An integrated population modelling workflow for supporting mesopredator management

Chloé R. Nater[1,*,†], Stijn P. Hofhuis[2,*], Matthew Grainger[1], Øystein Flagstad[1], Rolf A. Ims[2], Siw Killengreen[3], Dorothee Ehrich[2]

[1] Department of Land and Biodiversity, Norwegian Institute for Nature Research, Trondheim, Sør-Trøndelag, Norway

[2] Department of Arctic and Marine Biology, UiT – The Arctic University of Norway, Troms, Tromsø, Norway

[3] Department of Education, UiT – The Arctic University of Norway, Troms, Tromsø, Norway

* These authors share first authorship

† Corresponding author: chloe.nater@nina.no

Key words: culling; demography; harvest; hunting; immigration; IPM; mortality; population dynamics; red fox; reproducibility; tundra; Vulpes vulpes

Open Research: Raw data on harvested foxes (Ehrich et al. 2025a, 2025c) and small rodent abundance (Ehrich et al. 2025b) are stored in the COAT Data Portal (https://data.coat.no/). The datasets are subject to a 2-year embargo and will be released on 14th April 2027. Earlier access can be requested through Dr. Dorothée Ehrich (dorothee.ehrich@uit.no). The genetic data, opportunistic den survey data, complete model input data, posterior summaries from the models, and additional supplementary figures are stored in OSF: https://osf.io/756re/ (Nater and Hofhuis 2025). All code, including the "targets" pipeline and all necessary documentation for reproducing and adapting the workflow can be found on GitHub (https://github.com/ChloeRN/VredfoxIPM. Version 2.0 of the code, which was used to create the results presented in this paper, is provided via Zenodo (Nater et al. 2025).

ABSTRACT

Expanding populations of mesopredators threaten biodiversity and human health in many ecosystems across the world. Lethal control through harvest is commonly implemented as a mitigation measure, yet its effects on mesopredator population dynamics in interaction with compensatory mechanisms and environmental conditions has rarely been assessed quantitatively due to data constraints. Recent advances involving integrated population models (IPMs) have enabled promising new avenues for overcoming these constraints by jointly analysing multiple datasets while simultaneously accounting for bias and uncertainty. Here we developed a versatile IPM workflow for studying mesopredator population dynamics under different management regimes and applied it to an expanding population of red foxes in Arctic Norway. Our model combined routinely collected data on age, reproductive status, and genetic similarity from >4000 harvested red foxes with opportunistic field observations and information published on red foxes elsewhere. This allowed us to quantify population dynamics over a period of 20 years and identify the drivers of changes in population growth rates using retrospective (transient Life Table Response Experiments, tLTREs) and prospective (population viability analyses, PVAs) perturbation analyses. We found dramatic year-to-year fluctuations in red fox population size due to natural mortality and immigration responding to changes in rodent prey availability and population density. Forward projections indicated that current harvest levels were likely sufficient to prevent population increase over longer time periods. However, even substantial increases in harvest levels were unable to evoke population decline due to strong buffering effects of density-dependence, especially through immigration. Our study highlights the potential of IPMs for studying population dynamics even when no structured surveys of living animals are available and illustrates the value of extracting and curating information from harvested animals. Our semi-automated and reproducible modelling workflow is ready to be re-run periodically when new data becomes available for our study population and can easily be transferred and adapted to other harvested species, contributing to the development of cost-effective population analyses that are of high relevance for informing management strategies and mitigating biodiversity loss in practice.

INTRODUCTION

Spread and abundance increases of both alien and native invasive species are among the main drivers of ongoing global biodiversity loss (IPBES 2019). In many ecosystems around the world, population growth and range expansion of predators that occupy mid-ranking positions in the food-web (mesopredators) are particularly problematic (Prugh et al. 2009, Moore et al. 2023). Mesopredators of concern are often generalists that benefit from a variety of anthropogenic changes to ecosystems. One the one hand, increased food availability in human-dominated landscapes relaxes bottom-up constraints on mesopredators (Larivière 2004, Pasanen-Mortensen and Elmhagen 2015). On the other hand, mesopredators face less top-down constraints following the eradication of many apex predator populations (Elmhagen and Rushton 2007, Prugh et al. 2009). Mesopredator populations that are thus released from both top-down and bottom-up constraints increase in abundance, leading to high predation pressure on their prey and causing negative cascading effects down the food chain (Prugh et al. 2009, Roos et al. 2018). Declines and even local extinctions of numerous bird, reptile, and ungulate populations have been the result (Brashares et al. 2010, Read and Scoleri 2015, Kämmerle et al. 2017). Population growth, human spread, and climatic changes also help mesopredators expand into new habitats, become invasive, and displace native species (Salo et al. 2008, Elmhagen et al. 2017). Besides having negative impacts on biodiversity, the expansion of mesopredators can also pose a threat to human health as some mesopredators (e.g. red foxes, *Vulpes vulpes*) are vectors for zoonotic diseases such as rabies and alveolar echinococcosis (Holmala and Kauhala 2006, Laurimaa et al. 2016).

Given the negative effects of mesopredator population growth and expansion, control through harvest (also referred to as “culling”) is widely implemented as a management action. However, the effect of harvest is difficult to quantify and often unclear (Conner and Morris 2015), partly owing to demographic resilience that allows mesopredator populations to compensate for increased mortality (Salo et al. 2010, Minnie et al. 2016). Assessing the impacts of management interventions thus requires unbiased estimates of population sizes and demographic rates under different harvest pressures and environmental conditions (Henden et al. 2021). Traditionally, obtaining such estimates hinged on the availability of long-term individual-based demographic data from marked individuals (Clutton-Brock and Sheldon 2010), but this type of data is difficult to obtain, particularly for predators that are highly mobile, elusive, and nocturnal (Karanth and Chellam 2009). Furthermore, long-term monitoring of marked individuals in heavily harvested populations is often impossible due to high mortality. Data obtained from harvested animals, on the other hand, are readily available but traditional methods of analysing them (e.g. life table analysis) are prone to bias and unable to reliably estimate demographic parameters (Williams et al. 2002).

The solution to both insufficient individual-based data and analytical biases lies in data integration, and – specifically – in using integrated population models (IPMs). IPMs jointly analyse multiple datasets, allowing both rich and sparse datasets, as well as expert knowledge and other published studies, to contribute information to a model for the true, latent population dynamics (Schaub and Kéry 2021). This makes IPMs ideal tools for harnessing information from harvest data while accounting for biases and maximizing information gain from sparse auxiliary data, as illustrated by the rapid growth in their popularity for studying harvested populations over recent years (Arnold et al. 2018, Nater et al. 2021, Gamelon et al. 2021). Bayesian implementations of IPMs have the additional advantage of full propagation of uncertainty and the possibility to connect directly to simulations of population trajectories under different harvest and management scenarios (Saunders et al. 2018, Schaub and Kéry 2021), making them highly relevant in the context of mesopredators management.

Irrespective of the exact method, another crucial aspect for analyses geared towards informing management decisions is reproducibility. Ensuring effective predator control and sustainable management of fish and wildlife populations more generally requires estimates of population size and key vital rates not just once but repeatedly over time (Nichols et al. 2019). This stands in stark contrast to the fact that the vast majority of analyses in ecology are not documented to an extent that allows re-running and reproducing workflows (Culina et al. 2020). For applied ecology to be truly capable of empowering managers and decision-makers, it has to produce not only research articles but also accessible and reproducible workflows that can be re-run routinely and cost-effectively whenever new data becomes available (Powers and Hampton 2019).

In this study, we develop a versatile IPM workflow for studying mesopredator population dynamics under different harvest regimes and apply it to a case study of an expanding red fox population in the tundra of Northern Norway. Capitalizing on data integration, our IPM combines information from harvested foxes (age, reproduction, and genetic similarity), opportunistic surveys (pup counts from hunters and camera traps at dens), and prior knowledge on natural mortality derived from other studies. We then use the model to estimate population size and key vital rates of red foxes in our study area over the last 20 years (2005-2024) of intense harvest. We further investigate the potential role of environmental conditions (food availability via the abundance of small rodents), density dependence, and harvest compensation on population regulation, and identify the key demographic drivers of past population change through transient life table response experiments (tLTREs, Koons et al., 2016, 2017). Finally, we couple our IPM with population viability analyses (PVAs, Morris & Doak, 2002; Saunders et al., 2018) to explore the effects of alternative management scenarios on future population trajectories. We thereby provide estimates and improved understanding of red fox population dynamics that are relevant for the conservation of a fragile tundra ecosystem. Beyond that, we publish an accessible, reproducible, and semi-automated IPM workflow that can be 1) re-run easily once new data becomes available and 2) readily adapted to other harvested species. We thus facilitate the implementation of cost-effective population analyses that are of high relevance for informing management and conservation in practice.

MATERIALS AND METHODS

Study species and area

Red foxes are one of the most widely distributed mesopredators in the world (Larivière and Pasitschniak-Arts 1996) and their influx into tundra regions of Eurasia and North America during the last century is one of the most striking examples of mesopredator expansion (Skrobov 1960, MacPherson 1964, Stickney et al. 2014, Gallant et al. 2020). This ongoing expansion threatens populations of endemic tundra species (Elmhagen et al. 2017, Henden et al. 2021), and has motivated intense management efforts not least through targeted harvest (Angerbjörn et al. 2013, Marolla et al. 2019). The red fox's success in colonizing and thriving in new habitats stems from its opportunistic diet and relatively fast life history: red foxes can reach sexual maturity towards the end of their first year of life and females typically give birth to 3-6 pups (range 1-12) per year. Survival beyond 5 years of age is rare in the wild (Larivière and Pasitschniak-Arts 1996).

Our study focuses on a population of red foxes located on Varanger Peninsula, which lies at the northeastern tip of Norway (70-71°N 28-31° E, Figure 1). The interior and northern and eastern coastal lowlands of the peninsula form a fringe of low Arctic tundra that is disconnected from the extensive Russian Arctic tundra to the east (Walker et al. 2005). Due to rapid climate warming this tundra ecosystem is currently on trajectory to shift towards a boreal climate (Pedersen et al. 2021), and this has contributed to an increase in local red fox abundance during the last century (Johnsen 1929, Ims et al. 2017). Small rodents are the most important prey of red foxes on Varanger (Killengreen et al. 2011), and red foxes are known to exhibit strong numerical response to rodent cycles (Henden et al. 2009a). Three species of rodent are of functional importance in our study area; the grey-sided vole (*Myodes rufocanus*), the tundra vole (*Microtus oeconomus*), and the Norwegian lemming (*Lemmus lemmus*) (Ims et al. 2017). All three species have spatially and temporally synchronous cycles with a 4 to 5-year periodicity, but lemming peak abundances occur only during some of the vole peak years (Ims et al. 2011, 2017). In addition, red foxes feed on reindeer carcasses, which are readily available in inland areas in winter due to widely practiced reindeer herding, and also exploit marine resources along the coastline (Killengreen et al. 2011).

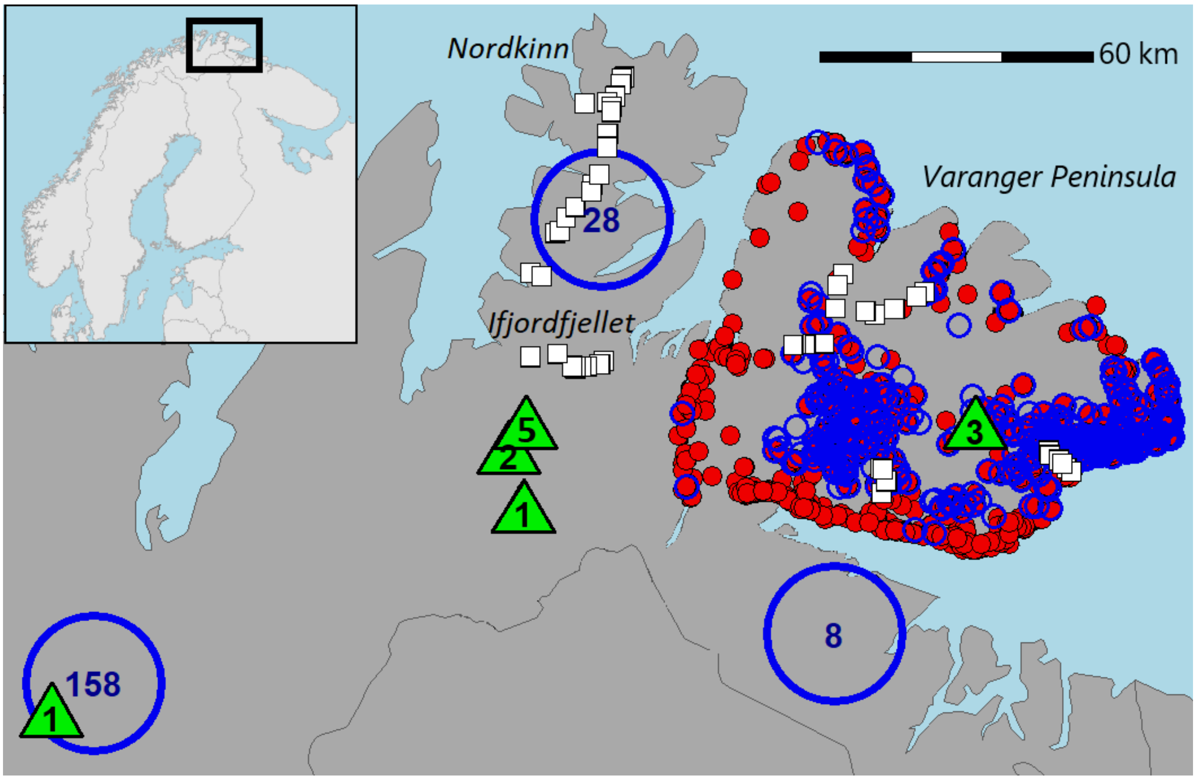

Figure 1. The study area within Fennoscandia and spatial representation of used data sources. Red circles = harvested females; Small blue circles = genetic samples of harvested females and males; Large blue circles = genetic samples from three possible immigrant source populations and corresponding sample sizes; Green triangles = opportunistic surveys of live pups upon den emergence and corresponding sample sizes; White boxes = small rodent trapping sites.

