Contributions from terrestrial and marine resources stabilize predator populations in a rapidly changing climate

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Abstract. Climate change has different and sometimes divergent effects on terrestrial and marine food webs, and in coastal ecosystems, these effects are tightly interlinked. Responses of opportunistic coastal predators and scavengers to climate change may thus be complex and potentially highly flexible, and can simultaneously serve as indicators of, and have profound impacts on, lower trophic levels. Gaining mechanistic understanding of these responses is therefore important, but often not feasible due to lack of long-term data from marked individuals. Here, we used a Bayesian integrated population model (IPM) to elucidate the effects of arctic warming and concurrent changes in terrestrial and marine resource availability on population dynamics of the opportunistic arctic fox (*Vulpes lagopus*) in Svalbard. Joint analysis of four types of data (den survey, age-at-harvest, placental scars, mark-recovery) revealed relatively stable population size and age structure over the last 22 yr (1997–2019) despite rapid environmental change linked to climate warming. This was related to the fact that terrestrial resources (reindeer carcasses, geese) became more abundant while the availability of marine resources (seal pups/carrion) decreased, and was driven by divergent trends in different vital rates (e.g., increased pregnancy rate but decreased pup survival). Balanced contributions of survival vs. reproduction and of immigration vs. local demography further stabilized population size. Our study thus sheds light on the mechanisms underlying population dynamics of opportunistic carnivores exploiting terrestrial and marine resources and suggests that exploitation of resources across different ecosystems can buffer predators against climate change. Additionally, it highlights the large potential of IPMs as tools to understand and predict the effects of environmental change on wildlife populations, even when data on marked individuals are sparse.

Key words: arctic fox; cause-specific mortality; demography; harvest; immigration; integrated population model; marine resources; population dynamics; sea ice; terrestrial resources; transient life table response experiment.

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INTRODUCTION

The Arctic is currently warming at a rate twice the global average (Serreze and Barry 2011, IPCC 2018), with profound consequences for the functioning of ecosystems (Post et al. 2009, 2013, Hansen et al. 2013, Ims et al. 2013). The impacts of such rapid warming may, however, be expressed very differently in terrestrial and marine ecosystems. While loss of sea ice threatens ice-dependent marine food webs (Kovacs et al. 2011, Post et al. 2013), warming-induced increase

in terrestrial primary productivity (e.g., arctic greening) may boost higher trophic levels in tundra food webs (Legagneux et al. 2014, Le Moullec et al. 2019). Much of the arctic tundra biome borders directly on the coast of the Arctic Ocean and thus includes seasonally sea ice-covered marine habitats (Post et al. 2009, Ims et al. 2013). With such an extensive contact zone between the marine and terrestrial ecosystems, climate change impacts in either are closely and intricately linked to changes in the other. Assessing the potential impacts of climate change on arctic ecosystems therefore requires not only predicting its potentially diverging effects on marine and terrestrial food webs, but also understanding how these effects are interlinked.

Coastal ecosystems around the world are inhabited by a variety of opportunistic predators and scavengers that exploit both marine and terrestrial resources and thereby constitute a link between both ecosystems (Rose and Polis 1998, Moore 2002, Carlton and Hodder 2003, Mellbrand et al. 2011). The Arctic is no exception, and many arctic mammal species, from small rodents to iconic apex predators such as the polar bear (*Ursus maritimus*), fall into this category (Prop et al. 2015). As a consequence of their varied diet spanning across sea and land, these opportunistic predators may show more complex, and possibly also more flexible, responses to climate change than specialist predators and/or predators that are strictly limited to a single food web (Moore 2002, Moritz and Agudo 2013, Pereira et al. 2014). Apex predators in particular have also been suggested as sentinels of ecosystem impacts of climate warming, as their responses may reflect bottom-up changes in food webs (Moore 2002, Sergio et al. 2008, Hazen et al. 2019). Following these responses, population-level changes in apex predators may then, in turn, exert strong top-down controls on lower trophic levels (Estes et al. 2011). Understanding the impacts of climate warming on populations of generalist apex predators is therefore a challenging but important step toward assessing the large-scale consequences for intertwined marine and terrestrial ecosystems (Ehrich et al. 2015).

Climate change-induced alterations in environmental conditions affect the dynamics of populations via vital rates (i.e., survival and reproduction) of individuals (Caswell 2001,

Jenouvrier et al. 2012, Nater et al. 2018). Assessing the impacts of environmental changes thus requires a mechanistic understanding of how changes in resource availability affect vital rates and of how variation in vital rates, in turn, translates into population-level patterns (Williams et al. 2002, Lawson et al. 2015). Such knowledge can be obtained from structured demographic models (Caswell 2001), but hinges on the availability of long-term individual-based data (Clutton-Brock and Sheldon 2010). Collecting the necessary data on marked individuals for periods long enough to allow studying impacts of environmental change is costly and challenging. This is particularly pertinent for longer-lived species that are highly mobile and difficult to capture (such as many apex predators). Data limitations have consequently precluded detailed demographic analyses for such species in many cases. However, integrated population models (IPMs) (Schaub and Abadi 2011), which have recently been adopted from fisheries sciences into wildlife ecology (Maunder and Punt 2013), now offer new opportunities: joint analysis of multiple types of data allows efficient use of sparse data, increased precision in estimation of vital rates and their relationships with environmental variables, and quantification of processes for which data collection is particularly challenging, such as immigration (Abadi et al. 2010, Lee et al. 2015, Plard et al. 2019).

