availability, we used the number of reindeer carcasses found between 1998 and 2016 in the herding areas of Karasjok West and Kautokeino East, which include the main goose breeding area (Figure 1c). This index does not result from a rigorous sampling design, as the search for dead reindeer is opportunistic. Thus, carcass abundance is likely to be underestimated. However, the number of livestock found dead strongly correlates with the number of animals claimed lost by reindeer herders (r = 0.76, 95% CI [0.39, 0.92], n = 14), a metric used in previous studies (e.g. Tveraa et al., 2014), and with the estimated minimum available carrion biomass (r = 0.99, 95% CI [0.98, 1.00], n = 14; see Appendix S3).

We used Normalized Difference Vegetation Index (NDVI) remote sensing data from the Global Inventory Modeling and Mapping Studies (GIMMS), with 8-km spatial and bimonthly temporal resolution, to measure vegetation green up in spring in the study area (Pettorelli, 2013; Figure S4). We used this NDVI product as a measure of phenology because it is the only satellite product available over the whole period of our study. GIMMS-based NDVI correlates well with winter snow depth and spring temperature (Nielsen et al., 2012) and gives a spatially explicit measure of spring conditions. See Appendix S4.

2.4 | Data analysis

We used three measures of the annual goose performance. First, the proportion of breeding pairs that were successful in year t, $b(t) = \frac{B_a(t)}{P_s(t)}$, where B_a is the number of breeding pairs that had at least one fledgling counted during the autumn monitoring, and P_s is the number of potential breeding pairs counted during the spring monitoring. Second, the average brood size, $j(t) = \frac{F_a(t)}{P_s(t)}$, where F_a is the total number of fledglings counted during the autumn monitoring. These two variables were highly correlated (r [95% CI] = 0.97 [0.93, 0.99], n = 19), but we decided to analyse both as they reflect different aspects of the breeding success. Lastly, we calculated the ratio of adult birds in the autumn (A_a) to adult birds in the spring (A_s), $a(t) = \frac{A_a(t)}{A_s(t)}$. The ratio can exceed 1 because in some years more adult birds are counted during the autumn monitoring than in the spring monitoring. This ratio is assumed to give an inverse estimate of how common the use of the eastern and likely more risky migration route is among adults, because adults that fly that route should have left before the autumn surveys were conducted. The correlations between this ratio and the other two measures of annual performance were 0.66 (95% CI [0.30, 0.86], n = 19) and 0.74 (95% CI [0.42, 0.89], n = 19), respectively. To evaluate the different hypotheses regarding the impact of fox culling on the performance of the goose population, we developed a suite of seven a priori models that included different combinations of confounding factors while avoiding overparameterization. The seven models were fitted to each of the three measures of goose performance. We then assessed the influence of each parameter

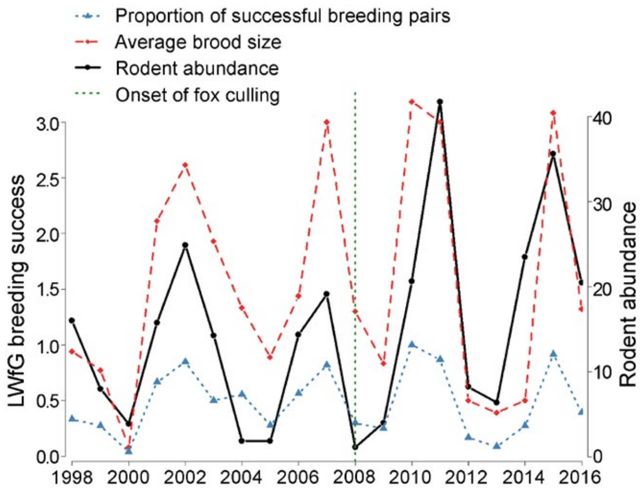

FIGURE 3 Time series of measures of Lesser White-fronted Goose (LWfG) breeding success (proportion of breeding pairs that were successful and average brood size) and rodent abundance (average catches per grid). Note that the scale on the two *y*-axes is different. The vertical green line indicates the onset of the red fox culling programme

TABLE 1 Mean, minimum and maximum values of the different variables before and after the onset of the culling programme. Rodent abundance is expressed as average voles captured per trapping grid. Note that the ratio of adults counted in the autumn to spring can be higher than 1 (see Section 2). Onset of spring represented vegetation green up, with higher values representing greener vegetation and thus earlier spring

Variable	Before (n = 10 years)	After (n = 9 years)
Proportion successful pairs	0.49 (0.04–0.85)	0.47 (0.09–1.00)
Fledglings per pair	1.51 (0.08–3.00)	1.57 (0.39–3.18)
Ratio adults autumn to spring	0.71 (0.16–1.50)	0.89 (0.50–1.40)
Rodent abundance	12.00 (1.88–24.88)	17.97 (1.13–41.75)
Number of carcasses	263 (88–544)	384 (181–621)
Onset of spring	0.43 (0.28–0.61)	0.42 (0.30–0.56)

by evaluating whether effect sizes were similar across models. We did not use model selection criteria or model averaging methods because our aim was to assess the consistency of parameters across different models, not to find the most supported models or to provide an overall estimate. For sensible interpretation of effects, this approach is preferred to other approaches such as model averaging, especially when interactions among predictors are tested (Cade, 2015). Rodent abundance, number of reindeer found dead, rodent abundance the previous year, onset of spring and the categorical variable "culling" indicating the absence or presence of red fox culling, were entered as predictor variables. Density-dependence was not included, given the low goose population density in the breeding area. Because we expected small rodent abundance to be a key driver of variation in breeding success, this variable was present in all the models. We tested for an interaction between rodent abundance and number of reindeer carcasses to evaluate whether red fox responses might reach some degree of saturation during the rodent peak. We also tested for interactions between culling and both rodent abundance and number of reindeer carcasses, because we expected the effect of the latter two variables to become weaker after the onset of the fox culling programme. Similarly, we tested for an interaction between culling and rodent abundance the previous year, because we expected any delayed effect of rodent abundances through predator numerical responses to be dampened by fox culling.

We used generalized linear mixed models to model annual variation in the proportion of breeding pairs that were successful, the average brood size and the ratio of adults in autumn to spring. We used a logit link function and assumed a binomial distribution to analyse the proportion of breeding pairs that were successful. For both average brood size and ratio of adults in autumn to spring, we used a log link function assuming a Poisson distribution, modelling F_a as the response with log (P_s) as an offset for average brood size, and A_a as the response with log(A_s) as the offset for the ratio of adults in autumn to spring. Because of overdispersion, we used quasi-likelihood methods for all models (Ver Hoef & Boveng, 2007). Model fit was evaluated by residual diagnostics. To avoid systematic patterns in the residuals, we included a random rodent cycle effect (five categories reflecting the five rodent cycles in our time series: 1998–2000, 2001–2004, 2005–2008, 2009–2012, 2013–2016; Figure 3) in the models for proportion of successful pairs and average brood size. We assessed multicollinearity with correlation plots and Variance Inflation Factors, and excluded highly correlated variables from the same models. We performed all statistical analyses with R 3.4.3 (R Core Team, 2017). Estimates of effect sizes and uncertainty of covariates on average brood size from the function GLMMPQL in the MASS package (Venables & Ripley, 2002) were similar to those provided by the glmmTMB function in the more recent GLMMTMB package (Magnusson et al., 2017). We chose to use GLMMPQL because it allows fitting quasi-likelihood methods also with binomial-distributed data for mixed models, that is, for analysis of $b(t)$. Parameter estimates of all fitted models are provided in Tables S1–S3.

3 | RESULTS

The proportion of breeding pairs that were successful ranged between 0.04 (in 2000) and 1.00 (in 2010), while average brood size ranged between 0.08 (in 2000) and 3.18 (in 2010; Figure 3). The ratio of adults in autumn to spring varied between 0.16 (in 2000) and 1.50 (in 2007; Figure S5). The average proportion of successful pairs and the average brood size in the 9 years after the onset of fox culling was similar to the 10 years before, while the ratio of adults in autumn to spring slightly increased (Table 1). The 19-year study included four full rodent cycles with a period of 4–5 years between the peaks (Figure 3). The two cycles after the onset of the fox culling programme tended to show somewhat higher peak densities than the cycles before (Figure 3; Table 1). Number of reindeer

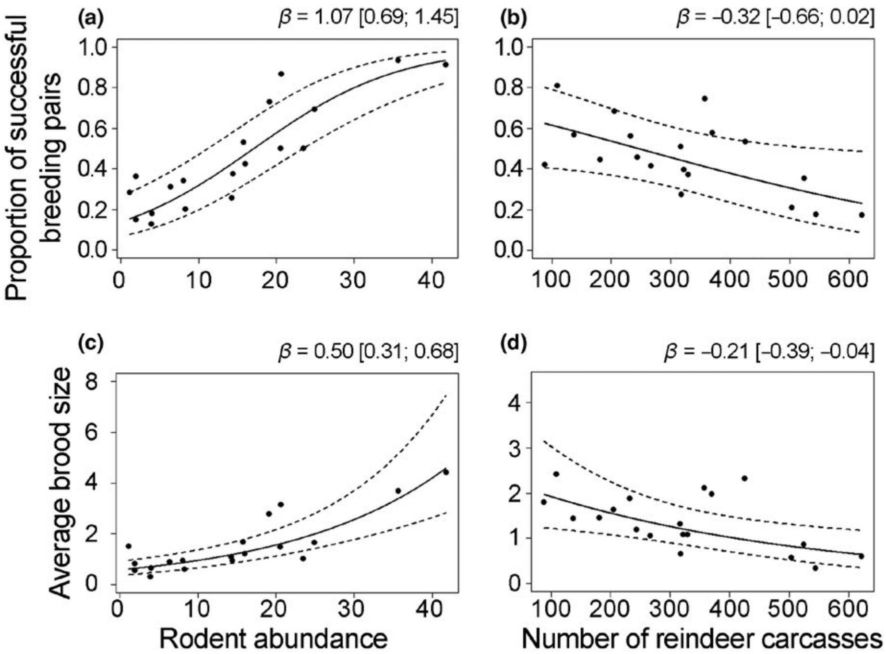

FIGURE 4 Effect of small rodent abundance and reindeer carcass abundance on the proportion of Lesser White-fronted Goose breeding pairs that were successful (a, b) and average brood size (c, d). Full line indicates model prediction (based on model 2 in Tables S1 and S2 respectively), dashed lines indicate 95% confidence interval, dots are partial residuals. Slope (β) estimates (95% CI) on the logit (a and b) and the log scale (c and d) are provided on top of each panel. Predictors are here rescaled (rodents/10, carcasses/100). Note that the scale on the *y*-axes differs between (c) and (d)

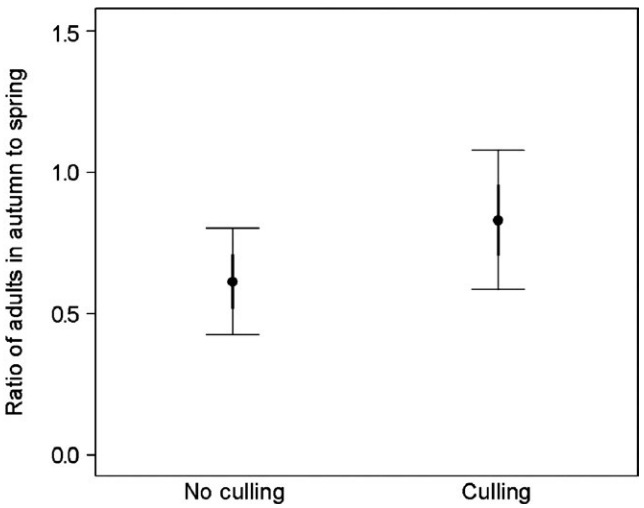

FIGURE 5 Effect of red fox culling on the ratio of adult geese counted in the autumn to the spring. This measure is assumed to reflect the portion of the Lesser White-fronted geese that takes the alternative, likely riskier migration route through western Russia. Nine years of fox culling (2008–2016) are compared to 10 years without management actions (1998–2007). Predicted values, *SE*s (thick black lines) and 95% CIs (whiskers) are based on model 5 in Table S3. Note that the ratio of adults in the fall to adults in the spring can be higher than 1 (see Section 2)

found dead was on average higher after the onset of the culling programme (Table 1) and ranged between 88 (in 2003) and 621 (in 2011; Figure 1c).

Rodent abundance showed a positive effect on both the proportion of breeding pairs that were successful (Figure 4a; Table S1) and average brood size (Figure 4c; Table S2). On average, 92% of breeding pairs were successful in years with rodent peaks (i.e. ~40 voles/grid), while on average only 21% was successful in the rodent crash phase (i.e. ~5 voles/grid). Similarly, fledgling success was on average 4.2 during a peak phase and 0.7 in the crash phase. In all models that included a reindeer carrion effect (Tables S1 and S2), an increase in the number of reindeer found dead tended to show a negative effect on the measures of breeding success (Figure 4b,d). Approximately 24% of breeding pairs were successful and 0.7 fledglings were produced per breeding pair in years with high carrion abundance (i.e. ~600 reindeer found dead), whereas approximately 61% of breeding pairs were successful and 1.9 fledglings were produced per breeding pair in years with low carrion abundance (i.e. ~100 reindeer found dead). Estimated effect sizes for carrion abundance were consistent among the models (Tables S1 and S2). There was no evidence for an effect of onset of spring, rodent abundance the previous year or an interaction between rodent and carcass numbers on the measures of breeding success (Tables S1 and S2). Most importantly, there was no evidence for the fox culling programme and its interactions with other predictors to affect measures of breeding success (Tables S1 and S2).

With respect to the ratio of adults in autumn to spring, the models only suggested a weak effect of small rodent abundance (Table S3). We did not find support for an effect of other predictors and their interactions (CIs widely overlapping 0), but point estimates for the effect of carrion abundance were consistently negative in all the models (Table S3). In addition, the model including rodent abundance, carrion abundance and culling suggested that culling could increase the ratio (Figure 5), but the evidence is inconclusive because of wide confidence intervals and considerable variation in effect size estimated from different models.

4 | DISCUSSION

Using 19 years of data, we contrasted 9 years of conservation action (red fox control) against 10 years of non-action, on measures of annual performance of the Fennoscandian Lesser White-fronted Goose population while accounting for food web components expected to affect predation pressure. As expected, we found goose breeding success to fluctuate in synchrony with the rodent cycle (i.e. apparent facilitation, Figure 2b,c), and to decrease in years with high abundance of reindeer carcasses (i.e. apparent competition, Figure 2b,c). This suggests that temporal variation in predation, mediated by major fluxes in the tundra food web, is likely to be an important driver of goose population dynamics. While red foxes were expected to play a pivotal role in these dynamics, we found no evidence for red fox culling to affect these food web interactions.

As is typical for most critically endangered populations, the targeted goose population is so small and spatially restricted that using replicates and controls in a rigorous experimental management design is not feasible. An equivalent red fox culling action performed in the context of Arctic fox conservation in Fennoscandia (Angerbjörn et al., 2013) benefited from the existence of several remaining populations, among which different actions could be allocated to provide evidence of a positive effect of red fox culling. Here, despite a design based on a single before–after comparison, the lack of evidence for a positive effect on goose breeding success after 9 years of intensive red fox control suggests that the management action has not been effective in this respect. Both failing at emptying the area of foxes and/or compensatory immigration (Lieury et al., 2015; Newsome, Crowther, & Dickman, 2014) after the completion of the culling may explain this result. Alternatively, the biological impact of red fox predation on goose dynamics may have been overrated, as the importance of other generalist predators such as corvids and eagles (Henden et al., 2014) may have been overlooked. Also, the possibility of a substitutable effect by other nest predators, such as mustelids (Parker, 1984), may disguise the effect of fox removal on goose dynamics. We found a tendency for the ratio of adult geese in autumn to spring to be higher after the onset of the red fox control programme. This may suggest that fewer adults embarked on the likely riskier migration through western Asia. Thus, the red fox culling may have affected goose behaviour in a way that made them stay in the sub-Arctic for longer and then use the putatively safer migration route. Such a positive effect of culling may have contributed to the recent increase in the goose population, but the uncertainty in the model estimates makes it impossible to draw firm conclusions at this point.

The role of rodent cycles as drivers of predation pressure on eggs and chicks has previously been shown for many tundra-nesting birds (e.g. Ims et al., 2013; McKinnon et al., 2014) as well as other Arctic geese (e.g. Gauthier, Bêty, Giroux, & Rochefort, 2004; Summers & Underhill, 1987). Nonetheless, the relationship between Lesser White-fronted Goose reproductive success and the vole cycle appears to be exceptionally strong and temporally consistent (Figure 3). Northern rodent cycles show systematic changes over time (Henden et al., 2009) and appear to be particularly sensitive to climatic change (Kausrud et al., 2008). Thus, the Fennoscandian population may be negatively impacted if the rodent cycles become more irregular and dampened due to increased climate warming (Nolet et al., 2013).

The negative relation between reindeer carrion abundance and goose breeding success provides the first empirical support for the hypothesis that resource-driven (i.e. bottom-up) mesopredator release (Killengreen et al., 2011) may negatively affect tundra-breeding birds (Henden, Ims, Fuglei, & Pedersen, 2017; Henden et al., 2014). In Finnmark, 56% of the carcass availability occurs in the mid-late winter (i.e. February–May, Figure S6), when body conditions of mesopredators/scavengers are likely to be at their lowest. Hence, high carrion availability likely enhances red fox survival during this critical period, increasing the probability of predation during the bird's nesting season in June/July. Therefore, with respect to the conservation of the Lesser White-fronted Goose and tundra birds in general, changes in reindeer management strategies should be considered.