Intense red fox harvest has been implemented in our study area and some neighbouring areas since 2005 to conserve the remaining population of regionally endangered arctic foxes (*Vulpes lagopus*) and ground nesting birds (Hamel et al. 2013, Ims et al. 2017). While this may have contributed to recent increases in ptarmigan (*Lagopus lagopus*) densities (Henden et al. 2021), sparse monitoring data has so far precluded robust assessments of whether and how harvesting, together with environmental drivers, has affected the red fox population itself.

Data collection and processing

Harvested foxes – Age

Over 4500 red foxes (~ 40% females, 50% males, 10% sex not recorded) have been harvested on Varanger Peninsula from 2005 to 2024. The main hunting season lasts from July 15th to April 1st, and most foxes (85 %) were shot by local hunters along the inhabited coastline at baits, by tracking, or by using a caller. Field inspectors from the Norwegian Nature Inspectorate shot 15 % of foxes, most of which in the inner parts of the peninsula during March-April and rarely in May. Age was determined for a subset of harvested foxes (17 – 100% of females per hunting season, see Appendix S1: Table S1 for details) by analysis of cementum annuli of one of the upper canines (Grue and Jensen 1979). We subsequently arranged data on all aged females shot during the primary (winter) hunting season into an age-at-harvest matrix. The resulting winter age-at-harvest matrix included a total of 879 females shot during the period October- May in each season from 2004-2005 to 2023-2024. Foxes shot in the summer months (July-September) were not included in the age-at-harvest data due to inconsistent and biased aging; they were, however, accounted for during analysis (see description of data likelihoods under "IPM construction" below).

Harvested foxes – Reproduction

We inferred pregnancy rates from placental scars for females > 1 year and harvested between July 1st and March 20th (n= 290). This period reflects the start of harvest after the reproductive season until the period in which we observed that the proportion of uteri with placental scars decreased at the onset of gestation (Englund 1970). Foxes harvested from April 10th until May 20th (n=121) were used to infer pregnancy rate from embryos. This period reflects the time during which we observed the highest pregnancy rate, which corresponded well with the pregnancy rate inferred from placental scars after the reproductive season. Litter sizes in utero were inferred from the number of placental scars or embryos. Sample sizes and proportions for reproductive data extracted per year are summarised in Appendix S1: Table S1.

Harvested foxes – Genetic population assignment

We obtained information on immigration by comparing the genotypes from foxes harvested on the Varanger Peninsula (505 samples from 2005-2015) to the gene pool of three possible immigrant source populations further west (Finnmarksvidda, 158 samples from 2008-2013; Nordkinn Peninsula, 28 samples from 2011) and south (South Varanger, 8 samples from 2016, Figure 1). All samples were genotyped at 12 microsatellite loci (Ostrander et al. 1995, Moore et al. 2010). We then used genetic assignment tests in the program Geneclass (Piry et al. 2004) to identify likely first-generation immigrants among the genotyped foxes from the Varanger Peninsula. The results consisted of individual-level p-values for the hypothesis that a fox originated from the Varanger population given its likely genetic composition in the birth year of the respective fox. We used the recommended threshold of 0.05 to assign immigrant (1) and resident (0) status to individuals. For more information on collection, analysis, and processing of genetic data, see Appendix S2.

Opportunistic surveys – Pup counts on dens

Numbers of live pups (= litter size upon emergence from the den) were counted opportunistically when red fox reproduction occurred in Arctic fox dens monitored by the Norwegian den monitoring programme (Ulvund et al. 2023, n=8), and when field inspectors removed red fox litters from dens (n=4). These observations were made during the months of June and July in eight different years and on a selection of five dens, one of which was located within the study area and four within a 160 km radius east of the study area (Figure 1).

Environment – Rodent abundance

In addition to data on red foxes, our analyses included an environmental covariate representing the availability the most important food resource for red foxes on Varanger: small rodents (Killengreen et al. 2011). We obtained a proxy for small rodent abundance from snap trapping of lemmings and voles using the small quadrat method of Myllymäki et al. (1971). Snap trapping was conducted for 2 days in late June (spring) and 2 days in early September (autumn) in 49 sites within the study area and 48-60 sites located to the west of the study area (Figure 1, see Ims, Yoccoz, and Killengreen (2011) for more details). To capture spatial and temporal scales relevant to the different red fox vital rates, we created two different rodent covariates: 1) winter (average of autumn and subsequent spring trapping) rodent abundance within Varanger relevant for local demography and 2) autumn rodent abundance at a larger spatial scale (including the sites within – and west of Varanger) relevant for immigration (red fox dispersal is known to peak in autumn; Storm et al. 1976, Gosselink et al. 2007, Soulsbury et al. 2008). As there is no clear evidence in literature on red fox preference for either voles or lemmings (Barth et al. 2000, Elmhagen et al. 2002, Savory et al. 2014), we considered both groups of species to be of equal importance and summed their abundances. However, to account for the much lower capture probability of lemmings compared to voles (Jensen et al. 1993), we additionally calculated our annual small rodent abundance covariates by first z-standardizing the two species groups separately, and subsequently summing them (see Appendix S6 for more details on background and procedure).

IPM construction

Age-structured population model

Our IPM was developed based on a previously published IPM for harvested arctic foxes (Nater et al., 2021). The model's core is a population model that considers female red foxes in five distinct age classes at an annual census in June that coincides with pup emergence from breeding dens (post-breeding census, Figure 2). Age class 1 corresponds to females < 1 year of age and is made up of all locally recruited female pups of the year, and immigrants that enter the population between the current and next census. Age classes 2 to 4 correspond to females aged 1 to 3 years, while age class 5 encompasses all females that are 4 years old or older. The population projection matrix for the time interval t to $t + 1$ can be expressed as:

$$\begin{bmatrix} (1 + immR_{t+1})S_{1,t}\mathrm{F}_{2,t+1} & S_{2,t}\mathrm{F}_{3,t+1} & S_{3,t}\mathrm{F}_{4,t+1} & S_{4,t}\mathrm{F}_{5,t+1} & S_{5,t}\mathrm{F}_{5,t+1} \\ (1 + immR_{t+1})S_{1,t} & 0 & 0 & 0 & 0 \\ 0 & S_{2,t} & 0 & 0 & 0 \\ 0 & 0 & S_{3,t} & 0 & 0 \\ 0 & 0 & 0 & S_{4,t} & S_{5,t} \end{bmatrix}$$

Females in each age class a survive from year t to $t + 1$ with a an annual survival probability $S_{a,t}$ (July to June). This can be decomposed further into age- and year-specific harvest ($mH_{a,t}$) and natural ($mO_{a,t}$) mortality hazard rates as: $S_{a,t} = \exp\left(-\left(mH_{a,t} + mO_{a,t}\right)\right)$ (Ergon et al. 2018). We assumed that harvest morality was different for juveniles and adults ($mH_{1,t} \neq mH_{2,t} = mH_{3,t} = mH_{4,t} = mH_{5,t}$) while natural mortality differed for all age classes. Conditional on survival, age a females advance to the next age class $(a+1)$ and reproduce according to a composite rate $\mathrm{F}_{a+1,t+1}$ just prior to next year's census $(t+1)$. Successful reproduction requires females to mate and get pregnant (probability $\Psi_{a,t}$), conceive a litter with an expected size $\rho_{a,t}$, and for the pups to survive from gestation to emergence from the den (= census, probability $S_{0,t}$), hence

$$F_{a,t} = 0.5\Psi_{a,t}\rho_{a,t}S_{0,t}$$

The factor 0.5 is the assumed even sex ratio at emergence from the den and limits $F_{a,t}$ to represent female pups only.

Immigrating foxes are expected to enter the population in autumn/early winter in their first year of life (Jensen 1973, Storm et al. 1976). We therefore modelled immigration into age class 1 as taking place prior to the harvest period (i.e. all immigrants are available for harvest) and formulated it as a rate ($immR_t$) that expresses the ratio of immigrated age 1 individuals to locally recruited age 1 individuals. While modelling immigration as a rate as opposed to numbers may lead to estimation issues in some IPMs (Schaub and Fletcher 2015, Zipkin and Saunders 2018), this parameterization gave more precise estimates in our case and was more straightforward to link to our data on immigration (see below).

We implemented the population model including demographic stochasticity (sensu Caswell, 2001) to account for uncertainty resulting from chance individual outcomes in population processes. The resulting variables represent the realized numbers of age class a females ($N_{a,t}$), age class a breeders ($B_{a,t}$), female embryos carried by age class a mothers ($L_{a,t}$), and female pups born to age a mothers and recruited into the population ($R_{a,t}$, Figure 2). See published code for the detailed implementation on this.

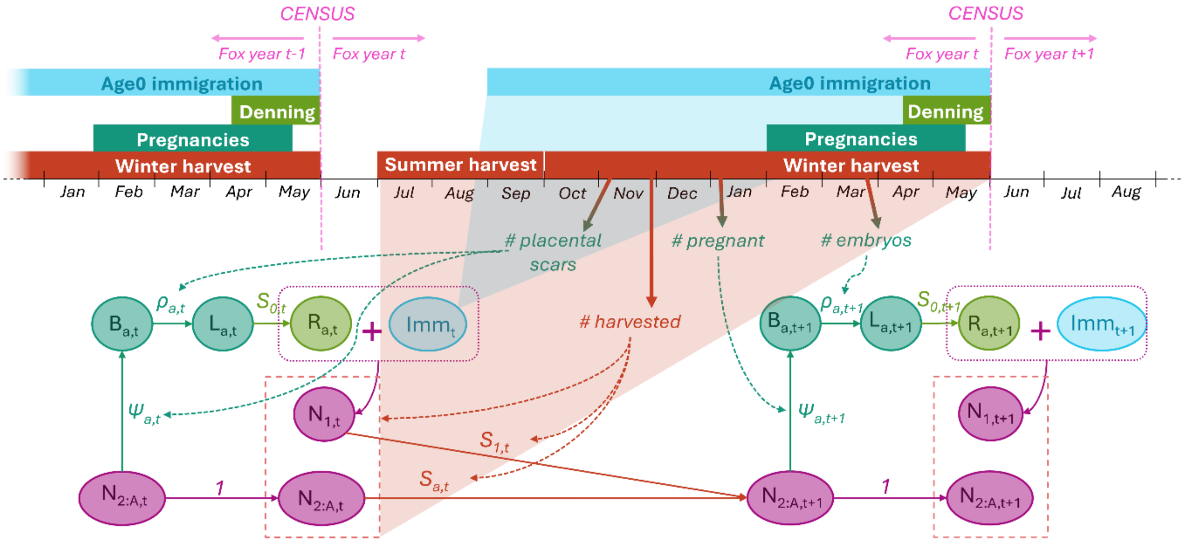

Figure 2. Schematic overview of the red fox annual cycle, timing of data collection, and the female-based age-structured population model. The round bubbles are the age- (index a, with A = index of oldest age class) and year- (index t) specific population-level metrics modelled by the IPM: N = population size in June, B = breeding population size, L = number of locally produced pups in utero, R = number of locally produced recruits (pups survived to emergence from the den), Imm = number of age class 1 immigrants. They are linked by the vital rates survival (S, where $S_{1:A}$ = annual survival and S_0 = survival to emergence from den), pregnancy rate (Ψ), and litter size in utero (ρ). The shaded areas visualize the time-matching between the annual life cycle and the quantities in the population model. The dashed arrows show how the different parts of collected data are linked to model parameters.

Data likelihoods

The role of data likelihoods in IPMs is to link the different available datasets to the relevant parameters in the population model. Our red fox IPM contains five types of data likelihoods adding information on 1) harvest and population size, 2) pregnancy rate, 3) litter size in utero, 4) denning survival, and 5) immigration rate.

The first likelihood uses counts and age-structure from the harvested foxes arranged in an age-at-harvest matrix $C_{a,t}$. Each cell in the matrix corresponds to the number of age a individuals harvested between the censuses of years t and $t+1$, and these numbers are linked to true female population size ($N_{a,t}$) in June via

$$C_{a,t} \sim Binomial(N_{a,t}, h_{a,t}p_t)$$

The probability in the binomial likelihood is composed of an age- and year-specific harvest rate, $h_{a,t}$, and a yearly data proportion parameter, p_t. The former is the probability of a fox being harvested and is defined as $(1 - S_{a,t})\frac{mH_{a,t}}{mH_{a,t}+mO_{a,t}}$, while the latter is the a priori known proportion of harvested foxes that have 1) been delivered for dissection and 2) been aged, and hence added to the age-at-harvest matrix, in a given year. All foxes harvested in summer were also accounted for via p_t as we treated them as "not aged" due to known aging bias. An underlying assumption of this likelihood is that detection is perfect, i.e., we accurately know the number of foxes harvested each year. This assumption is reasonable as the red fox hunt on Varanger Peninsula not only has mandatory reporting but also offers monetary rewards for each fox delivered to the project.