Here, we capitalize on the benefits of integrated data analysis to estimate vital rates, model population dynamics, and assess the roles of marine and terrestrial resources for a generalist apex predator and scavenger, the arctic fox (*Vulpes lagopus*). As the only endemic terrestrial mammalian predator in the Arctic, the arctic fox is well adapted to the wide variety of ecological settings found in different tundra biomes around the North Pole (Fuglei and Ims 2008). In high-arctic and insular arctic food webs, it exploits both terrestrial and marine resources (Roth 2003, Ehrich et al. 2015) and may therefore be affected by climate change through cascades in both food webs (Post et al. 2009, 2013). On the high-arctic Svalbard Archipelago, one of the fastest-warming locations on Earth (warming with an increase in annual ambient temperature of 3–5°C over the last 50 yr, Nordli et al. 2020), rapidly increasing temperatures are causing drastic

changes in both the marine and the terrestrial ecosystems (Descamps et al. 2017). Spring sea ice in the fjords on the west coast of Svalbard provides arctic foxes with access to marine mammal prey and carrion (Lydersen and Gjertz 1986, Hamilton et al. 2017). While sea ice used to be extensive until 2005–2006, it has been largely absent since (Isaksen et al. 2016, Muckenhuber et al. 2016, Dahlke et al. 2020). The availability of sea ice-based marine resources for arctic foxes has thus been declining. However, the opposite appears to be true for their most important terrestrial food resources: Svalbard reindeer (*Rangifer tarandus platyrhynchus*), pink-footed goose (*Anser brachyrhynchus*), and Svalbard rock ptarmigan (*Lagopus muta hyperborea*) have all been increasing in numbers over the last decades (Le Moullec et al. 2019, Fuglei et al. 2020, Johnson et al. 2020).

In this study, we aim to elucidate how the arctic fox population on the west coast of Svalbard has responded to the profound changes in marine and terrestrial ecosystems over the last two decades (1997–2019). For this purpose, we jointly analyzed several types of population monitoring data, each of which is unable to provide mechanistic insights when analyzed on its own: (1) den survey data, (2) age-at-harvest data, (3) reproductive data from placental scars of harvested individuals, and (4) sparse mark-recovery data available for only a few years within the study period. The resulting IPM not only allowed us to estimate changes in population size and age structure over the course of 22 yr, but also shed light on which demographic rates have been driving population dynamics. Finally, the analysis also provided new insights into how changes in marine and terrestrial resource availability may have contributed to changing demographic rates and patterns in population dynamics.

METHODS

Study area

Svalbard is a high-arctic archipelago in the Barents Sea situated between the North Pole and the mainland of Norway (74–81° N, 15–30° E). Due to the relatively low productivity of the high-Arctic tundra and its isolated geographic position, Svalbard harbors not only one of the northernmost but also structurally simplest terrestrial food webs of the world (Ims et al. 2013, Descamps et al. 2017). Key herbivores are two resident species, the Svalbard rock ptarmigan and the Svalbard reindeer, and three migratory Arctic breeding geese, the pink-footed goose, barnacle goose (*Branta leucopsis*), and brent goose (*Branta bernicla*, Descamps et al. 2017). Except for a very small, spatially restricted introduced population of sibling voles (*Microtus levis*), there are no small rodents in Svalbard (Henttonen et al. 2001). The predator/scavenger guild consists of two resident species, the arctic fox and the polar bear, and the migratory glaucous gull (*Larus hyperboreus*). In summer, migratory passerines, shorebirds, and sea birds contribute to the variety of prey (Descamps et al. 2017).

The study area (~900 km²) is located in the northeastern part of Nordenskiöld Land penninsula on central Spitsbergen, the largest island of the Svalbard archipelago. It encompasses the shoreline of Isfjorden and consists mainly of two large U-shaped broad valleys, Adventdalen and Sassendalen, surrounded by peaks reaching 1200 m (Appendix S1: Fig. S1). The landscape is mountainous and moderately glaciated, and situated in the middle Arctic tundra zone with no erect shrubs (Raynolds et al. 2019).

Study species

The arctic fox is the only endemic terrestrial mammalian predator with a circumpolar distribution in the tundra biome (Dalén et al. 2004). This widespread, highly flexible top predator lives in many different ecosystems and food web contexts (Ehrich et al. 2015). Some populations rely heavily on small rodents and lemmings, while others—often those with access to coastal areas—consist of generalists exploiting a variety of terrestrial and marine resources. This variation in diet is linked to substantial differences in life history and demography within the species (Braestrup 1941, Tannerfeldt and Angerbjörn 1998). In Svalbard, arctic foxes are abundant generalists and functionally important apex predators and scavengers with no natural enemies or competitors. They rely heavily on food resources from both the terrestrial (reindeer carcasses, tundra birds) and the marine (seal pups/carrion, sea birds) ecosystems (Prestrud 1992, Eide et al. 2005). Although cyclic rodent prey is lacking in Svalbard, arctic foxes do

show year-to-year variation in population size, which has previously been linked to availability of reindeer carcasses (Fuglei et al. 2003, Eide et al. 2012, Hansen et al. 2013).