Contrary to previous studies on bird breeding success (Madsen et al., 2007; Reed et al., 2004), we found no direct effect of spring phenology on both measures of goose reproductive success, although estimates were in the expected direction. The spatial resolution of the GIMMS data may have been too coarse to catch the precise phenology of the relatively small goose breeding area. However, using the higher resolution MODIS NDVI data on a shorter time period did not reveal any effect of spring phenology (Tables S4–S6). This suggests that Arctic geese might be able to start nesting as soon as enough suitable nest sites have become free of snow, even at a time when much of the tundra is still snow covered (Madsen et al., 2007). Alternatively, NDVI might have been a low-quality proxy compared with a more direct measure of timing of snowmelt, which was not available for our study.

5 | CONCLUSIONS

The Lesser White-fronted Goose case study has both general and specific implications. Generally, it highlights challenges in assessments of management efforts applied to small populations that are subjected to complex food web dynamics, especially when such dynamics involves compensatory mechanisms (e.g. predator functional and numerical responses) or transience (e.g. changing rodent cycle). This emphasizes the need for obtaining long-term data, not only on the conservation target itself but also on important drivers in the food web. Here, we benefited from long time series on the dynamics of rodent and reindeer carrion, which could be linked to the performance of the goose population, allowing us to conclude that the red fox culling action has not improved goose reproductive success. To determine the cause of this lack of effect, we would have required direct time-series data on predator functional and numerical responses, which are extremely hard to obtain.

Another important insight is that subtle changes, but still demographically influential changes in performance, may be involved in the response of the target population to management actions. As indicated by our analysis, it is possible that red fox culling has increased the survival rate of adult geese by affecting their migratory behaviour. Nevertheless, the high uncertainty in our estimates implies that more data are required to determine whether nest predation rates truly influences adult survival. In addition, comprehensive demographic analyses will be necessary to assess the influence of nest predation on the long-term growth rate of this goose population.

Our study provided also the first empirical support for the hypothesis that high availability of ungulate carrion exert a negative impact on ground-nesting tundra birds (Killengreen et al., 2011). The hypothesized mechanism involves mesopredator species that act also as facultative scavengers, which both expand into carrion-rich ecosystems and respond numerically to the surge in the carrion pool (Henden et al., 2014), thereby exerting a cascading impact on native species. Given the large extent of occurrence of semi-domesticated reindeer in the Eurasian tundra, and the acknowledged range expansion of boreal mesocarnivores like the red fox into the Arctic (Elmhagen et al., 2017), the implications of our study extend beyond the borders of Northern Fennoscandia. Furthermore, changes in climate and herding strategies are likely to affect patterns of reindeer mortality. Although earlier springs and longer growing seasons should benefit semi-domesticated reindeer (Tveraa et al., 2013), density dependence and unfavourable snow condition (e.g. ice-crusted snow from more frequent thaw-freeze cycles) may lead to very high winter mortality, subsidizing the facultative scavenger community. Accordingly, we suggest that management strategies for both semi-domestic and wild populations of reindeer, as well as other boreal and Arctic ungulates, should account for the potential subsidizing effect of carrions. In the case of the endangered Lesser White-fronted Goose population, new management actions could aim at regulating herd size to reduce winter mortality or removing carcasses in the surroundings of the breeding area, although distant carcasses may still exert an impact by sustaining populations of highly mobile predators. Overall, it is important to continue both the population monitoring and the management assessment including new data, in order to better assess the importance of red fox culling in the population recovery.

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AUTHORS' CONTRIBUTIONS

All authors contributed to conceive the ideas and collect the data; F.M., J.P.M., N.G.Y. and A.S. analysed the data; F.M. and R.A.I. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.c18qh26 (Marolla et al., 2019).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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Supplementary Information

Appendix S1

Generating predictions for how alternative prey abundance affects predation on geese

Motivated by the work of Suryawanshi *et al.* (2017), we were interested in developing a theoretical framework to explore under which conditions we observe the hypothesized mechanisms. We generated the predictions shown in Fig. 2c based on a model of how alternative resource supplies (i.e. small rodents or reindeer carcasses) may affect predation pressure, in this case exerted by red foxes on geese. Predation pressure can be a combination of numerical and functional responses, thus we combined these responses following a previously published model (Fryxell & Lundberg 1994) that allowed us to make explicit our assumptions on how different prey resources affect predation. Unfortunately, we are not aware of any direct measurements of red fox foraging behaviour on rodents or carcasses, so we rely on qualitative evidence to build the model assumptions.

Red foxes can respond both functionally and numerically to rodent cyclic dynamics. Red foxes have been shown to have high proportion of rodents in their diet when rodent abundance becomes high, i.e. towards the peak phase of the rodent population cycle (Killengreen *et al.* 2011; Ims *et al.* 2017). This likely means there is a minimum density of rodents that, if exceeded, makes the foxes behaviourally switch to and consume almost exclusively rodents. This follows optimal foraging theory, assuming rodents are the most profitable prey item (Macarthur & Pianka 1966; Charnov 1976; Fryxell & Lundberg 1994). In addition, red foxes can respond numerically to small rodents, usually showing higher density the year after a rodent peak (Lindström 1989; Henden, Ims & Yoccoz 2009).

Reindeer carrion can also be an important resource. For example, in Finnmark red foxes subsist primarily on reindeer carcasses during the low phase of the rodent cycle (Killengreen *et al.* 2011). Reindeer carcasses are more abundant in the late winter (56% of dead livestock is found between February and May) so we expect carrion consumption by foxes to happen mostly in this period, i.e. before the goose-breeding period. Therefore, given that food has been shown to be a limiting factor for red fox populations (Lindström 1989), we expect foxes to respond numerically in the same year to reindeer carrion through increased survival and reproduction. Our modelling does not distinguish between survival and reproduction, but assumes that the numerical response includes the combined effects of these processes.

To generate predictions based on these assumptions, we used a diet choice model following Fryxell & Lundberg (1994). In this model, the probability a_R for attacking an alternative resource R (rodents or carrion) depends on the density of the alternative resource R so that

$$a_R(R) = \frac{R^b}{1 + h_R R^b}$$

where b is a shape parameter and h_R is the handling time of that alternative resource. This form allows us to create curves of different shapes for different values of b. We assume small values of b ($b < 2$) to account for some likely behavioural variation, because assuming high values for b would create curves that are very close to a step function and thus represent perfect diet choice based on optimal foraging theory. The attacking of geese is assumed to be of secondary importance to the other prey types, so that abundance of other prey types is primarily what determines responses of foxes.

We included this probability of attack a_R in the multispecies disc equation (Macarthur & Pianka 1966; Charnov 1976; Fryxell & Lundberg 1994), which determines the predation rate on the focal prey item (i.e. the G geese). Predation rate on the geese $z_G(G)$ is then defined as

$$z_G(G) = \frac{a_G G P}{1 + a_R R h_R + a_G G h_g}$$

Where a_G is the probability for attacking geese G and h_g is the handling time of geese. We assumed the geese population G to be at a relatively constant low value, therefore what drives the change in predation rate $z_G(G)$ is largely a function of attack $a_R(R)$ on alternative resources (rodents or carrion), abundance of alternative resources R, and abundance of predators P. We included this predation function in the dynamical predator-prey model based on Fryxell & Lundberg (1994) to determine how predation changes as a function of the different alternative resource abundances R (rodents or carrion) and the abundance of predators P (foxes). For the sake of reducing complexity, we considered the alternative resources (rodents and carrion) to act independently of one another on the focal prey (geese) in the model, meaning that we modelled two different systems, one with rodents and one with carrion. Future theoretical work could look at the interactive effect of all three species, although this is challenging because it is unlikely that they can easily coexist in a model. We also do not consider other prey or caching behaviour.

The model defines the rate of change of alternative resource R, geese G, and predators P to be governed by

$$\frac{dR}{dt} = \mu_R R \left(1 - \frac{R}{K_R}\right) - \frac{a_R R P}{1 + a_R R h_R + a_G G h_g} - m_R R \tag{1}$$

$$\frac{dG}{dt} = \mu_G G \left(1 - \frac{G}{K_G}\right) - \frac{a_G G P}{1 + a_R R h_R + a_G G h_g} - m_G G \tag{2}$$

$$\frac{dP}{dt} = P \left(\frac{a_R e_R R + a_G e_G G}{1 + a_R R h_R + a_G G h_g} - m_P\right) \tag{3}$$

where μ_i is the maximum growth rate of prey species i, K_i represents carrying capacity of prey species i, m_i is the mortality rate of species i, and e_i is the energy conversion of prey species i into predators.

We ran numerical simulations of this model (see Fig. S7 for an example output of a simulation). Simulations started from low initial conditions for the state variables and were stopped after state variables had reached their attractor. We used these final densities from the attractor (for rodents, densities over the last full predator-prey cycle) to calculate the predation rate on geese (shown in Fig. 2c). The result was the combined multi-species functional and numerical responses of the predators to their prey.

A range of patterns can be generated depending on exact parameters, especially for the rodent cycles, which can have slightly different shapes. Predation can increase or decrease with rodent abundance depending on the phase of the cycle. However, we generally found patterns similar to the one shown in Fig. 2c, i.e. we observed low predation rate on geese at high rodent abundance and high predation rate on geese at high carrion supply.

Parameters for Fig. 2c are $b = 2$, $\mu_R = 8, \mu_G = 1.4, K_R = 16, K_G = 8, m_R = 0.01, m_G = 0.01, m_P = 0.6, h_R = 1, h_G = 4, e_R = 1, e_G = 1$ and changes in abundance due to the endogenously-generated predator-prey cycles are used to generate the predation curve for rodents. Parameter values of $b = 0.1$, $\mu_R = 4, m_R = 0.01, m_P = 0.2, h_R = 1, e_R = 1$ while manipulating carrying capacity K_R to get different abundances are used to generate the predation curve for carrion. For both predation curves, we set $G = 1$ to calculate the predation rate since we assumed goose abundance to be low and most parameter values lead to unstable equilibria for two prey species with only one predator (Fryxell & Lundberg 1994). We also tested whether results changed when we imposed a constraint that the probability a_R for attacking the alternative resource R versus the probability a_G for attacking geese G must sum to 1, so that $a_R + a_G = 1$, but it did not qualitatively change results. We found that the ranges of parameters $b = [0.1; 2]$, $\mu_R = [4;\ 8]$, $m_P = [0.5;\ 0.6]$, led to cycles, while the ranges of parameters $b = [0.1; 2]$, $\mu_R = [4;\ 8]$, $K_R = [2;\ 16]$, $m_P = [0.2;\ 0.4]$, did not lead to cycles. For parameters where we observed cycles, we found a positive influence of the alternative prey on the geese (apparent facilitation) in agreement with previous predictions on the impact of predator switching (Abrams & Matsuda 1996). For parameters where we did not observe cycles, we found a negative influence of the alternative prey on the geese (apparent competition), as it is often observed (Holt & Bonsall 2017). Thus, we used the model assumptions and output as support that our hypothesized predictions are feasible. However, we caution that more data is needed on fox responses to different prey types in order to make more accurate predictions on how predation on geese should be affected by rodents and carrion.

Appendix S2

Removal and catch per unit effort models for the fox population

We estimated the total population size of the fox population based on the reduction in catch per unit effort over time within a culling season. The red fox culling program commenced in 2008. In the period 2012-2016, the field inspectors from the Norwegian Environment Agency who culled red foxes also recorded the search effort on the days they were searching for foxes as the distance driven (km) by snowmobiles.

Assuming a closed fox population over the culling season (no immigration, emigration, mortality or reproduction of significance), the population size will decrease as animals are removed by the culling, and the catch per unit effort is expected to decrease due to the reduction in the density of animals.

Let N_t be the population size at survey day t and $Removed_t$ being the number of individuals that has been removed by culling from the population in the period from day 0 to day $t-1$. We then have that

$$N_t = N_0 - Removed_t \qquad \text{(eq. 1)}$$

where N_0 is the initial fox population size before culling commences. Assuming all animals have the same probability of being detected and culled, p_t, and detections are independent between occasions, the number of animals culled on day t, $Cull_t$, will follow a binomial distribution (Borchers *et al.* 2002):

$$Cull_t \sim Binomial(N_t, p_t) \qquad \text{(eq. 2)}$$

The probability of detecting and culling a fox is expected to depend on the search effort. Here we model the relationship between the search effort on day t, $Effort_t$ and p_t using the model:

$$p_t = 1 - e^{-\theta \times Effort_t} \qquad \text{(eq. 3)}$$

We assume the detection parameter, θ, to be constant accross surveys.

If culling has no effect on N_t, we suggest as an alternative to eq. 1 to model the data:

$$N_t = N_0 \qquad \text{(eq. 4)}$$

We fitted the removal/cpue model (eq. 1-3), and the pure cpue model (eq. 2-4) to the data on foxes culled using a maximum likelihood approach. The parameter N_0 was allowed to vary among years. Using AIC as criteria, it was clear that the removal/cpue model (AIC = 480.6) fitted the data better than the pure cpue model (AIC = 488.7).

The estimated reduction in the fox population size due to culling, estimated as sum(C_t)/ N_0, varied among years between 22% and 43 % (Fig. S2, top-left). Variation in initial fox population size N_0, estimated reduction in the fox population size, number of shot foxes, and effort followed the same among-year pattern (Fig. S2).

Appendix S3

Details of carrion biomass calculation

Herders can obtain compensation for animal loss due to predation by large carnivores (lynx *Lynx lynx*, wolverine *Gulo gulo*, wolf *Canis lupus*, brown bear *Ursus arctos*, golden eagle *Aquila chrysaetos*) upon suitable documentation of the type of predation. Qualified personnel of the management authorities use differences in killing techniques to decide upon the cause of death of livestock found dead, whenever possible. For the scavengers, the available reindeer carrion biomass is likely to be more important than the raw number of carcasses. Thus, we initially used data on livestock found dead in the herding regions of Karasjok West and Kautokeino East to calculate the minimum yearly amount of biomass available for scavenging. We divided the dataset by sex and age (calf, adult) of the carcass found, and extracted frequencies for each cause of death (lynx, wolverine, golden eagle, wolf, brown bear, other causes). The number of brown bear kills was very small and was included in the category "other causes". We multiplied sex- and age- specific mean body weight by the frequency of carcasses in each category to get an estimate of the biomass available, and we subtracted estimates of predator-specific daily food requirement obtained from the literature (Brown & Watson 1964; Andren *et al.* 2011; Wikenros *et al.* 2013). We assumed daily food requirement to reflect the amount of biomass immediately consumed by a given predator and, therefore, not available for scavenging. The estimated mean annual biomass was 5093 kg for Karasjok West (range = 1179, 9925) and 2325 kg for Kautokeino East (range = 800, 3740). Although being corrected for predator consumption, the estimated reindeer biomass was highly correlated with the number of reindeer found dead (r = 0.99, 95% CI [0.98, 1.00], n = 14). Thus, we chose to use the latter to elongate the time series (1998-2016), because body weight data are available only for the period 2000-2015. Data on body weights were obtained from annual reports of the Norwegian agriculture agency, which summarise data from government approved slaughter houses (see e.g. Anonymous. 2012. Ressursregnskap for reindriftsnæringen. Reindriftsforvaltningen, Alta. 126 p.).

Appendix S4

We extracted Normalized Difference Vegetation Index (NDVI) remote sensing data for the study area using the Minimum Convex Polygon (MCP) delimiting the Lesser White-fronted Goose core breeding area, and one-pixel buffer around this MCP. We calculated the average NDVI in the study area for June (i.e. when the geese start reproducing) as an estimate of annual variation in vegetation green-up. Because Global Inventory Modeling and Mapping Studies GIMMS data is available until 2015, while Moderate Resolution Imaging Spectroradiometer (MODIS) data on 250 m spatial resolution is available for the period 2000-2016, we used the linear relationship between estimates obtained from GIMMS and MODIS from 2000-2015 to predict GIMMS value for 2016. The correlation between these two variables for the period 2000-2015 is r = -0.67 (95% CI [-0.88, -0.27], n = 16). The linear regression with GIMMS as response variable and MODIS as predictor variable had the following form:

$$y = 0.0087x + 1.8123$$

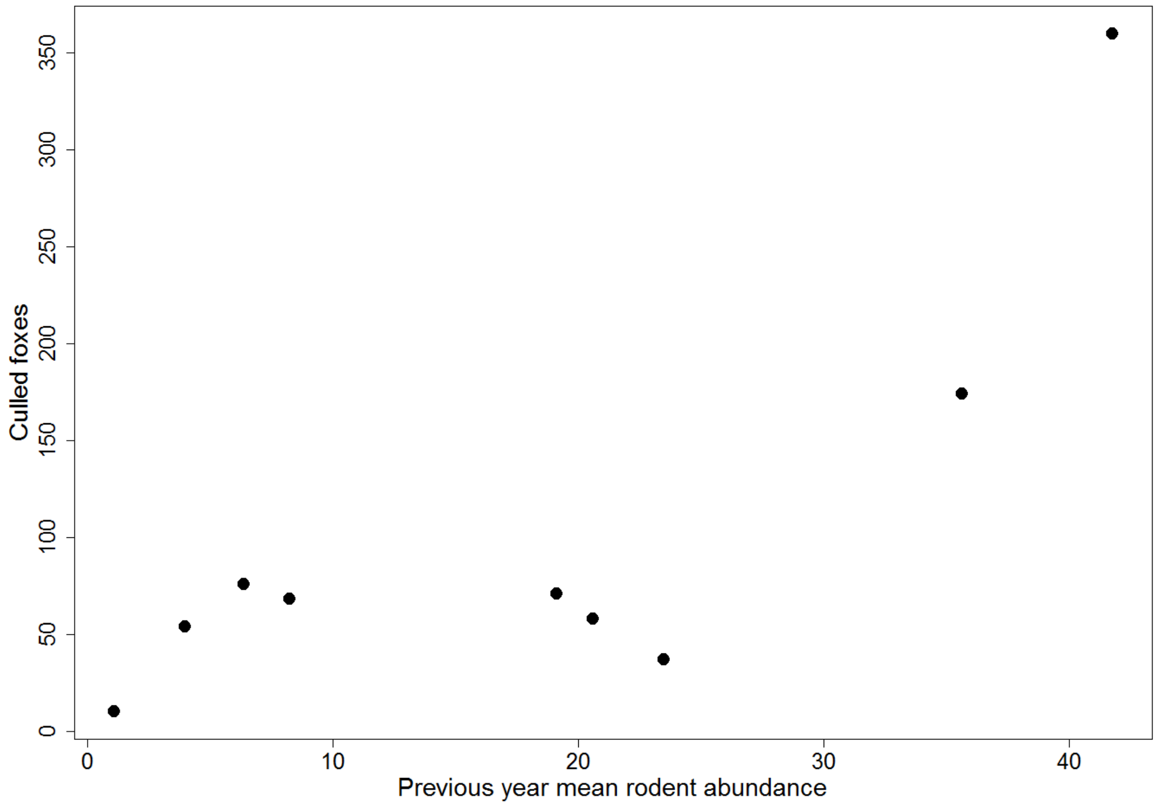

Fig. S1. Culled red foxes in relation to rodent abundance in the previous year (mean catches per trapping grid). Fox culling started in 2008.