The second and third likelihoods link information on reproduction from necropsies of harvested females to age- and year-specific pregnancy rates ($\Psi_{a,t}$) and litter sizes ($\rho_{a,t}$), respectively. Both likelihoods are based on observations of reproductive activity determined using placental scars and embryos present in uteri of harvested females as described in the "Data collection and processing" section. The proportion of harvested females of age a showing signs of reproductive activity in year t among all harvested females of the same age and time period is determined by pregnancy rate and we expressed this as a Bernoulli likelihood for individual observations ($P2$) of reproductively active (= 1) or not (=0):

$$P2_x \sim Bernoulli(\Psi_{age_x,year_x})$$

Here, x is the index for each individual observations and age_x and $year_x$ represent the age and year of female x in the year of the reproductive event. The likelihood involving litter size is set up in the same way, with the data ($P1$) being the number of embryos detected for reproducing female x:

$$P1_x \sim Poisson(\rho_{age_x,year_x})$$

The fourth data likelihood feeds in information from opportunistic observations of number of live pups post emergence from dens. Pup counts on dens ($NoPups_x$, with x = index of the observation) were treated as realizations of a Poisson distribution with an expected value equal to the estimated total number of pups of both sexes ($R \times 2$) divided by the estimated total number of breeding females (B) in the relevant year:

$$NoPups_x \sim Poisson\left(\frac{sum(R_{1:A,year_x}) \times 2}{sum(B_{1:A,year_x})}\right)$$

$R_{a,t}$ and $B_{a,t}$ are linked by both litter size in utero ($\rho_{a,t}$) and survival to emergence from the den ($S_{0,t}$, Figure 2). Since the above likelihood for litter size in utero provides substantial information on $\rho_{a,t}$, the likelihood for live pup counts on dens contributes information primarily towards denning survival $S_{0,t}$ (= the probability of pups surviving from conception to emergence from the den).

The final data likelihood links information on immigration status derived from Geneclass 2 analyses of genetic data to immigration rate. We tested out several different ways of formulating this data likelihood with regards to a) whether we used a priori determined immigration status using a p-value threshold or (rescaled) p-values directly and b) whether we pooled data across years to provide information on time-average immigration rate (μ^{immR}) or analysed data on a year-by-year basis to provide information on yearly immigration rates ($immR_t$). In the remainder of the manuscript, we focus on a model employing a likelihood for a priori determined immigration status (p-value threshold of 0.05) pooled across years and thus estimating average immigration rate from the data:

$$genObs_{Imm} \sim Poisson(genObs_{Res}\mu^{immR})$$

Here, $genObs_{Imm}$ and $genObs_{Res}$ are the total numbers of individuals that were determined to be first generation immigrants and locally recruited residents, respectively, relative to the reference population in their year of birth. For details on the other tested versions of this likelihood and a comparison of models using different versions, see Appendix S2.

Temporal variation in vital rates

We modelled among-year variation in (age-specific) vital rates $X_{a,t}$ using covariates, density feedbacks, direct compensation, and random effects according to the following general equation:

$$link\left(X_{a,t}\right) = link(\mu_a^X) + \beta_R^X rodent_t + \beta_D^X density_t + \gamma^X harvestLogD_t + \epsilon_t^X$$

Here, the intercept μ_a^X represents the age-specific vital rate average; β_R^X and β_D^X, are the slopes for the effects of rodent abundance ($rodent_t$) and log local population density ($density_t$), respectively; γ^X is the effect of harvest compensation that scales with the deviation of annual harvest mortality from the overall mean ($harvestLogD_t = \log(mH_{a,t}) - \log(\mu_a^{mH})$). ϵ_t^X are random year effects assumed to be normally distributed on the relevant link scale. We used a log-link for mortality hazard rates ($mH_{a,t}$, $mO_{a,t}$), litter size in utero ($\rho_{a,t}$), and immigration rate ($immR_t$) and a logit-link for pregnancy rate ($\Psi_{a,t}$). We included effects of local rodent abundance in winter in Varanger on natural mortality, litter size in utero, and pregnancy rate and of rodent abundance in fall across a larger region (Varanger, Nordkinn, and Ifjordfjellet) on immigration rate. Density feedback was included for immigration rate and natural mortality of the youngest age class. For natural mortality of all age classes, we additionally included a compensatory effect of harvest. We did not include covariates for harvest mortality as we did not have sufficient information on, for example, harvest effort. Temporal random effects, however, were included on all vital rates except denning survival, which we assumed to be the same in all years due to lack of data. Estimates of temporal variation vital rates were partially obtained directly from analysing specific data sets (litter size in utero, pregnancy rate, harvest mortality) and partially informed by variation across the integrated data streams (natural mortality, immigration rate).

Bayesian implementation

We implemented our IPM in a Bayesian framework using the software package NIMBLE (de Valpine et al. 2017) for R (R Core Team 2022). We capitalized on NIMBLE's functionality for definition-time if-else to write a user-friendly implementation that allows for easy adjustment of different model parameters and functions (see code for details). Our final model runs were based on four MCMC chains with 200,000 iterations each, using NIMBLE's standard samplers. 75,000 iterations per chain were discarded as burn-in and the remainder thinned by a factor of twenty, resulting in a posterior of 4×6,250 = 25,000 samples.

Prior information – Natural mortality

Bayesian implementation of models offers the possibility of adding auxiliary information via priors. This was essential in our case study because we lacked observational data on natural mortality. We tested three different approaches for defining prior distributions: 1) using published values for another red fox population (Devenish-Nelson et al., 2013), 2) using a meta-analytic model (see Appendix S3) of survival estimates from multiple red fox populations collated in Devenish-Nelson et al. (2013), and 3) using the Hoening model developed by Porteus et al. (2018) to calculate natural mortality from maximum observed age. More information on the different approaches, a comparison of models employing them, and detailed conclusions thereof can be found in Appendix S3.

For initializing age-specific population sizes in the first year of study, we used weakly informative discrete uniform priors with lower and upper bounds of 1 and 800 (youngest age class) / 400 (older age classes), respectively (this translated to a density of roughly 0.7

foxes/km^2, which is well above expected densities based on estimates from forested areas in Norway that are expected to support higher densities than tundra habitats, Lindsø et al. 2022). For all other parameters, we used non-informative priors (see model code for details).

Model assessment

To assess the adequacy of our model, we investigated the consequences of our choice of a) likelihood for immigration data and b) informative priors as described above (see Appendices S2 & S3). The specific choice of likelihood for the genetic data determined estimates of immigration rate and degree of among-year variation therein but had very little effect on model outputs otherwise (Appendix S2). The choice of informative prior for natural mortality not only affected natural mortality itself, but also estimates of average denning survival, harvest mortality, and absolute (but not relative changes in) population size (Appendix S3). Directly "borrowing" survival estimates from two other red fox populations, North Sweden and Bristol, seemed to be a less suitable approach (as indicated by highly inflated estimates of among-year variation in natural mortality) than using estimates from either meta-analysis or the Hoening model. Based on these assessments we defined our main model with a likelihood for a priori determined immigration status (estimated from genetic data) with a p-value threshold of 0.05 and used natural mortality priors derived from a meta-analysis of red fox survival estimates collated in Devenish-Nelson et al. (2013).

Additionally, we confirmed that there was no major lack of fit of our man model by checking posterior overlaps for parameters estimated by the IPM vs. estimated by independently fit models (Appendix S4, Gelman et al., 2013; Schaub & Kéry, 2021).

Demographic drivers of population dynamics

Life Table Response Experiments (LTREs) are retrospective perturbation analyses that identify the relative contributions of demographic drivers to population changes that have occurred in the past (Caswell 2001). Koons et al. (2017) suggested transient LTREs (tLTREs) for analysing past changes in realized annual population growth rates as estimated in typical IPMs, and here we implemented both a random design and a fixed design tLTRE. The random design tLTRE quantifies the contributions of variation in vital rates to variation in annual population growth rate across the entire study period while the fixed design tLTRE allowed us to investigate how year-to-year changes in vital rates contributed to differences in annual population growth rates for each pair of years within the study period (growth rate for interval t-1 to t vs. t to t+1). Further details on the implementation of the tLTRE analyses, including the associated calculation of transient sensitivities, are provided in Appendix S5.

Responses to management scenarios

After using the tLTRE analyses to investigate the drivers of past population dynamics, we coupled our IPM to a Population Viability Analysis (PVA, Morris & Doak, 2002) to explore the potential impacts of different management strategies on future population trajectories for red foxes on Varanger. In practice, this involved extending the time-coverage of our IPM to project the population for an additional ten years beyond data collection (until 2034) while simultaneously applying changes to vital rates during this additional time period (Schaub and Kéry 2021). We first focused primarily on the most relevant and realistic management action in the context of red foxes on Varanger: modification of harvest practices. Specifically, we ran scenarios in which harvest was completely removed, reduced by 50%, and increased by 50-200% from 2024 onwards to explore the role of harvest for longer-term population dynamics. As populations that are driven by cyclical resource availability are likely differently susceptible to management during different phases of the cycle (Bieber and Ruf 2005, Henden et al. 2009b), we also explored whether increasing harvest was more effective in years with either below or above average rodent abundance. Subsequently, we also investigated the buffering capacity of (compensatory) immigration by running scenarios with substantially less or no immigration, alone or in combination with increased harvest.

For implementing the PVA, we had to make two types of adjustments for ensuring relatively realistic predictions. First, we accounted for autocorrelation / cyclic dynamics in rodent abundance by predicting future rodent abundance in Varanger using the following second-order autoregressive model fit to the rodent covariate data:

$$RodA_t = \beta_1^{RA} * RodA_{t-1} + \beta_2^{RA} * RodA_{t-2} + \beta_3^{RA} * RodA_{t-1} * RodA_{t-2} + \epsilon_t^{RA}$$

Rodent abundance in the larger area surrounding Varanger was then estimated from $RodA_t$ using a correlation model for rodent abundance within Varanger versus the larger area. Second, we constrained the number of immigrants per year to not exceed twice the maximum number estimated during the study period to avoid unrealistically high population size predictions and consequential haywire density feedbacks.

Reproducible workflow setup

We set up our entire coding workflow (Figure 3) as an openly accessible, semi-automated, and reproducible “R targets” pipeline (Landau 2021) that integrates directly with the COAT database, where much of our data is stored (see Open Research statement). Together with rich documentation for every step of the workflow, this ensures that our analysis can be reproduced and re-run with additional data later in a robust and efficient way.

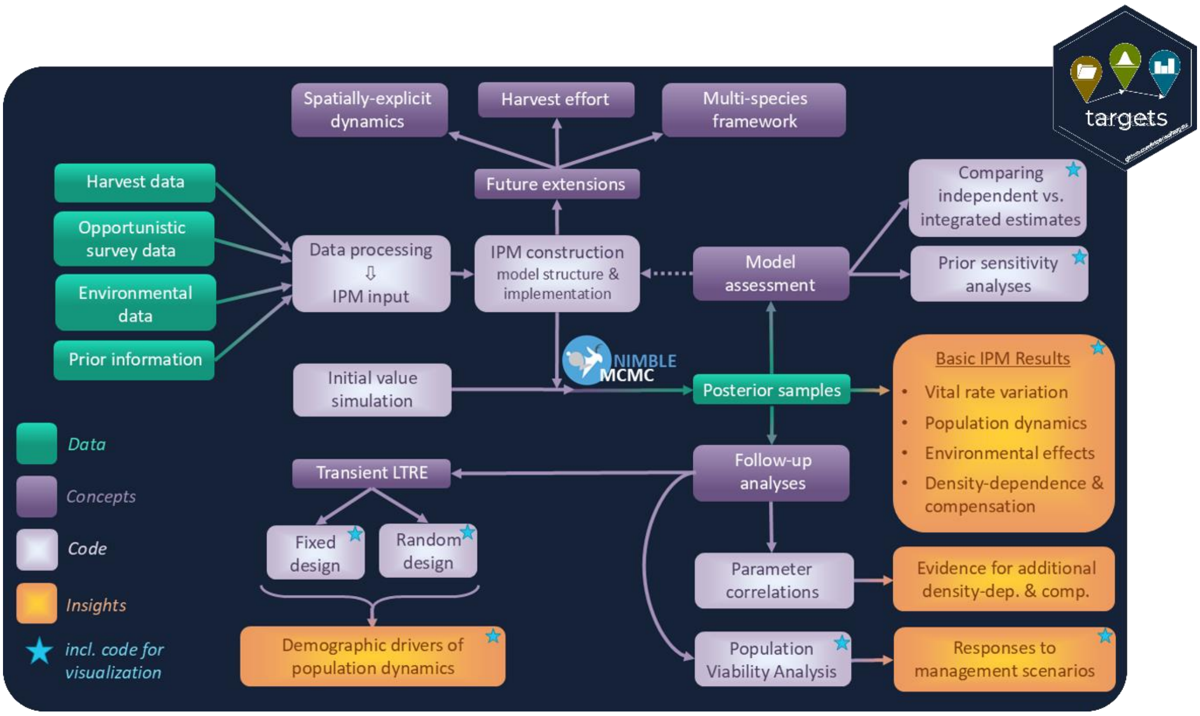

Figure 3: Schematic representation of the different components and steps in the semi-automated "targets" workflow for the analysis of population dynamics of red foxes on the Varanger peninsula. The latest version of the pipeline, including documentation, can be found on GitHub: https://github.com/ChloeRN/VredfoxIPM. Nimble logo © 2014, Perry de Valpine, Christopher Paciorek, Daniel Turek, Clifford Anderson-Bergman, Duncan Temple Lang; source and license (BSD-3): https://github.com/nimble-dev/nimble. Targets hex logo © 2025 Eli Lilly and Company; source and license (MIT): https://github.com/ropensci/targets.

