An integrated population modelling workflow for supporting mesopredator management

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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 the effects of harvest and its interaction with environmental conditions on mesopredator population dynamics have rarely been assessed quantitatively due to data constraints. Recent advances involving integrated populations models (IPMs) have enabled promising alternative approaches for quantitative assessments. Efficient use of multiple datasets, together with the ability to account for bias and uncertainty, make IPMs ideal tools for studying impacts of management actions and environmental conditions on harvested populations for which limited data is available.

Here we developed a versatile IPM workflow for studying mesopredator population dynamics under different harvest 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 variation from >3600 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 18 years, and to identify the drivers of changes in population growth rates using retrospective (Life Table Response Experiments, LTREs) and prospective (population viability analyses, PVAs) perturbation analyses. We found no long-term trends in population size over the course of our study period, not least due to intense harvest limiting the growth potential of the population. On shorter, year-to-year timescales, however, the numbers of red foxes could change dramatically due to responses of natural mortality and immigration to fluctuations in the availability of rodent prey.

Our study highlights the potential of integrated modelling approaches 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 (J. H. Moore et al. 2023; Prugh et al. 2009). 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; J. 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 morality (Salo et al. 2010; Minnie, Gaylard, and Kerley 2016). Assessing the impacts of management interventions thus requires unbiased estimates of population sizes and demographic rates under different harvest pressures and environmental conditions (J. 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 from predators that tend to be 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, Nichols, and Conroy 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 of 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; Gamelon et al. 2021; Nater 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, Cuthbert, and Zipkin 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, Kendall, and Boomer 2019). This stands in stark contrast to the fact that the vast majority of analyses in ecology are not documented to an extend 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 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 18 years (2005-2022) of intense harvest. We further investigate the potential role of environmental conditions (food availability via the abundance of small rodents and reindeer carcasses) for population regulation and identify the key demographic drivers of population change through transient life table response experiments (tLTREs, Koons et al., 2016, 2017). Finally, we couple our IPM with a population viability analysis (PVA, Morris & Doak, 2002; Saunders et al., 2018) to explore the effects of alternative management scenarios. 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, Obritschkewitsch, and Burgess 2014; Gallant, Lecomte, and Berteaux 2020). This ongoing expansion threatens populations of endemic tundra species (Elmhagen et al. 2017; J. 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 1-year lagged numerical response to rodent cycles (J. Henden, Ims, and Yoccoz 2009). 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 more rarely during only some of the vole peak years (Ims, Yoccoz, and Killengreen 2011; Ims et al. 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 food subsidies along the coastline (Killengreen et al. 2011).

Intense red fox harvest has been implemented in our study area since 2005 to conserve remaining populations of 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 (J. 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.

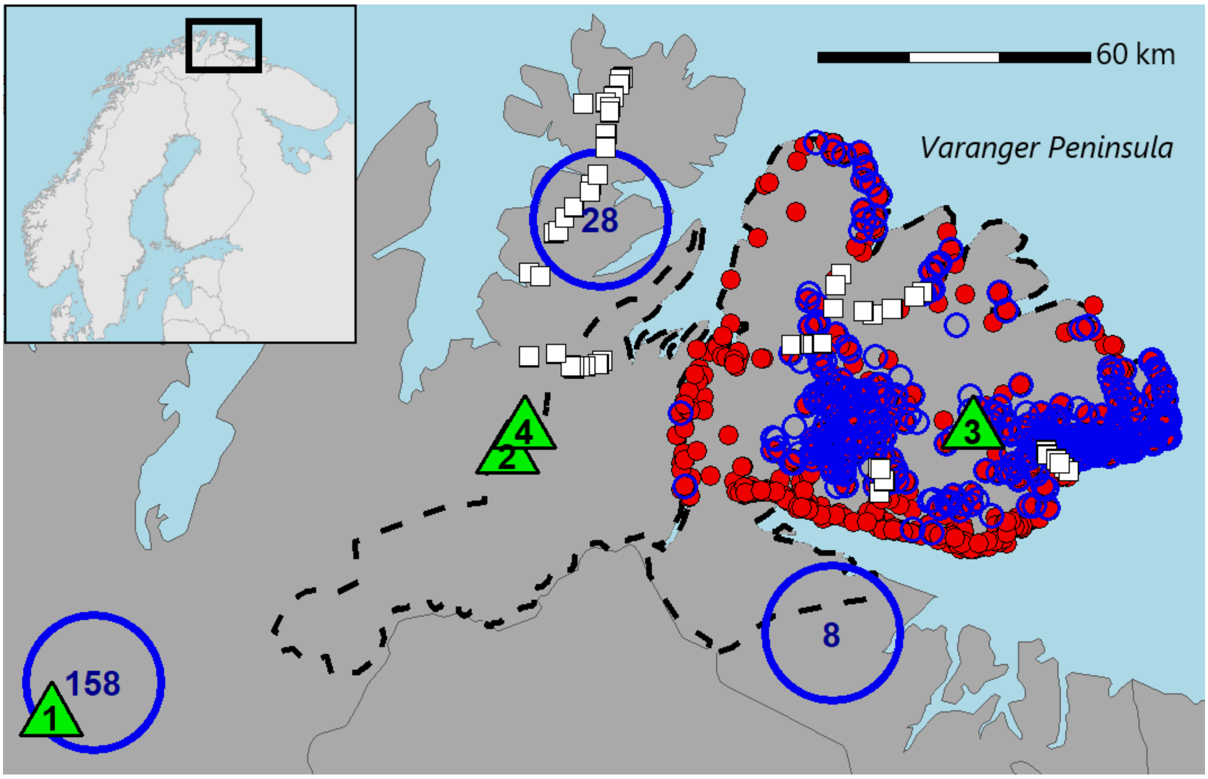

Figure 1. The study area within Fennoscandia and spatial representation of used data sources. Red circles = harvested females; Small blue circles = genetic samples of harvested females and males; Large blue circles = genetic samples from three possible immigrant source populations and corresponding sample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

Data collection and processing

Harvested foxes – Age

A total of 3678 red foxes have been harvested on Varanger Peninsula from 2005 to 2022. Most foxes (83 %) 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 17 % of foxes, most of which in the inner parts of the peninsula during March-April. Age was determined for a subset of harvested foxes (20 – 100% of females per hunting season) by analysis of cementum annuli of one of the upper canines (Grue and Jensen 1979).We subsequently arranged data on all aged females in age-at-harvest matrices. The resulting winter age-at-harvest data included a total of 744 females shot during the period October-

May in each season from 2004-2005 to 2021-2022. Summer age-at-harvest data included 85 females shot during the period July-September in years 2005 to 2012. Data from summer harvest after 2012 was excluded as aging was not done consistently in later years.

Harvested foxes – Reproduction

We inferred pregnancy rates from placental scars for females > 1 year and harvested from July 1st until March 20th (n= 258). 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=109) 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.

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 Penninsula, 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; M. Moore, Brown, and Sacks 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 Penninsula. 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 Supporting Information (SI) 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=6), and when field inspectors removed red fox litters from dens (n=4). These observations were made during the months of June and July in seven different years and on a selection of four dens, one of which was located within the study area and three within a 160km radius east of the study area (Figure 1).

Environment – Food availability

In addition to data on red foxes, our analyses included environmental covariates representing availability of important food resources for red foxes on Varanger: small rodents and reindeer carcasses (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) throughout the study period 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) a winter (average of autumn and spring trapping) rodent abundance within Varanger relevant for local demography and 2) an autumn rodent abundance at a larger spatial scale relevant for immigration (as red fox dispersal is known to peak in autumn (Storm et al. 1976; Gosselink et al. 2007; Soulsbury et al. 2008). To account for the much lower capture probability of lemmings compared to voles (P. M. Jensen, Stenseth, and Framstad 1993), we additionally calculated our annual small rodent abundance covariates by first z-standardizing the two species groups separately, and subsequently summing them.

Data on the availability of reindeer carcasses was retrieved from www.rovbase.no, which provides records on the yearly number of reindeer carcasses reported by reindeer herders from November until the end of June within the six municipalities that overlap with our study area (Berlevåg, Båtsfjord, Vardø, Vadsø, Nesseby, Tana). This reindeer covariate was also z-standardized for further analysis.

IPM construction

Age-structured population model

Our IPM is based on an IPM previously developed 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:

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

Females in each age class a survive from year t to $t+1$ first with a summer (July to September) survival probability $Ss_{a,t}$, then with an annual survival probability $S_{a,t}$ (October to June). Summer survival is modelled separately as it represents the probability of not being harvested in summer, which is different in terms of intensity and drivers from harvest throughout the rest of the year. We assume no natural mortality between July and September, resulting in $Ss_{a,t} = \exp\left(-mHs_{a,t}\right)$, where $mHs_{a,t}$ is summer harvest mortality hazard rate. Annual survival probability $S_{a,t}$, on the other hand, can be decomposed 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). 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.

The model includes immigration because our case study concerns an open population. Immigrating foxes are expected to enter the population in autumn/early winter in their first year of life (B. Jensen 1973; Storm et al. 1976). We therefore modelled immigration into age class 1 as taking place between the summer and winter harvest periods (i.e. immigrants are available for winter but not summer 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 (Figure S2.4) 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 and refer the reader to the published code for the detailed implementation on this.

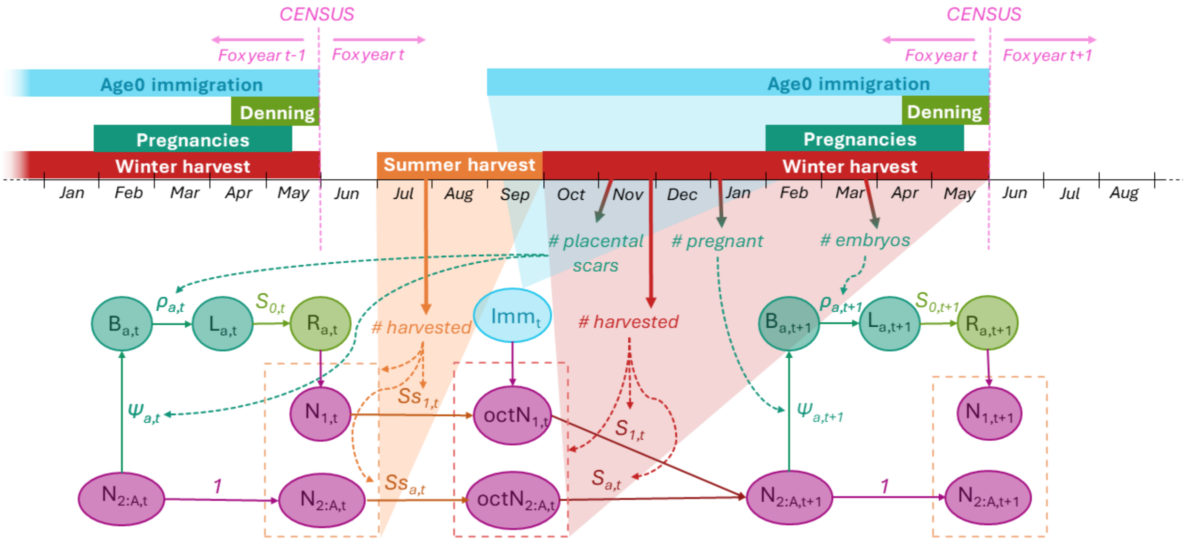

Figure 2. Schematic overview of the red fox annual cycle, timing of data collection, and the age-structured population model. The round bubbles are the age- (index a, with A = index of oldest age class) and year- (index t) specific population-level metrics modelled by the IPM: N = population size in 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), octN = population size in October, Imm = number of age class 1 immigrants. They are linked by the vital rates survival (S, where $Ss_{1:A}$ = summer survival, $S_{1:A}$ = 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 (for both summer/June and winter/Oct), 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 $C_{a,t}$, one each for the summer and winter harvest seasons. 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 population size ($N_{a,t}$) in June (for summer harvest) and October (for winter harvest) 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 $(1 - Ss_{a,t})$ for summer and $(1 - S_{a,t}) \frac{mH_{a,t}}{mH_{a,t} + mO_{a,t}}$ for winter, while the latter is the a priori known proportion of harvested foxes that have been aged (and hence added to the age-at-harvest matrix) in a given year. 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 Penninsula 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 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:

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

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 SI S2.

Temporal variation in vital rates

We modelled among-year variation in (age-specific) vital rates $X_{a,t}$ according to the following general equation:

$$link(X_{a,t}) = link(\mu_a^X) + \beta_1^X covA_t + \beta_2^X covB_t + \beta_3^X covA_t covB_t + \epsilon_t$$

Here, the intercept μ_a^X represents the age-specific vital rate average; β_1^X, β_2^X, and β_3^X are the slopes for the single effects of covariates A and B and the interactive effect of both, respectively; ϵ_t 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. For natural mortality, we additionally included an effect of reindeer carcass availability, as well as of its interaction with rodent abundance. 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 treated as constant due to lack of data.

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 three MCMC chains with 30,000 iterations each, using NIMBLE's standard samplers. 5000 iterations per chain were discarded as burn-in and the remainder thinned by a factor four, resulting in a posterior of 3×6250 = 18750 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 SI 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 SI 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, respectively. The slope parameters for the single rodent and reindeer effects on natural mortality were assigned one-sided, but otherwise non-informative, priors that constrained them to be negative to facilitate convergence. 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 SI S2 & S3). Including genetic data resulted in more precise estimates for some vital rates and population sizes as well as much faster model runtimes (~ 3 times faster). 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 (SI S2). The choice of informative prior for natural mortality not only affected natural mortality itself, but also denning survival, harvest mortality in summer and winter, and absolute (but not relative changes in) population size (SI 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 (S1 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 for analysing changes in realized population growth rate as estimated in typical IPMs, and we here implemented both the random design and the fixed design versions. Further details on the implementation of the LTRE analyses, including the associated calculation of transient sensitivities, are provided in SI S5.

Responses to management scenarios

We explored the potential impacts of different management strategies on the dynamics of the red fox population on Varanger by coupling our IPM to a Population Viability Analysis (PVA, Morris & Doak, 2002). In practice, this involved extending the time-coverage of our IPM to project the population for an additional nine years beyond data collection (until 2030) while simultaneously applying changes to vital rates and environmental covariates during this additional time period (Schaub and Kéry 2021). We 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 six scenarios in addition to a baseline scenario. The first scenario simulated a complete termination of harvest from 2022 onwards, while the second scenario assumed an overall increase of harvest by 50% from 2022 onwards. While neither of these constitute realistic options in practice, we ran them to explore the general role of harvest for short- to mid-term population dynamics.

Populations that are driven by cyclical resource availability are likely differently susceptible to management during different phases of the cycle (Bieber and Ruf 2005; J.-A. Henden et al. 2009). We tested this in the third to sixth scenario by increasing harvest mortality by 50% following (= delayed) or during (= matched) years with either below or above average rodent abundance. To account for autocorrelation / cyclic dynamics in rodent abundance, we predicted 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.

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 Data & Code availability 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.

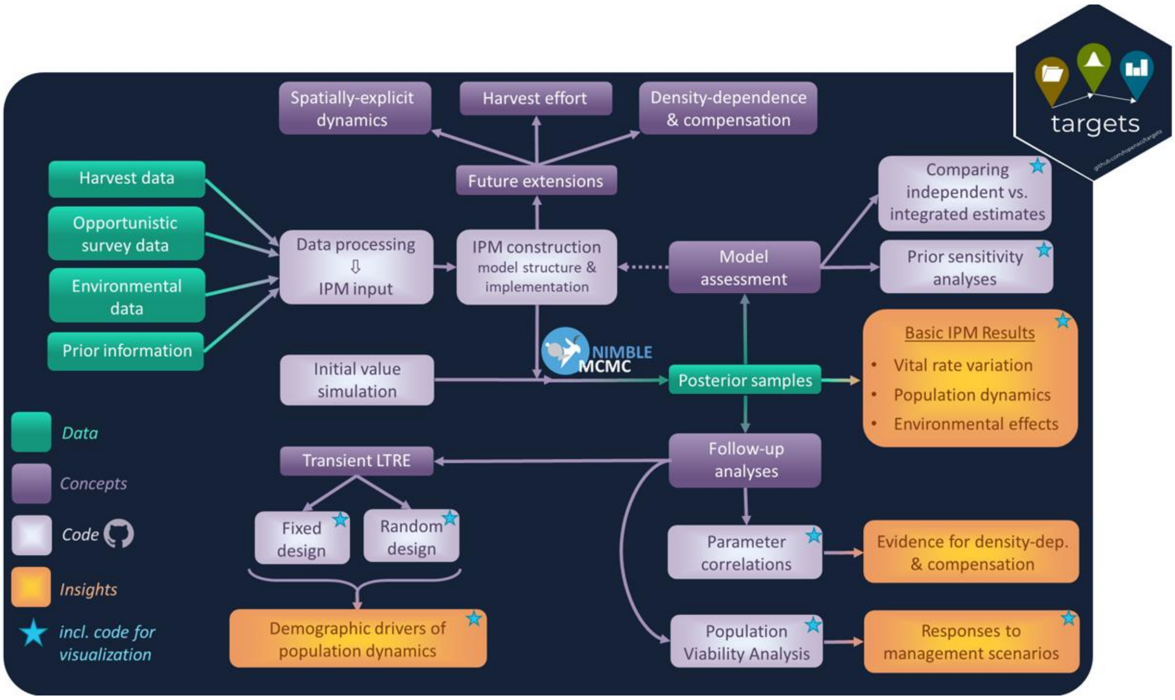

Figure 3: Schematic representation of the different components and steps in the semi-automated "targets" workflow for the analysis of population dynamics of red foxes on Varanger. The latest version of the pipeline, including documentation, can be found here: https://github.com/ChloeRN/VredfoxIPM

RESULTS

Vital rate variation & environmental effects

Numerical results in the following are given as median [95% credible interval] unless otherwise indicated.