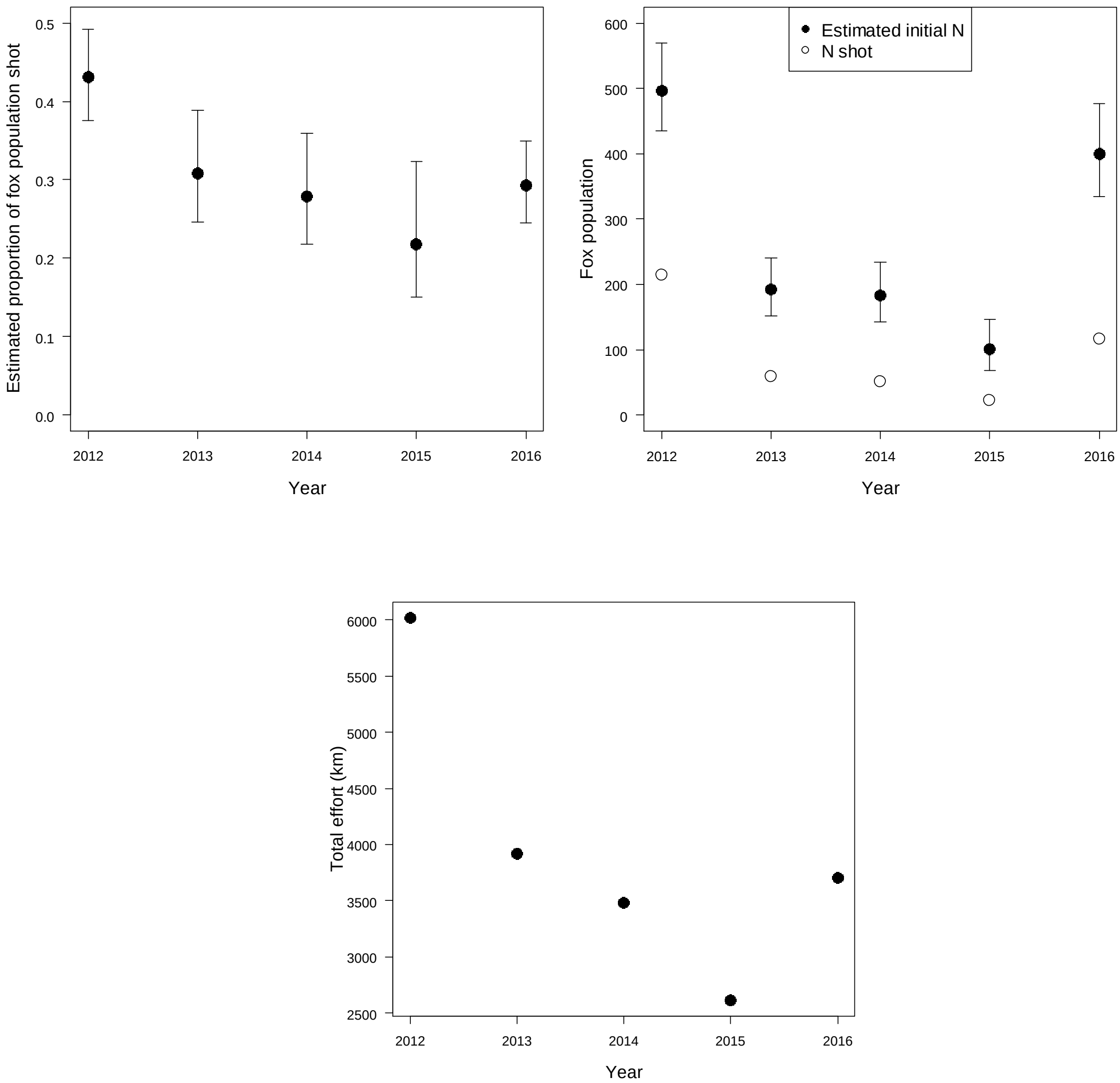

Fig. S2. (Top-left) Estimated annual reduction in the fox population size because of culling with 95% profile likelihood confidence interval bars. (Top-right) Estimated initial population size of foxes (N_0) with 95% profile likelihood confidence interval bars, and number shot each year (N shot). (Bottom) Total effort per year.

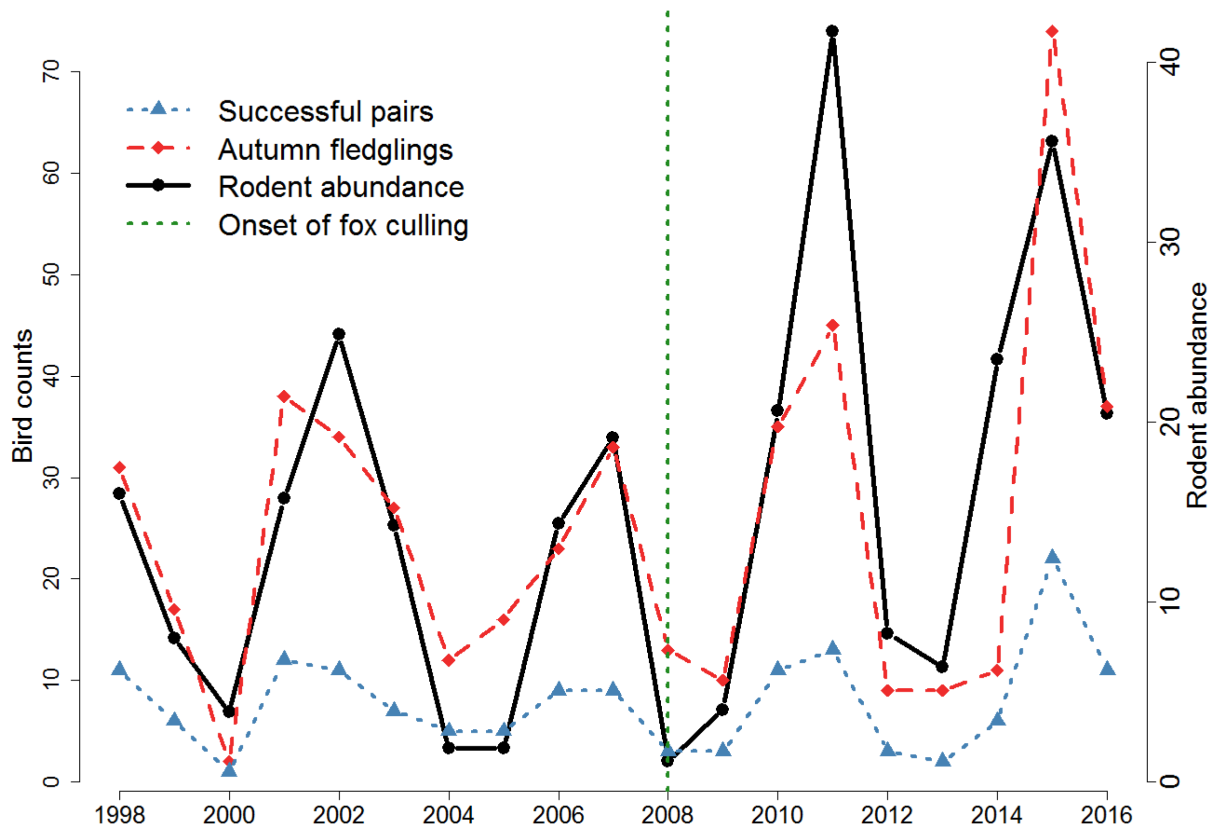

Fig. S3. Time series of the number of Lesser-White fronted Goose breeding pairs that were successful, the number of fledglings in the autumn, and rodent abundance (average catches per grid). Note that the scale on the two y-axes is different. The green line indicates the onset of the red fox culling program.

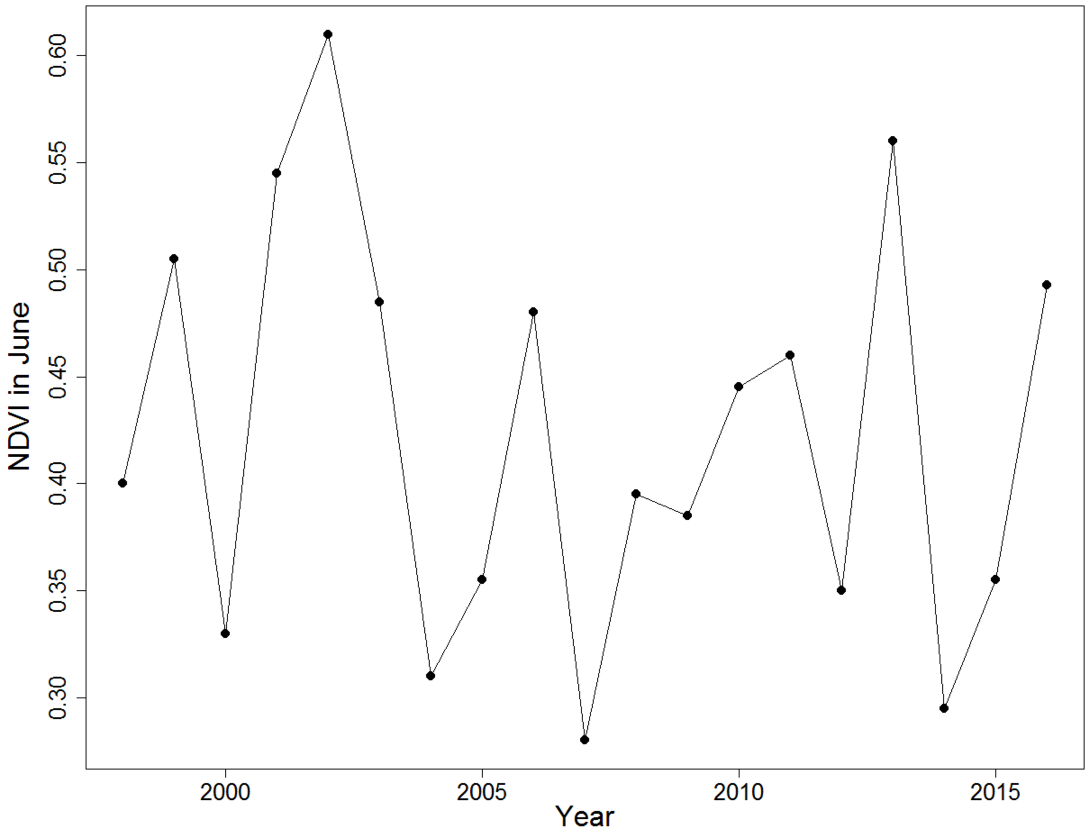

Fig. S4. Annual variation in the Normalized Difference Vegetation Index (NDVI) computed in June from the Global Inventory Modeling and Mapping Studies (GIMMS), measuring vegetation green-up. NDVI values close to zero represent absence of vegetation (thus late spring) while higher values, towards 1, represent greener vegetation (thus earlier spring).

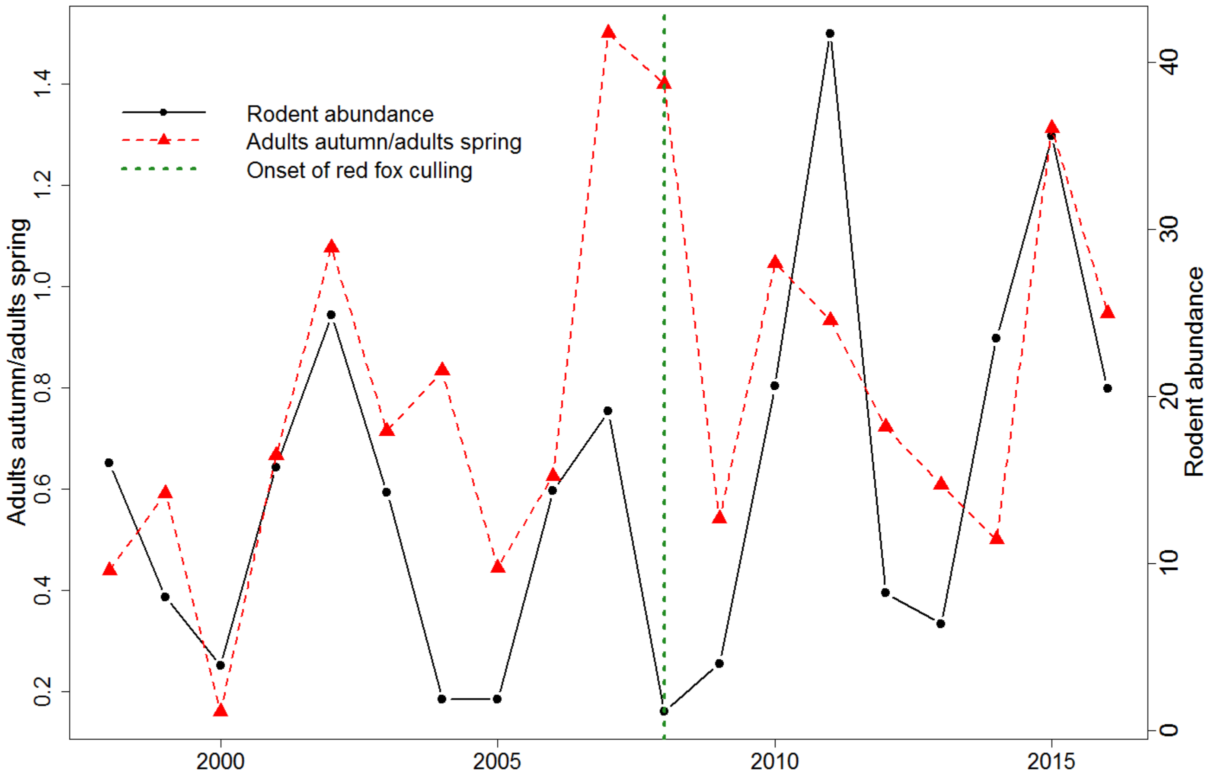

Fig. S5. Time series of rodent abundance (average catches per grid) and ratio of adult birds counted in autumn to adult birds counted in spring, in the Lesser White-fronted Goose population. Note that the scale on the two y-axes is different. The green line indicates the onset of the red fox culling program.

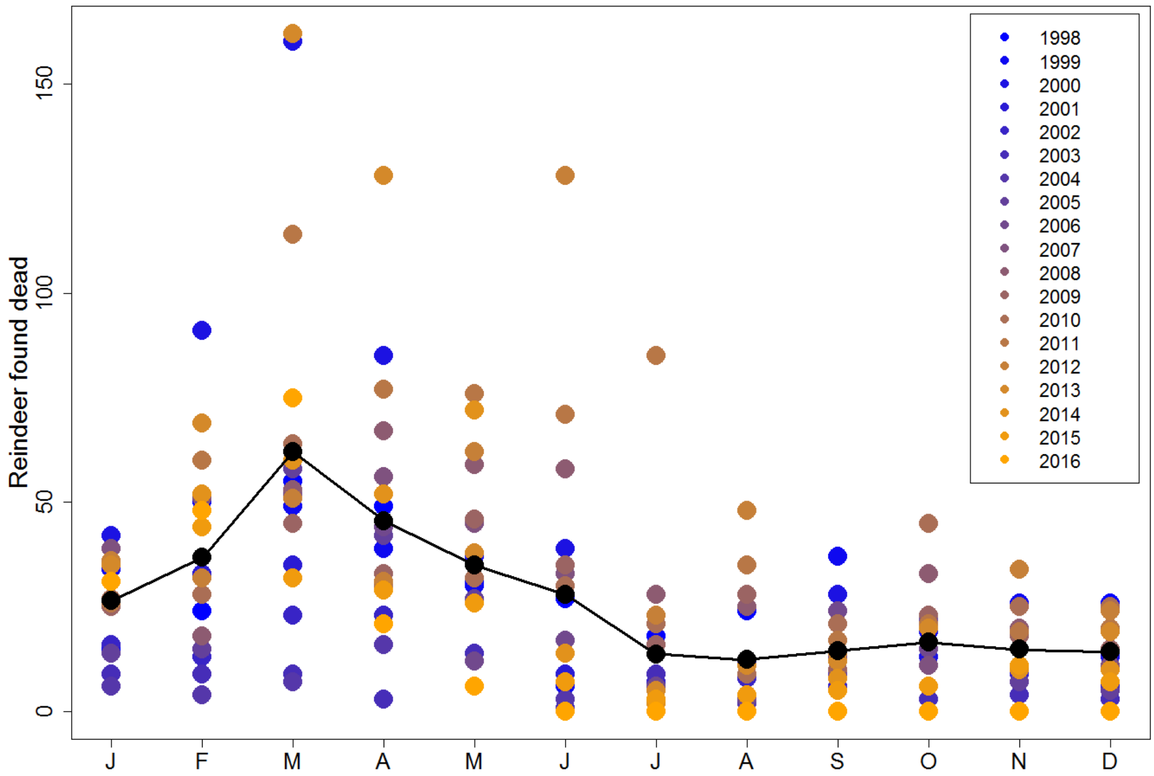

Fig. S6. Number of reindeer found dead across years (in colors) and months (x-axis). 56% of the carcasses is found between February and May. Black line represents the mean.