RESULTS

Vital rate variation, environmental effects, and compensatory mechanisms

Numerical results in the following are given as median [95% credible interval] unless otherwise indicated. Survival probabilities were highest for the oldest foxes (0.593 [0.517, 0.665]) and lowest for juveniles, including new immigrants (0.280 [0.170, 0.456], Figure 4). For juveniles and 3-year old foxes, natural mortality was the dominant factor determining survival: only ~17 [10, 27] % of juvenile and 30 [13, 59] % of 3-year old mortality was due to harvest on average, while the corresponding estimates for the other age classes ranged from 52 [24, 91] % to 57 [28, 90] %.

Pregnancy rates increased with age from, on average, 0.468 [0.359, 0.576] for 1-year old females to 0.857 [0.764, 0.922] for females older than 4 years (Appendix S1: Figure S1).

Older vixens also conceived more pups, with litters of 3-year-old females containing one (1.099 [0.379, 1.850) extra pup on average relative to litters of 1-year old first-time breeders. Denning survival of pups was estimated at 0.708 [0.512, 0.937] (Appendix S1: Figure S1).

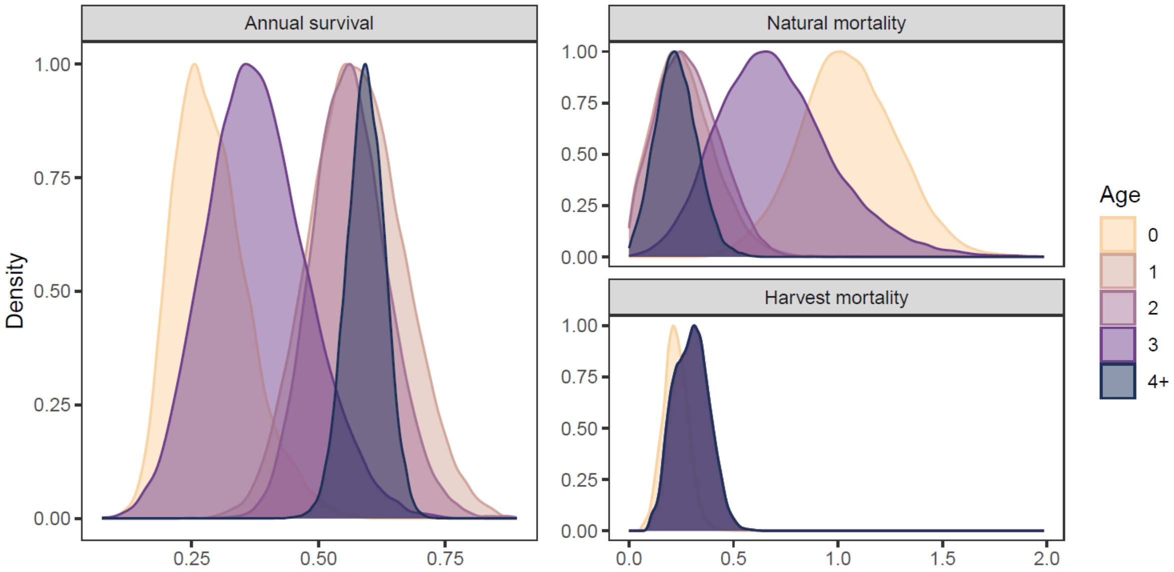

Figure 4. Scaled posterior distributions for age-specific average survival probabilities and mortality hazard rates.

The model estimated an average immigration rate of ~ 1 immigrant per 10 locally born pups (0.107 [0.079, 0.140], Appendix S1: Figure S1) but immigration rate, and consequently the number of immigrants, varied substantially across years (Appendix S1: Figures S2 & S5). Among-year variation was also evident for the other vital rates (Appendix S1: Figure S2), for example, with clear peaks in pregnancy rate and fetus numbers in 2011 and 2023 and survival from 2011 to 2012 and 2015 to 2016, as well as exceptionally high harvest mortality in the hunting season 2019-2020 (Appendix S1: Figure S2).

A part of among-year variation in vital rates could be attributed to variation in rodent abundance (Figures 6). We found evidence for lower natural mortality during and higher pregnancy rates and larger litters following winters with higher rodent abundance on Varanger peninsula (Figure 5). Model estimates also suggested a positive effect of autumn rodent abundance at the larger spatial scale on immigration rate, although uncertainty was high (Figure 5).

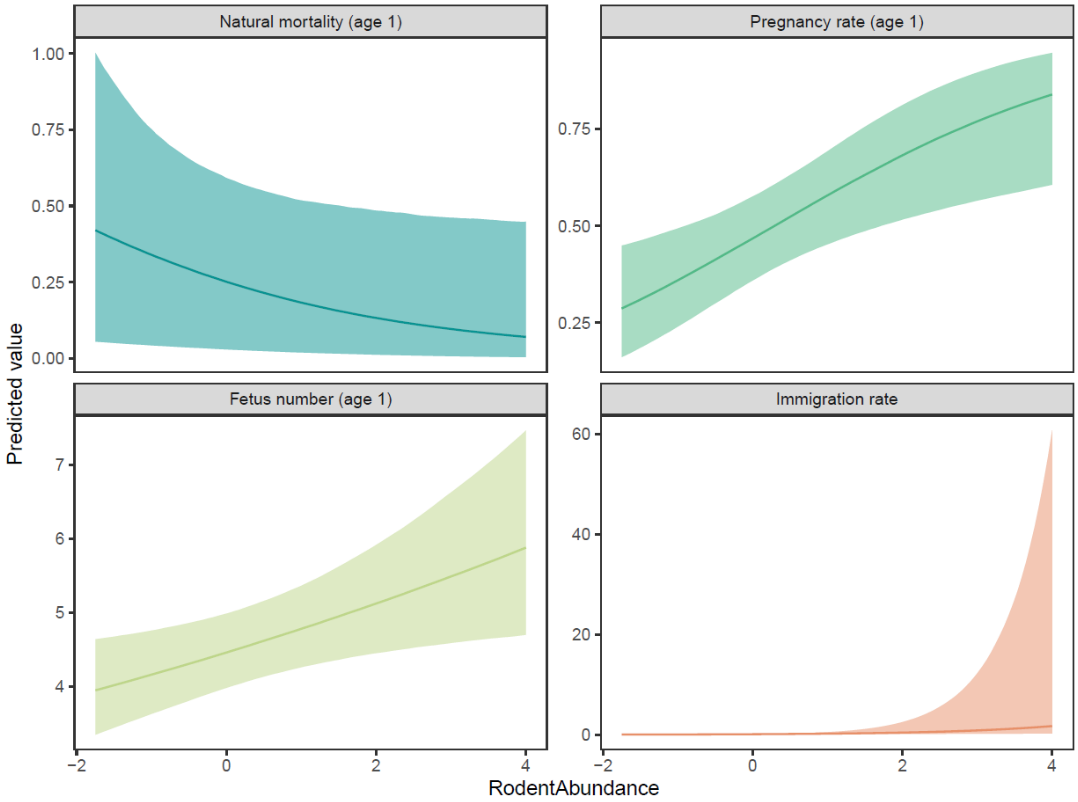

Figure 5. Predicted effects of z-standardized rodent abundance during winter on Varanger peninsula on natural mortality, pregnancy rate and fetus number, and rodent abundance during autumn at the larger spatial scale on immigration rate. The solid line represents the posterior median while the ribbon marks the 95% credible interval.

While the model was unable to estimate harvest compensation in natural mortality directly (γ^{mO}= 0.004 [-1.262, 1.686]), it provided evidence for density-dependence in both natural mortality and immigration and suggested that higher population densities led to increased natural mortality of the youngest age class (β_D^{mO}= 0.607 [0.091, 1.499]) and less immigration into the population (β_D^{immR}= -2.181 [-6.095, 0.260], Appendix S1: Figure S3).

Population dynamics during the study period

While the average growth rate of the red fox population on Varanger was stable and more likely to be positive than negative during the study period (geometric mean = 1.043 [0.996, 1.075], representing ~ 4% increase on average), there was large variation in annual population growth rates among years, amounting to population peaks lagging one year behind cyclic peaks in rodent abundance in 2007-08, 2010-11, 2014-15, 2018-19, and 2022-23 (Figure 6). Between 2016 and 2021, the population appeared to be declining and only had a weak numerical response to the rodent peak in 2018-2019, (Figure 6). However, this trend reversed with the latest rodent peak in 2022-23, resulting in a marked population increase in the latest years. The consequences of sharp population size fluctuations were visible in the population's age structure, showing a high proportion of young (1-year old) breeders in years following population increase and vice-versa following decrease (Appendix S1: Figure S4).

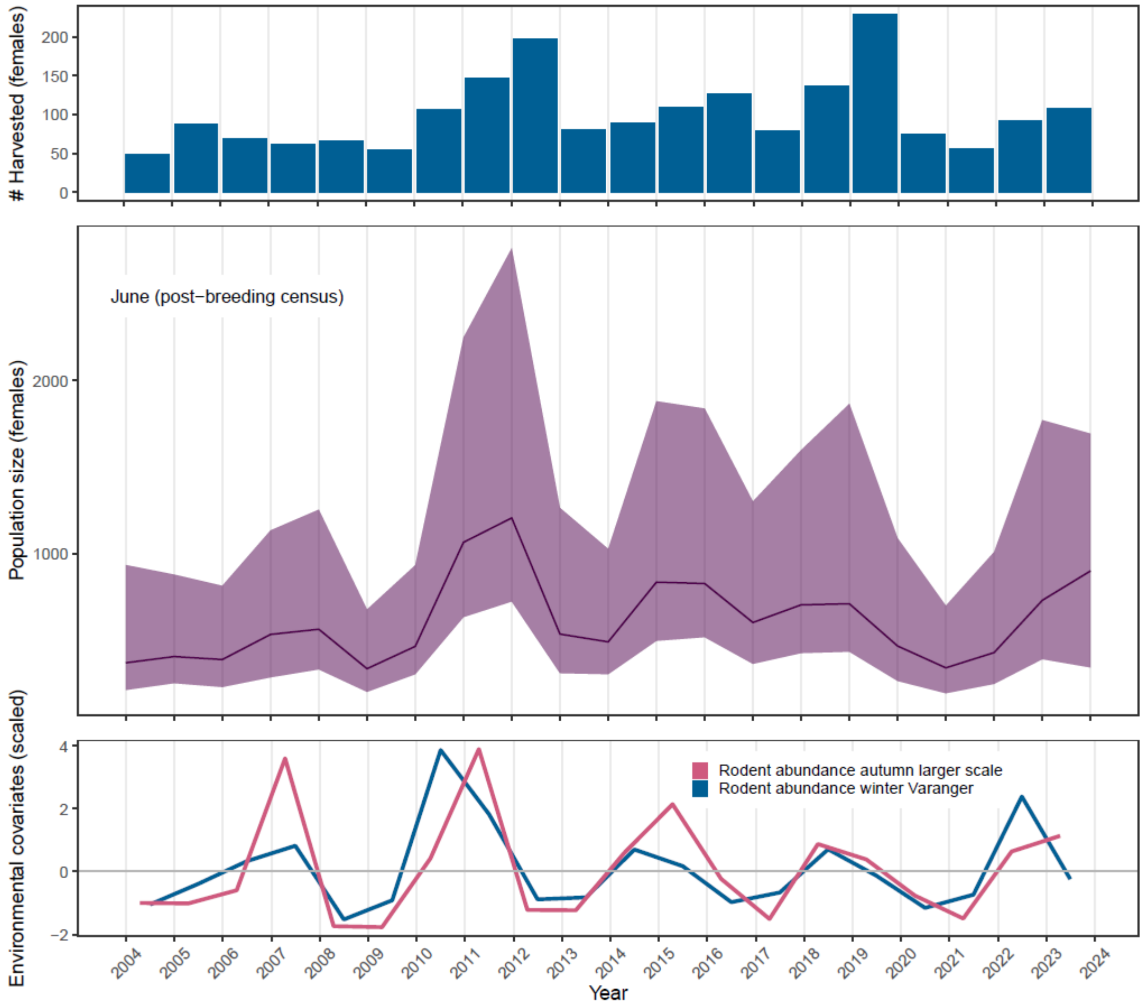

Figure 6. Number of female foxes harvested per year (top),estimated annual population sizes in June (middle), and observed rodent abundance per year (bottom). In the middle panel, the solid line represents the posterior median, the ribbon marks the 95% credible interval.

The results of the random design tLTRE indicated that the two factors that had contributed most to variation in population growth rate over the period 2005-2023 were fluctuations in natural mortality (especially of juveniles) and immigration rate (Figures 7 & Appendix S1: Figure S6). Harvest, reproduction, and population structure had contributed relatively little.