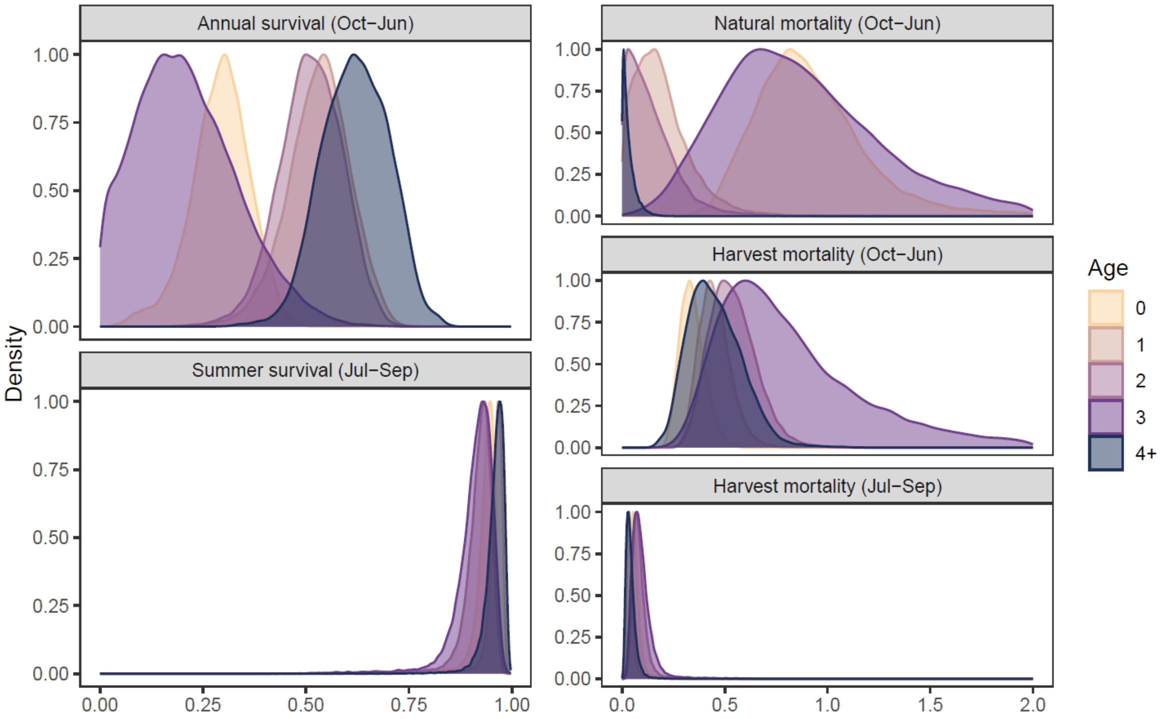

Figure 4. Scaled posterior distributions for age-specific average survival probabilities and mortality hazard rates.

Throughout both the summer season and the remainder of the year, survival probabilities were highest for the oldest foxes (Oct-Jun: 0.621 [0.461, 0.767]; Jul-Sep: 0.964 [0.899, 0.988]) and both lowest and most uncertain for 3-year old foxes (Oct-Jun: 0.196 [0.013, 0.473]; Jul-Sep: 0.919 [0.793, 0.963], Figure 4). Annual survival of juveniles (and new immigrants) was also relatively low at 0.295 [0.130, 0.420], and unlike for the older age classes, natural mortality was the dominant factor determining it: only ~31 [18, 49] % of juvenile mortality was due to harvest on average, while the corresponding estimates for older age classes varied between 52 [31, 76] % and 96 [78, 100] %.

Pregnancy rate increased with age from, on average, 0.474 [0.358, 0.583] for 1-year old females to 0.851 [0.744, 0.923] for females older than 4 years (Figure S1.1). Older vixens also conceived more pups, with litters of 3-year-old females containing one (1.035 [0.270, 1.815) extra pup on average relative to litters of 1-year old first-time breeders. Denning survival was estimated at 0.664 [0.478, 0.923] (Figure S1.1).

The model estimated an average immigration rate of ~ 1 immigrant per 10 locally born pups (0.107 [0.080, 0.141], Figure S1.1) but immigration rate, and consequently the number of immigrants, varied substantially across years (Figures S1.2 & S1.5). Among-year variation was also evident for the other vital rates (Figure S1.2), for example with clear peaks in pregnancy rate and fetus numbers in 2011, and survival from 2011 to 2012, as well as exceptionally high harvest mortality in the hunting seasons 2010-2011 and 2019-2020 (Figure S1.2).

A part of among-year variation in vital rates could be attributed to variation in rodent abundance (Figure S1.7). We found evidence for higher pregnancy rates and larger litters following winters with higher rodent abundance on Varanger (Figure 5).

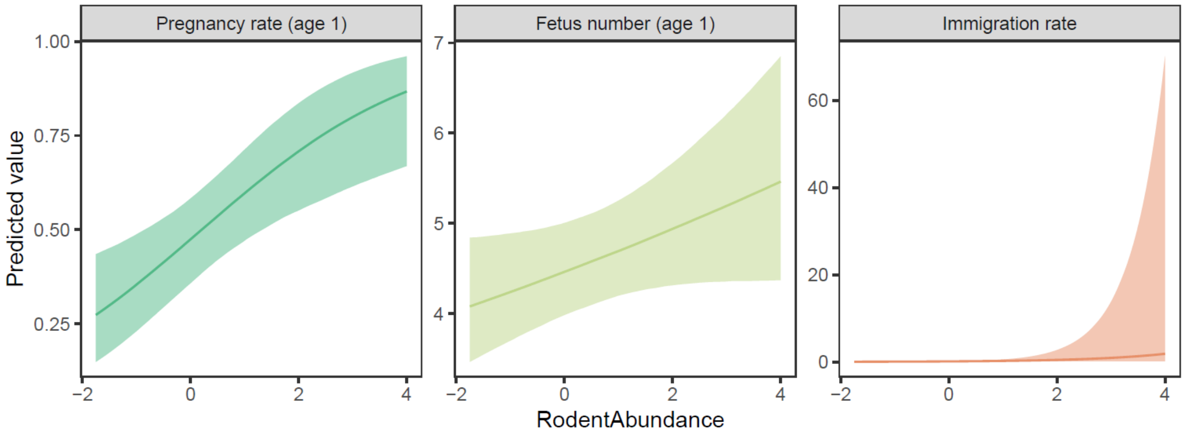

Figure 5. Predicted effects of z-standardized rodent abundance on pregnancy rate, fetus number, and immigration rate. The solid line represents the posterior median while the ribbon marks the 95% credible interval.

The model also estimated a positive effect of autumn rodent abundance at the larger spatial scale on immigration rate, although uncertainty was high (Figure 5). Attempts to estimate effects of joint rodent and reindeer effects on natural mortality were inconclusive due to high uncertainty and relatively low statistical power (Figure S1.3).

Population dynamics during the study period

While the average growth rate of the red fox population on Varanger was positive during the study period (1.093 [1.024, 1.185], representing ~ 10% increase on average), there was large variation in annual population growth rates among years up to 2016. Since 2016, population size has been in decline (Figure 6). 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 (Figure S1.4).

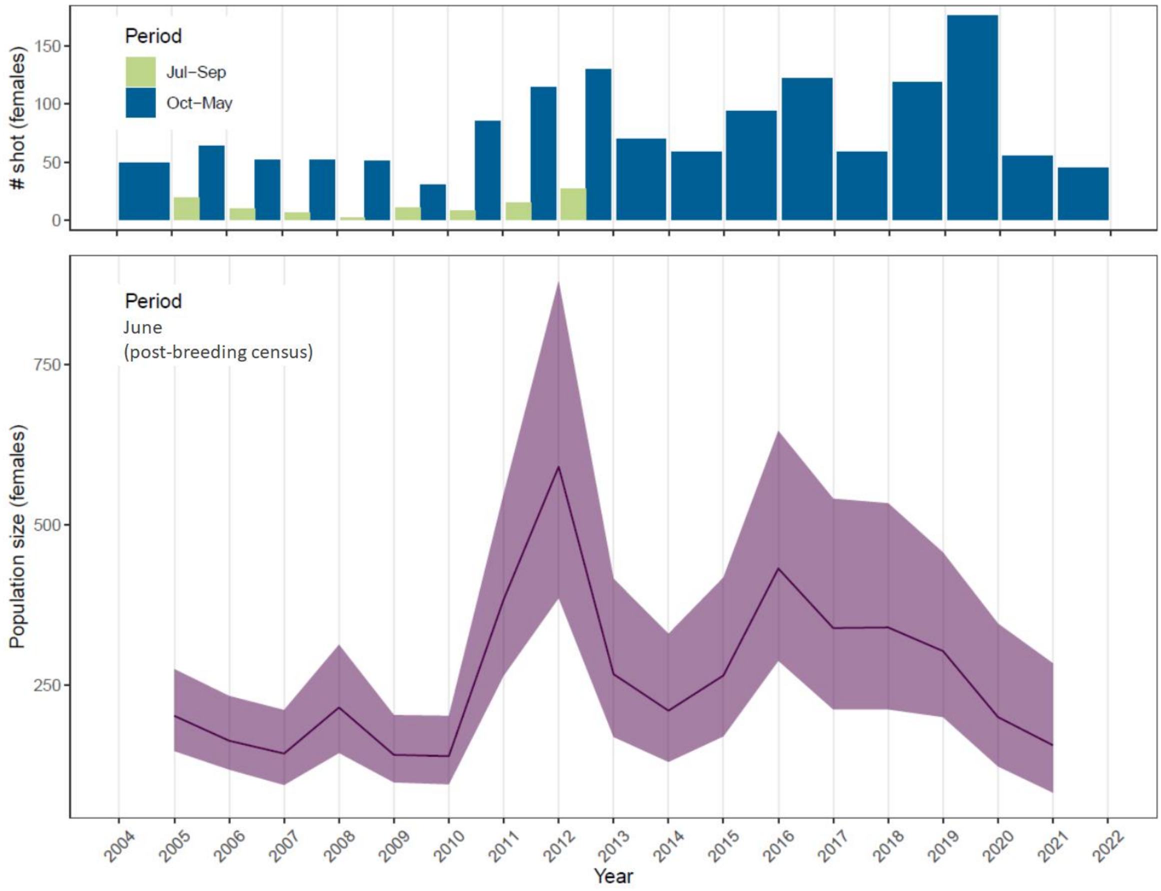

Figure 6. Number of female foxes harvested per year (top) and estimated annual population sizes in June (bottom). The solid line represents the posterior median, the ribbon marks the 95% credible interval. 2004 is the first year in the model, but population size estimation started in October 2004,

hence there is no estimate for June population size in that year. Foxes harvested in Jul-Sep after 2012 were not consistently aged and excluded in the model.

The results of the random design LTRE indicated that the two factors that contributed most to variation in population growth rate over the period 2005-2021 were fluctuations in natural mortality (especially of juveniles) and immigration rate (Figures 7 & S1.6). Harvest, reproduction, and population structure contributed relatively little.

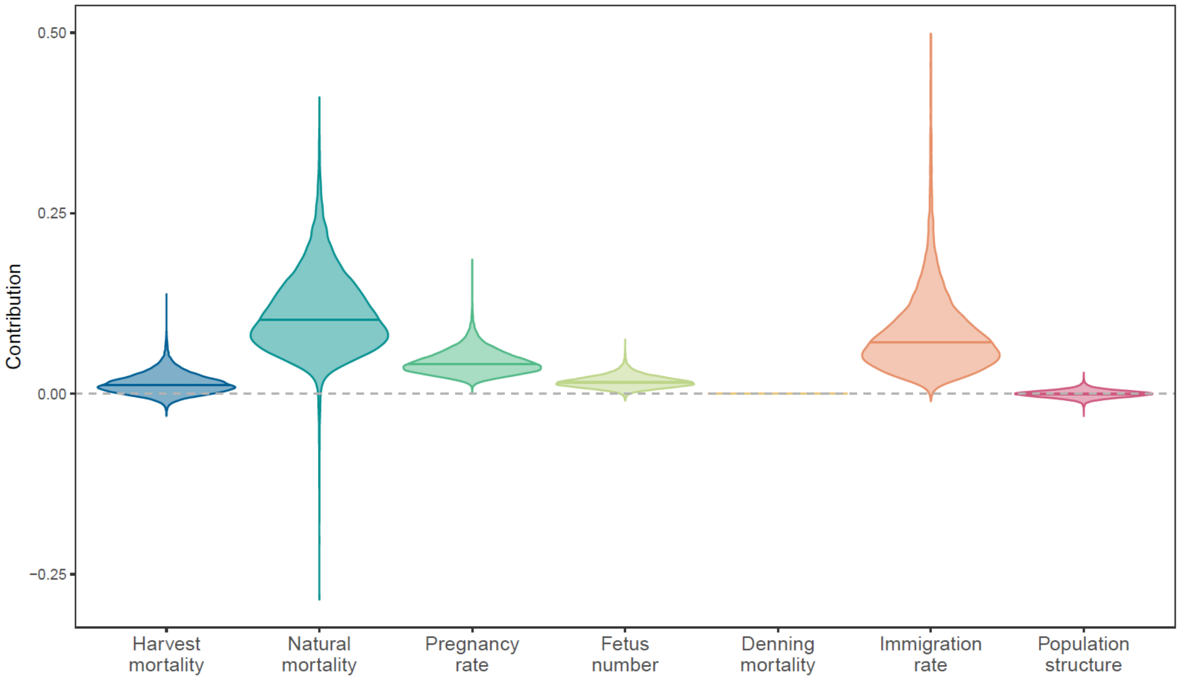

Figure 7. Posterior distributions of the contributions of variation in different demographic rates and population structure to changes in population growth rate between 2005-2006 and 2020-2021 (random design LTRE). Violins visualize distributions, solid lines mark posterior medians. Harvest mortality encompasses both summer and winter harvest, and all components are summed across age classes (see Figure S1.6 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 LTRE 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 (Figure 6) that changes in natural mortality and immigration rate were the primary drivers (Figure 8).

The relatively smaller changes in population growth rate during more recent years were characterized by more balanced contributions from different vital rates and population structure, and in particular changes in harvest mortality seem to have been more important recently (Figure 8).

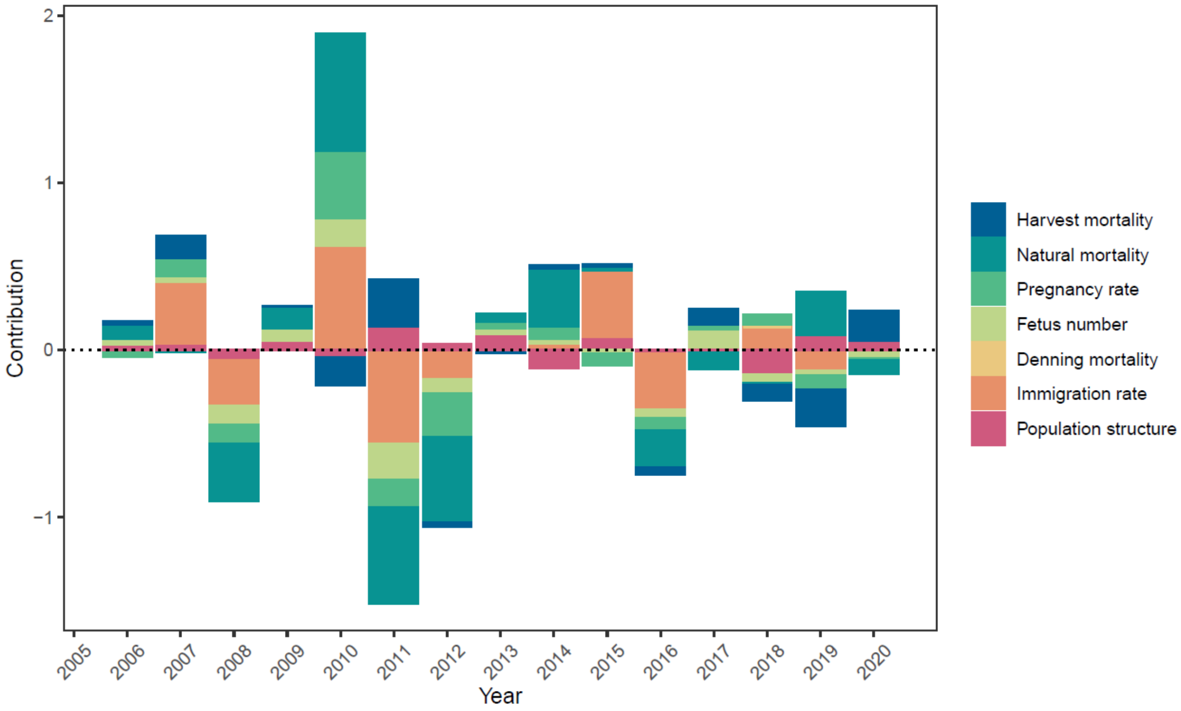

Figure 8. Posterior medians of the contributions of changes in different demographic rates and population structure to changes in population growth rate from one year to the next (fixed design LTRE). The bar for year t above represents contributions to change from population growth rate for the interval 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. Harvest mortality encompasses both summer and winter harvest, and 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 9 years beyond the study period (until 2030) revealed that continued population decline is likely if all parameters including environmental drivers remain unchanged (Figure 9A). Without harvesting, on the other hand, the population is likely to increase instead (Figure 9A). Conversely, increasing harvest mortality leads to faster population decline. Results from our simulations indicate that timing increased harvest to coincide with small rodent peaks may result in initially faster population decline (Figure 9B). Notably, however, this difference persisted as overall lower abundance but the rate of population decline after the first few years was similar irrespective of the timing of increased harvest relative to rodent abundance. The precision of population predictions into the future was low for all scenarios due to rapidly propagating uncertainty.

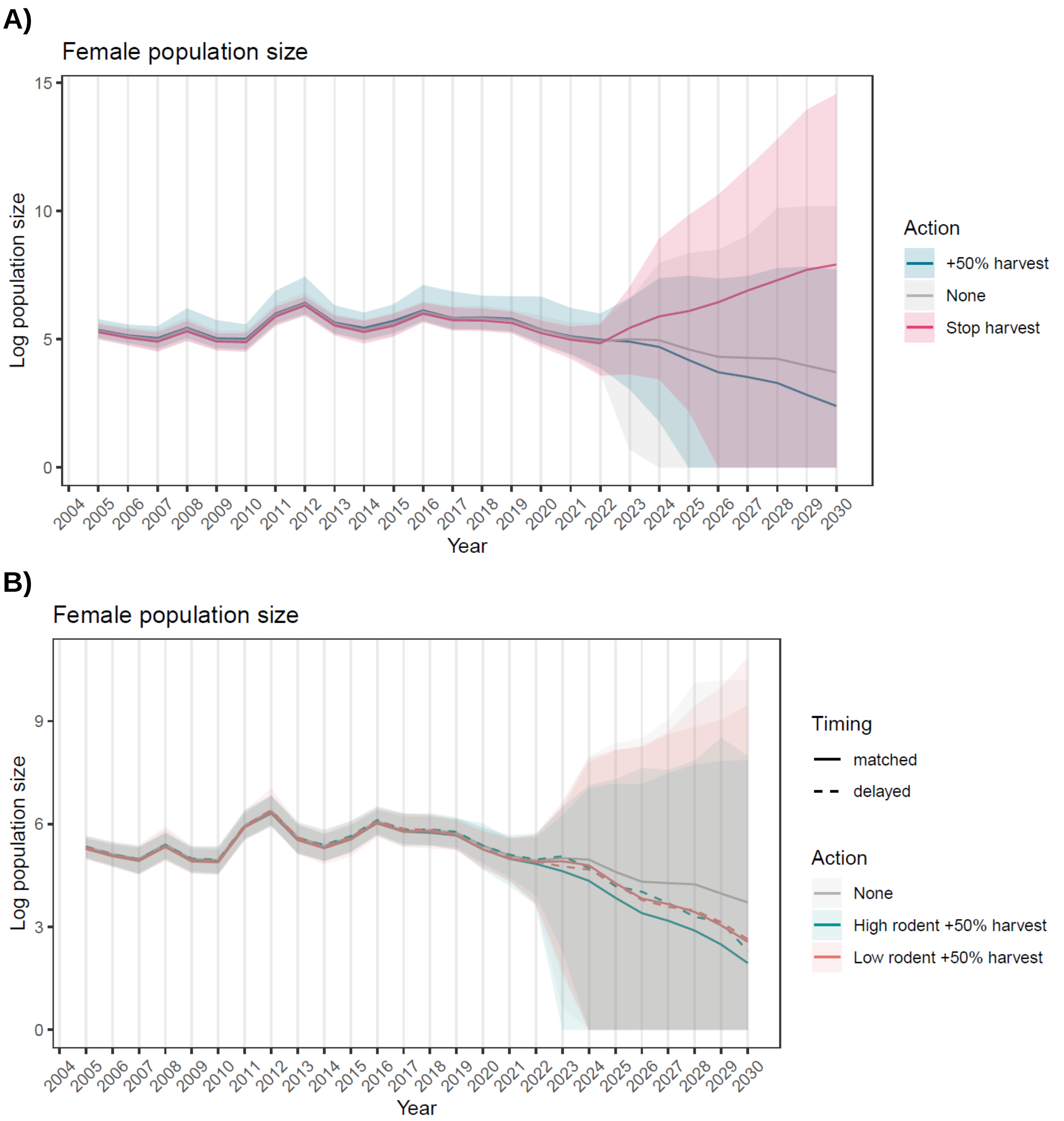

Figure 9. Population forecasts for the periods 2022-2030 under different management scenarios. Note that population size is plotted on the log scale. The baseline projection assumes unchanged parameters. Changes for the other scenarios are: “Stop harvest ” = summer and winter harvest mortality set to 0 from 2022; “+50% harvest” = winter harvest mortality increased by 50% in all years; “High rodent +50% harvest” = winter harvest mortality increased by 50% following/in years with above-average rodent abundance; “Low rodent +50% harvest” = winter harvest mortality increased by 50% following/in years with below-average rodent abundance. In (B), solid lines indicate scenarios in which the action depends on rodent abundance in the year of harvest, while dashed lines indicated scenarios in which the action depends on rodent abundance the preceding year.