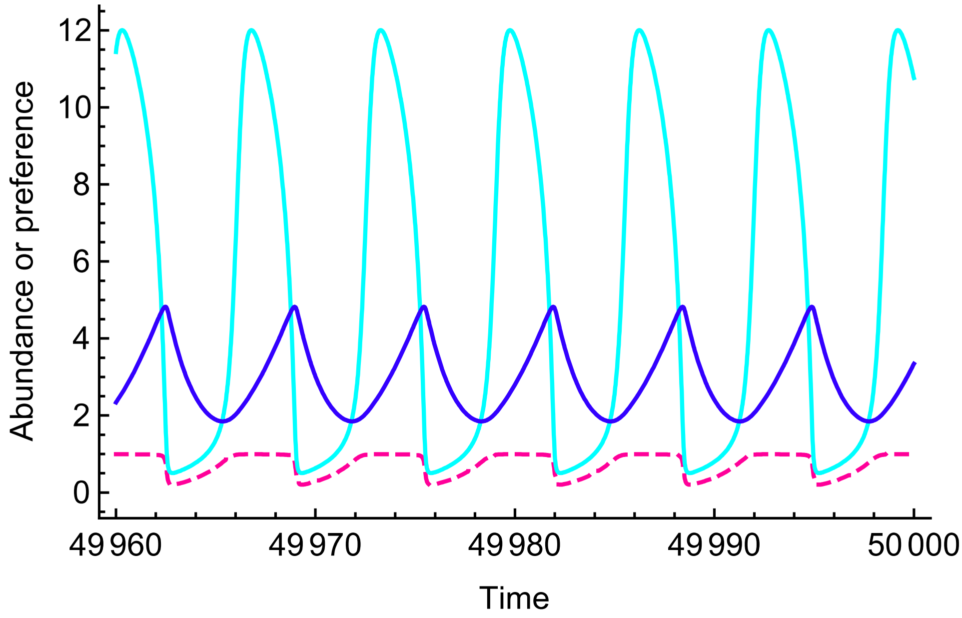

Fig. S7. Example numerical simulation results illustrating the cycles of the alternative prey R (light blue line), predator P (dark blue line), and probability of attack $a_R(R)$ (magenta dashed line). In this case, the alternative resource is assumed to be the rodents.

Table S1. Coefficient estimates and 95% confidence intervals for the 7 *a-priori* models explaining between-year variation in the proportion of Lesser White-fronted Goose breeding pairs that were successful. Estimates are on logit scale.

Variables/Model	**(1)** **R*C + S**	**(2)** **R + C + S**	**(3)** **R + C*Cu**	**(4)** **R*Cu + C**	**(5)** **R + C + Cu**	**(6)** **R + R_{t-1}*Cu**	**(7)** **R + R_{t-1} + Cu**
Rodents (R)	0.1067 (0.0176 ; 0.1959)	0.1070 (0.0687 ; 0.1454)	0.1067 (0.0671 ; 0.1463)	0.1013 (0.0328 ; 0.1699)	0.1071 (0.0684 ; 0.1457)	0.1143 (0.0660 ; 0.1625)	0.1146 (0.0669 ; 0.1624)
Carrion (C)	-0.0032 (-0.0081 ; 0.017)	-0.0032 (-0.0066 ; 0.0002)	-0.0035 (-0.0092 ; 0.0022)	-0.0031 (-0.0067 ; 0.0004)	-0.0031 (-0.0067 ; 0.0003)	-	-
Spring Onset (S)	0.3003 (-3.7406 ; 4.3411)	0.2988 (-3.6805 ; 4.2781)	-	-	-	-	-
Rodents t-1 (R_{t-1})	-	-	-	-	-	0.0034 (-0.0775 ; 0.0844)	-0.0060 (-0.0414 ; 0.0295)
Culling (Cu)	-	-	-0.3514 (-2.8782 ; 2.1754)	-0.2305 (-1.9188 ; 1.4578)	0.1278 (-1.3826 ; 1.1271)	-0.4762 (-2.1492 ; 1.1967)	-0.6263 (-1.8742 ; 0.6216)
Rodents*Carrion	8.4e-7 (-0.0002 ; 0.0002)	-	-	-	-	-	-
Carrion*Culling	-	-	0.0006 (-0.0066 ; 0.0079)	-	-	-	-
Rodents*Culling	-	-	-	0.0088 (-0.0743 ; 0.0919)	-	-	-
Rodents t-1*Culling	-	-	-	-	-	-0.0116 (-0.1018 ; 0.0785)	-

Table S2. Coefficient estimates and 95% confidence intervals for the 7 *a-priori* models explaining between-year variation in the Lesser White-fronted Goose average brood size. Estimates are on log scale.

Variables/Model	**(1)** **R*C + S**	**(2)** **R + C + S**	**(3)** **R + C*Cu**	**(4)** **R*Cu + C**	**(5)** **R + C + Cu**	**(6)** **R + R_{t-1}*Cu**	**(7)** **R + R_{t-1} + Cu**
Rodents (R)	0.0464 (0.0027 ; 0.0901)	0.0496 (0.0314 ; 0.0678)	0.0503 (0.0323 ; 0.0683)	0.0554 (0.0164 ; 0.0943)	0.0497 (0.0317 ; 0.0677)	0.0498 (0.0255 ; 0.0742)	0.0501 (0.0258 ; 0.0745)
Carrion (C)	-0.0023 (-0.0054 ; 0.0008)	-0.0021 (-0.0039 ; -0.0004)	-0.0020 (-0.0053 ; 0.0014)	-0.0022 (-0.0040 ; -0.0003)	-0.0022 (-0.0040 ; -0.0004)	-	-
Spring Onset (S)	0.1142 (-2.1993 ; 2.4277)	0.1067 (-2.1599 ; 2.3733)	-	-	-	-	-
Rodents t-1 (R_{t-1})	-	-	-	-	-	0.0093 (-0.0414 ; 0.0599)	0.0006 (-0.0259 ; 0.0271)
Culling (Cu)	-	-	0.2542 (-1.1506 ; 1.6589)	0.1763 (-0.8194 ; 1.1720)	0.0717 (-0.6665 ; 0.8098)	-0.3344 (-1.3828 ; 0.7139)	-0.5021 (-1.1404 ; 0.1362)
Rodents*Carrion	7.5e-6 (-9.4e-5 ; 0.0001)	-	-	-	-	-	-
Carrion*Culling	-	-	-0.0005 (-0.0044 ; 0.0035)	-	-	-	-
Rodents*Culling	-	-	-	-0.0073 (-0.0513 ; 0.0366)	-	-	-
Rodents t-1*Culling	-	-	-	-	-	-0.0118 (-0.0707 ; 0.0471)	-

Table S3. Coefficient estimates and 95% confidence intervals for the 7 *a-priori* models explaining between-year variation in the ratio of adult Lesser White-fronted geese counted in the autumn to the spring. Estimates are on log scale.

Variables/Model	**(1)** **R*C + S**	**(2)** **R + C + S**	**(3)** **R + C*Cu**	**(4)** **R*Cu + C**	**(5)** **R + C + Cu**	**(6)** **R + R_{t-1}*Cu**	**(7)** **R + R_{t-1} + Cu**
Rodents (R)	0.0249 (-0.0196 ; 0.0709)	0.0199 (0.0011 ; 0.0380)	0.0138 (-0.0058 ; 0.0331)	0.0405 (-0.0013 ; 0.0836)	0.0140 (-0.0056 ; 0.0331)	0.0158 (-0.0024 ; 0.0339)	0.0164 (-0.0015 ; 0.0341)
Carrion (C)	-0.0004 (-0.0032 ; 0.0023)	-0.0007 (-0.0022 ; 0.0007)	-0.0020 (-0.0046 ; 0.0005)	-0.0009 (-0.0023 ; 0.0005)	-0.0010 (-0.0025 ; 0.0004)	-	-
Spring Onset (S)	0.1380 (-2.2622 ; 2.5047)	0.1033 (-2.2124 ; 2.3966)	-	-	-	-	-
Rodents t-1 (R_{t-1})	-	-	-	-	-	0.0230 (-0.0198 ; 0.0649)	0.0106 (-0.0072 ; 0.0282)
Culling (Cu)	-	-	-0.1279 (-1.1221 ; 0.8825)	0.7735 (-0.0149 ; 1.5963)	0.3048 (-0.1468 ; 0.7568)	0.2372 (-0.5628 ; 1.0454)	0.0314 (-0.4423 ; 0.5013)
Rodents*Carrion	-1.3e-5 (-0.0001 ; 9.1e-5)	-	-	-	-	-	-
Carrion*Culling	-	-	0.0015 (-0.0018 ; 0.0046)	-	-	-	-
Rodents*Culling	-	-	-	-0.0323 (-0.0790 ; 0.0135)	-	-	-
Rodents t-1*Culling	-	-	-	-	-	-0.0150 (-0.0613 ; 0.0319)	-

Table S4. Coefficient estimates and 95% confidence intervals for the 2 *a-priori* models explaining between-year variation in the proportion of Lesser White-fronted Goose breeding pairs that were successful and including MODIS-based NDVI data as a measure of spring phenology, for the time period 2000-2016. Estimates are on logit scale.

Variables/Model	**(1) R*C + S**	**(2) R + C + S**
Rodents (R)	0.1090 (0.0122; 0.2057)	0.1097 (0.0681 ; 0.1513)
Carrion (C)	-0.0027 (-0.0081 ; 0.0027)	-0.0027 (-0.0065 ; 0.0011)
Spring Onset (S)	-0.0231 '(-0.0792 ; 0.0331)	-0.0230 (-0.0779 ; 0.0319)
Rodents*Carrion	1.9e-6 (-0.0002 ; 0.0002)	-

Table S5. Coefficient estimates and 95% confidence intervals for the 2 *a-priori* models explaining between-year variation in the Lesser White-fronted Goose average brood size and including MODIS-based NDVI data as a measure of spring phenology, for the time period 2000-2016. Estimates are on log scale.

Variables/Model	**(1) R*C + S**	**(2) R + C + S**
Rodents (R)	0.0448 (-0.0040; 0.2057)	0.0491 (0.0294 ; 0.0689)
Carrion (C)	-0.0021 (-0.0056 ; 0.0014)	-0.0019 (-0.0038 ; 0.0001)
Spring Onset (S)	-0.0132 (-0.0491 ; 0.0227)	-0.0130 (-0.0478 ; 0.0218)
Rodents*Carrion	1.0e-5 (-0.0001 ; 0.0001)	-

Table S6. Coefficient estimates and 95% confidence intervals for the 2 *a-priori* models explaining between-year variation in the ratio of adult Lesser White-fronted geese counted in the autumn to the spring and including MODIS-based NDVI data, for the time period 2000-2016. Estimates are on log scale.

Variables/Model	**(1)** **R*C + S**	**(2)** **R + C + S**
Rodents (R)	0.0228 (-0.0212; 0.0681)	0.0188 (0.0001 ; 0.0370)
Carrion (C)	-0.0005 (-0.0032 ; 0.0023)	-0.0007 (-0.0022 ; 0.0008)
Spring Onset (S)	-0.0015 (-0.0345 ; 0.0304)	-0.0012 (-0.0327 ; 0.0294)
Rodents*Carrion	1.0e-5 (-0.0001 ; 0.0001)	-

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Paper IV

Life cycle analysis of an endangered migratory bird shows no evidence that predator control drove population recovery

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Abstract

To be effective, management interventions that aim to halt the decline of endangered populations should target those demographic rates that are more likely to influence population growth rate. Demographic investigations are particularly challenging for migratory species because limiting factors can operate at any stage of the life cycle. The critically endangered Fennoscandian population of lesser white-fronted goose *Anser erythropus* is monitored at several staging areas across its migration and breeding range and it is also subjected to conservation actions, including culling of red foxes in the breeding area. A goal of the fox culling is to induce adult birds to avoid an alternative autumn migration route through Western Asia where mortality is expected to be higher than on the regular migration route through Eastern Europe. After a long-term decline, the population has recently shown signs of recovery, which has been linked to the conservation efforts. We used 17 years of counts carried out at breeding, wintering, and intermediate staging areas to parameterize a seasonal state-space model describing population dynamics throughout the annual cycle. We found no evidence that adult goose survival is lower on the allegedly riskier migration route. We conclude that there is no current evidence that red fox culling contributed to the recent population recovery, given our model, the available data and previous analyses of reproductive success. Still, we found indications that adult survival at staging and wintering sites may have improved in the latest years, possibly due to the positive impacts of another set of conservation actions carried out approximately at the same time the red fox culling started. This study highlights the challenge of assessing the efficacy of separate conservation actions when proper experimental designs are unfeasible and suggests that a combination of cross-national efforts is likely needed for conservation of endangered migratory populations.

1. Introduction

Information on demographic processes such as survival, fecundity and recruitment is crucial to develop effective population management strategies (Mills, 2007; Williams, Nichols, & Conroy, 2002). When this information is lacking, the risk is to direct management efforts towards vital rates that have little impact on the population growth rate (Johnson, Mills, Stephenson, & Wehausen, 2010). In avian management, for instance, focusing on improving nesting success is common even when its contribution to population performances is unknown (Gaines, Dinsmore, & Murphy, 2020). For small and endangered populations, we typically lack detailed data and thereby rely on life-history expectations based on other populations or species to identify management targets. This may be hazardous because the relative importance of vital rates can differ largely between healthy and declining populations of the same species, let alone of different species (Beissinger & Westphal, 1998; Johnson et al., 2010).

Understanding the demographic processes underlying population dynamics is even more challenging for migratory species, because factors that limit population growth can operate at any stage of the annual cycle (Sutherland, 1996). The environmental conditions experienced at each stage of the annual cycle can have both direct (i.e. immediate) and carry-over (i.e. delayed) effects on the population dynamics, adding another layer of complexity (e.g. Layton-Matthews, Hansen, Grotan, Fuglei, & Loonen, 2019; Rockwell, Bocetti, & Marra, 2012). So far, most studies on migratory birds have focused on the breeding season. However, birds usually spend more time at non-breeding sites (Faaborg et al., 2010) and limitations during the non-breeding period can actually drive population dynamics (Rushing et al., 2017; Wilson et al., 2018). Thus, more investigations assessing population dynamics throughout the full-annual cycle are needed (Hostetler, Sillett, & Marra, 2015; Marra, Cohen, Loss, Rutter, & Tonra, 2015; Rushing, Ryder, & Marra, 2016).

The lesser white-fronted goose *Anser erythropus* is a migrant goose species that breeds in sub- and low-arctic tundra and overwinters in temperate wetlands across Eurasia. Once common in northern Fennoscandia, the Fennoscandian lesser white-fronted goose population experienced a drastic decline during the 20th century, reaching the lowest size in 2008 with less than 20 breeding pairs estimated (Aarvak, Leinonen, Øien, & Tolvanen, 2009). A large conservation network spanning several countries across the population's range was built already in the mid-1980s to improve knowledge and conservation status of the population (Ekker & Bø, 2017). Among several interventions, 12 years of predator control (red fox culling) in the core breeding area in northern Norway were claimed as one of the main reasons for the recent recovery of the population, which consists now of approximately 100 birds (Aarvak, Øien, & Karvonen, 2017). Red fox control was started with a double goal: increasing reproductive success and avoiding early reproductive failure. Early failed breeders seem to leave the breeding areas earlier in the season and embark on a long migratory journey through Western Asia, where mortality is expected to be higher than on the regular migration route through Eastern Europe (Øien, Aarvak, Ekker, & Tolvanen, 2009). Since 2008, an estimated 22-43% of the local red fox population was culled every year between February and May, before the arrival of the geese at their breeding site (Marolla et al., 2019). We recently demonstrated that there is no current evidence that fox culling improved goose breeding success (Marolla et al., 2019). Breeding success appeared to be primarily driven by the functional response of predators to cyclic dynamics of small rodent populations, and partly by the numerical response of predators to the abundance of ungulate carcasses during winter. Still, it remains unclear whether a more subtle influence of fox culling on the choice of the goose autumn migration route could have influenced adult survival and contributed to the population recovery (Marolla et al., 2019).

The Fennoscandian population of lesser white-fronted goose performs a seasonal migration between the wintering grounds in Greece and the breeding areas in Troms and Finnmark County, northern Norway (Fig. 1). The reproductive season lasts from late-May to mid-August. Adult birds leave the breeding areas along with the fledglings in September, after a staging period of about three weeks at the coastal Valdak Marshes, Stabbursnes, Norway (70°10′N 24°40′E). The regular migration route, here termed the "European Route", takes them first to the Kanin Peninsula in northwestern Russia. Then, the birds fly southward through eastern Germany/western Poland, have an important stopover at Hortobágyi in eastern Hungary, and finally reach the wintering areas at Lake Kerkini and in the Evros Delta in northern Greece. Spring migration starts in March and follows approximately the same route, simply in the opposite direction. Birds return at the staging areas at Valdak Marshes in early- to mid-May and move to the core inland breeding area about a week later (Aarvak & Øien, 2003). Field observations suggest that, to reach the wintering grounds in Greece, non-breeders and breeders that failed early in the season could undertake an alternative moulting migration through western Russia and north-western Kazakhstan, here termed the "Asian Route" (Øien et al., 2009). There, the risk of geese being illegally shot is expected to be high (Jones, Whytock, & Bunnefeld, 2017). Recoveries of shot birds in these areas provide anecdotal support to this hypothesis (Marolla et al., 2019). Lower adult survival on the supposed riskier migration route through Western Asia was perceived as a major cause of population decline (Øien & Aarvak, 2009). Reducing early breeding failure, and thus the number of birds venturing on the supposed dangerous route, was a reason behind the implementation of the red fox culling program.