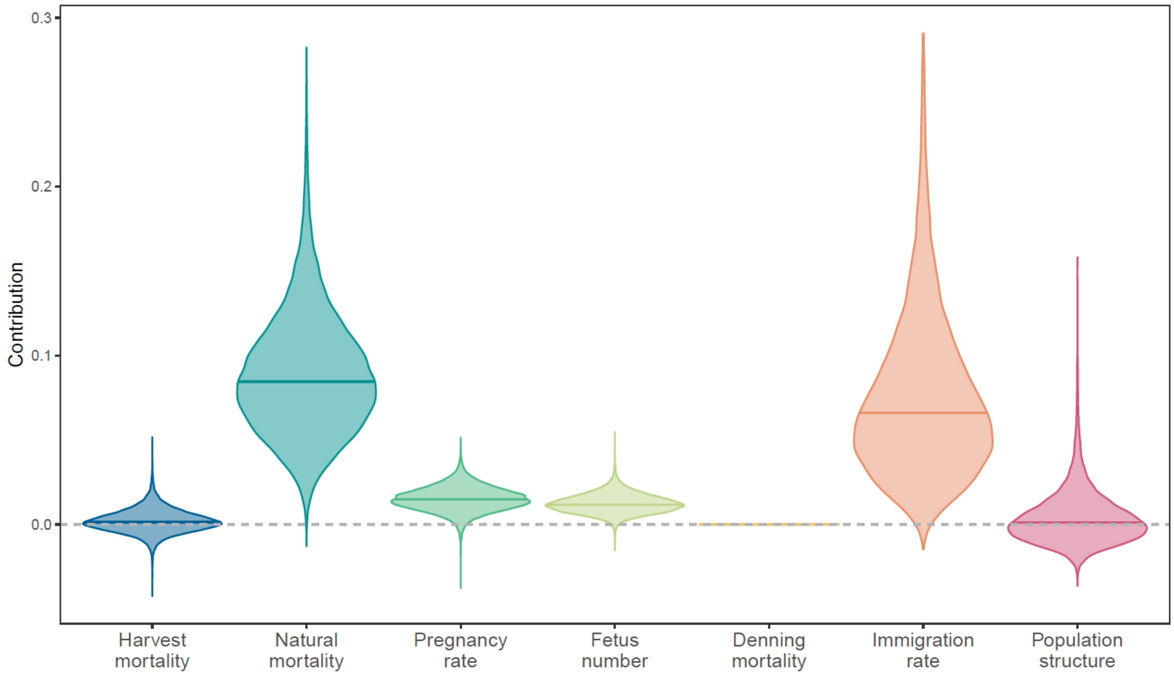

Figure 7. Posterior distributions of the contributions of variation in different demographic rates and population structure to changes in population growth rate between 2005-2006 and 2022-2023 (random design tLTRE). Violins visualize distributions, solid lines mark posterior medians. All components are summed across age classes (see Appendix S1: Figure S6 for a breakdown into age classes). Note that the contribution of denning mortality is 0 as this parameter was modelled as constant over time.

The results from the fixed design tLTRE gave some more nuanced insights, revealing that it was predominantly during the drastic changes in population growth rate in the first two thirds of the study period, as well as for the two most recent years, that changes in natural mortality and immigration rate were the primary drivers (Figure 8).

The relatively smaller changes in population growth rate during the period of population decline between 2015/2016 and 2021 were characterized by more balanced contributions, and changes in population structure and harvest mortality in particular seem to have been relatively more important in that period (Figure 8).

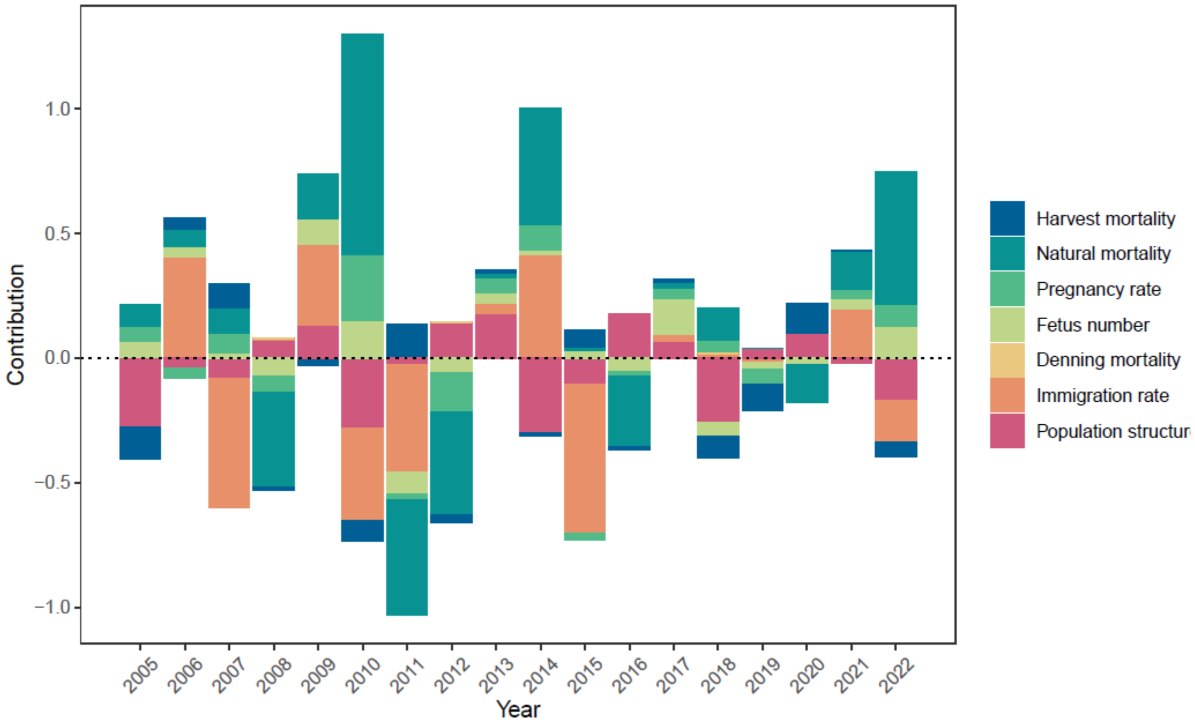

Figure 8. Posterior medians of the contributions of changes in different demographic rates and population structure to changes in population growth rate from one year to the next (fixed design tLTRE). The bar for year t above represents contributions to change from population growth rate for the interval t-1 to t to population growth rate for the interval t to t+1. Overall positive bars indicate increases in population growth rate over the relevant interval, while overall negative bars indicate decreases. All components are summed across age classes. Note that the contribution of denning mortality is 0 as this parameter was modelled as constant over time.

Management scenarios

Forecasting population dynamics for an additional 10 years beyond the study period (until 2034) revealed that a fluctuating but overall stable future population trajectory is likely if all parameters including environmental drivers remain unchanged (Figure 9). Without harvesting, on the other hand, the population is likely to increase instead, although uncertainty around this prediction becomes high (Figure 9A). Increasing harvest mortality, even by as much as 200%, is unlikely to evoke population decline and instead results in the population stabilizing at slightly lower levels (Figure 9A). Simulations further indicated that the timing of harvest increases (years with high versus low rodent densities) did not affect population size projections substantially (Appendix S1: Figure S7B). Immigration functioned as a stabilizing mechanism, as indicated by rapid population decline in a scenario without future immigration (Figure 9B). Models further suggested that moderate (50%) increases in harvest and decreases in immigration functioned best in tandem (Appendix S1: Figure S7A).

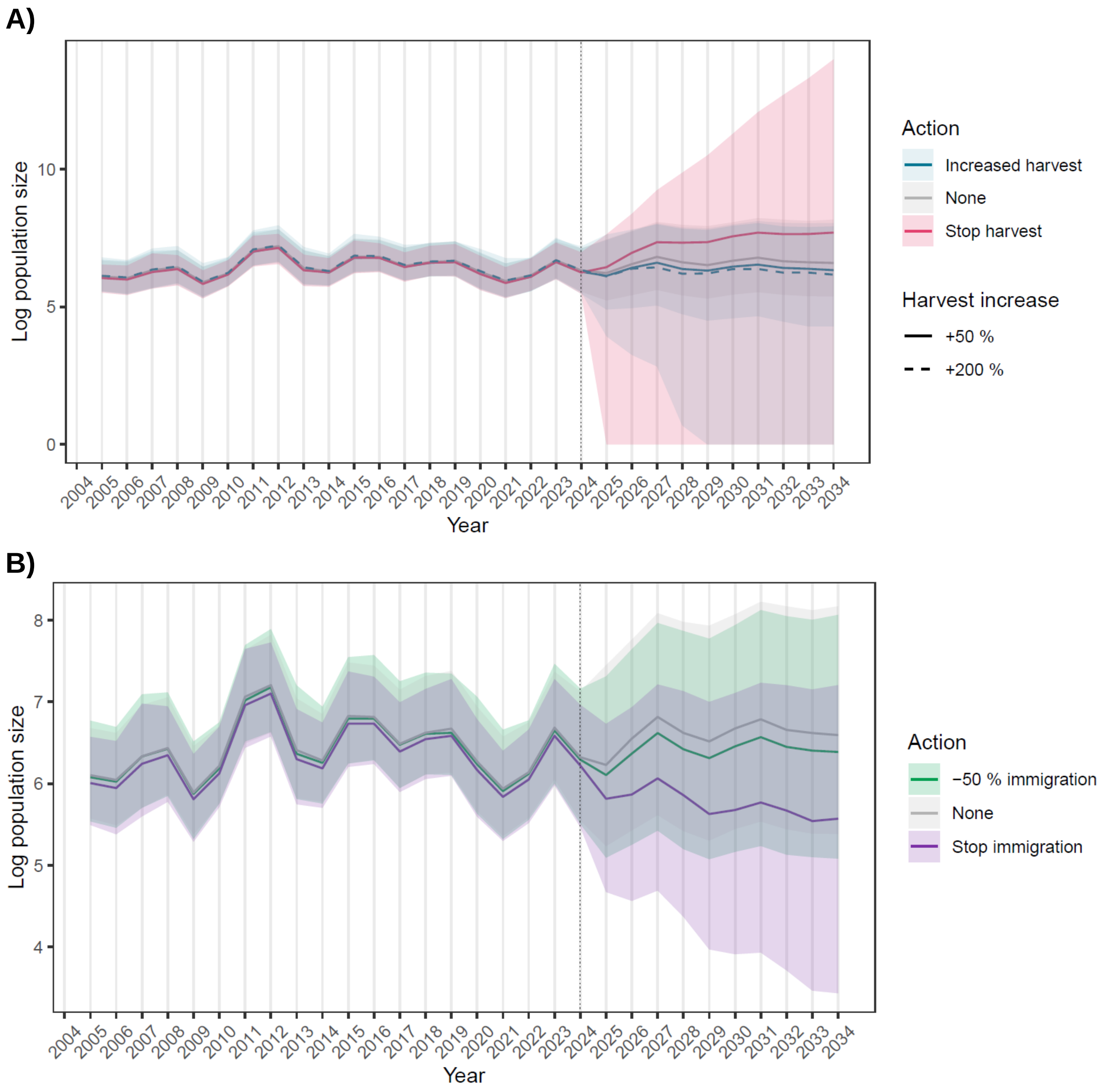

Figure 9. Population estimates for the study period 2004-2024 and subsequent population forecasts until 2034 under different management scenarios for harvest (A) and immigration (B). Note that population size is plotted on the log scale. The baseline projection (grey) assumes unchanged parameters. “Stop” scenarios involved setting harvest mortality/immigration rate to 0 from 2024 onwards. Remaining scenarios included percent decreases/increases in harvest mortality/immigration rate. Additional scenarios are shown in Appendix S1: Figure S7.

DISCUSSION

Successfully controlling and mitigating impacts of expanding mesopredator populations is an important and widespread challenge for wildlife management (Prugh et al. 2009). However, assessing the effects of management interventions is often severely hampered by a lack of observational data for estimating mesopredator population sizes and vital rates. This limits our understanding of how control efforts (e.g. harvest), compensatory mechanisms, and environmental conditions affect population dynamics together (Henden et al. 2021). In this study, we capitalized on data integration and designed a IPM workflow to overcome these limitations. We showed the potential of this workflow in a case study where we jointly analysed harvest, genetic, and environmental data, opportunistic field observations, and prior knowledge from literature. This allowed us to quantify population size and vital rate variation of a tundra red fox population over a time-period of 20 years. Using a combination of retrospective and prospective analyses, we identified natural mortality and immigration rate as the primary drivers of short-term changes in past population dynamics and highlighted how the interplay of harvest, immigration, rodent, abundance, and density feedbacks is likely to stabilize population size across a range of future management scenarios.

Reproductive output in a fluctuating environment

We obtained estimates of average pregnancy rates and litter sizes in utero that increased with age of the mother (Appendix S1: Figure S1) and resembled equivalent estimates from other ecologically similar red fox populations (Englund 1980, Devenish-Nelson et al. 2013). Carnivore reproduction is closely tied to food availability (Fuller and Sievert 2001) and for tundra red foxes that means small rodent abundance in particular (Killengreen et al., 2011, Henden et al. 2009a). In accordance with this, we found substantially higher pregnancy rates and litter sizes following winters with high rodent abundance (Figure 5). The effects of rodent abundance constituted ~54 % and 45 % of among-year variation in pregnancy rate and litter size, respectively. The remaining variation was modelled as random, representing the joint effects of other potentially important factors such as alternative food sources (e.g.

reindeer carcasses, ptarmigan, marine subsidies; Killengreen et al. 2011), abiotic conditions (e.g. winter severity; Bartoń and Zalewski 2007), and density feedbacks (Heydon and Reynolds 2000). For the latter, we found some preliminary evidence as post-hoc parameter correlations suggested that breeding probability (but not litter size) may be density-dependent (Appendix S1: Table S2). Future applications should therefore investigate potential density feedback in reproductive parameters in addition to natural mortality and immigration. Another aspect worth investigating is to what degree environmental conditions may differentially affect younger and older foxes; here we used the same rodent and random effects on reproductive rates of foxes in all age classes, but age-specific sensitivity to resource constraints is not uncommon in carnivores (Rauset et al. 2015) and may also have played into our estimates of unexplained variation.