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) and environmental conditions affect population dynamics in tandem (J. 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 18 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 population growth rate and highlighted the role of harvest in limiting population growth.

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 (Figure S1.1) 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 ~72 % and 40 % 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), density feedbacks (Heydon and Reynolds 2000), and abiotic conditions (e.g. winter severity; Bartoń and Zalewski 2007). Furthermore, we assumed that rodent abundance and other environmental conditions affected foxes in all age classes similarly, but age-specific sensitivity to resource constraints is likely for carnivores (Rauset, Low, and Persson 2015) and may also have played into the estimated unexplained variation.

Natural vs. harvest mortality

Natural mortality hazard rate estimates were strongly dependent on prior information (SI S3). Nonetheless, priors for all age classes except age class 3 were updated noticeably, indicating that other data across the IPM did contribute some information on natural mortality (Figure S4.1). Juvenile natural mortality was high compared to that of other age classes (Figure 4) which, in addition to low reproductive rates of yearlings (Figure S1.1), 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). Despite natural mortality being confounded with emigration in our model, substantial juvenile emigration is unlikely in a sink population (see next section). Natural mortality decreased with age as expected, with the exception of 3-year-olds whose estimate was highly uncertain due to lower precision in the prior (SI S3) and a lower sample size of harvested individuals (n = 53) compared to other age classes (n = 93 - 333).

Peaks in natural mortality during 2008 and 2012 (Figure S1.2), and the all-time low in 2010 were linked to small rodent abundance (Figure S1.7), despite covariate effects being highly uncertain (Figure S1.3). In addition to natural prey, human food subsidies are an important dietary component in many mesopredator populations (Newsome et al. 2015). We attempted to account for this by using reindeer carcass availability as a covariate, but low statistical power precluded us from drawing conclusions about the effect of carrion on natural mortality (Figure S1.3). This may also be partially linked to the fact that reindeer carcasses are not evenly distributed across our study area and future studies that aim to disentangle the drivers of variation in natural mortality will likely benefit from considering known spatial heterogeneity in the importance of different food resources (Killengreen et al. 2011; Chevallier et al. 2020).

Unlike for natural mortality, we found no evidence for age-dependence in harvest mortality hazard rates (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 (Baker et al. 2001; Storm et al. 1976). 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, DeVault, and Belant 2019). Harvest mortality was relatively constant during the study period except for high estimates in the 2019-2020 winter season (Figure S1.2). Including potentially relevant covariates, such as harvest effort, will help interpret observed variation in harvest mortality (Soininen, Fuglei, and Pedersen 2016).

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, Kilgo, and Rhodes 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), 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 (Figure S1.2). Even though uncertainty was high, several immigration peaks coincided with high rodent abundance (Figure 5, S1.7). Indeed, dispersal is a key strategy to cope with temporal resource variation (Holt 2008), and immigrant pulses following small rodent peaks have previously been described in Arctic foxes (Norén et al. 2011). However, high uncertainty in 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 (SI S2), but much of this could be accounted for by extending data integration to include the genetic assignment analysis in the IPM. Genetic monitoring is becoming increasingly attractive as an addition to or even replacement of traditional monitoring approaches (Schwartz, Luikart, and Waples 2007), and the model and code developed in 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.

Drivers of past 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 (Figure S1.4), suggesting a key role of reproductive output, survival of young, and possibly immigration for population increase. The results from our LTRE 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 & S1.6). Furthermore, years of population increase followed winters of small rodent peak abundance in 2007-08, 2010-11, and 2014-15 (Figures 6 & S1.8), 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, Sidorovich, and Izotova 2006; J. Henden, Ims, and Yoccoz 2009). The final rodent abundance peak during our study period (2018-19) 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 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 LTRE analyses showed relatively low contributions of harvest mortality overall (Figure 7). However, LTRE analyses focus on the contribution of *changes* in vital rates (Koons et al. 2016; Koons, Arnold, and Schaub 2017), and as harvest mortality has been relatively constant over the course of our study period (Figure S1.2), this limits the degree to which such 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 the population's decline to continue if all parameters remain unchanged but suggested that increase is likely in absence of harvest (Figure 9A). Current harvest levels thus appear to control population growth. In addition to our finding that harvest prevented population increase during the most recent rodent peak (see above), these results contribute new evidence to the debate on whether large-scale and long-term harvest constitutes effective mesopredator control (e.g. Heydon and Reynolds 2000; Rushton et al. 2006; Robley et al. 2014; J. Henden et al. 2021; Lazure and Weladji 2024). By extension, increasing harvest overall is likely to result in faster population decline (Figure 9A), but several studies have suggested that management of populations driven by cyclical resource availability should be "cyclic-phase-dependent", i.e. that control actions should be focused on years when target populations are most responsive to the action (Henden et al., 2009; Wilkinson et al., 2024). In a range of scenarios in which we increased harvest in response to rodent abundance, we found that that increasing harvest during winters with high rodent abundance was most effective at reducing population size, at least initially (Figure 9B). This was not only due to a high rodent winter – and hence harvest increase – being likely to occur within the first two years of the simulation, but also because increased mortality during high rodent winters reduced the population's total reproductive output the following year. It is unclear, however, to what degree this harvest strategy translates into mitigating detrimental effects on other species. (J.-A. Henden et al. 2010) found that red fox densities during and following small rodent peaks are less detrimental to Arctic foxes than mean red fox densities, suggesting that increased red fox harvest during peak rodent winters may not be the ideal strategy for protecting arctic foxes. Future work should therefore focus on a multi-species perspective (Mellard et al. 2022) and integrated community models (Zipkin et al. 2023) constitute a promising approach given our initial work on red foxes here and the ecosystem-level monitoring conducted in and surrounding Varanger (Climate-ecological Observatory for Arctic Tundra, COAT, Ims et al., 2013).

It is important to note that the results from our PVA simulations must be interpreted with caution, particularly on longer time scales, as we did not explicitly model compensatory mechanisms. It is well known that decreased natural mortality, due to either density feedback or heterogeneity in individual quality, can compensate for intensive harvest in many species (Doherty and Ritchie 2017; Péron 2013). Increased reproductive output and immigration are common compensatory mechanisms in mesopredators in particular (Lieury et al. 2015; Minnie, Gaylard, and Kerley 2016; Kierepka, Kilgo, and Rhodes 2017). Looking at posterior correlations among population sizes and vital rates, we indeed found evidence for density-dependence in population growth rate, natural and harvest mortality, and immigration, as well as compensation of harvest by natural mortality (Table S1.1). While these findings may be partially explained by sampling correlation, it is not unlikely that compensatory mechanisms are at play in our study population also. To further improve population forecasts and management strategies, future work should therefore focus on extending our modelling framework to mechanistically account for density dependence and compensation (e.g. Riecke et al., 2022).

IPM workflows as promising management tools

There is an urgent need for evidence-based management of mesopredators and quantitative assessments of control efforts (Doherty and Ritchie 2017; J.-L. Kämmerle, Ritchie, and Storch 2019; Lennox et al. 2018), yet lack of sufficient data and appropriate statistical tools often prevent the necessary analyses (Hradsky et al. 2019). Here we presented a modelling framework that tackles these challenges through integration of data that is available for many species of management concern: demographic and genetic data from harvested animals, sparse opportunistic surveys, and prior knowledge extracted from literature through meta-analysis. To enhance transferability of the modelling framework to other populations/species and to facilitate re-running the analyses when new data becomes available, we set up the entire analysis workflow – from data retrieval to plotting of results – as a reproducible and semi-automated “targets” pipeline (Landau 2021). Reproducibility of analytical workflows is key for successful adaptive management (Dietze et al. 2018; Nichols, Kendall, and Boomer 2019). Furthermore, 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). By making our workflow available as an accessible, reproducible, and well documented pipeline, we therefore 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. compensatory mechanisms, spatial representation) but also for better representation of the human dimension, such as how hunting regulations translate into harvest mortality (Eriksen, Moa, and Nilsen 2018) and how additional actions targeted at human subsidies (Jahren et al. 2020; Killengreen et al. 2011) might augment control through hunting. We finally stress that setting aside resources to leverage the data made available through management (i.e. harvested carcasses) is essential for the qualitative assessment of management.

ACKNOWLEDGEMENTS

This project would not have been possible without the large efforts of local hunters, field inspectors from the Norwegian Environmental Directorate, 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.

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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.

DATA AND CODE ACCESSIBILITY

Raw data on harvested foxes (Ehrich et al. 2023) and small rodent abundance (Ehrich et al. 2022) are archived on the COAT Data Portal (https://data.coat.no/). Both datasets are currently under embargo; 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 model, and supplementary files are archived on OSF: https://osf.io/756re/ (Nater and Hofhuis 2024). 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. The results presented in this paper were created using version 1.0 of the code (Nater et al. 2024).

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Supporting Information for:

An integrated population modelling workflow for supporting mesopredator management

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S1: Supplementary Figures and Tables

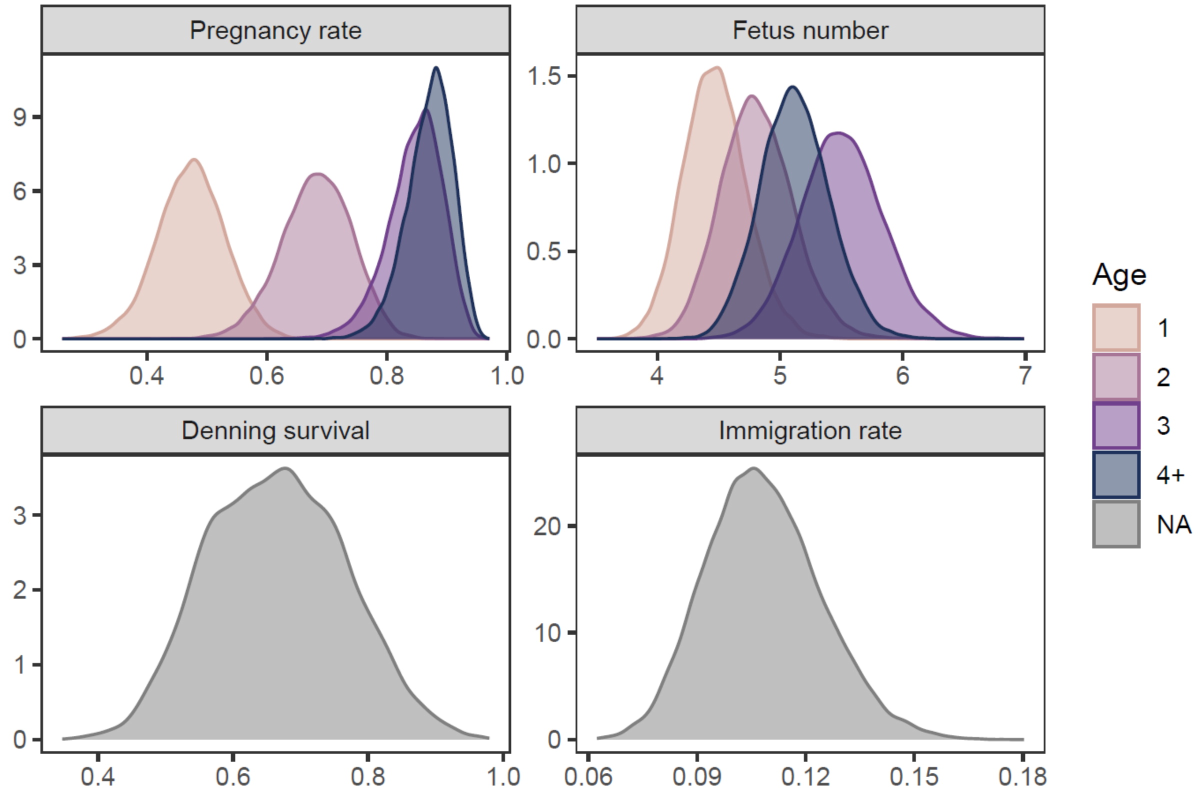
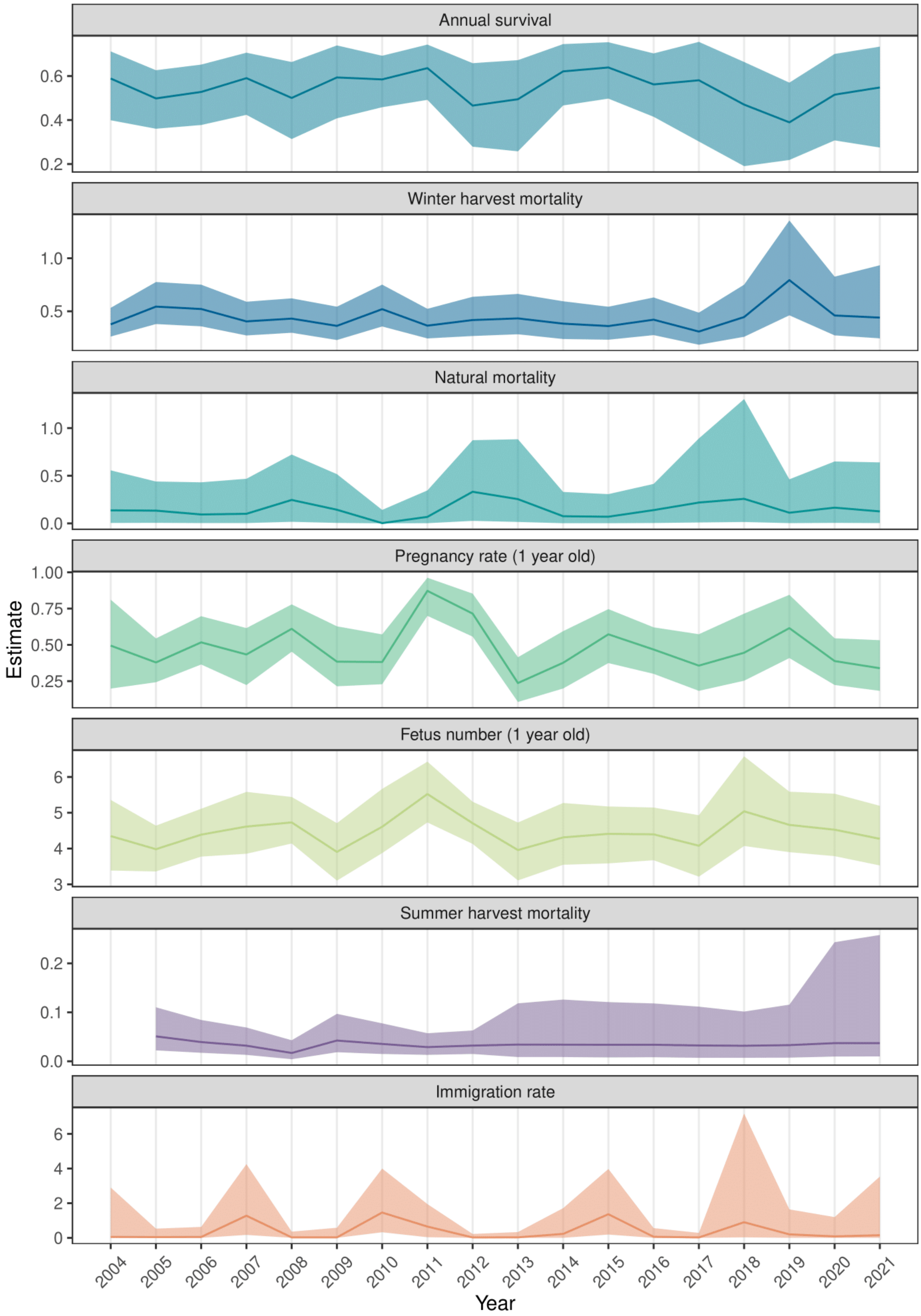


Figure S1.1: Posterior distributions for age-specific average pregnancy rates and litter sizes, as well as denning survival probability and immigration rate of red foxes on Varanger Peninsula.