Data collection

Den survey data.—The breeding population of arctic foxes in the study area has been monitored annually between 1997 and 2019 by surveying 23 potential breeding dens spread across the study area (Appendix S1: Table S1). Dens were visited in late June to early August, and breeding activity—defined as the presence of alive and/or dead pups—was determined using two methods. From 1997 to 2013, we monitored dens using binoculars/telescopes from a distance of approximately 150–200 m (see Eide et al. 2012 for more details). From 2014 onwards, we used automatic cameras on dens in addition to the manual binocular/telescope method. We mounted automatic cameras (Reconyx PC800; Reconyx, Holmen, Wisconsin, USA) on poles approximately 2–8 m from den entrances for a period of 1–30 d. The camera was programmed on a motion sensor at high sensitivity to take five pictures for each trigger (Ehrich et al. 2017). Based on pup observations, both the number of occupied dens (den with documented breeding) and litter size (the minimum number of pups observed at the same time by use of binocular/telescope or seen on pictures from automatic cameras) were registered.

Mark-recovery data.—We captured and individually marked 142 arctic foxes in the study area between 1997 and 2003. Pups ($n = 111$) were trapped by rushing the den or through the use of baited Tomahawk live cage traps (Tomahawk, Hazelhurst, Wisconsin, USA) at known den sites in July/August and along the shoreline from August to October. Adults ($n = 31$) were mostly trapped using either a net that released using a remote control device, or a snare system consisting of a spring-mounted plastic-coated foot snare mounted on a modified padded leg-hold trap system (Victor No. 1 Soft-Catch; see Eide et al. 2004 for details). All foxes were marked using ear tags with a unique color combination and number. Four marked foxes were recaptured alive within the study area in a later year, and 34 were reported dead after having been trapped during the hunting season as part of the legal harvest (see section "Harvest data"). Here, we analyzed capture

histories from all 142 marked individuals (72 females, 69 males, one individual of unknown sex; see also Appendix S1: Table S1). In line with results from other studies (Samelius and Alisauskas 2017, Chevallier et al. 2020), we therefore assumed that there were no sex differences in survival (and by extension, harvest, and natural mortality).

Harvest data.—Restricted harvesting of arctic foxes is permitted by the Governor of Svalbard and regulated by the Svalbard Environmental Protection Act (https://www.sysselmannen.no/en/hunting-trapping-and-fishing/). Since 1997, arctic fox harvest has required both a hunting license and reporting of trapping effort (number of traps and number of days trapping) and the number of trapped foxes. The trapping season for arctic foxes lasts from 1 November to 15 March. Following the 2008–2009 trapping season, both the number of trapping areas (licenses) and the number of traps per trapping area became more tightly restricted. All trappers were asked to deliver the skinned carcasses of harvested foxes for scientific purposes. The Norwegian Polar Institute then collected and conducted a necropsy of each carcass at the Norwegian Veterinary Institute in Tromsø, Norway. Carcass necropsy allowed extracting individual-level information on sex, age, and size of the previous litter for females. Age was estimated at the Norwegian Institute of Nature Research, Trondheim, Norway, by cementum annuli aging of lower canine teeth (Grue and Jensen 1976, Bradley et al. 1981). Foxes in their first year of life were denoted as age 0. The size of the previous litter (breeding season prior to harvest) was determined by counting the number of dark placental scars in each female's uterus. Notably, this method may overestimate the litter size at birth as it cannot account for intrauterine mortality, and because scars from earlier pregnancies may sometimes be difficult to distinguish from those from the latest pregnancy (Macpherson 1969, Englund 1970, Lindström 1981, Allen 1983).

Over the 22 harvest seasons between 1997 and 2019, a total of 670 arctic fox carcasses were obtained from the study area in Adventdalen and Sassendalen. Of these, 243 were confirmed females that had been aged, and we used these data for estimating local population size and age structure (age-at-harvest data). For analyses of reproductive parameters, we used data on

placental scars from a total of 898 aged females that had been trapped either in the study area, or elsewhere on Svalbard in the same harvest season (Appendix S1: Table S1).

Environmental data.—We considered three different annual environmental covariates as potential drivers of temporal variation in vital rates: sea ice extent, reindeer carcass availability, and goose reproduction. Below, we describe the expected relationships and data collection for each covariate.