Natural vs. harvest mortality

Natural mortality hazard rate estimates were strongly dependent on prior information (Appendix S3). Nonetheless, priors for all age classes were updated noticeably, indicating that other data across the IPM did contribute some information on natural mortality (Appendix S4: Figure S1). Juvenile natural mortality was high compared to that of other age classes (Figure 4) which, in addition to low reproductive rates of yearlings (Appendix S1: Figure S1), suggests a challenging first year of life in our study area. This is common in many mammalian species (Sibly et al. 1997) and in foxes can be related to inexperience, fitness costs of dispersal, and poorer body condition (Gosselink et al. 2007, Soulsbury et al. 2008). Natural mortality decreased with age as expected, with the exception of 3-year-olds whose estimate was more uncertain due to a lower sample size of harvested individuals (n = 59) compared to other age classes (n = 105 - 408).

Peaks in natural mortality during 2008, 2013, 2017 and 2020 (Appendix S1: Figure S2), and the all-time lows in 2010 and 2022 were clearly associated with small rodent abundance and local population densities (Figures 6 & Appendix S1: Figure S8), despite covariate effects being rather uncertain (Figures 5 & Appendix S1: Figure S3). As with reproduction, the model estimated a substantial portion of time variation as random, and part of this may be explained by alternative food sources that we did not model. Indeed, reindeer carcasses are known to be important in the inland parts of our study area when small rodents are scarce, while marine-derived subsidies are used along the coastline (Killengreen et al. 2011). Future studies that aim to disentangle the drivers of variation in natural mortality will therefore likely benefit from considering the importance of alternative food resources and known spatial heterogeneity therein (Killengreen et al. 2011, Chevallier et al. 2020).

Unlike for natural mortality, we found no evidence for higher harvest mortality hazard rates of juveniles as opposed to older foxes (Figure 4). This was somewhat surprising, as curiosity, naivety, and/or restricted access to food resources was expected to make juveniles more susceptible to harvest (Storm et al. 1976, Baker et al. 2001). Nonetheless, age-independent harvest mortality was also found in arctic foxes (Nater et al. 2021), and relatively low juvenile harvest mortality is common across a large number of terrestrial vertebrate species (Hill et al. 2019). Harvest mortality was relatively constant during the study period except for high estimates in the 2019-2020 winter season (Appendix S1: Figure S2). While we may speculate that this was linked to exceptionally high effort in 2019-2020, we did not have sufficient data on harvest effort to test this explicitly. Quantitative data on active hunter numbers and their time spent hunting are now being routinely collected, however, and we expect that these data will be able to help estimate and interpret observed variation in harvest mortality in the near future (Soininen et al. 2016).

Better data for quantifying time variation in harvest mortality may also improve our model's ability to pick up on compensatory mechanisms beyond density-dependence. While we did find higher natural mortality in years that started out with higher population densities, our current IPM failed to provide any evidence of natural mortality directly compensating for concurrent harvest mortality (Appendix S1: Figure S3) by means of other mechanisms such as survivorship bias and spatial or social redistribution (Péron 2013). While this may be at least partially attributed to the relatively constant harvest mortality in our study population, obtaining robust estimates of the degrees of compensatory/depensatory cause-specific mortalities is notoriously difficult and typically requires large amounts of high quality data on individual survival (e.g. Sandercock et al. 2011, Nater et al. 2020, Riecke et al. 2022). It is therefore not surprising that we did not obtain insightful estimates in our present analyses given that we lack long-term individual-based data on survival and cause-specific mortality for red foxes on Varanger peninsula.

Pulsed immigration in a sink population

Immigration from source populations into harvested sink populations is a much discussed mesopredator management issue (Beasley et al. 2013, Lieury et al. 2015, Kierepka et al. 2017). Our estimate of 1 immigrant per 10 locally born pups confirms previous speculation that substantial red fox immigration occurs even when control efforts are applied at a large regional scale (Heydon and Reynolds 2000, Norén et al. 2017). While our average estimate of ~10% immigrants among recruits (age class 1) is relatively low compared to a ~26 % average reported for mammals (Millon et al. 2019), we have to recall that the location of our study area on a peninsula likely limits immigration somewhat. Nonetheless and despite the relatively low average, immigration rates varied considerably across years. In low immigration years less than 3% of the new cohort originated from outside the study area.

Meanwhile, up to one third of recruits were immigrants in other years (Appendix S1: Figure S2). Even though uncertainty was high, several immigration peaks coincided with high rodent abundance (Figures 5 & Appendix S1: Figure S5). This supports the notion that dispersal is a key strategy to cope with temporal resource variation (Holt 2008), and similar immigrant pulses following small rodent peaks have previously been described in Arctic foxes (Norén et al. 2011). Our additional finding that higher population densities were associated with decreased immigration further underscores that relative environmental carrying capacity plays an important role in determining immigration rates. However, uncertainty in the estimates and the tendency of immigration to absorb unaccounted-for variation in IPMs (Paquet et al. 2021) limit our ability to draw firm conclusions on the drivers of variation in immigration rate in our study population.

In the vast majority of IPMs built and implemented to date, both immigration and time variation therein are estimated as “free parameters” without explicit data (Schaub and Kéry 2021). Here, we partially overcame the drawbacks of this (Paquet et al. 2021) by developing one of the first IPMs that anchors the estimate of average immigration rate using genetic data. Immigration rate estimates were sensitive to a range of assumptions made both by the a priori population assignment analysis and the implementation of the likelihood for the genetic data itself (Appendix S2), but much of this could be accounted for by extending data integration to include the genetic assignment analysis in the IPM.

Drivers of population dynamics

Annual population size estimates fluctuated greatly over the duration of the study, reaching up to 4 times as many foxes in peak years relative to low years (Figure 6). During peak years, the population’s age structure was characterised by a high proportion of young foxes in general and young breeders in particular (Appendix S1: Figure S4), suggesting a key role of reproductive output, survival of young, and possibly immigration for population increase. The results from our tLTRE analyses confirmed this, identifying changes in natural mortality of the youngest age class, immigration, and – to a lesser degree – pregnancy rates of 1- and 2-year-olds as the key drivers of changes in population growth rate over the course of the study period (Figures 4 & Appendix S1: Figure S6). Furthermore, years of population increase followed small rodent abundance peaks (Figure 6), adding to the body of evidence for delayed numerical responses of red fox populations to small rodent abundance (Chirkova 1953, Kolb and Hewson 1980, Lindström 1989, O'Mahony et al. 1999, Sidorovich et al. 2006, Henden et al. 2009a). The rodent abundance peak during 2018-2019 was not followed by a marked increase in red fox population abundance, and this was attributed to a substantial increase in harvest mortality in 2018 and 2019 (Figure 8). This suggest that sufficiently high harvest may be able to prevent temporary population growth prompted by high resource availability.

Potential impact of harvest changes

Given the large harvesting effort undertaken in our study area, it may seem surprising at first glance that the tLTRE analyses showed relatively low contributions of harvest mortality overall (Figure 7). However, tLTRE analyses focus on the contribution of *realized past changes* in vital rates (Koons et al. 2016, 2017), and as harvest mortality has changed little relative to other vital rates over the course of our study period (Appendix S1: Figure S2), this limits the degree to which tLTRE analyses can give insights into the role of harvest for population control on time scales beyond year-to-year transitions. PVAs, on the other hand, allowed us to investigate the effect of the absolute level of harvest on population trajectories across multiple years. Simulations predicted a stable population trajectory if all parameters remain unchanged but suggested that increase is more likely in absence of harvest (Figure 9A). Though uncertainty is high, current harvest levels thus appear to limit longer-term population growth. Further increases in harvest even up to triple of today's levels, on the contrary, were predicted to have rather limited effects on long-term population trajectories (Figure 9A). This is due to density-dependent mechanisms that mitigate increased harvest pressures and stabilise the population size through lower natural mortality and increased immigration. Indeed, rapid population decline in the absence of immigration (Figure 9B) highlights the potential of immigration to function as an important stabilising mechanism in our study population. This aligns with other studies that outline compensation of harvest by immigration as a key challenge for mesopredator management (e.g., Newsome et al. 2015, Lieury et al. 2015, Minnie et al. 2016, 2018, Kierepka et al. 2017, Porteus et al. 2019). One common piece of advice given in such situations is that control efforts should be conducted at large spatial scales (Conner and Morris 2015), yet we show that immigration poses a challenge even when intervention is conducted in an area spanning more than 6000 km^2. That said, our study area is located on a partially isolated peninsula and this may provide possibilities for interventions that limit immigration, such as targeted harvest along the immigration corridor and timed to coincide with the period when most migrant foxes are on the move. Working towards a better understanding of the movement ecology of both the source and sink populations is thus paramount for developing more efficient management strategies for red foxes on Varanger peninsula.

It is important to note that our PVAs here only consider the effect of management interventions on the red fox population itself. They make no predictions as to whether and how red fox management has any of the intended indirect effects on the endangered species they aim to conserve (arctic foxes and ground-nesting birds). For instance, while increased harvest mortality may have a limited effect on red fox population size in the long term, temporary reductions in population size may still benefit prey species or competitors at times when they are most vulnerable, such as during their respective breeding (Henden et al. 2010, Kämmerle et al. 2019, Wilkinson et al. 2024). Future work should therefore focus on a multi-species perspective (Mellard et al. 2022) and integrated community models (Zipkin et al. 2023), for example, constitute a promising approach given our initial work on red foxes here and the ecosystem-level monitoring conducted on the Varanger peninsula (Climate-ecological Observatory for Arctic Tundra, COAT, Ims et al., 2013).

IPM workflows as promising management tools

IPMs can be invaluable tools for quantitative population assessments in applied contexts, yet many are of limited use beyond their initial implementation because associated workflows are incompletely published, sparsely documented, and not set up for re-use. This stands in stark contrast to the facts that i) reproducibility of analytical workflows is key for successful adaptive management (Dietze et al. 2018, Nichols et al. 2019) and ii) openness, accessibility, and transparency of not just research results but entire workflows is essential for productive and equitable stakeholder inclusion in applied ecology and wildlife management (Powers and Hampton 2019). To address these challenges, we have made our entire workflow available as a semi-automated, accessible, reproducible, and well documented “targets” pipeline (Landau 2021). By doing so, we enable for analyses to be re-run in a swift and cost-efficient manner once new data become available, and set the stage for co-creation in further development of models, predictions, and management strategies. This paves the way not only for refining the biological aspects of the analysis (e.g. spatial representation, multi-species perspective) but also for better representation of the human dimension, such as how hunting regulations translate into harvest mortality (Eriksen et al. 2018) and how additional actions targeted at human subsidies (Killengreen et al. 2011, Jahren et al. 2020) might augment control through hunting. In addition, our workflow-approach also has the potential to greatly enhance transferability of our modelling framework to other populations and species; even if all IPMs are – to some degree – tailored to their respective study systems, their workflows are often comprised of the same steps (Figure 3). By emphasizing workflow architecture and providing generalisable code and functions whenever possible, we hope to facilitate others' efforts to build IPM workflows for their study species.

Conclusions

There is an urgent need for evidence-based management of mesopredators and quantitative assessments of control efforts (Doherty and Ritchie 2017, Lennox et al. 2018, Kämmerle et al. 2019) and here we have designed a reproducible IPM workflow that provides relevant insights using data that is readily available for many species of management concern: demographic data from harvested animals, sparse opportunistic surveys, and prior knowledge extracted from literature. In addition, ours is one of the first IPMs using genetic data. As genetic monitoring is becoming increasingly attractive as an addition to or even replacement of traditional monitoring approaches (Schwartz et al. 2007), this study can serve as a starting point for developing the next generation of IPMs, which are certain to include more sophisticated integration of genetic monitoring data via sub-models for genetic mark-recapture (Lukacs and Burnham 2005), close-kin mark-recapture (Bravington et al. 2016), estimation of (effective) population size and migration rates (Lowe and Allendorf 2010), and more.

ACKNOWLEDGEMENTS

This project would not have been possible without the large efforts of local hunters, field inspectors from the Norwegian Nature Inspectorate, and many students, assistant, researchers, and technicians that have been involved in collecting the data. It is thanks to the monitoring efforts and stewardship of COAT (Climate-ecological Observatory for Arctic Tundra) that these data are properly curated and available today.

This project has received financial support from the Norwegian Environment Agency (grant nr. 22SCD2B4, projects “Fjellrev i Finnmark” and “COAT arctic fox module”) and UiT – the Arctic University of Norway.

AUTHOR CONTRIBUTIONS

Chloé R. Nater: Conceptualization, Methodology, Software, Formal analysis, Writing - Original Draft, Writing - Review and editing, Visualization. Project administration, Supervision, Funding acquisition.

Stijn P. Hofhuis: Conceptualization, Investigation, Data curation, Software, Formal analysis, Writing - Original Draft, Writing - Review and editing, Visualization.

Matthew Grainger: Software, Formal analysis, Writing - Review and editing.

Øystein Flagstad: Investigation, Writing - Review and editing.

Rolf A. Ims: Conceptualization, Writing - Review and editing, Funding acquisition.

Siw Killengreen: Conceptualization, Investigation, Data curation, Writing - Review and editing.

Dorothée Ehrich: Conceptualization, Investigation, Data curation, Formal analysis, Writing - Original Draft, Writing - Review and editing, Supervision, Funding acquisition.

References

Angerbjörn, A., N. E. Eide, L. Dalén, B. Elmhagen, P. Hellström, R. A. Ims, S. Killengreen, A. Landa, T. Meijer, M. Mela, J. Niemimaa, K. Norén, M. Tannerfeldt, N. G. Yoccoz, and H. Henttonen. 2013. Carnivore conservation in practice: replicated management actions on a large spatial scale. Journal of Applied Ecology 50:59–67.