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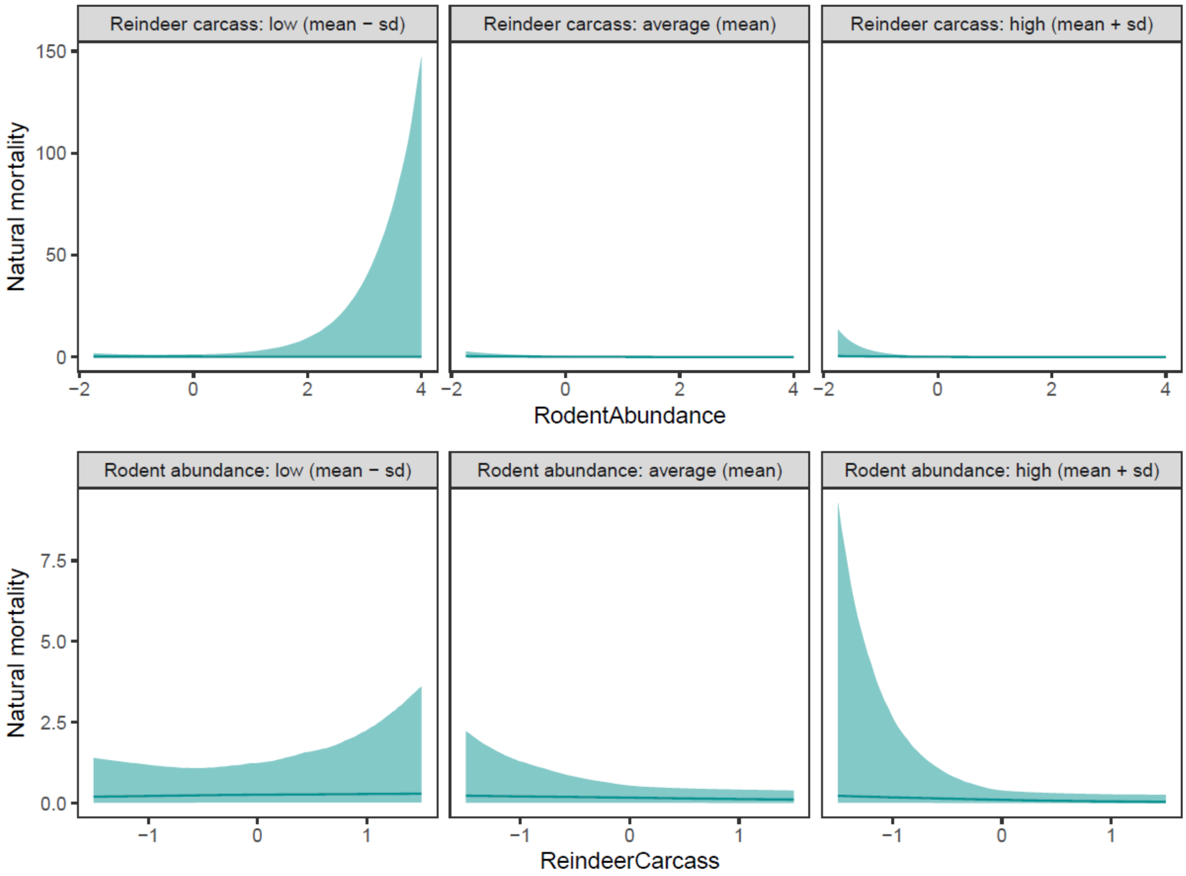

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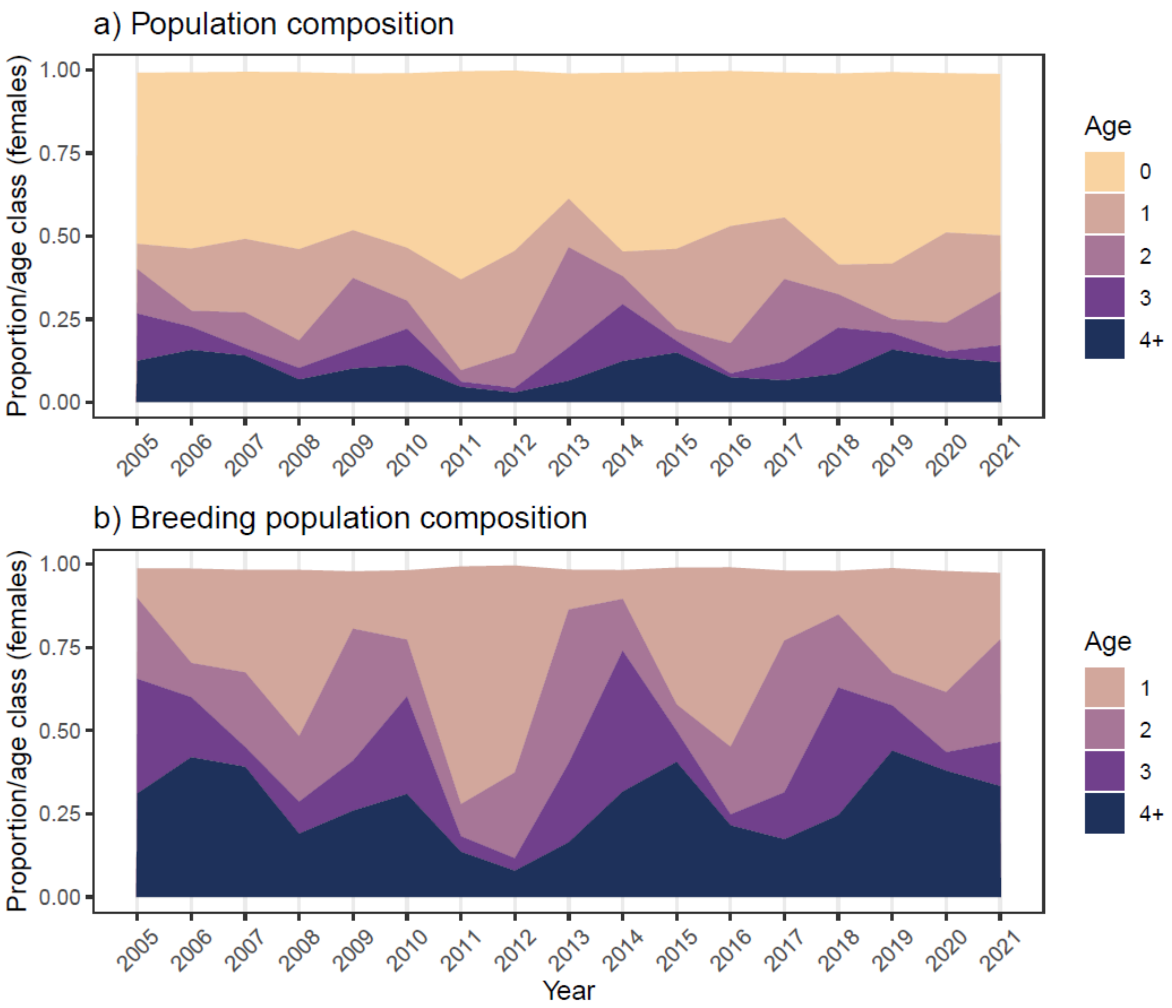

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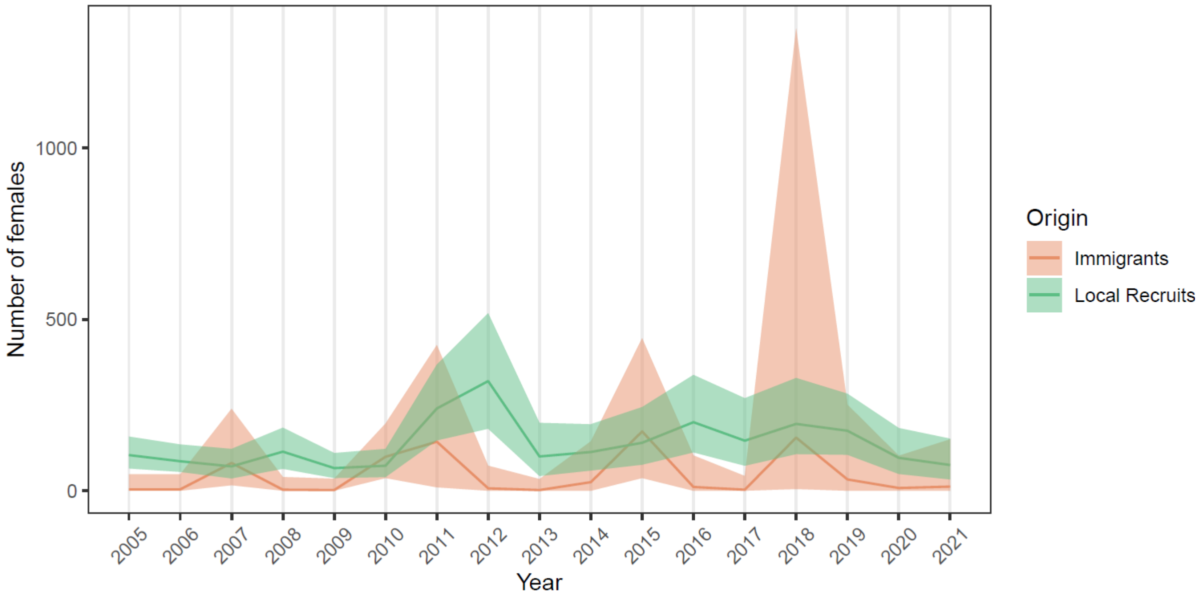
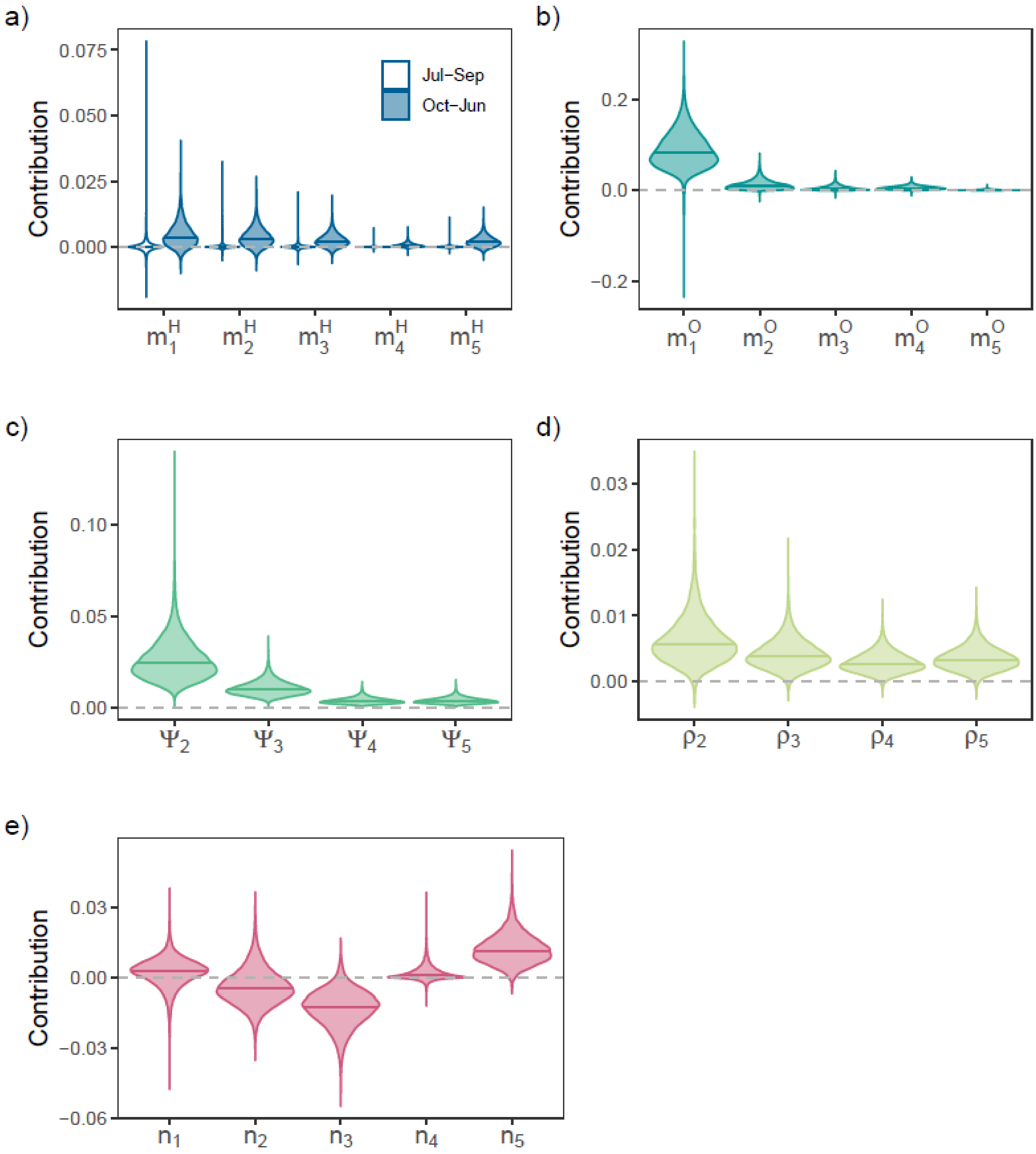


Figure S1.5: Estimated annual numbers of red fox juveniles recruited locally (green) on Varanger Peninsula and juveniles immigrating into the population from elsewhere (orange). The solid lines represent posterior medians, the ribbons marks the 95% credible intervals.



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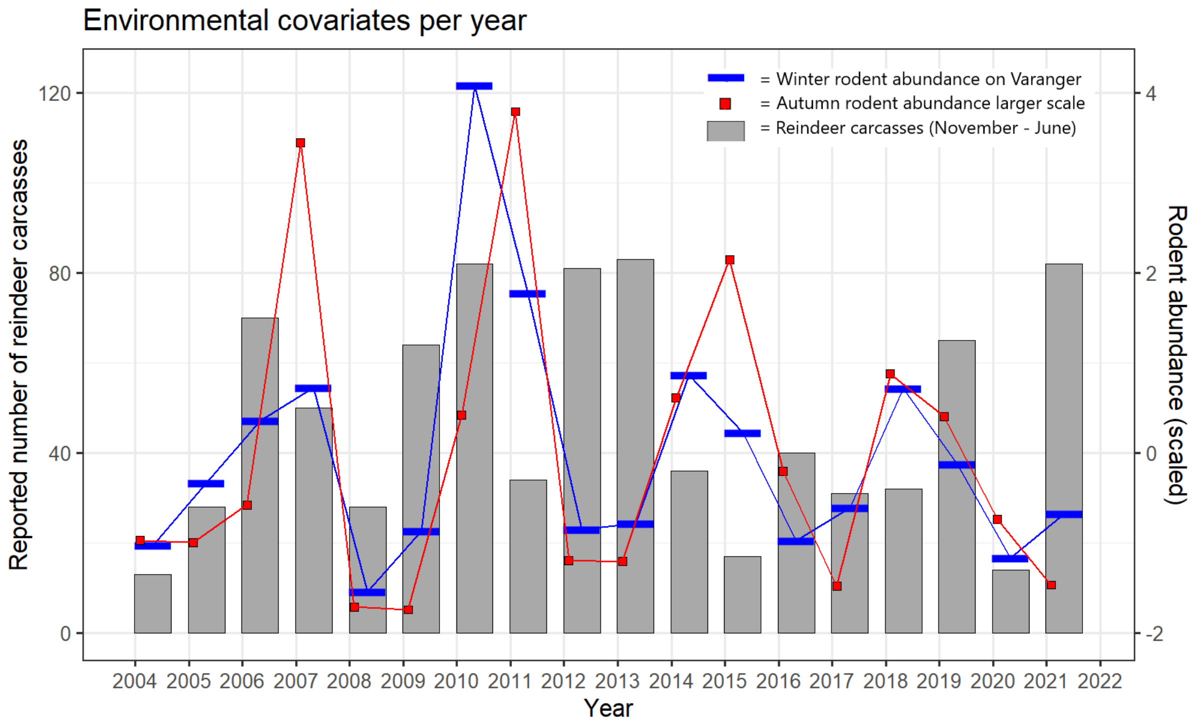


Figure S1.7: Environmental covariates used in the red fox IPM per year. Winter (average of autumn and spring trapping) rodent abundance within Varanger and reindeer carcass abundance were used as covariates for local mortality and reproduction of red foxes. Autumn rodent abundance at a larger spatial scale was used as a covariate for immigration.

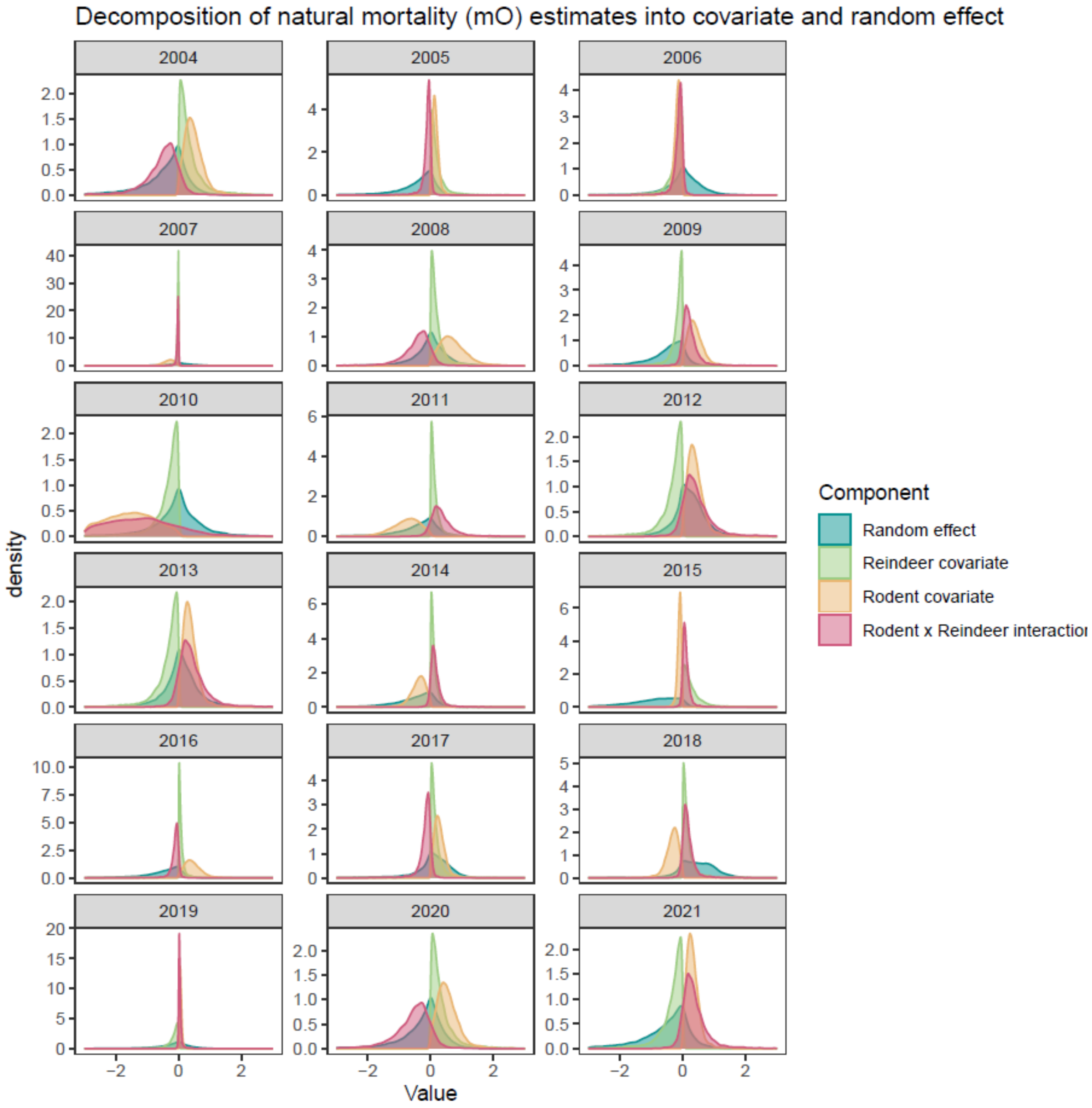


Figure S1.8: Decomposition of natural mortality (mO) posterior densities into covariates and random effect per year.