Sea ice extent.—Sea ice is important for arctic foxes both as hunting grounds and as a platform for dispersal (Lai et al. 2017, Fuglei and Tarroux 2019). Svalbard arctic foxes hunt seal pups on the sea ice in spring (Lydersen and Gjertz 1986), and foxes may follow polar bears on the sea ice to scavenge on their seal kills (Hiruki and Stirling 1989). The resulting marine input into the foxes' diet can be considerable, as shown by stable isotope analysis (Ehrich et al. 2015). Up until 2005, spring sea ice coverage has been extensive in many fjords in Svalbard. However, due to increases in water temperature the fjords have been mostly ice-free in recent years (Isaksen et al. 2016, Muckenhuber et al. 2016, Dahlke et al. 2020). This decline in fjord sea ice itself, but also the responsible climate warming more generally, may affect the availability of marine resources for arctic foxes and thus affect their vital rates. The study area borders Isfjorden, Central Spitsbergen, which consists of several fjord arms. The Norwegian Ice Service (NIS) routinely produces daily ice charts for this area using remote sensing digital imagery (Dahlke et al. 2020). They categorize sea ice into six classes with concentrations ranging from 0–10% (open water) to 100% (fast ice). For the present analyses, we defined the annual sea ice extent as the mean of all daily 90% sea ice concentrations (very close drift ice) over the period from 1 January to 30 June (Appendix S1: Fig. S1).

Reindeer carcasses.—The endemic Svalbard reindeer is the only resident large herbivore in Svalbard. The reindeer population has doubled since the 1980s and is currently estimated to be around 22,000 individuals (Le Moullec et al. 2019). Reindeer carcasses play an important role in the winter diet of the arctic fox (Prestrud 1992). A positive relationship between the number of carcasses available on the tundra in winter and arctic fox reproduction has previously been established (Eide et al. 2012). Reindeer carcasses are counted annually as part of a structural population census of reindeer in Adventdalen. The carcasses were easily spotted in the terrain by eye or using binoculars (10 × 42), and the total number was registered by five to six observers conducting the census on foot in late June/early July each year (Hansen et al. 2019). The count focused on (sub)adult individuals that perished during the previous winter, as fresh carcasses of recently born calves are rare and disappear quickly. Here, we treated the number of reindeer carcasses counted in the study area in summer as a measure of reindeer carcass availability for arctic foxes during the preceding winter/spring.

Goose reproduction.—Three seasonal migratory goose species (pink-footed goose, barnacle goose, and brent goose) arrive to the Svalbard archipelago in May, where they spend roughly four months (Madsen et al. 1999). Pink-footed geese are the most numerous, and their population has increased considerably in recent years (Madsen et al. 2017). Higher numbers and reproductive success of pink-footed geese may benefit arctic foxes—juveniles in particular—through an increase in prey availability during summer (Fuglei et al. 2003, Eide et al. 2005, McDonald et al. 2017). Adults and juveniles making up the pink-footed goose population breeding in Svalbard are counted on their wintering grounds in Denmark, the Netherlands, and Belgium between late September early November (Johnson et al. 2020). For further details on the field methods, see Heldbjerg et al. (2020). In the present study, we used the proportion of juveniles among all geese counted on the wintering grounds during autumn/winter as a proxy for goose reproductive success in the preceding summer.

Integrated population model construction

Integrated population models estimate population size and underlying demographic parameters by linking a structured model of population dynamics to several different types of observational data (Schaub and Abadi 2011, Plard et al. 2019). In the following, we describe (1) the female-based age-structured population model for arctic foxes, (2) the six likelihoods linking that model to four different types of data, and (3) the implementation of the resulting IPM in a Bayesian framework.

Age-structured population model.—We described the population dynamics of arctic foxes using a female-based age-structured population model with a post-breeding census. Females were grouped into five age classes with distinct, time-dependent survival probabilities $S_{\text{Age},t}$ (where Age = j for juveniles in their first year of life and Age = a for older individuals) and reproductive outputs $R_{\text{Age},t}$. All females aged four years or older were lumped together in the final age class (4+) as preliminary analyses indicated no substantial age differences in female reproductive parameters after four years of age, and data for older individuals were sparse. The dynamics of the female section of the population over the time interval t to $t + 1$ can be described as follows:

$$\| N_{,t+1} \| = \begin{bmatrix} S_{\text{j},t}R_{1,t+1} & S_{\text{a},t}R_{2,t+1} & S_{\text{a},t}R_{3,t+1} & S_{\text{a},t}R_{4,t+1} & S_{\text{a},t}R_{4,t+1} \\ S_{\text{j},t} & 0 & 0 & 0 & 0 \\ 0 & S_{\text{a},t} & 0 & 0 & 0 \\ 0 & 0 & S_{\text{a},t} & 0 & 0 \\ 0 & 0 & 0 & S_{\text{a},t} & S_{\text{a},t} \end{bmatrix} \begin{bmatrix} N_{0,t} \\ N_{1,t} \\ N_{2,t} \\ N_{3,t} \\ N_{4+,t} \end{bmatrix} + I_{t+1}$$