Here, we used 20 years (1998-2017) of count data of the Fennoscandian population of lesser white-fronted goose at different stopovers across its range to model population dynamics. Our primary interest was to estimate season-specific vital rates and compare survival probabilities on the two migration routes. We were also interested in assessing the effects of the red fox culling program at the breeding site and comparing these effects to the potential effects of other conservation initiatives carried out at some of the staging areas. These initiatives aimed at minimizing illegal shooting and improving habitat quality (Vougioukalou, Kazantzidis, & Aarvak, 2017). Ultimately, we were interested in obtaining insights on the relative contribution of vital rates to the recent population recovery. We expected 1) survival on the allegedly riskier Asian migration route to be lower than on the regular European Route; 2) the probability that birds avoid the Asian Route to increase after the start of the fox culling program in 2008; and 3) the change in this probability to contribute the most to the change in the realized population growth rate after the initiation of fox culling (i.e. predator control influences the population growth rate) as compared to potential changes in other vital rates.

2. Materials and methods

2.1 Population counts

The goose population is monitored at different locations along the European Route (Fig.1). We used data collected between 1998 and 2017 at the three major stopovers in northern Norway, Hungary, and Greece, where the population breeds, stages, and overwinters, respectively. Total counts are performed at each location, and birds are assigned to age classes whenever possible. In Norway, counts have been carried out at the staging sites at the Valdak Marshes in spring (May-June, since 1990) and autumn (August-September, since 1994), i.e. before and after the breeding period, under the assumption that all birds that breed in the core breeding area (~50 km away) also use these staging sites. Unique patterns in the black belly-patches of the geese allow individual recognition of the birds across the two seasons, but not across years because these patterns change between years (Aarvak et al., 2009). In spring, the number of yearlings (i.e. 2nd calendar-year birds), potential breeders (i.e. >2 years old birds that are part of a breeding pair) and non-breeders (i.e. >2 years old birds that are not part of a breeding pair) was recorded. In autumn, fledglings, successful breeders (i.e. birds in a breeding pair with at least one fledgling), and unsuccessful breeders (i.e. birds not part of a family group) were counted. Information on clutch size and early chick survival was not available because birds spread across the breeding area during summer and are difficult to survey.

In Hungary, counts have been performed at Hortobágyi National Park since 1990 during both the autumn and the spring migration. Long distances between birds and observers as well as frequent presence of heat haze in this hot steppe area do not allow differentiation between young and adult birds nor individual recognition. Therefore, only the maximum number of birds observed is available. For unknown reasons, very few individuals utilized the Hungarian stopover in 2018 and 2019. Because of this bias in the time series, we decided to exclude these two years from the analysis.

In Greece, reports of staging lesser white-fronted geese date back to the early 1900s. Total counts, however, have been systematically carried out only since 2005. Counts were carried out at the two major staging areas of Lake Kerkini and in the Evros Delta and on multiple occasions during the goose winter staging period (from as early as October until as late as March). At both sites, conditions allow identification of juveniles and adults, for which the overall maximum observed number is eventually reported.

2.2 Demographic model

Estimating demographic rates of animal populations typically requires marking and recapturing of individual animals. This method can be difficult to implement (Rodríguez-Caro et al., 2019) especially for endangered populations (Wielgus, Gonzalez-Suarez, Aurioles-Gamboa, & Gerber, 2008). Count data, however, are often available for birds and many other animal taxa (Link & Sauer, 1998). To circumvent the issue of marking animals, various statistical methods for demographic assessment based on count data have been developed (e.g. Gross, Craig, & Hutchison, 2002; Gross, Ives, & Nordheim, 2005; Link, Royle, & Hatfield, 2003; Rodríguez-Caro et al., 2019; Zipkin et al., 2014). These methods are typically referred to as “inverse modelling” (Caswell, 2000; González, Martorell, Bolker, & McMahon, 2016), where vital rates are estimated from age class-specific counts. Here, we built a seasonal state-space population model for the lesser white-fronted goose population based on age-structured count data. In the state-space modelling framework, an observation process that accommodates the measurement error of the results of a survey, as well as the lack of fit of the process model, is linked to an underlying population dynamics model for the true age-specific abundance, i.e., the process model (de Valpine & Hastings, 2002; Kéry & Schaub, 2011). The true population abundance, therefore, is modelled as a latent state variable, while the observations are modelled as conditional on these unknown states. We used Bayesian methods to implement our model and estimate demographic parameters and associated uncertainty, and thus obtain insights on important age-/stage-transitions in population dynamics of Fennoscandian lesser white-fronted geese.

2.2.1 Model of population dynamics

The life cycle model of the Fennoscandian lesser white-fronted goose population is shown in Fig. 2. The model included five stopover locations that matched the locations where the population counts are performed, i.e. Norway Spring (pre-breeding survey), Norway Autumn (post-breeding census), Hungary Autumn, Greece Winter, and Hungary Spring. We chose the annual cycle to start with Norway Spring, i.e. the pre-breeding survey at the Valdak Marshes staging sites in northern Norway. We included five stage classes that are a combination of three age classes (juveniles or 1st calendar-year birds; yearlings or 2nd calendar-year birds; adults or ≥ 3rd calendar-year birds) and three states of reproductive status for the oldest age class (non-breeders, failed breeders, and successful breeders). We assumed even sex ratio of fledglings and adults and no difference in survival between sexes. We also assumed that breeding begins at age 2, because yearlings have never been observed associated with fledglings during the post-breeding survey (T. Aarvak, pers. comm.). This is a sensible assumption because goose species typically do not breed before turning 2-years old (Finney & Cooke, 1978; Viallefont, Cooke, & Lebreton, 1995; Warren, Fox, Walsh, & P., 1992). The reproductive status and outcome of the adults determine whether an individual will undertake the migration to the wintering grounds in Greece through the European or the Asian Route (Fig. 2). Successful breeders are assumed to always fly along the European Route and non-breeders to always fly along the Asian Route, whereas potential breeders that failed breeding can make a choice between the two routes. Yearlings do not breed, so they are assumed to always fly the Asian Route. Because we adopted a seasonal model, age-specific abundances across consecutive stopovers are a function of survival, fecundity, and age-specific abundance at the previous stopover. To account for demographic stochasticity in this small population, age-specific abundances are described by stochastic processes. In the following equations, true latent population abundances (N) as well as observed counts (y) are indexed by age class, stopover location, and year, in this order.

Breeding season: from Norway Spring to Norway Autumn

The number of juveniles (J) in Norway Autumn (NA, i.e. after the breeding period) in year t is modelled as a Poisson process:

$$N_{J,NA,t} \sim Poisson\left(\alpha_t p_t N_{PB,NS,t}\right)$$

where α_t is the probability that a potential breeder (PB) in Norway Spring (NS) reproduces successfully, p_t is the product of the per capita fecundity (i.e. average number of fledglings per breeding individual) and the early chick survival, and $N_{PB,NS,t}$ is the number of potential breeders in Norway Spring.

In Norway Autumn, the adult component (Ad) of the goose population consists of successful breeders (SB) and potential breeders that failed breeding and chose to migrate over the European Route (FB). The number of successful breeders and the number of failed breeders at this stopover in year t are modelled as binomial processes:

$$N_{SB,NA,t} \sim Binomial\left(N_{PB,NS,t}, \alpha_t S_{Ad,NN,t}\right)$$

$$N_{FB,NA,t} \sim Binomial\left[N_{PB,NS,t}, (1-\alpha_t)\varphi_t S_{Ad,NN,t}\right]$$

where $S_{Ad,NN,t}$ is adult survival from Norway Spring to Norway Autumn (NN) and φ_t is the probability that a potential breeder that failed breeding remains in Norway and thus chooses the European Route.

Autumn migration: from Norway to Greece

Juveniles, successful breeders, and failed breeders that remained in Norway are assumed to follow the European Route and utilize the Hungarian stopover area. The number of juveniles and the number of adults in Hungary Autumn (HA) in year t ($N_{J,HA,t}$ and $N_{AdE,HA,t}$ where the E stands for European Route) are modelled as binomial processes:

$$N_{J,HA,t} \sim Binomial\left(N_{J,NA,t}, S_{J,NH,t}\right)$$

$$N_{AdE,HA,t} \sim Binomial\left(N_{SB,NA,t} + N_{FB,NA,t}, S_{Ad,NH,t}\right)$$

where $S_{J,NH,t}$ and $S_{Ad,NH,t}$ are, respectively, juvenile and adult survival from Norway Autumn to Hungary Autumn (NH).

Eventually, juveniles and adults fly from Hungary to the wintering grounds in Greece. The number of juveniles in Greece Winter (GW) in year t is modelled as a binomial process:

$$N_{J,GW,t} \sim Binomial\left(N_{J,HA,t}, S_{J,HG,t}\right)$$

where $S_{J,HG,t}$ is juvenile survival from Hungary Autumn to Greece Winter (HG). At the Greek stopover area, birds that took the Asian Route re-join the population. Therefore, the number of adults in Greece Winter at time t is given by:

$$N_{Ad,GW,t} = N_{AdE,GW,t} + N_{NB,GW,t} + N_{PBf,GW,t}$$

where $N_{AdE,GW,t}$ is the number of adults from Hungary Autumn that survived the last stretch of the European Route, $N_{NB,GW,t}$ is the number of adult non-breeders in Norway Spring that survived the Asian Route, and $N_{PBf,GW,t}$ is the number of potential breeders in Norway Spring that chose to leave Norway after failing the breeding attempt and survived the Asian Route. These three adult components are modelled as binomial processes:

$$N_{AdE,GW,t} \sim Binomial\left(N_{AdE,HA,t}, S_{Ad,HG,t}\right)$$

$$N_{NB,GW,t} \sim Binomial\left(N_{NB,NS,t}, S_{Ad,NG,t}\right)$$

$$N_{PBf,GW,t} \sim Binomial\left[N_{PB,NS,t}, (1-\alpha_t)(1-\varphi_t)S_{Ad,NG,t}\right]$$

where $S_{Ad,HG,t}$ is adult survival from Hungary Autumn to Greece Winter (HG), and $S_{Ad,NG,t}$ is adult survival from Norway Spring to Greece Winter (NG), i.e. on the Asian Route.

Because we assumed that yearlings do not reproduce, in the model they leave Norway before the breeding period and follow the Asian Route to join the population in Greece. Therefore, the number of yearlings in Greece Winter in year t is modelled as a binomial process:

$$N_{Y,GW,t} \sim Binomial\left(N_{Y,NS,t}, S_{Y,NG,t}\right)$$

where $N_{Y,NS,t}$ is the number of yearlings in Norway Spring and $S_{Y,NG,t}$ is yearling survival from Norway Spring to Greece Winter (NG).

Spring migration: from Greece to Norway

The whole population is assumed to follow the European Route to reach the breeding areas in northern Norway. Therefore, in Hungary Spring (HS), the number of juveniles ($N_{J,HS,t}$), yearlings ($N_{Y,HS,t}$), and adults ($N_{Ad,HS,t}$) in year t are modelled as binomial processes:

$$N_{J,HS,t} \sim Binomial\left(N_{J,GW,t}, S_{J,GH,t}\right)$$

$$N_{Y,HS,t} \sim Binomial\left(N_{Y,GW,t}, S_{Y,GH,t}\right)$$

$$N_{Ad,HS,t} \sim Binomial\left(N_{Ad,GW,t}, S_{Ad,GH,t}\right)$$

where $S_{J,GH,t}$, $S_{Y,GH,t}$, $S_{Ad,GH,t}$ are respectively juveniles, yearling, and adult survivals from Greece Winter to Hungary Spring (GH).

Eventually, the birds complete the annual cycle by moving to northern Norway. The number of yearlings in Norway Spring in year $t+1$ $\left(N_{Y,NS,t+1}\right)$ depends on the number of juveniles that make it from Hungary Spring to Norway Spring and thus move into the next age class. This is modelled as a binomial process:

$$N_{Y,NS,t+1} \sim Binomial\left(N_{J,HS,t}, S_{J,HN,t}\right)$$

where $S_{J,HN,t}$ is juvenile survival from Hungary Spring to Norway Spring (HN). Adults in Norway Spring include yearlings that move into the adult stage and individuals already in that stage. Of these adults, some become part of a breeding pair and thus turn into potential breeders, while others do not. Therefore, the number of potential breeders in Norway Spring in year $t+1$ $\left(N_{PB,NS,t+1}\right)$ is given by:

$$N_{PB,NS,t+1} = N_{PBY,NS,t+1} + N_{PBAd,NS,t+1}$$

where $N_{PBY,NS,t+1}$ is the number of yearlings that moved to the adult age class and became part of a breeding pair, and $N_{PBAd,NS,t+1}$ is the number of adults that became part of a breeding pair. These two components of the adult population are modelled as binomial processes:

$$N_{PBY,NS,t+1} \sim Binomial\left(N_{Y,HS,t}, \omega_t S_{Y,HN,t}\right)$$

$$N_{PBAd,NS,t+1} \sim Binomial\left(N_{Ad,HS,t}, \omega_t S_{Ad,HN,t}\right)$$

where ω_t is the probability that a bird becomes part of a breeding pair, and $S_{Y,HN,t}$ and $S_{Ad,HN,t}$ are respectively yearling and adult survivals from Hungary Spring to Norway Spring (HN). The number of non-breeders in Norway Spring in year $t+1$ $\left(N_{NB,NS,t+1}\right)$ is given by:

$$N_{NB,NS,t+1} = N_{NBY,NS,t+1} + N_{NBAd,NS,t+1}$$

where $N_{NBY,NS,t+1}$ is the number of yearlings that moved to the adult age class and did not become part of a breeding pair, and $N_{NBAd,NS,t+1}$ is the number of adults that did not become part of a breeding pair. These two components of the adult population are modelled as binomial processes:

$$N_{NBY,NS,t+1} \sim Binomial\left(N_{Y,HS,t}, (1-\omega_t) S_{Y,HN,t}\right)$$

$$N_{NBAd,NS,t+1} \sim Binomial\left(N_{Ad,HS,t}, (1-\omega_t) S_{Ad,HN,t}\right).$$

We point out that we view these survival probabilities as estimates of apparent survival. The migratory range of the Fennoscandian lesser white-fronted goose population partially overlaps that of the neighbouring West Russian population as they share part of the Asian migration route (Øien & Aarvak, 2009). Immigration of male individuals from the Russian population occurs (Ruokonen, Aarvak, Chesser, Lundqvist, & Merila, 2010) and may confound true survival in the statistical inference from our model. Still, the Fennoscandian population is considered a single management unit (Ruokonen et al., 2004).

2.2.2 Observation model

We modelled the observation processes (i.e. the mapping of the latent stage-specific population sizes on the observed counts, y) as normal distributions conditional on the true local population abundance and the stopover-specific residual error (τ_{obsx}). We assumed to have no systematic over- or underestimation of counts at any of the five stopovers. In Norway Spring, yearlings $\left(y_{Y,NS,t}\right)$, potential breeders $\left(y_{PB,NS,t}\right)$, and non-breeders $\left(y_{NB,NS,t}\right)$ are observed in every year t. Therefore:

$$y_{Y,NS,t} \sim Normal\left(N_{Y,NS,t+1}, \tau_{obs1}\right)$$

$$y_{PB,NS,t} \sim Normal\left(N_{PB,NS,t}, \tau_{obs1}\right)$$

$$y_{NB,NS,t} \sim Normal\left(N_{NB,NS,t}, \tau_{obs1}\right)$$

In Norway Autumn, juveniles $\left(y_{J,NA,t}\right)$, successful breeders $\left(y_{SB,NA,t}\right)$, and failed breeders that chose to migrate over the European Route $\left(y_{FB,NA,t}\right)$ are observed in every year t. Therefore:

$$y_{J,NA,t} \sim Normal\left(N_{J,NA,t}, \tau_{obs2}\right)$$

$$y_{SB,NA,t} \sim Normal\left(N_{SB,NA,t}, \tau_{obs2}\right)$$

$$y_{FB,NA,t} \sim Normal\left(N_{FB,NA,t}, \tau_{obs2}\right)$$

In Hungary Autumn, age classes are not separated. Therefore, in each year t we have a single count:

$$y_{TOT,HA,t} \sim Normal\left(N_{J,HA,t} + N_{Ad,HA,t}, \tau_{obs3}\right)$$

In Greece Winter, only juveniles $\left(y_{J,GW,t}\right)$ and adults $\left(y_{Ad,GW,t}\right)$ are observed in each year t because yearlings are counted as adults. Therefore:

$$y_{J,GW,t} \sim Normal\left(N_{J,GW,t}, \tau_{obs4}\right)$$

$$y_{Ad+Y,GW,t} \sim Normal(N_{Y,GW,t} + N_{Ad,GW,t}, \tau_{obs4})$$

In 2009 and 2010, however, only the total population size was recorded in Greece Winter, and therefore the observed counts for these years were modelled as:

$$y_{TOT,GW,t} \sim Normal(N_{J,GW,t} + N_{Y,GW,t} + N_{Ad,GW,t}, \tau_{obs4})$$

In Hungary Spring, age classes are again not separated. Therefore, in each year t:

$$y_{TOT,HS,t} \sim Normal(N_{J,HS,t} + N_{Y,HS,t} + N_{Ad,HS,t}, \tau_{obs5})$$

2.2.3 Population growth rate

We calculated annual population growth rate λ_t by dividing the total population size in Norway Spring in year $t+1$ by the total population size in Norway Spring in year t:

$$\lambda_t = (N_{Y,NS,t+1} + N_{PB,NS,t+1} + N_{NB,NS,t+1})/(N_{Y,NS,t} + N_{PB,NS,t} + N_{NB,NS,t})$$

2.2.4 Effect of small-rodent cycles

The reproductive success of the Fennoscandian lesser white-fronted geese is known to be strongly dependent on the population density of cyclic small rodent species (Marolla et al., 2019). To account for this, we modelled the product of the per capita fecundity and the early chick survival (p_t) as a function of rodent abundance on a log link scale:

$$log(p_t) = \mu_p + \beta_{rodents} \times RodentAbundance_t$$

where μ_p is the log of the mean vital rate and $RodentAbundance_t$ is an index of rodent abundance (average number of individuals per trapping grid each year) derived from a capture-mark-recapture survey described in Ehrich, Yoccoz, and Ims (2009) and conducted approximately 50 km from the goose breeding area. Small rodent species are known to have synchronized population cycles over much larger distances (Stenseth & Ims, 1993). The probability that a potential breeder reproduces successfully (α_t) and the probability that failed breeders avoid the allegedly riskier migration route (φ_t) may also be influenced by rodent abundance. Nonetheless, the effect of rodent abundance on these parameters was unidentifiable likely due to limited data and we decided to exclude it.