Parameter pairs	50 %	2.5 %	25 %	75 %	97.5 %	Evidence
Pop. growth rate ~ N	-0.41	-0.52	-0.45	-0.38	-0.32	**
Harvest mort. ~ N	-0.15	-0.46	-0.27	-0.03	0.21	*
Natural mort. ~ N	0.44	0.14	0.35	0.53	0.68	**
Immigration rate ~ N	-0.21	-0.45	-0.30	-0.11	0.10	*
Breeding pop. size ~ N	0.24	-0.05	0.14	0.33	0.49	*
Litter size ~ N	0.06	-0.29	-0.06	0.19	0.41	-
Harvest mort. ~ Natural mort.	-0.18	-0.48	-0.29	-0.06	0.19	*
Harvest mort. ~ Immigration rate	-0.09	-0.38	-0.20	0.03	0.33	-
Harvest mort. ~ Immigration rate [t+1]	-0.02	-0.35	-0.14	0.11	0.38	-
Harvest mort. ~ Nat.mort[t+1]	-0.14	-0.48	-0.26	0.00	0.29	-
Natural mort. ~ Immmigration rate	-0.24	-0.64	-0.41	-0.03	0.40	*
Harvest mort. ~ Reproduction	0.03	-0.29	-0.08	0.16	0.40	-
Natural mort. ~ Reproduction	-0.49	-0.84	-0.64	-0.34	-0.04	**

Table S1.1: Summaries of posterior distributions of post-hoc correlation analyses between different model parameters over all 18 years in the study. Correlations with population size (N) may indicate the presence of density feedbacks while correlations among other parameters may give insights into potential trade-offs and compensatory mechanisms. The results are presented as quantiles of 50% (posterior median), 2.5%, 25%, 75%, and 97.5%. The column “Evidence” expresses the strength of evidence for a correlation based on its credible interval (CI): ** = strong evidence (95% CI does not overlap 0), * = moderate evidence (50% CI does not overlap 0), - = no evidence (50% CI overlaps 0).

S2: Using genetic data in IPMs

S2.1 Additional information on genetic data processing and analysis

Genetic samples were collected from harvested foxes of both sexes; 505 from within Varanger from 2005-2015 (11-74 foxes per year), 158 from Finnmarksvidda (lake Iešjávri) from 2008-2013, 28 from Nordkynn Peninsula in 2011, and 8 from Sør-Varanger (Neiden) in 2016 (Table S2.1).

Table S2.1: Overview of genetic samples per area and hunting season.

	2004 2005	2005 2006	2006 2007	2007 2008	2008 2009	2009 2010	2010 2011	2011 2012	2012 2013	2013 2014	2014 2015	2015 2016
Varanger	45	59	54	50	36	29	45	51	51	74	11	0
Finnmarksvidda	0	0	0	31	10	29	30	28	30	0	0	0
Nordkinn	0	0	0	0	0	0	28	0	0	0	0	0
Sør-Varanger	0	0	0	0	0	0	0	0	0	0	0	8

DNA was extracted from muscle samples using the DNeasy 96 Blood & Tissue Kit (QIAGEN, GmbH, Hilden, Germany). All samples were genotyped at 12 microsatellite loci (REN54P11, FH2001, FH2848, FH2328, FH2054, CPH18, CPH11, CPH7, CPH2, C08.618, AHT133; An et al. 2010 and CXX-468; Ostrander et al. 1995). The markers were amplified using multiplex PCR followed by capillary electrophoresis as described in Moore et al. (2010). Genotypes were scored in GeneMarker 2.6.4 (SoftGenetics) and reviewed manually. Table S2.2 presents summary statistics for the genetic samples.

Table S2.2: Summary statistics for the genetic data from Varanger (per hunting season) and for the three regions sampled outside of Varanger. n = number of individuals, Ho = mean observed heterozygosity, Ho.sd = standard deviation of observed heterozygosity over loci, He = mean expected heterozygosity, He.sd = standard deviation of expected heterozygosity, Ar = mean allelic richness for a sample size of 8, Ar.sd = standard deviation of allelic richness, Fis = mean FIS, Fis.sd = standard deviation of FIS. Summary statistics were calculated in the R package *"hierfstat"* (Goudet, 2005).

	n	Ho	Ho.sd	He	He.sd	Ar	Ar.sd	Fis	Fis.sd
Varanger	505	0.721	0.167	0.753	0.182	6.018	2.221	0.036	0.056
Varanger_2004_05	45	0.694	0.205	0.73	0.203	5.638	2.196	0.052	0.092
Varanger_2005_06	59	0.742	0.174	0.755	0.186	6.103	2.272	0.011	0.076
Varanger_2006_07	54	0.67	0.168	0.742	0.189	5.942	2.146	0.095	0.093
Varanger_2007_08	50	0.737	0.173	0.751	0.189	5.992	2.333	0.009	0.078
Varanger_2008_09	36	0.69	0.226	0.741	0.204	5.91	2.32	0.082	0.108
Varanger_2009_10	29	0.701	0.191	0.744	0.192	5.888	2.209	0.056	0.074
Varanger_2010_11	45	0.731	0.179	0.748	0.173	5.742	2.06	0.016	0.121
Varanger_2011_12	51	0.73	0.171	0.76	0.168	6.019	2.096	0.035	0.09
Varanger_2012_13	51	0.739	0.157	0.769	0.156	6.139	2.15	0.036	0.103
Varanger_2013_14	74	0.747	0.159	0.748	0.182	5.895	2.186	-0.01	0.073
Varanger_2014_15	11	0.735	0.203	0.744	0.186	5.493	2.173	-0.008	0.225
Finnmarksvidda	158	0.727	0.163	0.773	0.168	6.298	2.307	0.059	0.068
Nordkynn	28	0.765	0.145	0.777	0.156	6.195	2.343	0.004	0.127
Sør- Varanger	8	0.719	0.161	0.756	0.197	6.667	2.674	0.013	0.223

We identified likely first-generation immigrants based on their genotypes applying genetic assignment as implemented in the program Geneclass 2 (Piry et al., 2004). Consistent with previous work (Norén et al., 2015), preliminary analyses of population structure did not show much differentiation among the possible immigrant source populations of Finnmarksvidda, Nordkynn and Sør-Varanger and all samples from these areas were therefore pooled into one combined potential source population (Figure S2.1).

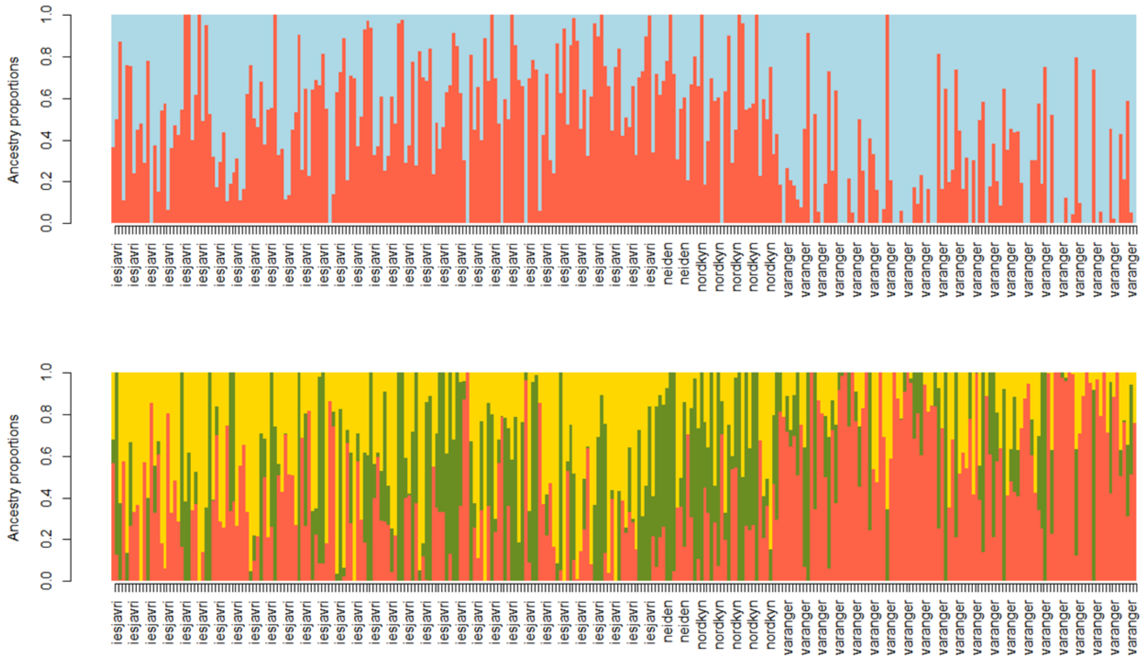


Figure S2.1: Populations structure of red foxes shot on Varanger peninsula in the first two years of the study (winter 2004-05 and 2005-06) shown as proportion of ancestry in 2 (top) or 3 (bottom) clusters. Population structure was assessed using the sparse Non-Negative Matrix Factorization algorithm developed by Frichot et al. (2015) implemented in the R package "*LEA*" (Frichot & François, 2015). Results provided most support for a subdivision into two groups: Varanger and the surrounding area.

We further refined the definition of the reference population from Varanger peninsula to represent the year in which the individual to be assigned was born (based on its harvest date and estimated age) to account for the fact that intensive hunting likely has led to a change in allele frequencies on Varanger over the 10 years covered by the genetic sampling (Lieury et al., 2015). For seven individuals lacking age, we assumed that they had been shot in their first winter. In addition to individuals shot in the focal individual's birth year, foxes known to be alive at that time based on their age and harvesting date were included in the reference population as well. Because of few samples available to describe the reference population, we excluded 18 individuals born before 2000. As recommended by Piry et al. (2004) we identified immigrants using a Bayesian likelihood estimation (Rannala & Mountain, 1997), a relative assignment criterion based on the comparison between the population of origin and the potential source population, and an exclusion test based on 1000 Monte Carlo resampling replicates (Paetkau et al. 2004) to identify immigrants. For each individual, Geneclass 2 thus provided individual-level p-values for the hypothesis that a fox originated from the Varanger population, given the genetic composition of the local and potential source population in the year of the individual's birth.

Figure S2.2 shows the distribution of p-values for all 487 individuals harvested in Varanger that were included in the analyses . 46 (9.4%) of individuals were assigned p-values below 0.05 and were thus assumed highly likely to be of immigrant origin. The percentage of likely immigrants ($p < 0.05$) was higher for males (15.8%) than females (5.4%) in the sample.

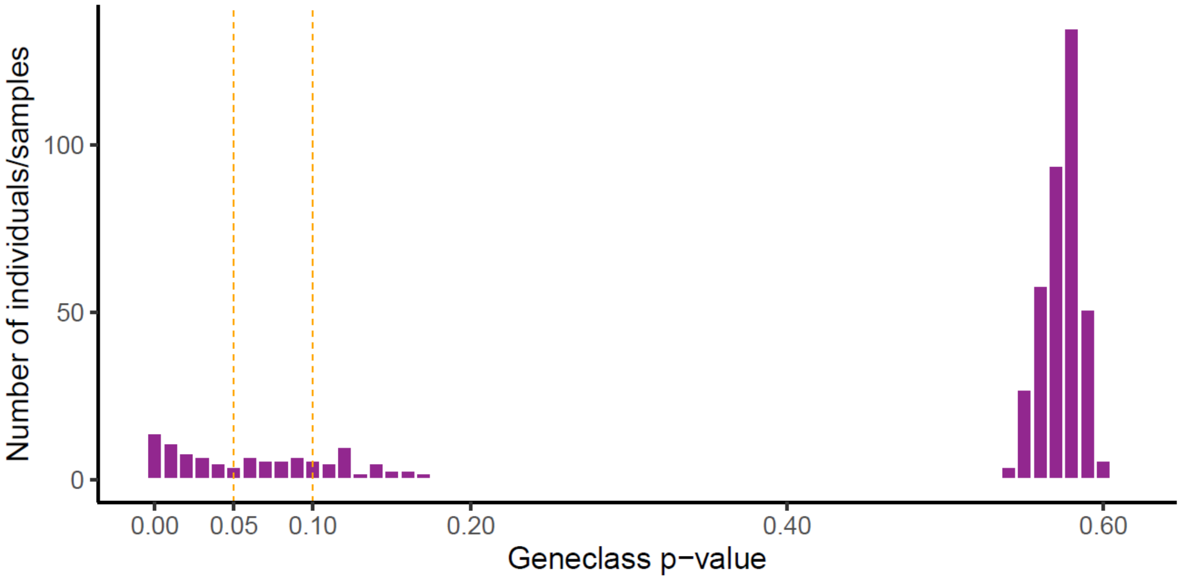


Figure S2.2: Distribution of individual-level p-values for the hypothesis that a fox originated from the Varanger population. The lower the p-value, the more likely that an individual is an immigrant into Varanger. The dashed orange lines mark the 0.05 and 0.10 thresholds.

S2.2 Different versions of genetic data likelihoods

The inclusion of information from genetic assignment tests in IPMs is new, and p-values as calculated by Geneclass 2 are not intuitively compatible with Bayesian modelling frameworks. We therefore considered several possible ways of specifying the likelihood for this information in our IPM. The likelihoods we tested differed in three aspects:

1) A priori immigrant status assignment vs. use of continuous data
2) The threshold chosen for a-priori immigrant status assignment
3) Use of genetic data to inform average vs. yearly immigration rate

The final version of our model (presented in the main article) employs a priori immigrant status assignment using the commonly accepted threshold of 0.05 ($p < 0.05$ equals immigrants, status = 1) and uses genetic data to estimate average immigration rate over the study period, but not time variation therein. The data likelihood is expressed as:

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

where $genObs_{Imm}$ and $genObs_{Res}$ are the total numbers of individuals that were determined to be first generation immigrants ($p < 0.05$) and locally born residents ($p \geq 0.05$), respectively, relative to the reference population in their year of birth. μ^{immR} is the average immigration rate over the course of the study period.

In an alternative approach, we attempted to use the continuous p-values directly to first estimate a true latent immigration status for each individual instead of using an arbitrary threshold. To do so, we made an assumption that the inverse of the p-value (1-p) was proportional to the probability that an individual is an immigrant and specified the data likelihood as follows:

$$ImmStatus_x \sim Bernouilli(pImm_x)$$

Here, $ImmStatus_x$ is the immigrant status (1 = immigrant, 0 = locally born) of individual x, and $pImm_x$ is a probability relative to the inverse of the p-value Geneclass 2 assigned for individual x. Immigration rate can then be calculated subsequently as:

$$\mu^{immR} = \frac{sum(ImmStatus_{1:X})}{X - sum(ImmStatus_{1:X})}$$

where X is the total number of individuals in the genetic data. We first tested this implementation assuming $pImm_x = 1 - p_x$ (where p_x is the p-value calculated by Geneclass 2). However, because even the highest p-values were no larger than ~0.6 (Figure S2.2), this severely overestimated immigration rate. Consequently, we tested this approach using an adjusted version of $pImm_x$ which had been rescaled to range from 0 to 1.

We also considered a second version of both likelihoods which linked information in the genetic data to annual immigration rates ($immR_t$) instead of time-average immigration rate (μ^{immR}). Both likelihoods had the same forms as above, but μ^{immR} was replaced with $immR_t$, and for each year t we only considered the subset of individuals that was between 0-1 years old. As such, this reinforced the assumption of immigration within the first year of life made by both the IPM and the Geneclass 2 analysis, and put a strong constraint on time-variation in immigration rate since that was now calculated as a derived quantity ($= SD(immR_{1:T})$, where T = last year in study).

S2.3 Comparison of models using different genetic data likelihoods

We performed two sets of model comparisons to assess the impact of different approaches to modelling genetic data.

In the first set, we compared models using a priori assignment of immigrant status using thresholds of 0.05 and 0.2, as well as a model using the rescaled p-values as continuous data (Figure S2.3, additional figures in supplementary folder "CompFinal_GenData"). All models in the comparison used the genetic data to inform average immigration rate. The choice of data likelihood and p-value threshold had very little effect on parameters beyond average immigration rate and time-variation in immigration rate. The 0.2 threshold model and the rescaled p-value model produced similar estimates of average immigration rate (~0.3-0.35), while the 0.05 threshold model estimated substantially lower immigration rate (~0.1). This difference did not propagate much into other parameters though because it was compensated by relatively higher time-variation in immigration rate and denning survival in the 0.05 threshold model.

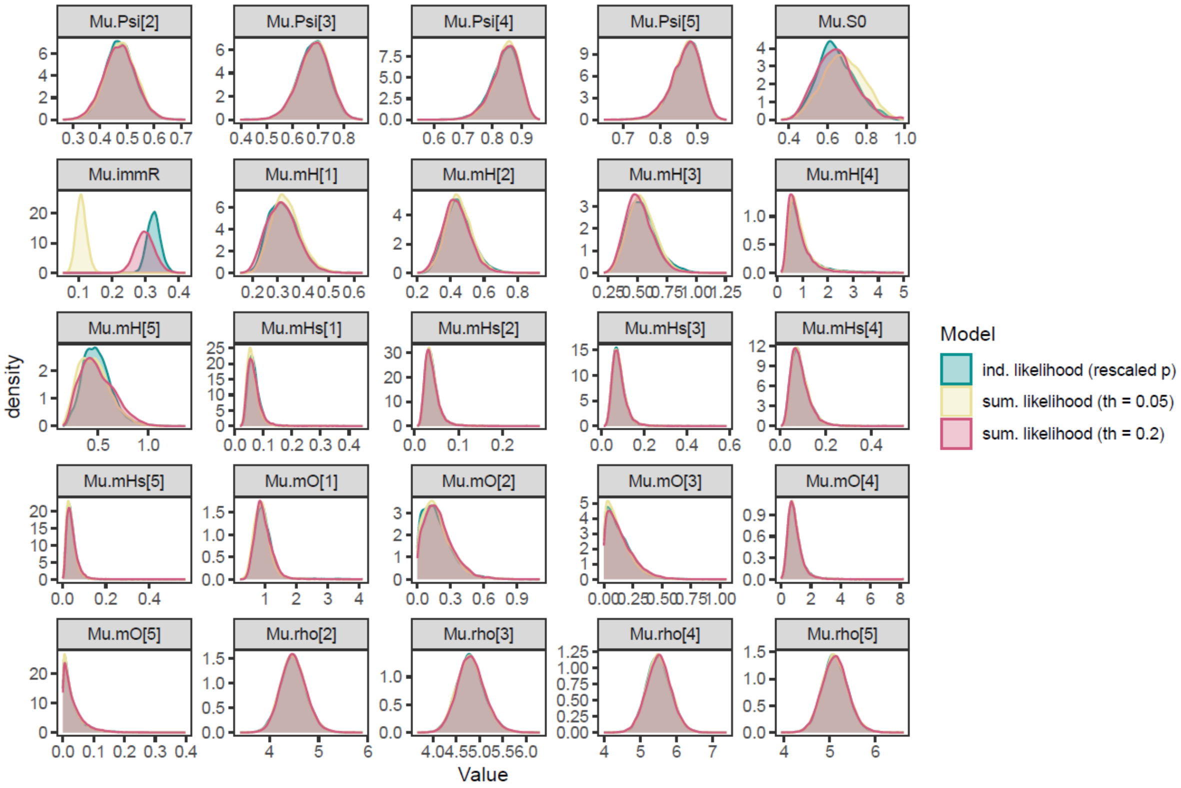


Figure S2.3: Posterior densities for (age-specific) vital rate averages from models employing different likelihoods for the genetic data. Mu.Psi[a] = age class a pregnancy rate; Mu.mH[a] = age class a winter harvest mortality hazard rate; Mu.mHs[a] = age class a summer harvest morality hazard rate; Mu.mO[a] = age class a natural mortality hazard rate; Mu.rho[a] age class a litter size in utero. The yellow model is the model presented in the main article. Graphical comparisons for other model parameters can be found in the supplementary folder “CompFinal_GenData”.