$N_{,t+1}$ represents the number of females in all age classes (hereafter "population size") in the summer of year $t + 1$ after the young of the year has appeared outside their natal dens and also includes all females that will immigrate prior to and during the following harvest season (I_{t+1}). Under the post-breeding census, local females in a given age class, $N_{\text{Age},t}$, can contribute to next year's population size by surviving and remaining in the population (probability $S_{\text{Age},t}$) and by subsequently reproducing in next year's breeding season (as females of the next age class, $R_{\text{Age}+1,t+1}$). We assumed apparent survival to differ only between juveniles (individuals in their first year of life = age class 0, index Age = j) and adults from the second year of life onwards (age classes 1 to 4+, index Age = a). Reproductive output, on the other hand, was assumed to be different for each age class. It was defined as the product of pregnancy rate Ψ, the number of fetuses ρ, and early/denning survival S_0 (= survival from conception to emergence from the den around 3–4 weeks of age). It was further multiplied by a factor 0.5 to consider only female offspring (assuming an even sex ratio):

$$R_{\text{Age},t} = 0.5\Psi_{\text{Age},t}\rho_{\text{Age},t}S_{0,t}$$

Since the numbers of individuals in our study area are relatively small, we built the population model to take full account of demographic stochasticity (randomness in outcomes of survival and reproduction at the individual level; see Caswell 2001). To do so, we treated the numbers of individuals surviving, survivors reproducing, offspring produced, and immigrants entering the study area as outcomes of stochastic binomial and Poisson processes (see model code ArcticFox_IPM.R in Data S1 for details).

Data likelihoods.—The parameters of the population model were estimated through the integrated analysis of four different types of data: age-at-harvest data, mark-recovery data, reproduction data obtained from placental scar counts of harvested foxes, and den survey data (see Appendix S1: Table S1 for a summary of sample sizes). Each type of observation was linked to the relevant model parameters (vital rates, population sizes) through a specific data likelihood as described in the following and depicted in Fig. 1.

Age-structured harvest data are the outcome of both population dynamics and a sampling process (reported harvest) and can be modeled using a state-space framework (Conn et al. 2008). Specifically, we described the number of female foxes of each age class reported as harvested within the study area during the time interval t to $t + 1$ ($C_{\text{Age},t}$) as

$$C_{\text{Age},t} \sim \text{Binomial}(N_{\text{Age},t}, h_{\text{Age},t}p_t^{\text{AS}}p_t^{\text{L}})$$

Here, $N_{\text{Age},t}$ is the total number of females in a given age class in the population at time t. The product $h_{\text{Age},t}p_t^{\text{AS}}p_t^{\text{L}}$ represents the probability of any of those females to become part of the age-at-harvest matrix $\mathbf{C}$. In our case, inclusion in $\mathbf{C}$ required that an individual was harvested during the relevant time interval (probability $h_{\text{Age},t}$) and that sufficient information was available to place its carcass in the age-at-harvest matrix. The latter was only possible if age and sex (probability p_t^{AS}), as well as harvest location (probability p_t^{L}), could be determined. The harvest rate $h_{\text{Age},t}$ is estimated by the model. p_t^{AS} and p_t^{L}, on the other hand, were calculated a priori as the annual proportions of individuals harvested in the study area for which information on both age
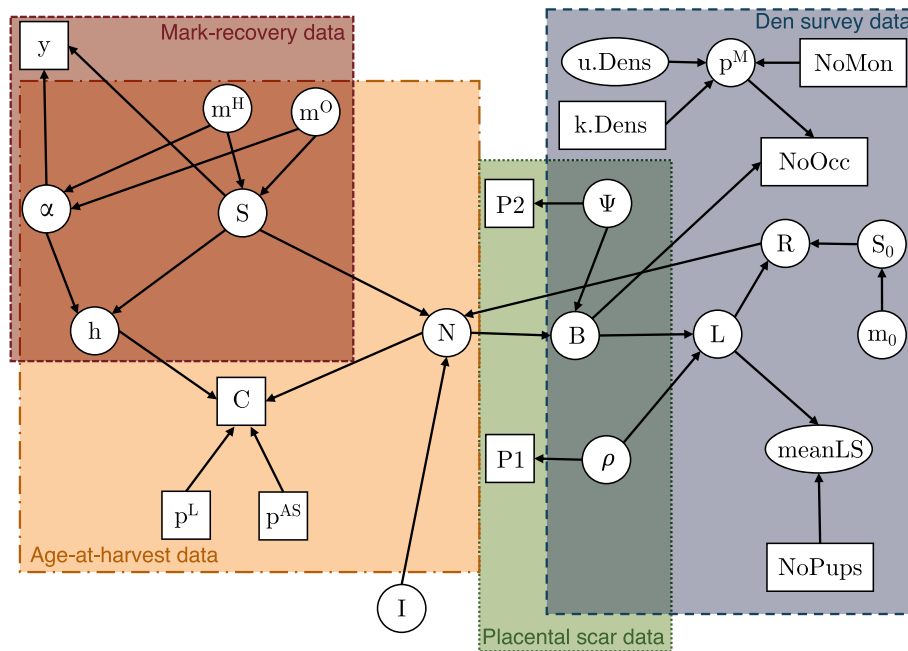
Fig. 1. Structure of the arctic fox integrated population model represented as a simplified DAG (directed acyclic graph). Hyperparameters, priors, and age/time indices are omitted for improved legibility. Small squares represent data, circles represent parameters, and arrows indicate flow of information. Colored squares mark the different data modules. Data node definitions: y = individual capture histories, $\mathbf{C}$ = age-at-harvest matrix, p^L = proportion of carcasses for which trapping location was available, p^{AS} = proportion of carcasses for which age and sex had been determined, P1 = number of placental scars, P2 = presence/absence of placental scars, k.Dens = number known dens, NoMon = number monitored dens, NoOcc = number occupied dens, NoPups = number of pups counted on occupied dens. Parameter definitions: m^H = harvest mortality hazard rate, m^O = natural mortality hazard rate, α = proportion deaths due to harvest ($m^H/(m^H + m^O)$), S = survival probability, h = harvest probability, I = number of immigrants, N = population size, B = breeding population size, Ψ = breeding probability, u.Dens = number unknown dens, p^M = proportion of dens monitored, ρ = number of fetuses per female, L = total number of fetuses produced, R = number of pups emerging from dens, S_0 = denning survival probability, m_0 = denning mortality hazard rate ($-\log(S_0)$), meanLS = average litter size.