Arnold, T. W., R. G. Clark, D. N. Koons, and M. Schaub. 2018. Integrated population models facilitate ecological understanding and improved management decisions. The Journal of Wildlife Management 82:266–274.

Baker, P. J., S. Harris, C. P. J. Robertson, G. Saunders, and P. C. L. White. 2001. Differences in the capture rate of cage-trapped red foxes Vulpes vulpes and an evaluation of rabies control measures in Britain. Journal of Applied Ecology 38:823–835.

Barth, L., A. Angerbjörn, and M. Tannerfeldt. 2000. Are Norwegian lemmings *Lemmus lemmus* avoided by arctic *Alopex lagopus* or red foxes *Vulpes vulpes* ? A feeding experiment. Wildlife Biology 6:101–109.

Bartoń, K. A., and A. Zalewski. 2007. Winter severity limits red fox populations in Eurasia. Global Ecology and Biogeography 16:281–289.

Beasley, J. C., Z. H. Olson, W. S. Beatty, G. Dharmarajan, and O. E. Rhodes. 2013. Effects of Culling on Mesopredator Population Dynamics. PLoS ONE 8:e58982.

Bieber, C., and T. Ruf. 2005. Population dynamics in wild boar *Sus scrofa* : ecology, elasticity of growth rate and implications for the management of pulsed resource consumers. Journal of Applied Ecology 42:1203–1213.

Brashares, J. S., L. R. Prugh, C. J. Stoner, and C. W. Epps. 2010. Ecological and Conservation Implications of Mesopredator Release. Pages 221–240 *in* J. Terborgh and J. A. Estes, editors. Trophic Cascades: Predators, Prey and the Chaning Dynamics of Nature. Island Press, Washington.

Bravington, M. V., H. J. Skaug, and E. C. Anderson. 2016. Close-Kin Mark-Recapture. Statistical Science 31:259–274.

Caswell, H. 2001. Matrix Population Models: Construction, Analysis, and Interpretation. Sinauer Associates Incorporated.

Chevallier, C., G. Gauthier, S. Lai, and D. Berteaux. 2020. Pulsed food resources affect reproduction but not adult apparent survival in arctic foxes. Oecologia 193:557–569.

Chirkova, A. F. 1953. Dynamics of Fox Numbers in Voronezh province and Forecasting of Fox Harvests. Voprosy Biologii Pushnykh Zverey 13:50–69.

Clutton-Brock, T., and B. C. Sheldon. 2010. Individuals and populations: the role of long-term, individual-based studies of animals in ecology and evolutionary biology. Trends in Ecology & Evolution 25:562–573.

Conner, L. M., and G. Morris. 2015. Impacts of Mesopredator Control on Conservation of Mesopredators and Their Prey. PLOS ONE 10:e0137169.

Culina, A., I. van den Berg, S. Evans, and A. Sánchez-Tójar. 2020. Low availability of code in ecology: A call for urgent action. PLOS Biology 18:e3000763.

Devenish-Nelson, E. S., S. Harris, C. D. Soulsbury, S. A. Richards, and P. A. Stephens. 2013. Demography of a carnivore, the red fox, Vulpes vulpes: what have we learnt from 70 years of published studies? Oikos 122:705–716.

Dietze, M. C., A. Fox, L. M. Beck-Johnson, J. L. Betancourt, M. B. Hooten, C. S. Jarnevich, T. H. Keitt, M. A. Kenney, C. M. Laney, L. G. Larsen, H. W. Loescher, C. K. Lunch, B. C. Pijanowski, J. T. Randerson, E. K. Read, A. T. Tredennick, R. Vargas, K. C. Weathers, and E. P. White. 2018. Iterative near-term ecological forecasting: Needs, opportunities, and challenges. Proceedings of the National Academy of Sciences 115:1424–1432.

Doherty, T. S., and E. G. Ritchie. 2017. Stop Jumping the Gun: A Call for Evidence-Based Invasive Predator Management. Conservation Letters 10:15–22.

Ehrich, D., S. Kaino, J. E. Knutsen, State Nature Surveillance Vadsø and Tana, and R. A. Ims. 2025a. V_redfox_carcass_examination. COAT Data Portal. DOI: 10.48425/j3kth58t.

Ehrich, D., E. M. Soininen, R. A. Ims, and S. T. Killengreen. 2025b. V_rodents_snaptrapping_abundance_regional. COAT Data Portal. DOI: 10.48425/fl748uw6.

Ehrich, D., State Nature Surveillance Vadsø and Tana, S. Killengreen, and R. A. Ims. 2025c. V_redfox_hunting. COAT Data Portal. DOI: 10.48425/nxvs558z.

Elmhagen, B., D. Berteaux, R. M. Burgess, D. Ehrich, D. Gallant, H. Henttonen, R. A. Ims, S. T. Killengreen, J. Niemimaa, K. Norén, T. Ollila, A. Rodnikova, A. A. Sokolov, N. A. Sokolova, A. A. Stickney, and A. Angerbjörn. 2017. Homage to Hersteinsson and Macdonald: climate warming and resource subsidies cause red fox range expansion and Arctic fox decline. Polar Research 36:3.

Elmhagen, B., and S. P. Rushton. 2007. Trophic control of mesopredators in terrestrial ecosystems: top-down or bottom-up? Ecology Letters 10:197–206.

Elmhagen, B., M. Tannerfeldt, and A. Angerbjörn. 2002. Food-niche overlap between arctic and red foxes. Canadian Journal of Zoology 80:1274–1285.

Englund, J. 1970. Some aspects of reproduction and mortality rates in Swedish foxes (Vulpes vulpes), 1961-63 and 1966-69. Swedish Wildlife 8:1–82.

Englund, J. 1980. Pooulation dynamics of the Red Fox (Vulpes vulpes) in Sweden. Pages 107–122 *in* E. Zimen, editor. The Red Fox: Symposium on behaviour and ecology. Dr. W. Junk bv Publishers, The Hague.

Ergon, T., Ø. Borgan, C. R. Nater, and Y. Vindenes. 2018. The utility of mortality hazard rates in population analyses. Methods in Ecology and Evolution 9:2046–2056.

Eriksen, L. F., P. F. Moa, and E. B. Nilsen. 2018. Quantifying risk of overharvest when implementation is uncertain. Journal of Applied Ecology 55:482–493.

Fuller, T., and P. Sievert. 2001. Carnivore demography and the consequences of changes in prey availability. Page 163-in JL Gittleman, SM Funk, DW Macdonald, et RK Wayne, éd. Carnivore conservation.

Gallant, D., N. Lecomte, and D. Berteaux. 2020. Disentangling the relative influences of global drivers of change in biodiversity: A study of the twentieth-century red fox expansion into the Canadian Arctic. Journal of Animal Ecology 89:565–576.

Gamelon, M., C. R. Nater, É. Baubet, A. Besnard, L. Touzot, J. Gaillard, J. Lebreton, and O. Gimenez. 2021. Efficient use of harvest data: a size-class-structured integrated population model for exploited populations. Ecography 44:1296–1310.

Gelman, A., J. B. Carlin, H. S. Stern, D. B. Dunson, A. Vehtari, and D. B. Rubin. 2013. Bayesian Data Analysis, Third Edition. CRC Press.

Gosselink, T. E., T. R. Van Deelen, R. E. Warner, and P. C. Mankin. 2007. Survival and Cause-Specific Mortality of Red Foxes in Agricultural and Urban Areas of Illinois. The Journal of Wildlife Management 71:1862–1873.

Grue, H., and V. Jensen. 1979. Review of the formation of incremental lines in tooth cementum of terrestrial mammals. Danish Review of Game Biology 11:48.

Hamel, S., S. T. Killengreen, J.-A. Henden, N. G. Yoccoz, and R. A. Ims. 2013. Disentangling the importance of interspecific competition, food availability, and habitat in species occupancy: Recolonization of the endangered Fennoscandian arctic fox. Biological Conservation 160:114–120.

Henden, J., D. Ehrich, E. M. Soininen, and R. A. Ims. 2021. Accounting for food web dynamics when assessing the impact of mesopredator control on declining prey populations. Journal of Applied Ecology 58:104–113.

Henden, J., R. A. Ims, and N. G. Yoccoz. 2009a. Nonstationary spatio-temporal small rodent dynamics: evidence from long-term Norwegian fox bounty data. Journal of Animal Ecology 78:636–645.

Henden, J.-A., R. A. Ims, N. G. Yoccoz, P. HellstrÃ¶m, and A. AngerbjÃ¶rn. 2010. Strength of asymmetric competition between predators in food webs ruled by fluctuating prey: the case of foxes in tundra. Oikos 119:27–34.

Henden, J.-A., N. G. Yoccoz, R. A. Ims, B.-J. Bårdsen, and A. Angerbjörn. 2009b. Phase-dependent effect of conservation efforts in cyclically fluctuating populations of arctic fox (Vulpes lagopus). Biological Conservation 142:2586–2592.

Heydon, M. J., and J. C. Reynolds. 2000. Demography of rural foxes (*Vulpes vulpes*) in relation to cull intensity in three contrasting regions of Britain. Journal of Zoology 251:265–276.

Hill, J. E., T. L. DeVault, and J. L. Belant. 2019. Cause-specific mortality of the world's terrestrial vertebrates. Global Ecology and Biogeography 28:680–689.

Holmala, K., and K. Kauhala. 2006. Ecology of wildlife rabies in Europe. Mammal Review 36:17–36.

Holt, R. D. 2008. THEORETICAL PERSPECTIVES ON RESOURCE PULSES. Ecology 89:671–681.

Ims, R. A., J. U. Jepsen, A. Stien, and N. G. Yoccoz. 2013. Science plan for COAT: climate-ecological observatory for Arctic Tundra. Fram Centre report series 1:1–177.

Ims, R. A., S. T. Killengreen, D. Ehrich, Ø. Flagstad, S. Hamel, J.-A. Henden, I. Jensvoll, and N. G. Yoccoz. 2017. Ecosystem drivers of an Arctic fox population at the western fringe of the Eurasian Arctic. Polar Research 36:8.

Ims, R. A., N. G. Yoccoz, and S. T. Killengreen. 2011. Determinants of lemming outbreaks. Proceedings of the National Academy of Sciences 108:1970–1974.

IPBES. 2019. Summary for policymakers of the global assessment report on biodiversity and ecosystem services. Zenodo.

Jahren, T., M. Odden, J. D. C. Linnell, and M. Panzacchi. 2020. The impact of human land use and landscape productivity on population dynamics of red fox in southeastern Norway. Mammal Research 65:503–516.

Jensen, B. 1973. Movements of the Red fox (Vulpes vulpes L.) in Denmark Investigated by Marking and Recovery. Danish Review of Game Biology 8:1–22.

Jensen, P. M., N. C. Stenseth, and E. Framstad. 1993. Trappability of the Norwegian lemming (Lemmus lemmus). Pages 545–554 *in* N. C. Stenseth and R. A. Ims, editors. The biology of lemmings: from papers presented at a meeting at the Konnevesi Research Station, Finland. Academic Press, for the Linnean society of London, London San Diego New York.

Johnsen, S. 1929. Rovdyr- og rovfuglstatistikken i Norge. Bergens Museums Årbok 2:1–140.

Kämmerle, J., J. Coppes, S. Ciuti, R. Suchant, and I. Storch. 2017. Range loss of a threatened grouse species is related to the relative abundance of a mesopredator. Ecosphere 8:e01934.

Kämmerle, J.-L., E. G. Ritchie, and I. Storch. 2019. Restricted-area culls and red fox abundance: Are effects a matter of time and place? Conservation Science and Practice 1:e115.

Karanth, K. U., and R. Chellam. 2009. Carnivore conservation at the crossroads. Oryx 43:1.

Kierepka, E. M., J. C. Kilgo, and O. E. Rhodes. 2017. Effect of compensatory immigration on the genetic structure of coyotes. The Journal of Wildlife Management 81:1394–1407.

Killengreen, S. T., N. Lecomte, D. Ehrich, T. Schott, N. G. Yoccoz, and R. A. Ims. 2011. The importance of marine vs. human-induced subsidies in the maintenance of an expanding mesocarnivore in the arctic tundra: *Importance of subsidies to mesopredators*. Journal of Animal Ecology 80:1049–1060.

Kolb, H. H., and R. Hewson. 1980. A Study of Fox Populations in Scotland from 1971 to 1976. The Journal of Applied Ecology 17:7.

Koons, D. N., T. W. Arnold, and M. Schaub. 2017. Understanding the demographic drivers of realized population growth rates. Ecol. Appl. 27:2102–2115.

Koons, D. N., D. T. Iles, M. Schaub, and H. Caswell. 2016. A life-history perspective on the demographic drivers of structured population dynamics in changing environments. Ecol. Lett. 19:1023–1031.

Landau, W. M. 2021. The targets R package: a dynamic Make-like function-oriented pipeline toolkit for reproducibility and high-performance computing. Journal of Open Source Software 6:2959.

Larivière, S. 2004. Range expansion of raccoons in the Canadian prairies: review of hypotheses. Wildlife Society Bulletin 32:955–963.

Larivière, S., and M. Pasitschniak-Arts. 1996. Vulpes vulpes. Mammalian Species:1–11.

Laurimaa, L., E. Moks, E. Soe, H. Valdmann, and U. Saarma. 2016. *Echinococcus multilocularis* and other zoonotic parasites in red foxes in Estonia. Parasitology 143:1450–1458.

Lennox, R. J., A. J. Gallagher, E. G. Ritchie, and S. J. Cooke. 2018. Evaluating the efficacy of predator removal in a conflict-prone world. Biological Conservation 224:277–289.