In the second set of comparisons, we evaluated the effect of using genetic data to inform average and annual immigration rates (Figure S2.4, additional figures in supplementary folder “CompFinal_ImmModels”). The first result from this comparison was that adding the genetic data as opposed to estimating immigration from priors and residual variation in the model only led to more precise estimates of natural mortality, immigration rates (and immigrant numbers), and population size. It also resulted in somewhat more among-year variation in natural mortality (attributed to both covariate effects and residual variation). Second, the comparison showed that adding genetic data to inform average immigration rate did not lead to substantial shifts or altered temporal patterns in most other parameters. When using genetic data to estimate annual immigration rates, however, the added constraints propagated into many other parameters, leading to higher denning survival and harvest mortality of young individuals, lower harvest mortality of the oldest age class, a stronger effect of rodent abundance on natural mortality, and higher population size early in the time series. Due to these shifts, the low degree of variation in immigration rate over time, and the fact that this time variation was constrained by data from relatively small numbers of foxes each year and strong assumptions, we decided to continue with a model that uses genetic data to estimate average immigration rate only. We do note, however, that our published code contains the option to implement all combinations of likelihoods and data thresholds.

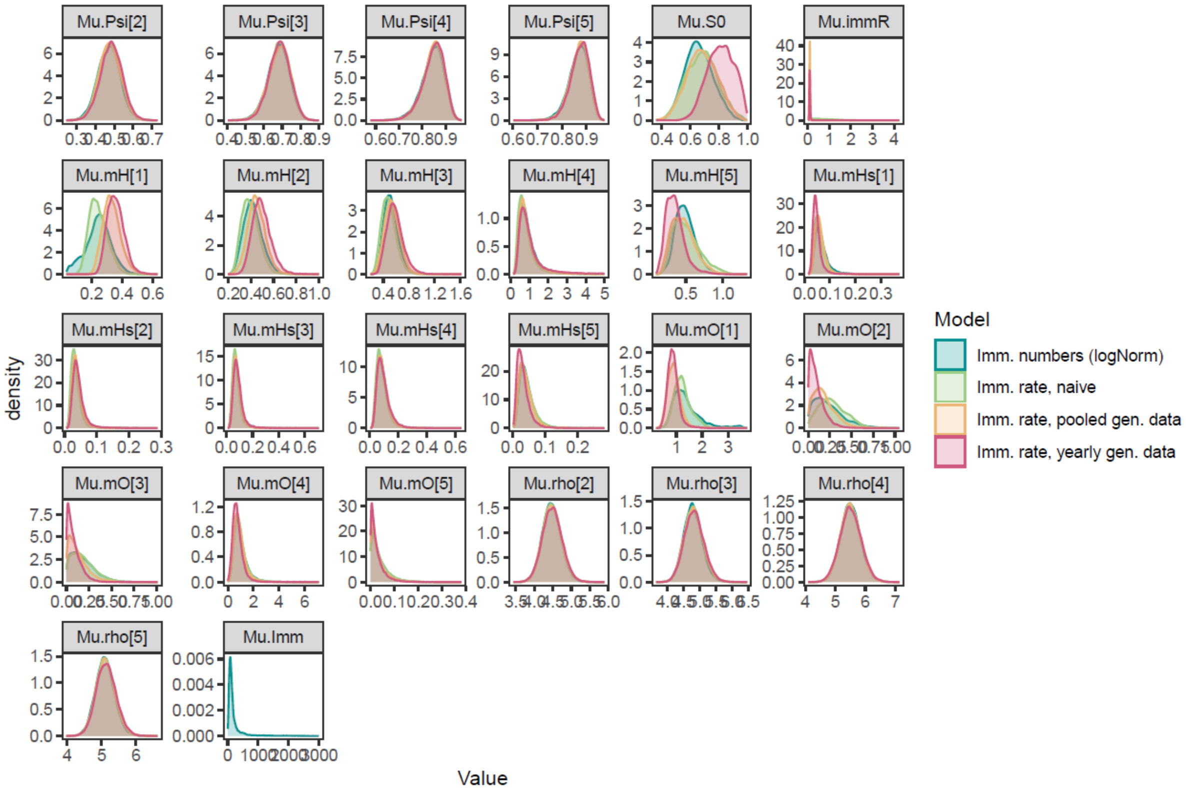


Figure S2.4: Posterior densities for (age-specific) vital rate averages from models employing different models for immigration. Mu.Psi[a] = age class a pregnancy rate; Mu.S0 = denning survival; Mu.immR = immigration rate; Mu.mH[a] = age class a winter harvest mortality hazard rate; Mu.mHs[a] = age class a summer harvest morality hazard rate; Mu.mO[a] = age class a natural mortality hazard rate; Mu.rho[a] age class a litter size in utero; Mu.Imm = number of immigrants. The yellow model is the model presented in the main article. Graphical comparisons for other model parameters can be found in the supplementary folder “CompFinal_ImmModels”.

S3: Informative priors and their implications

S3.1 Different options for natural mortality priors

Like many mesocarnivores, red foxes on Varanger are not subject to individual-based monitoring using marked animals (e.g. mark.recapture programmes). Monitoring using telemetry has been initiated in 2021 but is very limited so far (9 individuals collared over 3 years). Consequently, there is no observational data available that can be used to estimate the natural components of red fox mortality. We therefore opted for including available knowledge on red fox natural mortality in our model using informative priors for average age-specific natural mortality hazard rates (μ_a^{mO}, where a = age class). We tested three different approaches for specifying informative priors: 1) using published values for a single other red fox population (from collected survival estimates in Devenish-Nelson et al., 2013), 2) using meta-analysis of survival estimates from many populations of red foxes collated in Devenish-Nelson et al. (2013), and 3) using a phylogenetic Hoenig model developed by Porteus et al. (2018) to calculate natural mortality from maximum observed age. We describe all three approaches briefly below, and present a comparison in the next section. Approach 2 (meta-analysis) was implemented for the models presented in the main article and other model comparisons (e.g. SI S2 & S4).

Approach 1: Survival estimates from single other populations

Devenish-Nelson et al. (2013) collated vital rate estimates from red fox populations across the species' distribution. While they do conclude that there is a lot of variation across populations, using estimates from (ecologically) similar populations as substitutes is one possible approach to specifying informative priors. To test this in our model and assess the impacts that choice of estimates had on model parameters, we picked two populations highlighted in Devenish-Nelson et al. (2013): Bristol and North Sweden. The red fox population from Bristol is not hunted, meaning that the reported estimates of annual survival (S) can be directly translated into natural mortality hazard rates mO via $S = \exp{(-mO)}$. The red fox population from North Sweden is lightly hunted, but otherwise ecologically very similar to the red foxes in Varanger. In both cases, we used the means ($Snat.mean_a$) and standard deviations ($Snat.sd_a$) of annual survival of age classes 1-4 presented in Table 1 in Devenish-Nelson et al. (2013), and assumed that age class 5 in our model had the same underlying parameters as age class 4 (Table S3.1).

Table S3.1: Mean and standard deviation for annual survival of red foxes derived from the review by Devenish-Nelson et al. (2013). Values for populations "Bristol" and "North Sweden" are taken from Table 1 in the review. Values under "Meta-analysis" were calculated through weighted regression of multiple populations presented in Table A2 in the review's supplementary.

	Bristol		**North Sweden**		**Meta-analysis**	
	Mean	*SD*	*Mean*	*SD*	*Mean*	*SD*
Age class 1	0.30	0.07	0.33	0.02	0.402	0.182
Age class 2	0.35	0.05	0.71	0.04	0.467	0.181
Age class 3	0.57	0.07	0.50	0.05	0.541	0.182
Age class 4	0.70	0.06	0.59	0.04	0.403	0.182
Age class 5	0.70	0.06	0.59	0.04	0.600	0.236

Within the IPM, we then used these parameters to specify the informative prior on μ_a^{mO} as follows:

$$\mu_a^{m0} = -\log(\mu_a^{Snat})$$
$$\mu_a^{Snat} \sim Normal(Snat.mean_a, Snat.sd_a)T[0,1]$$

Here, μ_a^{Snat} is the (hypothetical) average survival probability in the absence of harvest, and we used a truncated normal distribution to constrain values to be bounded by 0 and 1.

Approach 2: Survival estimates from meta-analysis of studies of other populations

Given the large variation in red fox vital rates across populations, Devenish-Nelson et al., (2013) advised caution when substituting vital rates across populations. An alternative approach to picking a single, presumably “suitable” population to borrow information from (Approach 1) is to account for variation across a large number of populations by first running a meta-analysis. In this second approach, we therefore estimated the parameters $Snat.mean_a$ and $Snat.sd_a$ for all parameters using a weighted regression on estimates from 20 of the populations presented in Table A2 in the supplementary of Devenish-Nelson et al., (2013). 23 populations in the review presented survival estimates for sufficient number of age classes and details on all are provided here: https://github.com/ChloeRN/VredfoxIPM/blob/main/Data/RedFox_LiteratureData.csv. We extracted maximum sample sizes of each study from Table A1 of the review when possible, and tried to reconstruct it from the original publications if it was not reported in Table A1. We also attempted to cross-check values with the original publications, but that was possibly for less than half as many of the original publications were not accessible. Prior to meta-analysis, we discarded 3 of the 23 populations due to inconclusive age class definition. We subjected the age-specific survival estimates from the remaining 20 populations to regression analysis weighted by maximum sample size. The resulting global estimates for age-specific annual survival ($Snat.mean_a$ and $Snat.sd_a$) are shown in Table S3.1 and Figure S3.1. The estimates were used to specify informative priors for natural mortality in the IPM in the same way as outlined under “Approach 1” above.

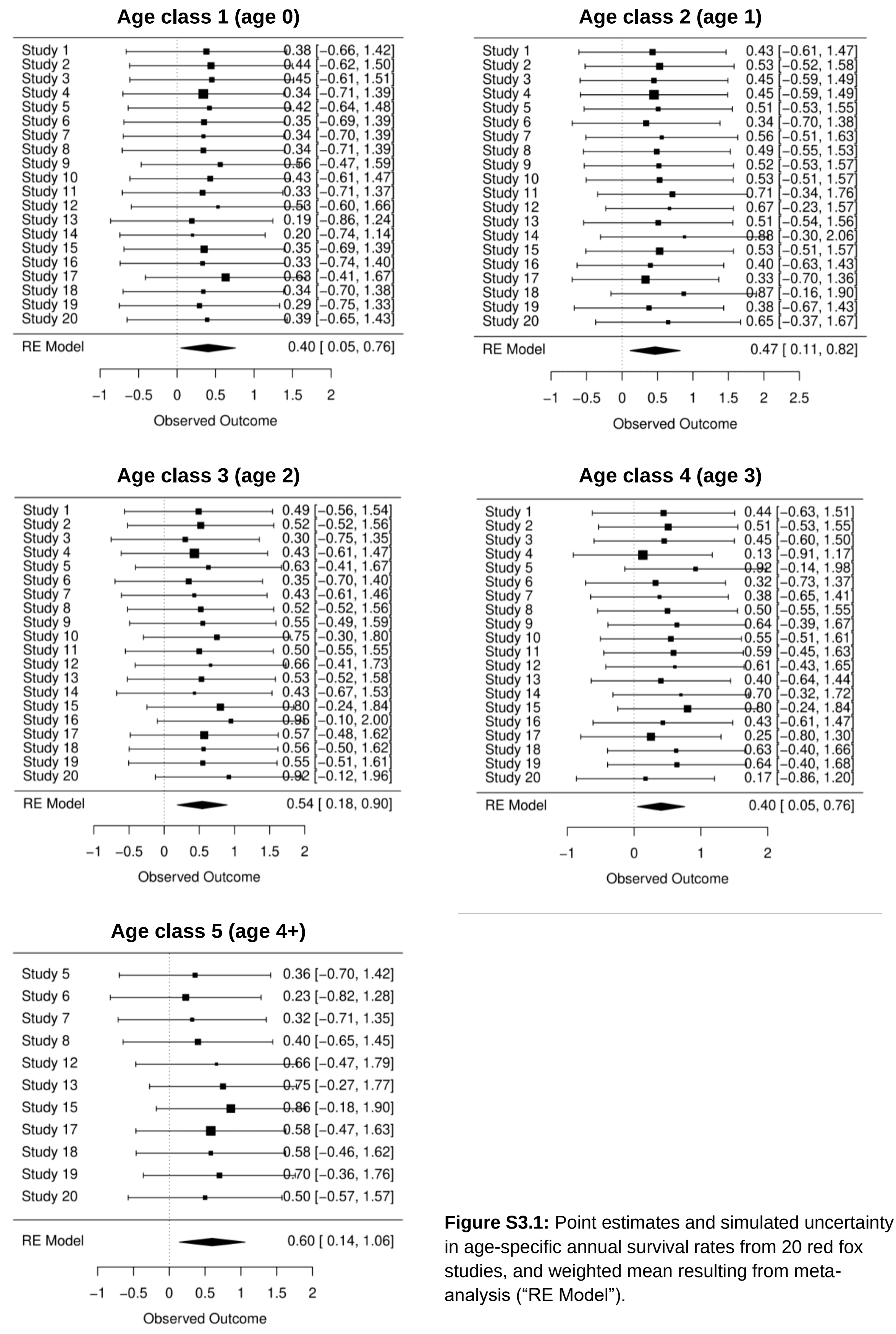
We note that our meta-analysis included populations irrespective of the degree of harvesting/hunting they were exposed to. We also ran the same analysis using only estimates from populations that were stated to be not or only lightly hunted (in original references), but this resulted in a low sample size and survival estimates that were extremely uncertain (and overlapped substantially with estimates from the full meta-analysis).

Approach 3: Natural mortality estimates from phylogenetic Hoenig model

Porteus et al. (2018) proposed an alternative approach to building informative priors for natural mortality of carnivores that involves phylogenetic models and life history characteristics. Specifically, they found that an implementation of the Hoenig model (Hoenig, J. M., 1983) works relatively well for red foxes. In practice, the Hoenig model uses a populations maximum individual age ($maxAge$) to calculate natural mortality ($m0$) according to:

$$log.m0 = a + b(\log(maxAge) - \log(\mu_{Tmax}))$$
$$m0 \sim logNormal(log.m0, \sigma)$$

The parameters a, b, σ, and μ_{Tmax} for the order carnivora where estimated by Porteus et al. (2018) using a Bayesian approach, and we obtain posterior samples for the former three and a point estimate from the latter from Tom Porteus upon request. Using these estimates and the age of the oldest female in our sample of harvested red foxes from Varanger (10) we



Age class 1 (age 0)

Age class 2 (age 1)

Age class 3 (age 2)

Age class 4 (age 3)

Age class 5 (age 4+)

Figure S3.1: Point estimates and simulated uncertainty in age-specific annual survival rates from 20 red fox studies, and weighted mean resulting from meta-analysis (“RE Model”).

calculated $log.mO$ for each posterior sample (n = 30) and subsequently simulated 30 replicate values from the log-normal distribution. We then derived the log mean ($mnat.logmean$) and log standard deviation ($mnat.logSD$) from the distribution of all resulting values, and used them to specify an informative prior for natural mortality of all adult age classes (2-5) in our model:

$$\mu_{2:5}^{mO} = \mu_{adult}^{mO}$$
$$\mu_{adult}^{mO} \sim logNormal(mnat.logmean, mnat.logSD)$$

The Hoenig model does not yield age-specific estimates, yet it is typical that juvenile animals have higher mortality. We accounted for this by adjusting the prior for the first age class using the ratio of juvenile to adult natural mortality estimated for harvested arctic foxes ($\mathrm{JA.mRatio}$, Nater et al., 2021) as follows:

$$\mu_{1}^{mO} = \mu_{adult}^{mO} \times JA.mRatio$$
$$JA.mRatio \sim logNormal(0.481, 0.355)$$

S3.2 Prior sensitivity analysis

Figure S3.2 presents a comparison of parameter estimates from models employing approaches 1, 2, and 3 from above.

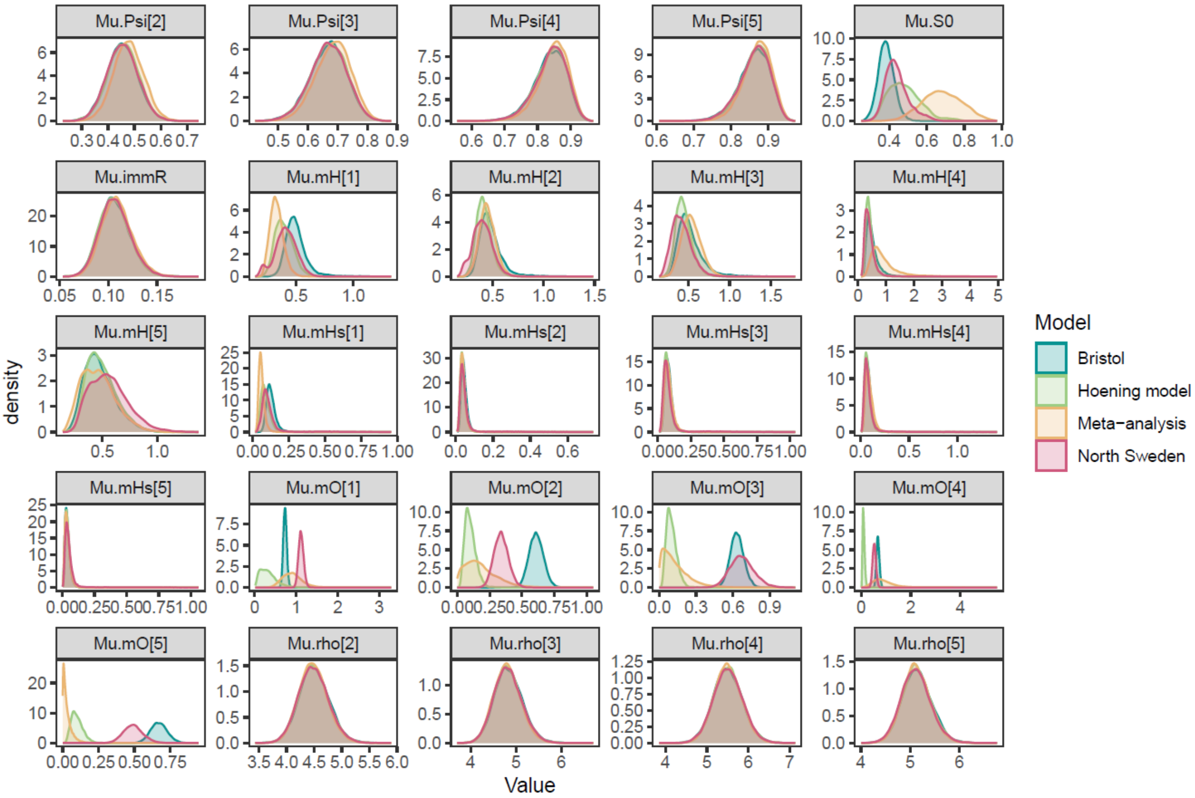


Figure S3.2: Posterior densities for (age-specific) vital rate averages from models employing different priors for natural mortality. The yellow model is the model presented in the main article. Graphical comparisons for other model parameters can be found in the supplementary folder “CompFinal_SurvPriors”.