2.2.5 Demographic assessment of goose management

When we tried to estimate the temporal variability in all vital rates in our fairly complex model, issues of parameter identifiability arose with our data set. With the limited count data available, we could only estimate probabilities of seasonal survival and choosing the riskier Asian route that are constant across years. To assess the effect of the red fox culling program on the probability that failed breeders avoid the allegedly riskier migration route, we adopted the strategy of (Marolla et al., 2019). We tested whether this probability (φ_t) changed after the implementation of the culling program in 2008 by modelling it as a function of a categorical variable 'Culling', which indicates whether fox culling occurred in a given year or not. We used a logit link function to model this probability:

$$logit(\varphi_t) = \mu_\varphi + \beta_{cull\varphi} \times Culling_t$$

where μ_φ is the logit of the mean vital rate.

Conservation initiatives other than red fox culling, however, were implemented approximately in the same period at the autumn and winter staging sites in Hungary and Greece. These initiatives aimed at minimizing poaching and accidental shooting as well as improving habitat quality, and could have been important for the population increase. Therefore, we also assessed whether adult autumn survival probabilities on the two legs of the European Route ($S_{Ad,NH,t}$ and $S_{Ad,HG,t}$) and adult winter survival ($S_{Ad,GH,t}$) were different before and after 2008. For consistency, we also tested for a change after 2008 in adult survival on the Asian Route ($S_{Ad,NG,t}$). These four survival probabilities were modelled with a customary logit function:

$$logit\left(S_{Ad,NH,t}\right) = \mu_{S_{Ad,NH,t}} + \beta_{cullS1} \times Culling_t$$

$$logit\left(S_{Ad,HG,t}\right) = \mu_{S_{Ad,HG,t}} + \beta_{cullS2} \times Culling_t$$

$$logit(S_{Ad,GH,t}) = \mu_{S_{Ad,GH,t}} + \beta_{cullS3} \times Culling_t$$

$$logit(S_{Ad,NG,t}) = \mu_{S_{Ad,NG,t}} + \beta_{cullS4} \times Culling_t$$

where μ_{S_x} is the logit of the mean survival probability. We point out that, because only the maximum number of birds observed throughout the winter in Greece was available, the parameter that we call 'adult winter survival' ($S_{Ad,GH,t}$) overlaps and thus is partly confounded with survival during both autumn and spring migration between Greece and Hungary.

2.2.5 Model fitting

We fitted the model using Markov chain Monte Carlo methods implemented in JAGS (Plummer, 2003) by the R package jagsUI (Kellner, 2015). We assigned vague priors to all parameters (see JAGS code in Appendix S1) and slightly more constrained priors to the β_{cullSx} parameters to enhance their rates of convergence (i.e. normal distributions with mean = 0 and variance = 10). To initiate the model, we provided initial population abundances in Norway Spring at $t = 1$ using available data. We ran four chains with 500,000 iterations, a thinning rate of 50, and burn-in of 100,000, yielding 32,000 draws from the joint posterior distribution of the parameters. Convergence of Markov chains was evaluated by visual inspections of time series plots of the draw and by ensuring that the Gelman-Rubin convergence statistics R-hat was below 1.1 (Brooks & Gelman, 1998). We summarised posterior distributions by their mean and 95% credible interval [CI].

2.3 Transient LTRE

We performed a *transient Life Table Response Experiment* (LTRE) as described by Koons, Iles, Schaub, and Caswell (2016) to estimate the contribution of the five vital rates modelled as a function of 'Culling' to the realized change in the population growth rate after the implementation of the fox-culling program. The transient LTRE is based on the idea that environmental conditions can influence the population growth rate not only directly through their effects on the vital rates, but also indirectly by inducing transient (i.e. ephemeral) changes in the structure of the population. The transient LTRE accounts for these changes and allows distinguishing between such direct and indirect effects. We were interested in estimating the contribution of variability in each vital rate θ_i to the change in λ_t between successive time steps, i.e. $\Delta\lambda_t$. Specifically, the drivers of change in geometric mean growth rates $\Delta log\lambda_g$ can be decomposed between two time intervals of equal duration, a and b, as follows:

$$contribution_{\theta_i}^{\Delta log\lambda_g} \approx \left(log_{\mu_{i,b}} - log_{\mu_{i,a}}\right)\left(\bar{e}_{\mu_i}^{A} + \bar{e}_{\mu_i}^{\hat{n}}\right)$$

where μ is the mean of vital rate i over a time interval (i.e. a or b), $\bar{e}$ is the so-called "real time elasticity" calculated for a reference population described by the mean of the interval-specific vital rates between intervals a and b, A describes the direct effect of a change in a vital rate on $\Delta log\lambda_g$, and $\hat{n}$ describes the indirect effect of a change in population structure on $\Delta log\lambda_g$ (see Koons et al., 2016 for details). For the implementation of the transient LTRE in R, we adapted the R code provided in Appendix S7 in Koons, Arnold, and Schaub (2017).

3. Results

Our model estimated that the Fennoscandian population of lesser white-fronted goose declined from 70 [61 – 79] birds in Norway Spring in 1998 to 38 [31 – 46] birds in Norway Spring in 2007, the year before the start of the red fox culling program. The population reached its lowest level in 2009 with 34 birds estimated [28 – 41], and then increased up to 109 birds [100 – 119] in 2017 (Fig. 3). Notably, the population did not increase gradually after 2009, but rather experienced abrupt positive changes in abundance after summers with high small rodent abundances in 2011 and 2015 (Fig. S1). Overall, the average annual population growth rate changed from 0.95 [0.77 - 1.15] on average before the onset of the fox-culling program to 1.15 [0.96 - 1.36] afterwards.

Estimates for all demographic parameters are shown in Fig. 4 and Table 1. Average apparent survival was quite high for all ages and migration legs (Fig. 1). Juvenile survival ranged from 0.77 to 0.86 between the migration legs, yearling survival ranged between 0.87 and 0.89, and adult survival ranged between 0.89 and 0.97. Importantly, and contrary to our expectations, average adult apparent survival on the supposedly riskier Asian Route (0.89 [0.64 - 1.00]) was estimated to be similar to the average adult apparent survival along the European Route (0.87 [0.65 - 0.98]). We calculated this value as the product of adult survival from Norway Autumn to Hungary Spring and adult survival from Hungary Spring to Greece Winter.

With respect to the effects of the management actions evaluated in our model, the probability that failed breeders avoid the Asian Route (φ) increased on average after the implementation of the red fox culling program, although high uncertainty around this estimate made this evidence inconclusive ($\beta_{cull\varphi}$ = 1.10, [-0.53 - 3.65] on logit scale, Fig. 5). Apparent adult survival probabilities on the European Route, the Asian Route, and on the wintering grounds also increased on average after the onset of fox culling, and by a larger magnitude compared to the probability that failed breeders avoid the Asian Route. However, these estimates also had a high uncertainty associated (on the logit scale: $S_{Ad,NH,t}$ = 2.11 [-1.94 - 7.06]; $S_{Ad,HG,t}$ = 2.71 [-1.19 - 7.37]; $S_{Ad,GH,t}$ = 2.84 [-0.69 - 7.31]; $S_{Ad,NG,t}$ = 2.40 [-1.59 - 7.20]; Fig. 5).

The transient LTRE analysis led to inconclusive results owing to the very diffuse posterior distributions of the vital rate contributions to the realized population growth rate, that is, due to the substantial uncertainty associated with our demographic estimates. The estimated mean of the overall contribution of the parameter describing winter survival ("Hun->Gre" in Fig. S2) was slightly higher than the mean of the contribution of the other parameters. The posterior probability distribution of this parameter had also a slightly heavier tail (Fig. S2). The direct effects of vital rates contributed more to the realized population growth rate compared to the indirect effects (Fig. S3).

4. Discussion

Benefiting from twenty years of seasonal population surveys producing count data at several stages across its entire year-round range, we parameterized a seasonal, demographic state-space model for the Fennoscandian population of lesser white-fronted goose in order to address unanswered and frequently-debated questions about the effects of conservation actions on the recent population recovery. As lack of effect of a predator control action on the reproductive success (parameters α and p) had already been demonstrated (Marolla et al., 2019), here we focused on the possibility that predator control could have influenced the goose population growth rate by affecting birds' migratory behaviour and the survival probabilities specific to the different migration routes. Indeed, red fox culling in the breeding area in northern Norway was initiated not only to increase reproductive success, but also to reduce early breeding failure that could induce birds to migrate through Western Asia instead of Eastern Europe. Illegal-hunting pressure and thus mortality was expected to be higher along the Asian than along the European migration route (Aarvak & Øien, 2003; Jones et al., 2017; Lorentsen et al., 1999; Øien et al., 2009).

Contrary to our expectations, we found no evidence that birds are exposed to a higher mortality risk on the Asian Route, with the estimated adult survival on the Asian Route being similar to that on the European Route. Although there was high uncertainty, the probability that failed breeders do not embark on the migration through Asia slightly improved during the culling period (Fig. 5). Still, even if the red fox culling program may have achieved its purpose of increasing this probability, this potential effect would be unlikely to have influenced population growth rate because the Asian Route appears not as risky as expected. This result is relevant for the conservation of the goose population, because significant efforts have been put in the culling program during the last decade. Combined with what Marolla et al. (2019) found, we conclude that, based on this model and the available data, there is currently not evidence that red fox culling influences the growth rate of this lesser white-fronted goose population. Nevertheless, we caution against strong inference because the potential immigration of individuals belonging to the Russian population during the autumn migration through western Asia may have confounded the estimates of survival.

Interestingly, our analysis suggested that the probability of avoiding the Asian Route might not be the only parameter that has changed in the years following the onset of fox culling. Survival probabilities on both migration routes and wintering grounds increased on average after 2008, by a higher magnitude compared to the probability of avoiding the Asian route. The large statistical uncertainty makes it impossible to draw firm conclusions about the degree of any such change in these demographic rates. This result, however, may reflect a positive effect of another set of conservation interventions that were implemented to improve bird safety at several staging areas along the European Route. Between 2005 and 2009, a first EU LIFE-Nature project laid the foundation for an international cooperation among many of the countries that host the Fennoscandian lesser white-fronted goose population during its annual cycle (Tolvanen, Øien, & Ruokolainen, 2009). This initiative led to the development of National Action Plans for the lesser white-fronted goose in Norway, Finland, and Estonia. It also identified the need of preventing poaching and accidental shooting in Greece, promoted public awareness campaigns in Estonia and Hungary, and recommended to carry out conservation efforts also in the countries located along the Asian Route. This cooperation was continued between 2011 and 2017 through a second LIFE project, which led to the implementation of patrolling systems in Greece and Bulgaria, hunting ban of all goose species including the similar greater white-fronted goose *Anser albifrons* at the Evros Delta in Greece, habitat restoration initiatives in Greece and Hungary, and the development of National Action Plans in Hungary, Bulgaria, and Greece (Vougioukalou et al., 2017). Remarkably, no lesser white-fronted geese were found shot at project sites during the second LIFE project (Vougioukalou et al., 2017), although the 2008's economic crisis may have contributed to decrease hunting activities in Greece (Kazantzidis, Vasiliadis, Ilias, & Makrygianni, 2015). Taken together, these conservation measures may have prevented the population from further decline by improving conditions at the staging areas. In addition, we acknowledge the possibility that the potential increase in survivals may be linked to the increase in some greater white-fronted goose populations that partially share the Asian Route with other goose species including the lesser white-fronted goose and are permitted to be hunted (Fox & Leafloor, 2018; Jones et al., 2017).

Unfortunately, the goose counts that were available prevented us from reliably estimating the contribution of each survival probability to the change in realized population growth rate after fox culling began in 2008. Although the mean contribution of the parameter describing winter adult survival was slightly higher than the contribution of the other survival probabilities, the statistical uncertainty around the estimates was too large to draw any strong inference. Therefore, we cannot really conclude that winter adult survival was more important than the other vital rates to invert the declining population trend. Moreover, winter survival here is partly confounded with survival during migration between Hungary and Greece, both in the autumn and in the spring, because only a single maximum count per winter was available for Greece. However, the fact that all the survival probabilities that were allowed to vary in the model may have increased after 2008 suggests that a comprehensive approach, with conservation actions implemented at different stopovers along the entire migration flyways, may be key to ensure the conservation of such a small population. Because reproductive success is tightly linked to small rodent population cycles in northern Fennoscandia (Marolla et al., 2019) and the amplitude of the rodent cycles may be becoming increasingly dampened (Cornulier et al., 2013; Kausrud et al., 2008; Nolet et al., 2013), ensuring protection at key staging sites of the population in good reproductive years may be fundamental to increase recruitment and thereby population size. Indeed, the goose population experienced abrupt increases in size following good reproductive years in the period when conservation actions were already in place.

Because of identifiability issues, we were unable to estimate temporal variability in the demographic parameters. This might be an important limitation, especially considering the large between-year variability in breeding success in the lesser white-fronted goose population (Marolla et al., 2019). It is possible that the lack of data from Greece in the period 1998-2004, combined with the absence of information on age-structure in Hungary and the fact that yearlings are distinguished nowhere but in Norway, has caused the parameters and their associated uncertainty to be unidentifiable. In integrated population models (Schaub & Abadi, 2010), most of the information to estimate apparent survival probabilities comes from capture-recapture data that are currently not available for our goose population. However, previous studies showed that with this type of inverse modelling that we used it is possible to estimate between-year variability (e.g. Gross et al., 2005; Link et al., 2003). Thus, this issue might be circumvented with more years of data that will come in as the monitoring proceeds. This could be investigated also with simulated data of different sample sizes.

Conservation and management implications

Evaluating the effectiveness of conservation/management actions on small populations is challenging, because proper experiments designed to include controls as well as temporal and spatial replications of actions are usually not achievable (Taylor et al., 2017). Removing or controlling predators is usually beneficial to declining bird populations, but unsuccessful programs are not rare (Dicks et al., 2019; Williams et al., 2019). Based on a management design including spatial contrasts, it has been shown that culling of red foxes likely contributed to increase the population density of ptarmigan *Lagopus lagopus* in northern Norway (Henden, Ehrich, Soininen, & Ims, MS). Moreover, red fox culling likely contributed to prevent local extinction of the arctic fox *Vulpes lagopus* (Ims et al., 2017). However, through a combination of food-web analysis (Marolla et al., 2019) and state-space modelling of the realized population dynamics (this study), we found no evidence for a contribution of fox culling to the recent increase in abundance of the Fennoscandian lesser white-fronted goose population. In Marolla et al. (2019), we discussed that compensatory immigration (Lieury et al., 2015; Newsome, Crowther, & Dickman, 2014), substitutable effect of other nest predators (Henden et al., 2014; Parker, 1984), and insufficient culling may explain the apparent lack of influence on goose reproductive success. Here, we found that apparent adult goose survival is unlikely to differ between the two major migration routes that were expected to differ in terms of illegal hunting pressure, although compensatory immigration from the neighbouring Russian population of lesser white-fronted goose may have masked some patterns in true survival. Still, we found indications that the remarkable effort of implementing conservation actions in several countries to ensure population protection throughout the annual cycle may have been beneficial to the population. That population dynamics at non-breeding sites can be as or even more important than dynamics at breeding sites is increasingly acknowledged (Hostetler et al., 2015; Marra et al., 2015). It is therefore plausible that increased safety at staging sites combined with improved habitat conditions has ensured high survival and recruitment, and that this has been particularly important in years with high reproductive success.

In this respect, it will be important not only to continue the monitoring at the currently surveyed staging sites, but also to include new locations in the monitoring scheme. For instance, the implementation of a systematic monitoring program at important bird areas in Kazakhstan has been proposed (T. Aarvak, pers. comm.), following on the heels of recent pilot surveys (Cuthbert et al., 2018). Including this data in the demographic model we have developed in this study could help disentangling whether a certain leg of the Asian Route is indeed affected by higher goose mortality. Another aspect of the model that could be improved in the near future is the partial confounding between survival during winter staging in Greece and survival during the migration between Hungary and Greece, both in the autumn and in the spring. Daily count data were not readily available for this study, but once organized, they will allow to specify arrival and departure time to and from the Greek sites, and thus define a winter staging period that does not overlap with migration. Moreover, we encourage to always trying providing age-structure counts; in staging areas where these data are difficult to obtain such as Hungary, even having the age-structure for a random sample of birds may aid getting better parameter estimates. We believe that iterating both the demographic analysis and the management evaluation over the coming years will be crucial to better understand whether the flyway conservation approach adopted for the Fennoscandian lesser white-fronted goose is actually preventing the extinction of the population and also to optimize the approach further.

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Author contributions: F. Marolla, S. Hamel, and N. G. Yoccoz conceived the idea; F. Marolla, M. Kéry, and M. Schaub designed the modelling strategy; T. Aarvak and M. Vougioukalou provided goose count data; R. A. Ims and N. G. Yoccoz provided data on small rodent abundance; F. Marolla organized the data; F. Marolla and C. R. Nater analyzed the data; F. Marolla led the writing of the manuscript. All authors contributed critically to the writing of the manuscript. None of the authors has conflict of interest to declare.