and sex was available, and of individuals harvested anywhere for which information on location (study area vs. outside) was available, respectively. In most cases, missing age/sex information was due to a carcass not being delivered for necropsy, and missing location information due to incomplete reporting from the trapper. Cases of missing data were overall rare (mean $p_t^{AS} = 0.92$, mean $p_t^L = 0.99$) and more prevalent early in the study period. The lowest proportions of aged and sexed carcasses (0.43) and located harvests (0.88) occurred in the 1998–1999 and 2000–2001 harvest seasons, respectively.

We used a dead-recovery model (Brownie et al. 1985) to describe the likelihood for the 142

capture histories in our mark-recovery data. The Bayesian implementation of this likelihood is described in detail elsewhere (Brooks et al. 2000, Gimenez et al. 2007) and contains two parameters: the age-dependent probability that an individual survives from year t to $t + 1$ ($S_{Age,t}$) and the probability of recovering a marked individual. Since we here only considered recoveries of harvested foxes and could further assume that all harvests of marked individuals were reported, this latter probability is equivalent to the age-specific harvest rates $h_{Age,t}$. Survival probabilities and harvest rates depend on one another, and we accounted for this by expressing both in terms of the underlying mortality hazard rates

such that $S_{\text{Age},t} = \exp(-(m_{\text{Age},t}^{\text{H}} + m_{\text{Age},t}^{\text{O}}))$ and $h_{\text{Age},t} = (1 - S_{\text{Age},t})m_{\text{Age},t}^{\text{H}}/(m_{\text{Age},t}^{\text{H}} + m_{\text{Age},t}^{\text{O}})$ (Ergon et al. 2018). Here, $m_{\text{Age},t}^{\text{H}}$ and $m_{\text{Age},t}^{\text{O}}$ represent the age- and time-dependent competing risks for death due to harvest and due to other (natural) causes. Hereafter, we refer to juvenile and adult mortality hazard rates, survival probabilities, and harvesting probabilities using indices age = j and age = a, respectively.

We split information on reproduction obtained from carcasses into two sets of data with separate likelihoods. First, we modeled the presence/absence of placental scars as a Bernoulli random variable with a probability equal to the age- and year-specific pregnancy rate, $\Psi_{\text{Age},t}$. Second, we described the number of observed placental scars (given that any were present) as realizations of a Poisson process whose expected mean was the age- and year-specific number of fetuses, $\rho_{\text{Age},t}$.

Den survey data were also described with two separate likelihoods for the distinct types of information contained in the data: the number of occupied dens and the number of pups observed on occupied dens. Under the assumptions that each breeding female occupies one den, the number of dens observed to be occupied in year t can be expressed as follows:

$$\text{NoOcc}_t \sim \text{Binomial}(\text{sum}(B_{,t}), p_t^{\text{M}})$$

where p_t^{M} is the proportion of dens monitored in year t and $\text{sum}(B_{,t})$ is the sum of breeding females in each age class in year t ($B_{\text{Age},t}$). If all dens within the study area were monitored, p_t^{M} could be calculated from the den survey data. However, this is not the case because there may be dens in the study area that have never been detected. We therefore estimated p_t^{M} as the number of monitored dens in year t divided by the sum of the number of known dens and the estimated number of unknown dens.

The number of pups (males and females) observed on each occupied den was modeled as a Poisson random variable with an expected value equaling the mean litter size (post emergence from the den) in year t, meanLS_t. This, in turn, was defined as $(\text{sum}(R_{,t}) \times 2)/\text{sum}(B_{,t})$: twice the number of female pups (again assuming equal sex ratio) produced in year t by breeding females of all ages divided by the total number of breeding females of all ages.

No explicit data were available to estimate the number of females immigrating into the study area in any given year, I_t. However, immigration can be estimated in IPM frameworks even when no data on it are available, as long as the age class distribution of immigrants is defined a priori (Abadi et al. 2010). Arctic foxes frequently disperse in their first year of life (Tannerfeldt and Angerbörn 1996, Eide et al. 2004), and in some years, more juveniles were harvested in the study area than had been born there (Ehrich et al. 2012). We therefore assumed that all immigrant females were age class 0 individuals and described I_t as following a Poisson distribution with an annually varying expected mean number of immigrants.