Lieury, N., S. Ruette, S. Devillard, M. Albaret, F. Drouyer, B. Baudoux, and A. Millon. 2015. Compensatory immigration challenges predator control: An experimental evidence-based approach improves management: Compensatory Immigration in Carnivore Management. The Journal of Wildlife Management 79:425–434.

Lindsø, L. K., P. Dupont, L. Rød-Eriksen, I. P. Ø. Andersskog, K. R. Ulvund, Ø. Flagstad, R. Bischof, and N. E. Eide. 2022. Estimating red fox density using non-invasive genetic sampling and spatial capture–recapture modelling. Oecologia 198:139–151.

Lindström, E. 1989. Food limitation and social regulation in a red fox population. Ecography 12:70–79.

Lowe, W. H., and F. W. Allendorf. 2010. What can genetics tell us about population connectivity? Molecular Ecology 19:3038–3051.

Lukacs, P. M., and K. P. Burnham. 2005. Review of capture–recapture methods applicable to noninvasive genetic sampling. Molecular Ecology 14:3909–3919.

MacPherson, A. H. 1964. A Northward Range Extension of the Red Fox in the Eastern Canadian Arctic. Journal of Mammalogy 45:138.

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

Mellard, J. P., J.-A. Henden, Å. Ø. Pedersen, F. Marolla, S. Hamel, N. G. Yoccoz, and R. A. Ims. 2022. Food web approach for managing Arctic wildlife populations in an era of rapid environmental change. Climate Research 86:163–178.

Millon, A., X. Lambin, S. Devillard, and M. Schaub. 2019. Quantifying the contribution of immigration to population dynamics: a review of methods, evidence and perspectives in birds and mammals. Biol. Rev. Camb. Philos. Soc. 94:2049–2067.

Minnie, L., A. Gaylard, and G. I. H. Kerley. 2016. Compensatory life-history responses of a mesopredator may undermine carnivore management efforts. Journal of Applied Ecology 53:379–387.

Minnie, L., A. Zalewski, H. Zalewska, and G. I. H. Kerley. 2018. Spatial variation in anthropogenic mortality induces a source–sink system in a hunted mesopredator. Oecologia 186:939–951.

Moore, J. H., L. Gibson, Z. Amir, W. Chanthorn, A. H. Ahmad, P. A. Jansen, C. P. Mendes, M. Onuma, C. A. Peres, and M. S. Luskin. 2023. The rise of hyperabundant native generalists threatens both humans and nature. Biological Reviews 98:1829–1844.

Moore, M., S. K. Brown, and B. N. Sacks. 2010. Thirty-one short red fox (Vulpes vulpes) micro-satellite markers. Molecular Ecology Resources 10:404–408.

Morris, W. F., and D. F. Doak. 2002. Quantitative conservation biology: theory and practice of population viability analysis. Sinauer Associates, Sunderland, Mass.

Myllymäki, A., A. Paasikallio, E. Pankakoski, and V. Kanervo. 1971. Removal experiments on small quadrats as a means of rapid assessment of the abundance of small mammals. Annales Zoologici Fennici 8:177–185.

Nater, C. R., N. E. Eide, Å. Ø. Pedersen, N. G. Yoccoz, and E. Fuglei. 2021. Contributions from terrestrial and marine resources stabilize predator populations in a rapidly changing climate. Ecosphere 12.

Nater, C. R., S. Hofhuis, D. Ehrich, and M. Grainger. 2025, May 30. ChloeRN/VredfoxIPM: v2.0. Zenodo. DOI: 10.5281/zenodo.15551983.

Nater, C. R., and S. P. Hofhuis. 2025. Red Fox IPM. https://doi.org/10.17605/OSF.IO/756RE.

Nater, C. R., Y. Vindenes, P. Aass, D. Cole, Ø. Langangen, S. J. Moe, A. Rustadbakken, D. Turek, L. A. Vøllestad, and T. Ergon. 2020. Size- and stage-dependence in cause-specific mortality of migratory brown trout. Journal of Animal Ecology 89:2122–2133.

Newsome, T. M., J. A. Dellinger, C. R. Pavey, W. J. Ripple, C. R. Shores, A. J. Wirsing, and C. R. Dickman. 2015. The ecological effects of providing resource subsidies to predators. Global Ecology and Biogeography 24:1–11.

Nichols, J. D., W. L. Kendall, and G. S. Boomer. 2019. Accumulating evidence in ecology: Once is not enough. Ecology and Evolution 9:13991–14004.

Norén, K., A. Angerbjörn, J. Wallén, T. Meijer, and B. N. Sacks. 2017. Red foxes colonizing the tundra: genetic analysis as a tool for population management. Conservation Genetics 18:359–370.

Norén, K., L. Carmichael, E. Fuglei, N. E. Eide, P. Hersteinsson, and A. Angerbjörn. 2011. Pulses of movement across the sea ice: population connectivity and temporal genetic structure in the arctic fox. Oecologia 166:973–984.

O'Mahony, D., X. Lambin, J. L. MacKinnon, and C. F. Coles. 1999. Fox Predation on Cyclic Field Vole Populations in Britain. Ecography 22:575–581.

Ostrander, E. A., F. A. Mapa, M. Yee, and J. Rine. 1995. One hundred and one new simple sequence repeat-based markers for the canine genome. Mammalian Genome 6:192–195.

Paquet, M., J. Knape, D. Arlt, P. Forslund, T. Pärt, Ø. Flagstad, C. G. Jones, M. A. C. Nicoll, K. Norris, J. M. Pemberton, H. Sand, L. Svensson, V. Tatayah, P. Wabakken, C. Wikenros, M. Åkesson, and M. Low. 2021. Integrated population models poorly estimate the demographic contribution of immigration. Methods in Ecology and Evolution 12:1899–1910.

Pasanen-Mortensen, M., and B. Elmhagen. 2015. Land cover effects on mesopredator abundance in the presence and absence of apex predators. Acta Oecologica 67:40–48.

Pedersen, Å. Ø., J. U. Jepsen, I. M. G. Paulsen, E. Fuglei, J. B. Mosbacher, V. T. Ravolainen, N. G. Yoccoz, E. Øseth, H. Böhner, K. A. Bråthen, D. Ehrich, J.-A. Henden, K. Isaksen, S. Jakobsson, J. Madsen, E. M. Soininen, A. Stien, I. Tombre, T. Tveraa, O. E. Tveito, O. P. L. Vindstad, and R. A. Ims. 2021. Norwegian Arctic Tundra: a Panel-based Assessment of Ecosystem Condition. Norwegian Polar Institute, Tromsø.

Péron, G. 2013. Compensation and additivity of anthropogenic mortality: life-history effects and review of methods. Journal of Animal Ecology 82:408–417.

Piry, S., A. Alapetite, J.-M. Cornuet, D. Paetkau, L. Baudouin, and A. Estoup. 2004. GENECLASS2: A Software for Genetic Assignment and First-Generation Migrant Detection. Journal of Heredity 95:536–539.

Porteus, T. A., J. C. Reynolds, and M. K. McAllister. 2018. Establishing Bayesian priors for natural mortality rate in carnivore populations: Establishing Natural Mortality Rate Priors. The Journal of Wildlife Management 82:1645–1657.

Porteus, T. A., J. C. Reynolds, and M. K. McAllister. 2019. Population dynamics of foxes during restricted-area culling in Britain: Advancing understanding through state-space modelling of culling records. PLOS ONE 14:e0225201.

Powers, S. M., and S. E. Hampton. 2019. Open science, reproducibility, and transparency in ecology. Ecological Applications 29:e01822.

Prugh, L. R., C. J. Stoner, C. W. Epps, W. T. Bean, W. J. Ripple, A. S. Laliberte, and J. S. Brashares. 2009. The Rise of the Mesopredator. BioScience 59:779–791.

R Core Team. 2022. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria.

Rauset, G. R., M. Low, and J. Persson. 2015. Reproductive patterns result from age-related sensitivity to resources and reproductive costs in a mammalian carnivore. Ecology 96:3153–3164.

Read, J. L., and V. Scoleri. 2015. Ecological Implications of Reptile Mesopredator Release in Arid South Australia. Journal of Herpetology 49:64–69.

Riecke, T. V., M. G. Lohman, B. S. Sedinger, T. W. Arnold, C. L. Feldheim, D. N. Koons, F. C. Rohwer, M. Schaub, P. J. Williams, and J. S. Sedinger. 2022. Density-dependence produces spurious relationships among demographic parameters in a harvested species. Journal of Animal Ecology 91:2261–2272.

Roos, S., J. Smart, D. W. Gibbons, and J. D. Wilson. 2018. A review of predation as a limiting factor for bird populations in mesopredator-rich landscapes: a case study of the UK. Biological Reviews 93:1915–1937.

Salo, P., P. B. Banks, C. R. Dickman, and E. Korpimäki. 2010. Predator manipulation experiments: impacts on populations of terrestrial vertebrate prey. Ecological Monographs 80:531–546.

Salo, P., M. Nordström, R. L. Thomson, and E. Korpimäki. 2008. Risk induced by a native top predator reduces alien mink movements. Journal of Animal Ecology 77:1092–1098.

Sandercock, B. K., E. B. Nilsen, H. Brøseth, and H. C. Pedersen. 2011. Is hunting mortality additive or compensatory to natural mortality? Effects of experimental harvest on the survival and cause-specific mortality of willow ptarmigan. Journal of Animal Ecology 80:244–258.

Saunders, S. P., F. J. Cuthbert, and E. F. Zipkin. 2018. Evaluating population viability and efficacy of conservation management using integrated population models. Journal of Applied Ecology 55:1380–1392.

Savory, G. A., C. M. Hunter, M. J. Wooller, and D. M. O'Brien. 2014. Anthropogenic food use and diet overlap between red foxes (*Vulpes vulpes*) and arctic foxes (*Vulpes lagopus*) in Prudhoe Bay, Alaska. Canadian Journal of Zoology 92:657–663.

Schaub, M., and D. Fletcher. 2015. Estimating immigration using a Bayesian integrated population model: choice of parametrization and priors. Environmental and Ecological Statistics 22:535–549.

Schaub, M., and M. Kéry. 2021. Integrated Population Models: Theory and Ecological Applications with R and JAGS. Academic Press.

Schwartz, M. K., G. Luikart, and R. S. Waples. 2007. Genetic monitoring as a promising tool for conservation and management. Trends in Ecology & Evolution 22:25–33.

Sibly, R. M., D. Collett, D. E. L. Promislow, D. J. Peacock, and P. H. Harvey. 1997. Mortality rates of mammals. Journal of Zoology 243:1–12.

Sidorovich, V. E., A. A. Sidorovich, and I. V. Izotova. 2006. Variations in the diet and population density of the red fox Vulpes vulpes in the mixed woodlands of northern Belarus. Mammalian Biology 71:74–89.

Skrobov, V. D. 1960. On the interrelations of the arctic fox and red fox in the tundra of the Nenets national region. Zoologicheskii Zhurnal 39:496–471.

Soininen, E. M., E. Fuglei, and Å. Ø. Pedersen. 2016. Complementary use of density estimates and hunting statistics: different sides of the same story? European Journal of Wildlife Research 62:151–160.

Soulsbury, C. D., P. J. Baker, G. Iossa, and S. Harris. 2008. Fitness costs of dispersal in red foxes (Vulpes vulpes). Behavioral Ecology and Sociobiology 62:1289–1298.

Stickney, A. A., T. Obritschkewitsch, and R. M. Burgess. 2014. Shifts in Fox Den Occupancy in the Greater Prudhoe Bay Area, Alaska. ARCTIC 67:196.

Storm, G. L., R. D. Andrews, R. L. Phillips, R. A. Bishop, D. B. Siniff, and J. R. Tester. 1976. Morphology, Reproduction, Dispersal, and Mortality of Midwestern Red Fox Populations. Wildlife Monographs 49:3–82.

Ulvund, K., Ø. Flagstad, L. Rød-Eriksen, L. G. Arntsen, L. B. Eriksen, C. Jackson, O. Kleven, B. K. Sandercock, and N. E. Eide. 2023. Fjellrev i Norge 2023. Resultater fra det nasjonale over-våkingsprogrammet for fjellrev. Norsk institutt for naturforskning, Trondheim.

de Valpine, P., D. Turek, C. J. Paciorek, C. Anderson-Bergman, D. T. Lang, and R. Bodik. 2017. Programming With Models: Writing Statistical Algorithms for General Model Structures With NIMBLE. Journal of Computational and Graphical Statistics 26:403–413.

Walker, D. A., M. K. Raynolds, F. J. A. Daniëls, E. Einarsson, A. Elvebakk, W. A. Gould, A. E. Katenin, S. S. Kholod, C. J. Markon, E. S. Melnikov, N. G. Moskalenko, S. S. Talbot, B. A. (†) Yurtsev, and The Other Members Of The Cavm Team. 2005. The Circumpolar Arctic vegetation map. Journal of Vegetation Science 16:267–282.

Wilkinson, C., J. Vigués, M. Stoessel, M. Vinka, A. Angerbjörn, and K. Norén. 2024. Phase-dependent red fox expansion into the tundra: implications for management. The Journal of Wildlife Management 88:e22569.

Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. Analysis and Management of Animal Populations. Academic Press.

Zipkin, E. F., J. W. Doser, C. L. Davis, W. Leuenberger, S. Ayebare, and K. L. Davis. 2023. Integrated community models: A framework combining multispecies data sources to estimate the status, trends and dynamics of biodiversity. Journal of Animal Ecology 92:2248–2262.

Zipkin, E. F., and S. P. Saunders. 2018. Synthesizing multiple data types for biological conservation using integrated population models. Biological Conservation 217:240–250.