6. Figures

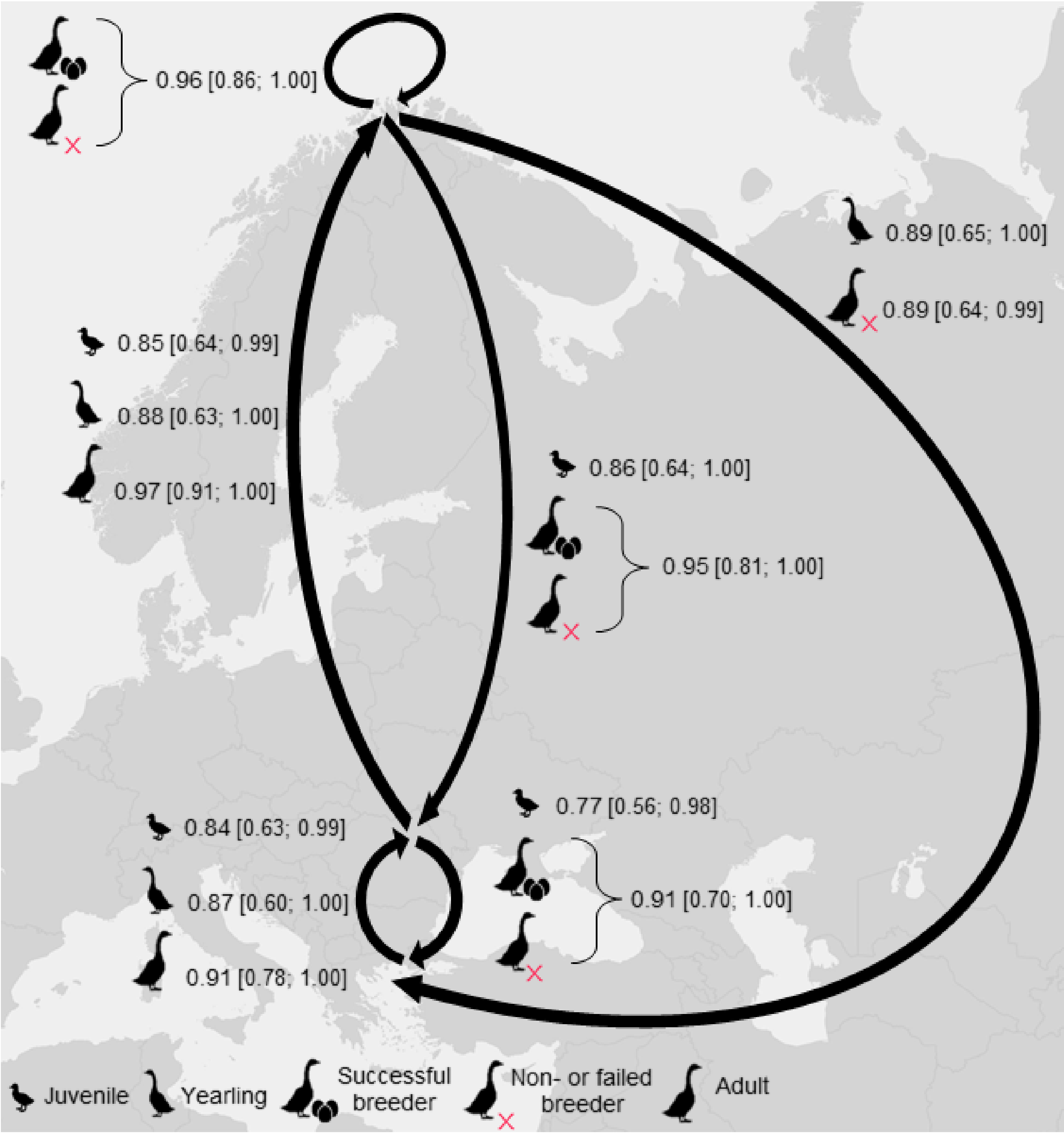

Fig. 1 – Simplified representation of the life cycle of the Fennoscandian lesser white-fronted goose population with the two autumn migration routes, i.e. the European Route and the Asian Route. Numbers are model estimates (mean ± 95% Credible Interval) of leg- and age-specific survival probabilities. For graphical purposes, the arrows do not show exactly the itinerary covered by the birds but only an approximation.

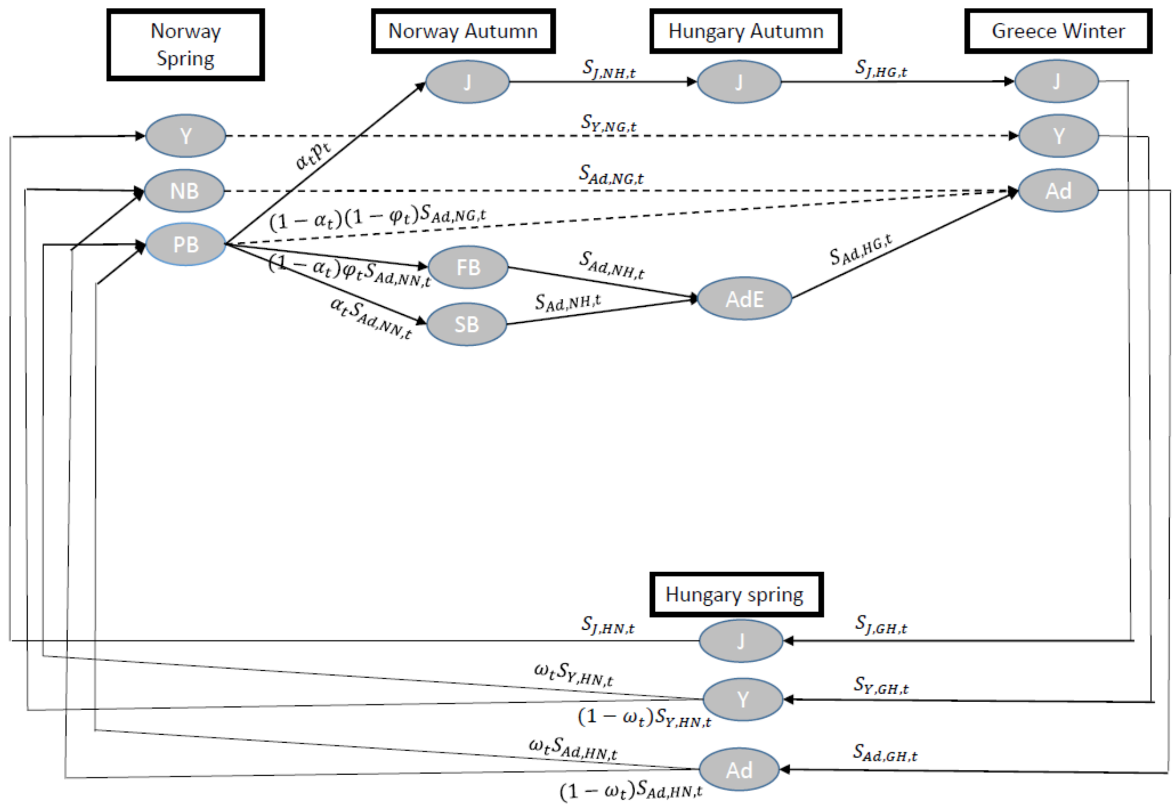

Fig. 2 – Life cycle of the Fennoscandian Lesser White-fronted Goose population. Dashed arrows depict the alternative, allegedly riskier, migration route through Western Asia (the Asian Route). Y = Yearling; NB = Non-Breeder; PB = Potential Breeder; J = Juvenile; FB = Failed Breeder; SB = Successful Breeder; Ad = Adult. Definitions of demographic parameters can be found in Table 1.

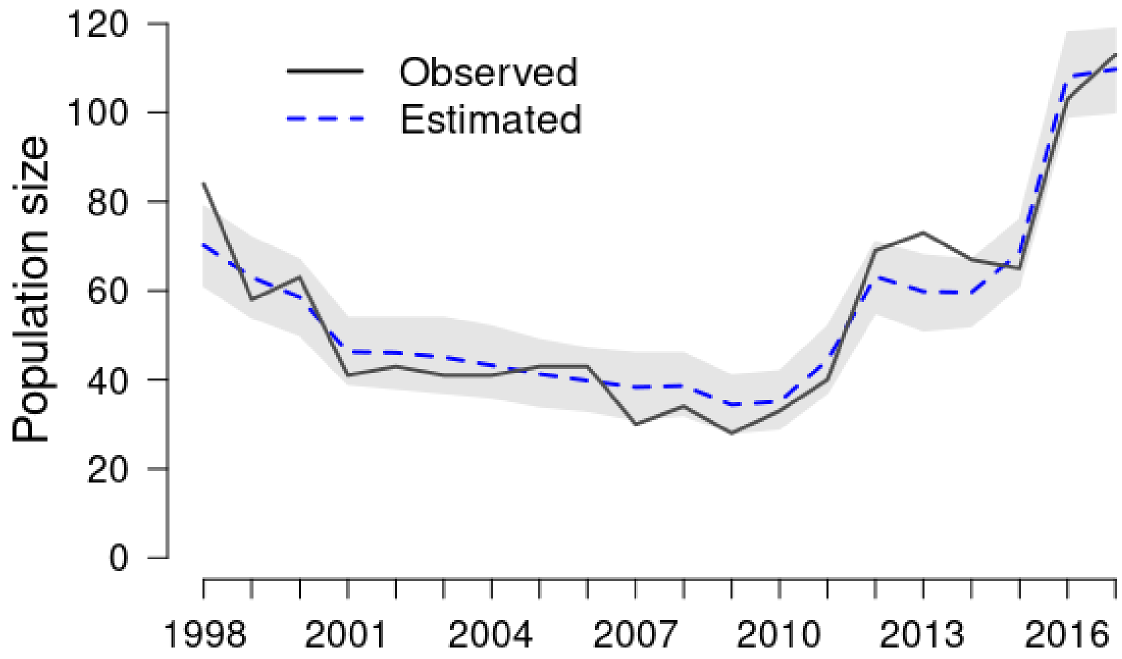

Fig. 3 – Observed (solid black line) and estimated (dashed blue line) total number of individuals of the Fennoscandian lesser white-fronted goose population. The grey area represents 95% credible intervals.

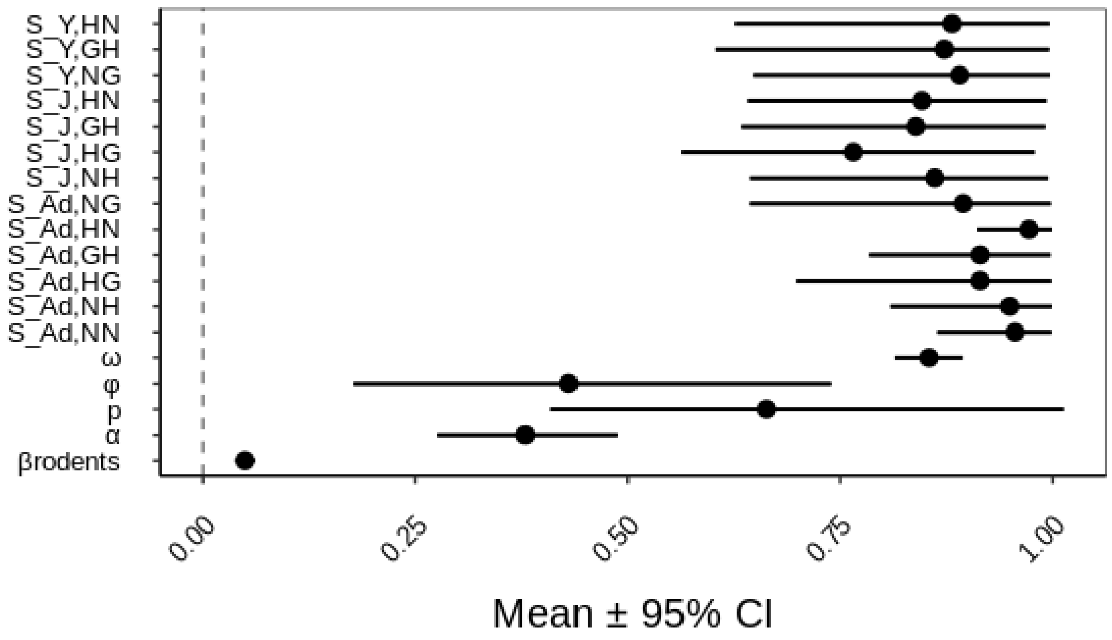

Fig. 4 – Mean ± 95% Credible Intervals of estimated posterior distributions of vital rates in the Fennoscandian lesser white-fronted goose population model. All parameters except $\beta_{rodents}$ and p are probabilities and thus vary between 0 and 1. Survival probabilities are grouped by age class and reported following the goose migration scheme (from bottom to top). For interpretation of the labels, see Table 1.

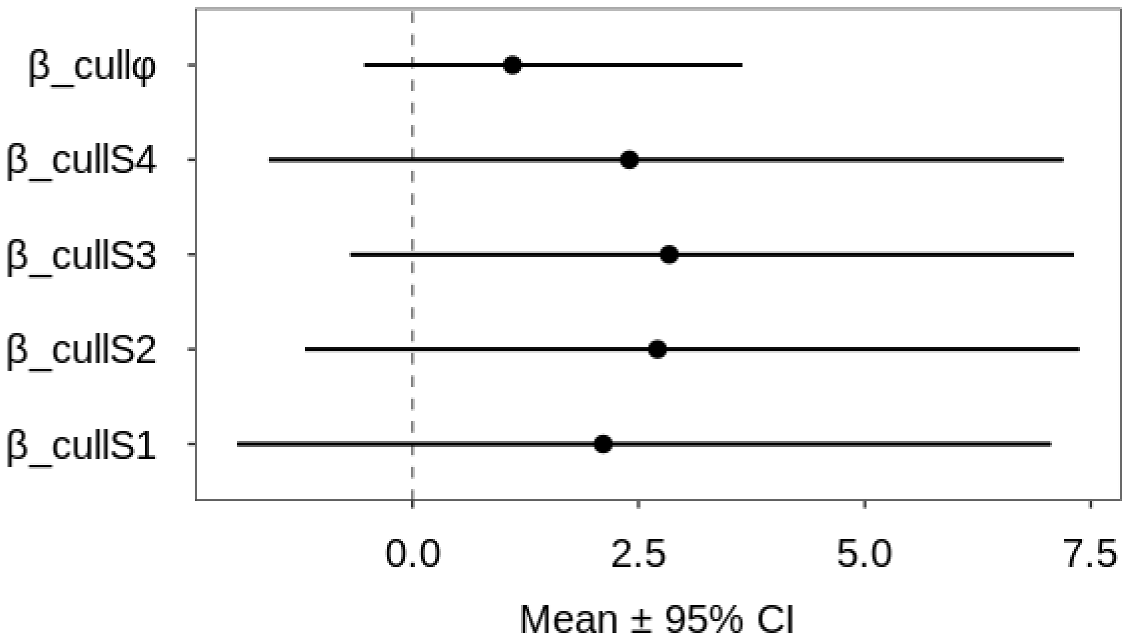

Fig. 5 – Mean ± 95% Credible Intervals of estimated posterior distributions of changes in the five selected vital rates after the implementation of the red fox culling program in 2008. β_cullS1 = change in adult survival from Norway Autumn to Hungary Autumn (i.e. first leg of autumn migration on the European Route). β_cullS2 = change in adult survival from Hungary Autumn to Greece Winter (i.e. last leg of autumn migration on the European Route plus a portion of winter staging). β_cullS3 = change in adult survival from Greece Winter to Hungary Spring (i.e. a portion of winter staging plus first leg of spring migration on the European route). β_cullS4 = change in adult survival from Norway Autumn to Greece Winter, i.e. autumn migration on the Asian Route. β_cullφ = change in probability that failed breeders avoid the Asian Route.

7. Tables

Table 1 – Definition of parameters in the Fennoscandian lesser white-fronted goose population model, along with estimated posterior means and 95% Credible Intervals for the whole study period (1998-2017).