Temporal variation in vital rates

To account for potential impacts of changes in abiotic (e.g., ambient temperature, sea ice extent) and biotic (e.g., prey availability) environment on arctic fox population dynamics, we modeled among-year variation in age-specific demographic parameters $X_{\text{Age},t}$. We did so by adding time trends (β_{trend}^{X}), fixed effects of variation in relevant environmental factors using detrended covariates (β_{cov}^{X}), and independently normally distributed random year effects (ε_t^{X}) representing residual variation on the relevant link scale:

$$\text{link}(X_{\text{Age},t}) = \text{link}(\mu_{\text{Age}}^{X}) + \beta_{\text{trend}}^{X} \times t + \beta_{\text{cov}}^{X} \times \text{cov}_t + \varepsilon_t^{X}$$

where μ_{Age}^{X} is the age-specific average value of $X_{\text{Age},t}$. The link scales were log for mortality hazard rates ($m_{\text{Age},t}^{\text{H}}$, $m_{\text{Age},t}^{\text{O}}$) and fetus numbers ($\rho_{\text{Age},t}$), logit for pregnancy rates ($\Psi_{\text{Age},t}$), and log-log for early survival ($S_{0,t}$). Effects of sea ice extent and reindeer carcass availability were fit on both mortality ($m_{\text{Age},t}^{\text{O}}$) and reproductive parameters ($\Psi_{\text{Age},t}$, $\rho_{\text{Age},t}$, $S_{0,t}$). Effects of goose reproduction were only fit on natural mortality, as geese arrive in Svalbard after foxes have given birth (Eide et al. 2012). For $m_{\text{Age},t}^{\text{H}}$, we did not fit any time trend or environmental covariate effects. Instead, we modeled the large change in harvest management (reduction in number of trapping areas) as a change in the intercept from the harvest season 2009–2010 onwards, effectively separating harvest mortality into two periods. Among-year variation in the number of female immigrants, I_t, was expressed only in terms of residual variation. In Table 1, we provide an overview over the fitted effects for each

Table 1. Overview over modeled effects on different arctic fox vital rates.

Vital rate	Abbreviation	Time trend	Period switch	Sea ice extent	Reindeer carcass availability	Goose reproduction	Random year variation
Harvest mortality	m^H_{Age}		▼				◆
Natural mortality	m^O_{Age}	◇		▼	▽	▽†	◇
Pregnancy rate	$\Psi_{Age,t}$	▲		△	△		◆
Number of fetuses	$\rho_{Age,t}$	▽		△	◇		◇
Denning survival	$S_{0,t}$	▽		◇	△		◇
Immigrant number	I_t						◆

Notes: ▲/▼ = positive/negative effect with 90% credibility interval (CI) not including 0. △/▽ = positive/negative effect with 50% CI not including 0. ◆ = variance component estimated ≠ 0. ◇ = effect indistinguishable from 0 (50% CI overlapping 0 for fixed effects, posterior distribution of standard deviation separate from 0 for variance components). Blank cells indicate that effects were not considered in the model. "Period switch" refers to the change in harvest regulations midway through the study period. For a detailed description of how all of the effects were incorporated on each parameter, see Appendix S2.
 † Effect only on juveniles (age class 0).

demographic parameter, and the hierarchical models used to fit the effects are described in more detail in Appendix S2.

Bayesian implementation.—The likelihood of an IPM is the product of the separate data likelihoods, given independence among the different data sets. While the independence assumption is not fully met in our case (i.e., some individuals are part of multiple datasets), simulation studies have shown that partial dependence has little influence on parameter estimates (Schaub and Fletcher 2015, Plard et al. 2019). We used noninformative priors for all parameters except for the number of unknown dens, for which we used an informative Poisson prior with an expected value of 4. This expected value was informed by expert knowledge about arctic fox biology and behavior, as well as about local topography and resource distribution in the study area. The experts were two of the authors (Nina E. Eide and Eva Fuglei) and Pål Prestrud, all of whom have been involved in fieldwork and research on arctic foxes in the study area for many years. A sensitivity analysis showed that the estimates of population sizes and demographic parameters were robust over a range of sensible priors (see Appendix S3: Section S3.1 for details).

We implemented the IPM in NIMBLE (de Valpine et al. 2017) using version 0.9.0 of the nimble R package and used Markov chain Monte Carlo (MCMC) for estimation (three chains of 25,000 iterations, of which the first 5000 were discarded as burn-in). Convergence was assessed by means of visual inspection of the chains and the Gelman-Rubin statistic (Gelman and Rubin 1992).