Prior choice had a strong impact on estimates of average natural mortality hazard rates, as would be expected given the lack of observational data. Borrowing estimates directly from populations in Bristol and North Sweden yielded higher estimates of natural mortality, while the meta-analytical approaches (literature meta-analysis, Hoenig model) gave lower values with higher uncertainty. However, directly borrowing from other populations led to difficulty estimating time-variation in natural mortality, as indicated by large uncertainty in year random effects standard deviation and covariate effects (Fig. S3.3). The choice of natural mortality prior also affected winter harvest mortality (especially of the first age class) and survival to emergence from the den. The model using priors derived from meta-analysis of literature yielded slightly lower first year harvest mortality and higher survival to den emergence, the latter of which was consistent with estimates of the same parameters in a population of closely related arctic foxes (Nater et al., 2021). This model consequently also produced higher average estimates of population size, but population level estimates of all models had highly overlapping credible intervals (see supplementary folder “CompFinal_SurvPriors”).

We selected the model using priors based on literature meta-analysis for further analysis and presentation in the main article due to it’s ability to make use of information from a wide range of other populations, its ability to estimate time-variation in natural mortality without issues, and its more realistic estimate of survival to emergence from the den compared to the other models.

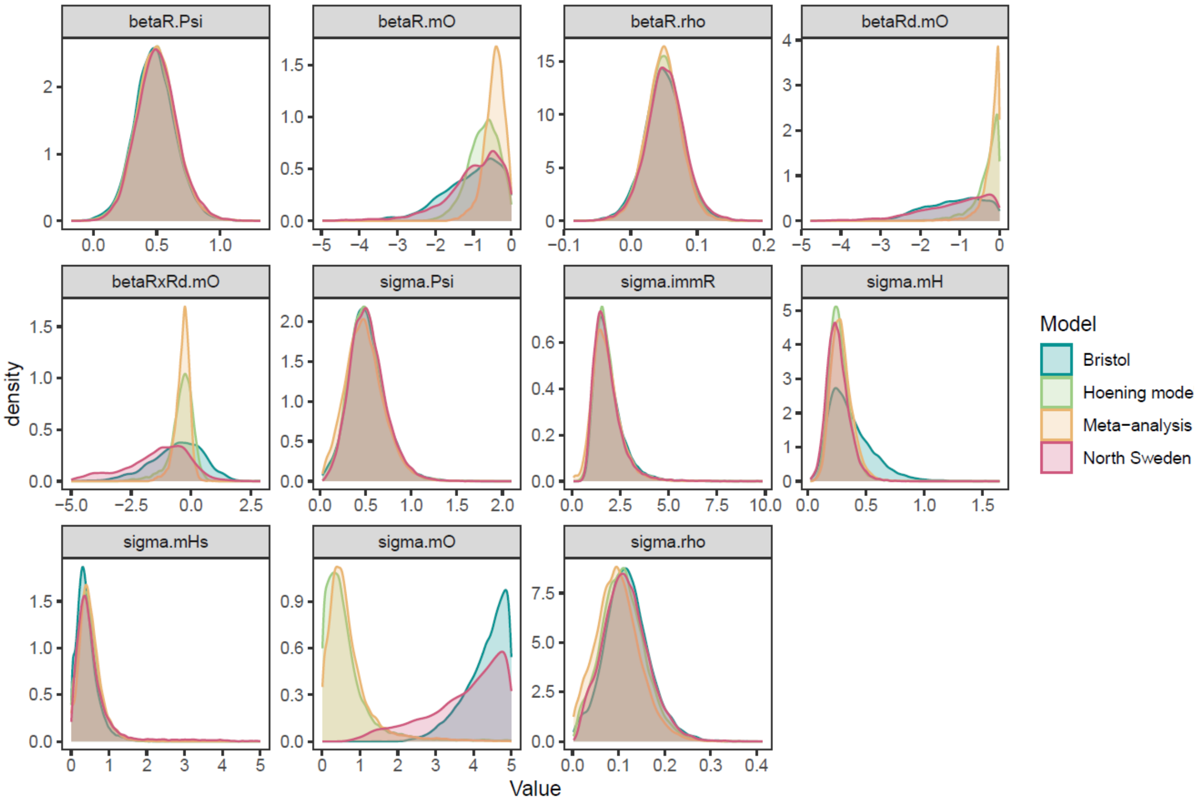


Figure S3.3: Posterior densities for parameters linked to time variation in vital rates from models employing different priors for natural mortality. The yellow model is the model presented in the main article. Graphical comparisons for other model parameters can be found in the supplementary folder “CompFinal_SurvPriors”.

S4: Testing effects of data integration

Severe lack of fit and assumption violation of integrated models can manifest as large discrepancies between parameter estimates by the integrated model and equivalent estimates from independent models. We tested for this by comparing posterior distributions of vital rate parameters from our IPM to independent models analysing only

a) data on presence/absence of placental scars/embryos (estimating pregnancy rates)
b) data on number of placental scars/embryos (estimating litter sizes in utero)
c) data on opportunistic pup counts on dens (estimating average numbers of pups on dens)
d) data on immigration status (estimating immigration rates)

In addition, we also compared estimates of natural mortality from the IPM to the naïve informative priors we used.

Overall, data integration did not affect the estimation of parameters informed by placental scar/embryo data and genetic data on immigration status (Figures S4.1 & S4.2). Integration did, however, lead to substantial updating of the natural mortality priors, with an increase in precision for the youngest age class, and an increase in precision and shift towards lower values for age classes 2, 3, and 5 (Figure S4.1). This is what we would expect given that the priors were built using data from both harvested and non-harvested populations and were thus likely to be overestimates for natural mortality only. Estimates of time-variation in and covariate effects on immigration rates and natural mortality were emergent properties of the model, and this is illustrated by the contrast between IPM estimates and independent model posteriors, which reflect the non- (or weakly) informative priors (Figure S4.2). Posterior distributions of average litter sizes clearly illustrated the benefits of data integration, as the independent model for opportunistic data clearly reflected both the large uncertainty and complete absence of information in some years inherent to these data (Figure S4.3).

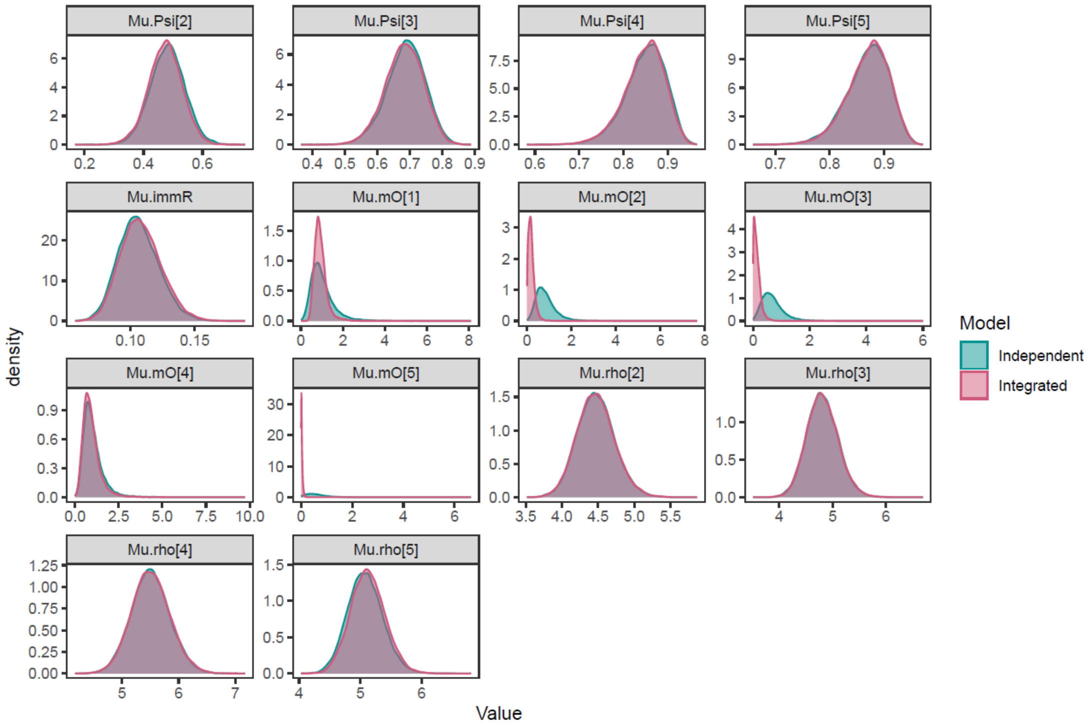


Figure S4.1: Posterior densities for (age-specific) vital rate averages from the IPM (red) and from equivalent but independent data models (blue).

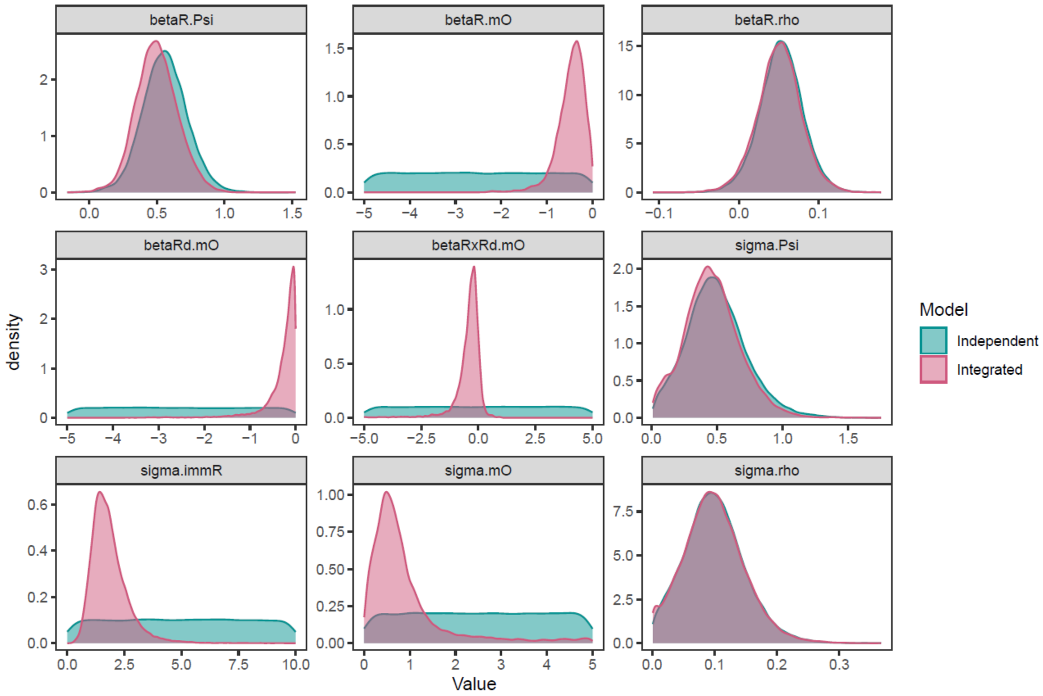


Figure S4.2: Posterior densities for parameters linked to variation in vital rates from the IPM (red) and from equivalent but independent data models (blue).

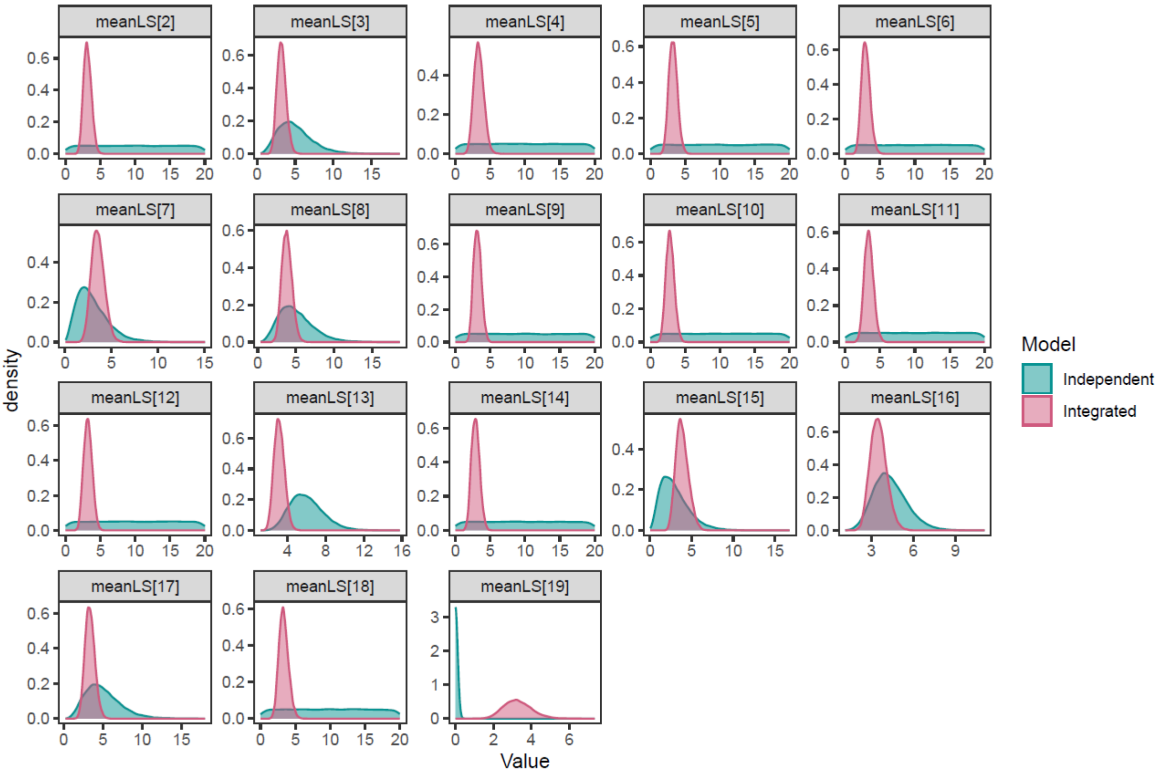


Figure S4.3: Posterior densities for time-dependent average number of pups on dens from the IPM (red) and from equivalent but independent data models (blue).

S5: Transient Life Table Response Experiment

Transient Life Table Response Experiments (tLTREs, Koons et al., 2016, 2017) are methods to quantify the relative importance of different demographic processes to changes in realized population growth rates. There are several different LTRE implementations and we used two in this study: the random design and the fixed design.

In a random design LTRE, variance in realized population growth rates (λ_t) across all years in the study period is partitioned into variance in different vital rates and population structure such that the contribution of each parameter θ_i is defined as:

$$Contribution_{\theta_i}^{var(\lambda_t)} \approx \sum_j cov(\theta_{i,t}, \theta_{j,t}) \frac{\delta\lambda_t}{\delta\theta_{i,t}} \frac{\delta\lambda_t}{\delta\theta_{j,t}} \bigg|_{\overline{\theta}}$$

Here, $cov(\theta_{i,t}, \theta_{j,t})$ is the variance covariance matrix of parameters i and j and $\frac{\delta\lambda_t}{\delta\theta_{i,t}}$ is the sensitivity of λ_t with respect to $\theta_{i,t}$ evaluated at the time-average value of θ_i (see SI S5).

The approach a the fixed-design LTRE is related but focuses on the difference in population growth rate in two distinct years – here denoted t and $t + 1$. Contributions are defined as:

$$Contribution_{\theta_i}^{\Delta\lambda_t} \approx (\theta_{i,t+1} - \theta_{i,t}) \frac{\delta\lambda_t}{\delta\theta_{i,t}} \bigg|_{\overline{\theta_i}}$$

Here, the sensitivity is evaluated at the mean value of the parameter in years t and $t + 1$ and multiplied with the difference. We implemented the fixed-design LTRE for all pairs of subsequent years within the study period.

Performing transient LTRE analyses requires derivation of transient sensitivities for all vital rates and population structure components. In matrix notation, the age-structured population model for red foxes can be expressed as:

$$\begin{bmatrix} N_{1,t+1} \\ N_{2,t+1} \\ N_{3,t+1} \\ N_{4,t+1} \\ N_{5,t+1} \end{bmatrix} = \begin{bmatrix} (1 + immR_t)Ss_{1,t}S_{1,t}\mathrm{F}_{2,t+1} & Ss_{2,t}S_{2,t}\mathrm{F}_{3,t+1} & Ss_{3,t}S_{3,t}\mathrm{F}_{4,t+1} & Ss_{4,t}S_{4,t}\mathrm{F}_{5,t+1} & Ss_{5,t}S_{5,t}\mathrm{F}_{5,t+1} \\ (1 + immR_t)Ss_{1,t}S_{1,t} & 0 & 0 & 0 & 0 \\ 0 & Ss_{2,t}S_{2,t} & 0 & 0 & 0 \\ 0 & 0 & Ss_{3,t}S_{3,t} & 0 & 0 \\ 0 & 0 & 0 & Ss_{4,t}S_{4,t} & Ss_{5,t}S_{5,t} \end{bmatrix} \times \begin{bmatrix} N_{1,t} \\ N_{2,t} \\ N_{3,t} \\ N_{4,t} \\ N_{5,t} \end{bmatrix}$$

The parameters are defined as follows:

$N_{a,t}$ = number of age class a individuals present in year t.

$immR_t$ = Immigration rate in year t.

$Ss_{a,t}$ = Summer survival (Jul-Sep) of age class a individuals in year t.
$Ss_{a,t} = \exp(-mHs_{a,t})$ where mHs = summer harvest mortality hazard rate.

$S_{a,t}$ = Annual survival (Oct-Jun) of age class a individuals from year t to $t + 1$.
$S_{a,t} = \exp(-(mH_{a,t} + mO_{a,t}))$ where mH = winter harvest mortality hazard rate and mO = natural mortality hazard rate.

$\mathrm{F}_{a,t} =$ Reproductive output of age class a individuals in year t.
$F_{a,t} = 0.5\Psi_{a,t}\rho_{a,t}S_{0,t}$ where Ψ = pregnancy rate, ρ = fetus number, and S_0 = survival from birth to den emergence (corresponding mortality hazard rate: m_0).

The realized growth rate from year t to $t+1$ (λ_t) is defined as $sum(N_{1:5,t+1})/sum(N_{1:5,t})$. If we define the population proportions in each age class, $n_{a,t}$, as $N_{a,t}/sum(N_{1:5,t})$, then:

$$\lambda_t = n_{1,t}(1 + immR_t)Ss_{1,t}S_{1,t}\left(1 + \mathrm{F}_{2,t+1}\right) + n_{2,t}Ss_{2,t}S_{2,t}\left(1 + \mathrm{F}_{3,t+1}\right) + n_{3,t}Ss_{3,t}S_{3,t}\left(1 + \mathrm{F}_{4,t+1}\right) + n_{4,t}Ss_{4,t}S_{4,t}\left(1 + \mathrm{F}_{5,t+1}\right) + n_{5,t}Ss_{5,t}S_{5,t}(1 + \mathrm{F}_{5,t+1})$$

The sensitivity of λ_t to changes in any parameter θ is then calculated as the derivative of λ_t with respect to θ, $\frac{\delta\lambda_t}{\delta\theta_t}$ (Caswell, 2001). In the following, we present the derivatives (sensitivity formulas) for all parameters as used in our LTRE analyses. Figures S5.1, S5.2, and S5.3 visualize the transient sensitivities and elasticities ($\frac{\theta_t}{\lambda_t}\frac{\delta\lambda_t}{\delta\theta_t}$) evaluated at the average over all years.