Parameter	Definition	Posterior Mean	95% CI
α	Probability of breeding successfully	0.38	0.28; 0.49
p	Product of fecundity and chick survival	0.66	0.41; 1.01
φ	Probability that a failed breeder chooses the European Route	0.43	0.18; 0.74
ω	Probability of becoming part of a breeding pair	0.85	0.81; 0.90
S_Ad,NN	Adult survival from Norway Spring to Norway Autumn	0.96	0.86; 1.00
S_Ad,NH	Adult survival from Norway Autumn to Hungary Autumn	0.95	0.81; 1.00
S_Ad,HG	Adult survival from Hungary Autumn to Greece Winter	0.91	0.70; 1.00
S_Ad,GH	Adult survival from Greece Winter to Hungary Spring	0.91	0.78; 1.00
S_Ad,HN	Adult survival from Hungary Spring to Norway Spring	0.97	0.91; 1.00
S_Ad,NG	Adult survival from Norway Spring to Greece Winter	0.89	0.64; 1.00
S_J,NH	Juvenile survival from Norway Autumn to Hungary Autumn	0.86	0.64; 1.00
S_J,HG	Juvenile survival from Hungary Autumn to Greece Winter	0.77	0.56; 1.00
S_J,GH	Juvenile survival from Greece Winter to Hungary Spring	0.84	0.63; 1.00
S_J,HN	Juvenile survival from Hungary Spring to Norway Spring	0.85	0.64; 1.00
S_Y,NG	Yearling survival from Norway Spring to Greece Winter	0.89	0.65; 1.00
S_Y,GH	Yearling survival from Greece Winter to Hungary Spring	0.87	0.60; 1.00
S_Y,HN	Yearling survival from Hungary Spring to Norway Spring	0.88	0.63; 1.00
βrodents	Effect of small rodent abundance on p	0.05	0.04; 0.06

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Supplementary material

Appendix S1

JAGS code for the state-space model

```
cat("
   model{
   # Seasonal stage-structured population model for the Fennoscandian LWfG
   # age at first breeding = 2 years
   # the 'year' starts with Norway Spring, for which we provide initial age-specific abundance
   # alfa = prob. of reproducing successfully
   # phi = prob. of staying in Norway given failed reproduction
   # omega = prob. of forming a breeding pair

   #---------------------------------------------------------
   # Define priors for the parameters
   #---------------------------------------------------------

   # Observation error
   tau.obs.1 <- pow(sigma.1, -2)
   sigma.1 ~ dunif(0.5,30)
   sigma2.1 <- pow(sigma.1, 2)
   tau.obs.2 <- pow(sigma.2, -2)
   sigma.2 ~ dunif(0.5,30)
   sigma2.2 <- pow(sigma.2, 2)
   tau.obs.3 <- pow(sigma.3, -2)
   sigma.3 ~ dunif(0.5,30)
   sigma2.3 <- pow(sigma.3, 2)
   tau.obs.4 <- pow(sigma.4, -2)
   sigma.4 ~ dunif(0.5,30)
   sigma2.4 <- pow(sigma.4, 2)
   tau.obs.5 <- pow(sigma.5, -2)
   sigma.5 ~ dunif(0.5,30)
   sigma2.5 <- pow(sigma.5, 2)

   # Initial population size

   N[1,1,1] ~ dpois(7)
   N[2,1,1] ~ dpois(2)
   N[3,1,1] ~ dpois(50)

   # Demographic parameters
   for(t in 1:nyears){

   # Seur (Survival European route) varies over two age classes (juv and ad), seasons, and year
   # Sy (Survival yearlings) varies over three seasons and year
   # Skaz (Survival Kazakhstan route) varies only over year
   # p (product of per-capita fecundity and early chick survival) varies over two age classes (2Y and
#3Y+) and year
   # alfa varies over two age classes (2Y and 3Y+) and year
   # phi varies over year
   # omega varies over year

```

```
SeurAd[1,t] <- mean.sad.1
SeurJuv[1,t] <- mean.sjuv.2
SeurJuv[2,t] <- mean.sjuv.3
SeurJuv[3,t] <- mean.sjuv.4
SeurJuv[4,t] <- mean.sjuv.5
SeurAd[5,t] <- mean.sad.5

# The following adult survivals are modelled as a function of red fox culling
logit(SeurAd[2,t]) <- mu.sad.2 + betaCull.sad.2*Culling[t] # Norway Autumn to Hungary Autumn
logit(SeurAd[3,t]) <- mu.sad.3 + betaCull.sad.3*Culling[t] # Hungary Autumn to Greece Winter
logit(SeurAd[4,t]) <- mu.sad.4 + betaCull.sad.4*Culling[t] # Greece Winter to Hungary Spring

Sy[1,t] <- mean.sy.1
Sy[2,t] <- mean.sy.2
Sy[3,t] <- mean.sy.3

logit(Skaz[t]) <- mu.skaz + betaCull.skaz*Culling[t]    # Survival on Asian route

log(p[t]) <- mu.p + betaRod*Rodents[t]

alfa[t] <- mean.alfa

logit(phi[t]) <- mu.phi + betaCull.phi*Culling[t]

omega[t] <- mean.omega
}

mean.sad.1 ~ dunif(0,1)
mean.sjuv.2 ~ dunif(0,1)
mean.sad.2 ~ dunif(0,1)
mu.sad.2 <- logit(mean.sad.2)
mean.sjuv.3 ~ dunif(0,1)
mean.sad.3 ~ dunif(0,1)
mu.sad.3 <- logit(mean.sad.3)
mean.sjuv.4 ~ dunif(0,1)

mean.sad.4 ~ dunif(0,1)
mu.sad.4 <- logit(mean.sad.4)

mean.sjuv.5 ~ dunif(0,1)
mean.sad.5 ~ dunif(0,1)

mean.sy.1 ~ dunif(0,1)
mean.sy.2 ~ dunif(0,1)
mean.sy.3 ~ dunif(0,1)

mean.skaz ~ dunif(0,1)
mu.skaz <- logit(mean.skaz)

betaRod ~ dnorm(0, 0.01)   # why did we use dunif(-10,10) for our effects on ptarmigans?
mean.p ~ dunif(0,5)
mu.p <- log(mean.p)

mean.alfa ~ dunif(0,1)
```

```
mean.phi ~ dunif(0,1)
mu.phi <- logit(mean.phi)
betaCull.phi ~ dnorm(0,0.1)
betaCull.sad.2 ~ dnorm(0,0.1)
betaCull.sad.3 ~ dnorm(0,0.1)
betaCull.sad.4 ~ dnorm(0,0.1)
betaCull.skaz ~ dnorm(0,0.1)

mean.omega ~ dunif(0,1)

#----------------------------------------
# Derived parameters
#----------------------------------------

# Population growth rate (from Norway Spring to Norway Spring)

for(t in 1:(nyears-1)){
lambda[t] <- Ntot[t+1]/(Ntot[t]+0.001)
}


#--------------------------------------------------------
# Likelihood for population count data (state-space model)
# -------------------------------------------------------

# System process

# Norway Autumn, i.e. season 2
for(t in 1:nyears){
meanjuv[t] <- N[3,1,t]*alfa[t]*p[t]#*0.5
N[1,2,t] ~ dpois(meanjuv[t])                                   # Juveniles
N[2,2,t] ~ dbin((1-alfa[t])*phi[t]*SeurAd[1,t], N[3,1,t]) # Failed Breeders
N[3,2,t] ~ dbin(alfa[t]*SeurAd[1,t], N[3,1,t])            # Successful Breeders

# Hungary Autumn, i.e. season 3
N[1,3,t] ~ dbin(SeurJuv[1,t], N[1,2,t])                  # Juveniles
N[2,3,t] ~ dbin(SeurAd[2,t], (N[2,2,t]+N[3,2,t]))       # Adults Europe

# Greece Winter, i.e. season 4
N[1,4,t] ~ dbin(SeurJuv[2,t], N[1,3,t])               # Juveniles
N[2,4,t] ~ dbin(Sy[1,t], N[1,1,t])                     # Yearlings
M[1,t] ~ dbin(Skaz[t], N[2,1,t])                       # transition Non-Breeders
M[2,t] ~ dbin((1-alfa[t])*(1-phi[t])*Skaz[t], N[3,1,t]) # transition Potential Breeders
M[3,t] ~ dbin(SeurAd[3,t], N[2,3,t])                  # transition Adults Europe
N[3,4,t] <- M[1,t] + M[2,t] + M[3,t]                  # Adults

# Hungary Spring, i.e. season 5
# observed values here are for the following calendar year, because the goose year start in June
N[1,5,t] ~ dbin(SeurJuv[3,t], N[1,4,t])               # Juveniles
N[2,5,t] ~ dbin(Sy[2,t], N[2,4,t])                    # Yearlings
N[3,5,t] ~ dbin(SeurAd[4,t], N[3,4,t])                # Adults

# Norway Spring, i.e. season 1
N[1,1,t+1] ~ dbin(SeurJuv[4,t], N[1,5,t])                # Juveniles
L[1,t] ~ dbin(Sy[3,t]*(1-omega[t]), N[2,5,t])             # Transition Yearling Non-Breeders
```

```
L[2,t] ~ dbin(SeurAd[5,t]*(1-omega[t]), N[3,5,t])          # Transition adults Non-Breeders
N[2,1,t+1] <- L[1,t] + L[2,t]                              # Non-Breeders
R[1,t] ~ dbin(Sy[3,t]*omega[t], N[2,5,t])                 # transition Yearling Potential Breeders
R[2,t] ~ dbin(SeurAd[5,t]*omega[t], N[3,5,t])             # transition Adult Potential Breeders
N[3,1,t+1] <- R[1,t] + R[2,t]                             # Potential Breeders

}

# Total population size in Norway Spring to calculate growth rate
for(t in 1:nyears){
Ntot[t] <- N[1,1,t] + N[2,1,t] + N[3,1,t]
}

# Observation process
for(t in 1:nyears){

# Norway Spring, i.e. season 1
y[1,1,t] ~ dnorm(N[1,1,t], tau.obs.1)              # yearlings
y[2,1,t] ~ dnorm(N[2,1,t], tau.obs.1)             # adults not in pairs (non-breeders)
y[3,1,t] ~ dnorm(N[3,1,t], tau.obs.1)             # adults in pairs (breeders)

# Norway Autumn, i.e. season 2
y[4,2,t] ~ dnorm(N[1,2,t], tau.obs.2)             # juveniles
y[5,2,t] ~ dnorm(N[2,2,t], tau.obs.2)             # failed breeders on European route
y[6,2,t] ~ dnorm(N[3,2,t], tau.obs.2)             # successful breeders

# Hungary Autumn, i.e. season 3
y[7,3,t] ~ dnorm(N[1,3,t] + N[2,3,t], tau.obs.3)  # total count

# Greece Winter, i.e. season 4
y[4,4,t] ~ dnorm(N[1,4,t], tau.obs.4)                # juveniles
y[8,4,t] ~ dnorm(N[2,4,t] + N[3,4,t], tau.obs.4)     # adults
y[7,4,t] ~ dnorm(N[1,4,t] + N[2,4,t] +
N[3,4,t], tau.obs.4)                               # total count

# Hungary spring, i.e. season 5
y[7,5,t] ~ dnorm(N[1,5,t] + N[2,5,t] +
N[3,5,t], tau.obs.5)                               # total count

}

}
", fill=TRUE)
```

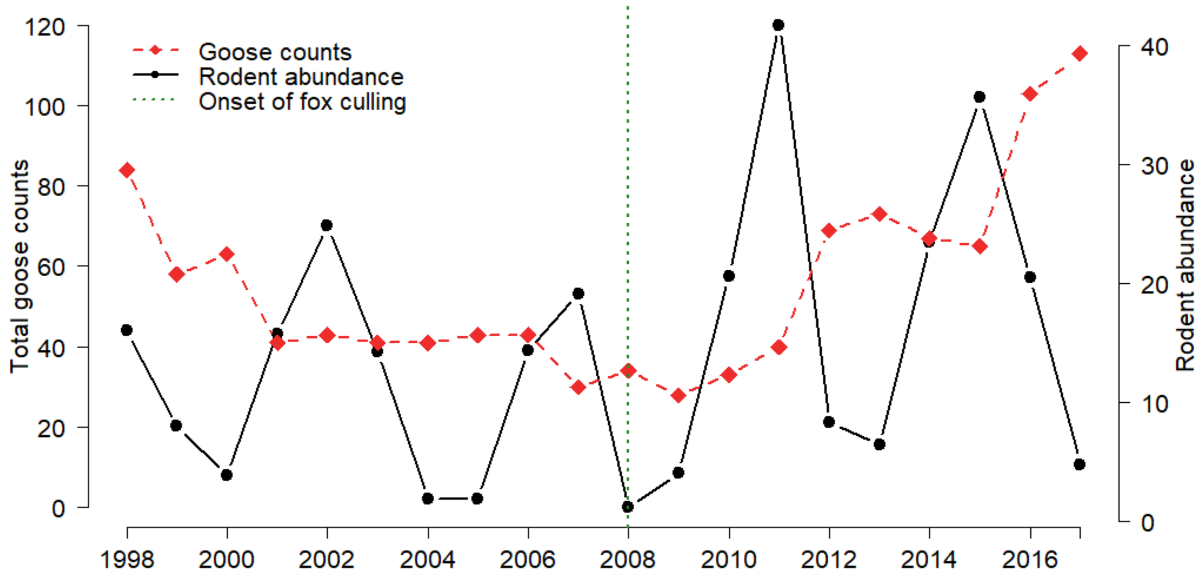

Fig. S1 – Time series of rodent abundance (average catches per grid) and population size of the Fennoscandian lesser white-fronted goose (total counts carried out in Norway in the spring). Note that the scale on the two y-axes is different. The vertical green line indicates the onset of the red fox culling programme

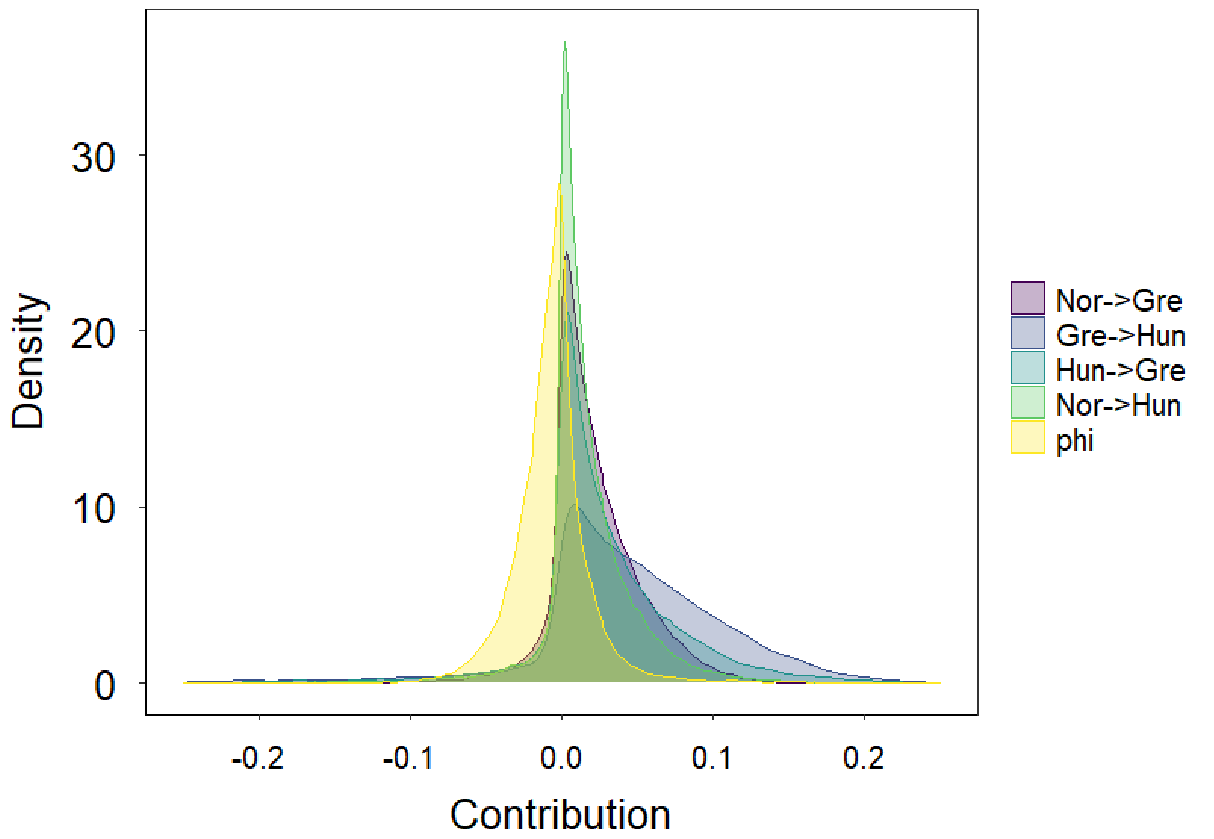

Fig. S2 – Results of the transient LTRE analysis. Posterior distributions of overall contributions (i.e. direct + indirect effect) of the five vital rates modelled as a function of 'Culling' to the realized change in population growth rate of the Fennoscandian Lesser White-fronted Goose population after the implementation of the fox-culling program.

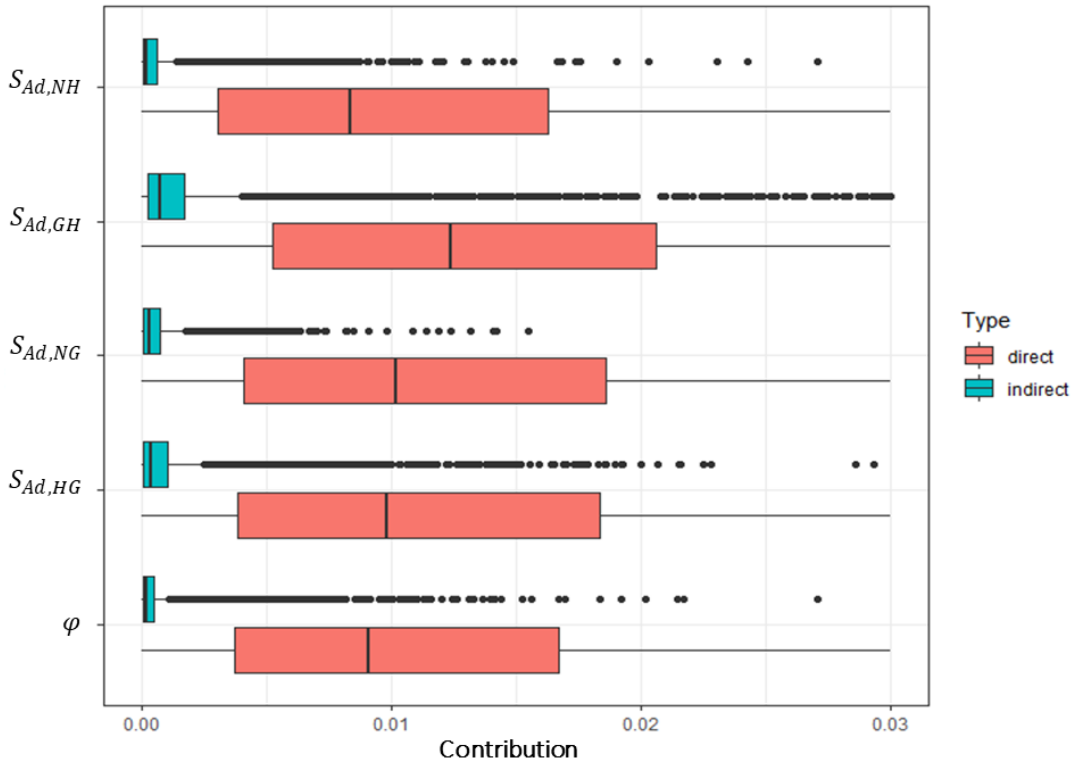

Fig. S3 – Contribution of direct and indirect effects of the five vital rates modelled as a function of 'Culling' to the realized change in the population growth rate of the Fennoscandian lesser white-fronted goose population after the implementation of the fox-culling program. Note that we magnified the portion of the figure with the boxes to emphasize the differences between mean contributions. However, large uncertainty makes impossible any reliable inference on which vital rates contributed the most.