Annual survival

$$\frac{\delta\lambda_t}{\delta S_{1,t}} = n_{1,t} * (1 + immR_t) * Ss_{1,t} * \left(1 + \Psi_{2,t+1} * 0.5 * \rho_{2,t+1} * S_{0,t+1}\right)$$

$$\frac{\delta\lambda_t}{\delta S_{a,t}} = n_{a,t} * Ss_{a,t} * \left(1 + \Psi_{a+1,t+1} * 0.5 * \rho_{a+1,t+1} * S_{0,t+1}\right) for\ a > 1$$

Winter harvest mortality & natural mortality

$$\frac{\delta\lambda_t}{\delta mH_{a,t}} = \frac{\delta\lambda_t}{\delta mO_{a,t}} = -\exp\left(-\left(mH_{a,t} + mO_{a,t}\right)\right) * \frac{\delta\lambda_t}{\delta S_{a,t}}$$

Summer survival

$$\frac{\delta\lambda_t}{\delta Ss_{1,t}} = n_{1,t} * (1 + immR_t) * S_{1,t} * \left(1 + \Psi_{2,t+1} * 0.5 * \rho_{2,t+1} * S_{0,t+1}\right)$$

$$\frac{\delta\lambda_t}{\delta Ss_{a,t}} = n_{a,t} * S_{a,t} * \left(1 + \Psi_{a+1,t+1} * 0.5 * \rho_{a+1,t+1} * S_{0,t+1}\right) for\ a > 1$$

Summer harvest mortality

$$\frac{\delta\lambda_t}{\delta mHs_{a,t}} = -\exp\left(-mHs_{a,t}\right) * \frac{\delta\lambda_t}{\delta S_{a,t}}$$

Pregnancy rate

$$\frac{\delta\lambda_t}{\delta\Psi_{1,t+1}} = 0$$

$$\frac{\delta\lambda_t}{\delta\Psi_{2,t}+1} = n_{1,t} * (1 + immR_t) * Ss_{1,t} * S_{1,t} * 0.5 * \rho_{2,t+1} * S_{0,t+1}$$

$$\frac{\delta\lambda_t}{\delta\Psi_{a,t}+1} = n_{a-1,t} * Ss_{a-1,t} * S_{a-1,t} * 0.5 * \rho_{a,t+1} * S_{0,t+1} \quad for\ 2 < a > 5$$

$$\frac{\delta\lambda_t}{\delta\Psi_{5,t}+1} = (n_{4,t} * Ss_{4,t} * S_{4,t} + n_{5,t} * Ss_{5,t} * S_{5,t}) * 0.5 * \rho_{5,t+1} * S_{0,t+1}$$

Fetus number

$$\frac{\delta\lambda_t}{\delta\rho_{1,t+1}} = 0$$

$$\frac{\delta\lambda_t}{\delta\rho_{2,t}+1} = n_{1,t} * (1 + immR_t) * Ss_{1,t} * S_{1,t} * 0.5 * \Psi_{2,t+1} * S_{0,t+1}$$

$$\frac{\delta\lambda_t}{\delta\rho_{a,t}+1} = n_{a-1,t} * Ss_{a-1,t} * S_{a-1,t} * 0.5 * \Psi_{a,t+1} * S_{0,t+1} \quad for\ 2 < a > 5$$

$$\frac{\delta\lambda_t}{\delta\rho_{5,t}+1} = (n_{4,t} * Ss_{4,t} * S_{4,t} + n_{5,t} * Ss_{5,t} * S_{5,t}) * 0.5 * \Psi_{5,t+1} * S_{0,t+1}$$

Survival to emergence from den

$$\frac{\delta\lambda_t}{\delta S_{0,t+1}} = n_{1,t} * (1 + immR_t) * Ss_{1,t} * S_{1,t} * \Psi_{2,t+1} * 0.5 * \rho_{2,t+1} + sum\big(n_{2:4,t} * Ss_{2:4,t} * S_{2:4,t} * \Psi_{3:5,t+1} * 0.5 * \rho_{3:5,t+1}\big) + n_{5,t} * Ss_{5,t} * S_{5,t} * \Psi_{5,t+1} * 0.5 * \rho_{5,t+1}$$

Mortality hazard rate to emergence from den

$$\frac{\delta\lambda_t}{\delta m_{0,t+1}} = -\exp(-m_{0,t+1}) \frac{\delta\lambda_t}{\delta S_{0,t+1}}$$

Immigration rate

$$\frac{\delta\lambda_t}{\delta immR_t} = n_{1,t} * (1 + immR_t) * Ss_{1,t} * S_{1,t} * \big(1 + \Psi_{2,t+1} * 0.5 * \rho_{2,t+1} * S_{0,t+1}\big)$$

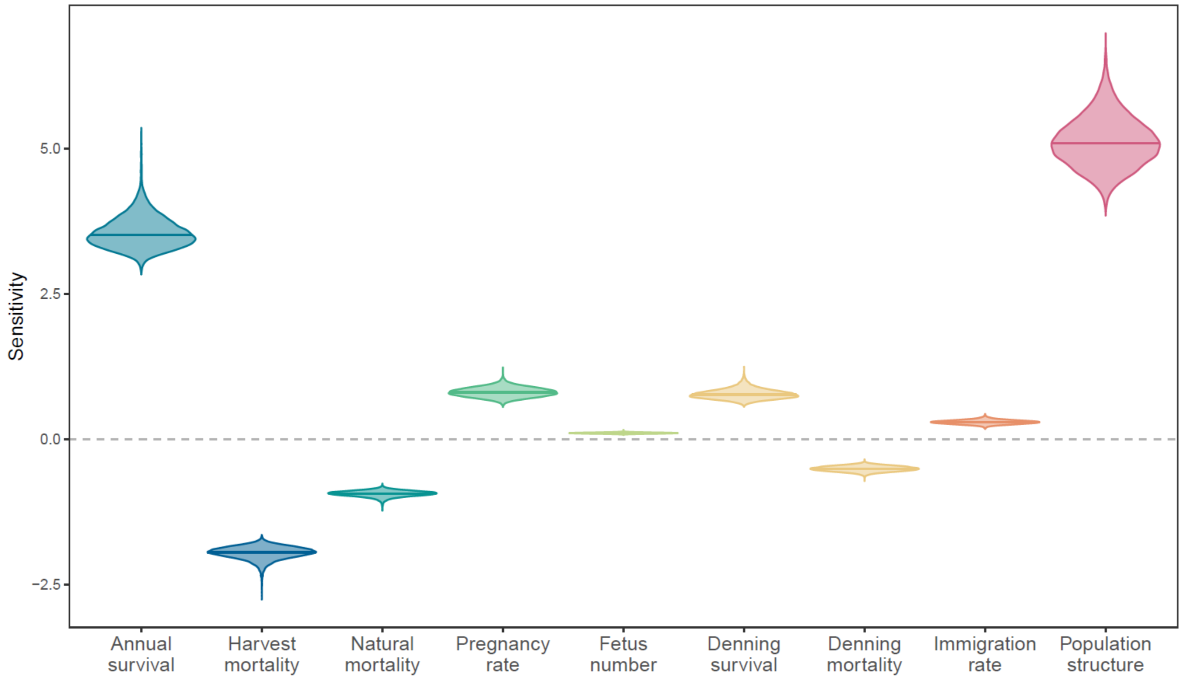
Population proportions per age class

$$\frac{\delta\lambda_t}{\delta n_{1,t}} = (1 + immR_t) * Ss_{1,t} * S_{1,t} * \big(1 + \Psi_{2,t+1} * 0.5 * \rho_{2,t+1} * S_{0,t+1}\big)$$

$$\frac{\delta\lambda_t}{\delta n_{a,t}} = Ss_{a,t} * S_{a,t} * \big(1 + \Psi_{a+1,t+1} * 0.5 * \rho_{a+1,t+1} * S_{0,t+1}\big) \quad for\ 1 > a < 5$$

$$\frac{\delta\lambda_t}{\delta n_{5,t}} = Ss_{5,t} * S_{5,t} * \big(1 + \Psi_{5,t+1} * 0.5 * \rho_{5,t+1} * S_{0,t+1}\big)$$

A) Sensitivities



B) Elasticities

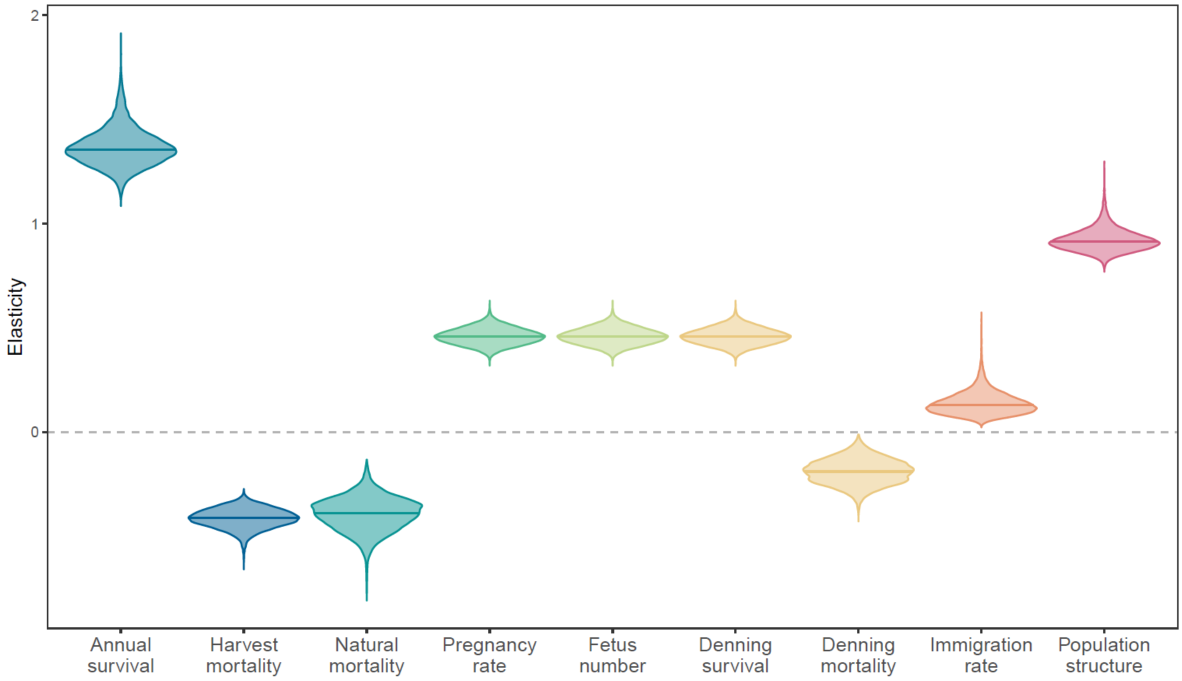


Figure S5.1: Posterior distributions of sensitivities (A) and elasticities (B) of population growth rate between 2005-2006 and 2020-2021 with respect to different demographic rates and population structure. Violins visualize distributions, solid lines mark posterior medians. Harvest mortality encompasses both summer and winter harvest, and all components are summed across age classes.

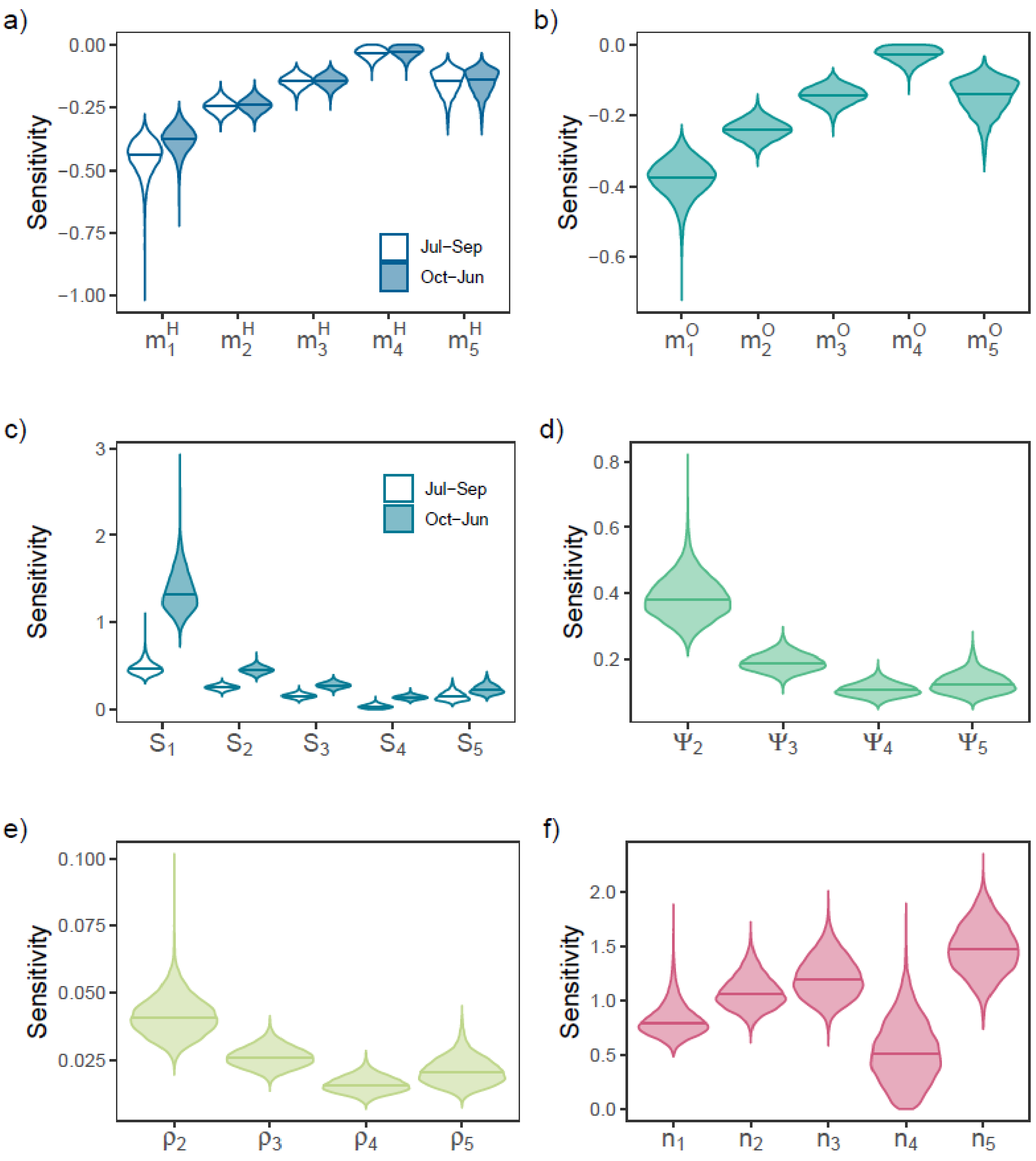


Figure S5.2: Posterior distributions of sensitivities of population growth rate between 2005-2006 and 2020-2021 with respect to different age-specific demographic rates and population proportions. Violins visualize distributions, solid lines mark posterior medians.

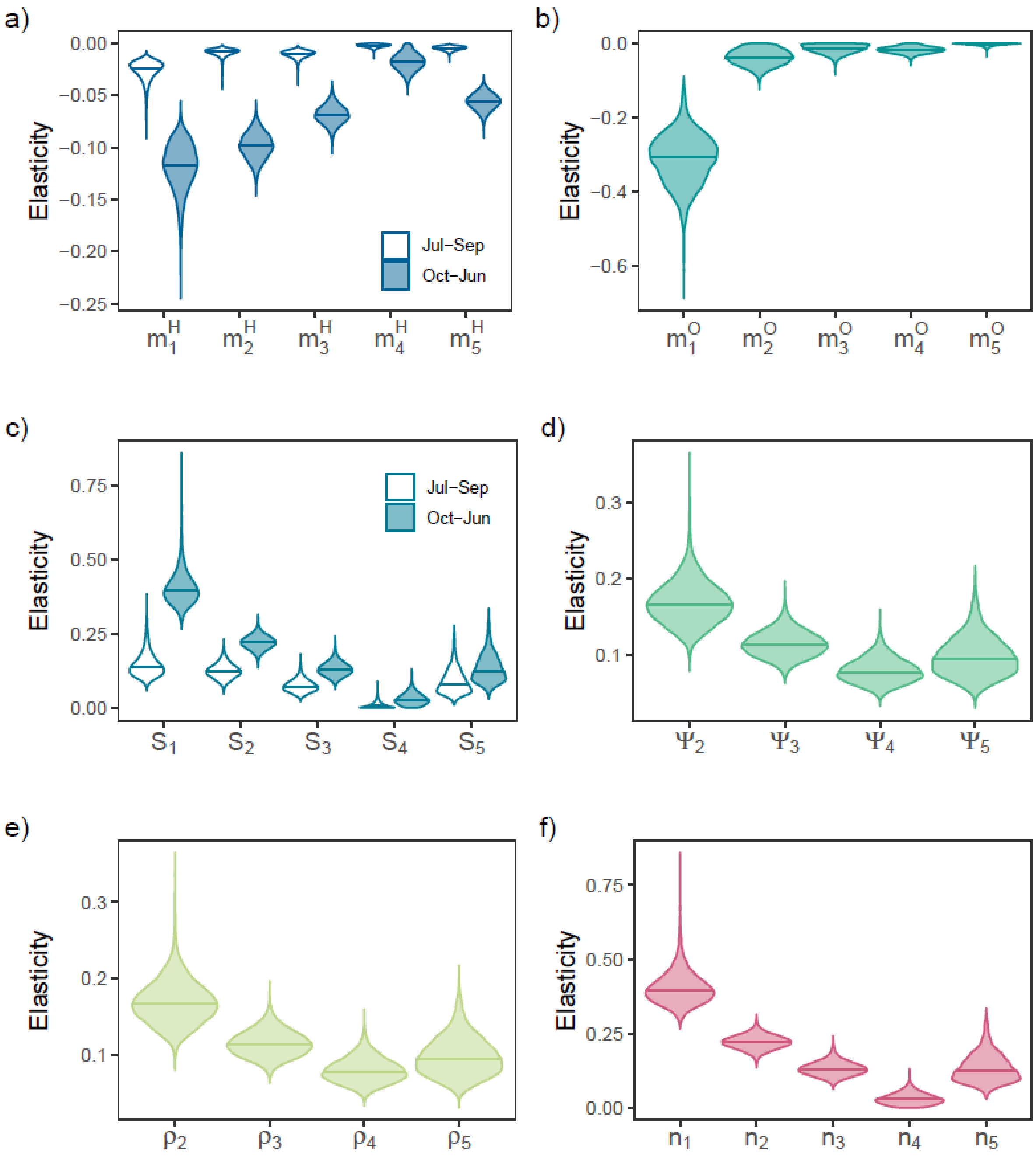


Figure S5.3: Posterior distributions of elasticities of population growth rate between 2005-2006 and 2020-2021 with respect to different age-specific demographic rates and population proportions. Violins visualize distributions, solid lines mark posterior medians.