Model testing

At present, no global goodness-of-fit test is available for IPMs (Schaub and Abadi 2011, Plard et al. 2019). Instead of separately assessing the fit of the IPM component models (Kéry and Schaub 2012, Plard et al. 2019), we tested the overall performance and fit, as well as potential bias in predictions, of our model by investigating four central aspects. First, we assessed the influence of informative priors on model predictions (Kéry and Schaub 2012, Gelman et al. 2013). Second, we compared vital rate estimates obtained from the IPM to estimates from independent analyses to make sure there was no major discrepancy among datasets, and between datasets and the population model (Kéry and Schaub 2012, Gelman et al. 2013). Third, we checked for major lack of fit by comparing model predictions for both vital rates and population-level patterns to observations (Gelman et al. 2013). Finally, we assessed the ability of the model to produce realistic predictions using stochastic simulations (Gabry et al. 2019). The results of these tests revealed little influence of informative priors (Appendix S3: Section S3.1), no major discrepancies among datasets and model structure

(Appendix S3: Section S3.2), good fit of model predictions to data (Appendix S3: Subsection S3.3.1), and realistic population trajectories resulting from model prediction (Appendix S3: Subsection S3.3.2).

Transient life table response experiments

We applied transient life table response experiments (LTREs, Koons et al. 2016) to assess the relative contributions of changes in different demographic rates and population structure to fluctuations in population size over time. Following the approach of Koons et al. (2017), we ran two types of LTRE on all posterior samples from the IPM. First, we used a random design LTRE to determine the contribution of overall variation in demographic rates and population structure to variation in population growth rate throughout the whole study period:

$$\text{Contribution}_{\theta_i}^{\text{var}(\lambda_t)} \approx \sum_i \text{cov}(\theta_{i,t}, \theta_{j,t}) \frac{\delta\lambda_t}{\delta\theta_{i,t}} \frac{\delta\lambda_t}{\delta\theta_{j,t}}\bigg|_{\bar{\theta}}$$

Here, λ_t is the population growth rate from t to $t + 1$ and $\theta_{,t}$ is a vector of all demographic rates and population structures (with first indices i and j). $\delta\lambda_t/\delta\theta_{i,t}$ thus constitutes the partial derivative of population growth rate with respect to demographic rates and population structure.

Second, we applied a fixed-design LTRE to calculate the contributions of changes in demographic rates and population structure from one year to the next to the change in population size over the same interval:

$$\text{Contribution}_{\theta_i}^{\Delta\lambda_t} \approx (\theta_{i,t+1} - \theta_{i,t}) \frac{\delta\lambda_t}{\delta\theta_{i,t}}\bigg|_{\bar{\theta}}$$

We present the derivation of transient sensitivities for the arctic fox model in Appendix S4 and provide the code to implement the LTRE (ArcticFox_randomLTRE.R, ArcticFox_fixedLTRE.R) in Data S1.

All analyses were run in R version 3.3.2 (R Core Team 2019).

RESULTS

Vital rate estimation

Average harvest mortality hazard rates (median [90% credibility interval]) for juveniles and adults were very similar, that is, 0.26 [0.17, 0.42]

and 0.23 [0.15, 0.36], respectively, in the first period (1997–2009), and 49 [8, 73]% lower on average in the second period following the change in harvest regulation (2010–2019). Average natural mortality for both age categories was substantially higher at 0.76 [0.44, 1.24] for juveniles and 0.47 [0.34, 0.62] for adults. This resulted in average juvenile survival probabilities of 0.35 [0.22, 0.50] in the first period and 0.40 [0.25, 0.56] in the second period (Appendix S1: Figs. S2, S3). For adults, average survival probabilities were 0.49 [0.42, 0.58] in the first period and 0.55 [0.47, 0.63] in the second period (Appendix S1: Figs. S2, S3). Natural mortality did not change directionally over time but fluctuated as a function of variation in environmental covariates (Appendix S1: Fig. S3). Specifically, natural mortality was higher in years with less sea ice, fewer reindeer carcasses, and/or lower goose reproduction (Table 1, Fig. 2; Appendix S1: Figs. S4–S6). The model was unable to reliably estimate additional random among-year variation in natural mortality, instead resulting in a posterior distribution for the standard deviation (SD) with a mode very close to 0. Random among-year variation in harvest mortality, on the other hand, was estimated successfully. The resulting time-dependent harvest mortality hazard rates correlated well not only with the total number of individuals harvested (age-at-harvest data), but also with independent preliminary data on hunting effort (Appendix S3: Fig. S7).

Pregnancy rate was estimated to be low for females below three years of age and to increase up to 0.93 [0.84, 0.99] for females in the oldest age class of 4+ (Appendix S3: Fig. S8). The model supported an increase in pregnancy rate over the study period (Appendix S1: Fig. S7) and indicated that more females were breeding following winters with relatively large sea ice extent and high availability of reindeer carcasses (Table 1, Fig. 2). Random year effects were estimated to have a SD of 0.89 [0.41, 1.52] on the logit scale.

Fetus number showed a slight increase with age, from an average 5.2 [4.5, 5.9] in age class 1 to 6.6 [6.1, 7.1] in age class 4+ (Appendix S3: Fig. S9). Estimated time variation in fetus number (Appendix S1: Fig. S8) was primarily attributed to a negative trend and a positive effect of the amount of sea ice. There was no evidence for an
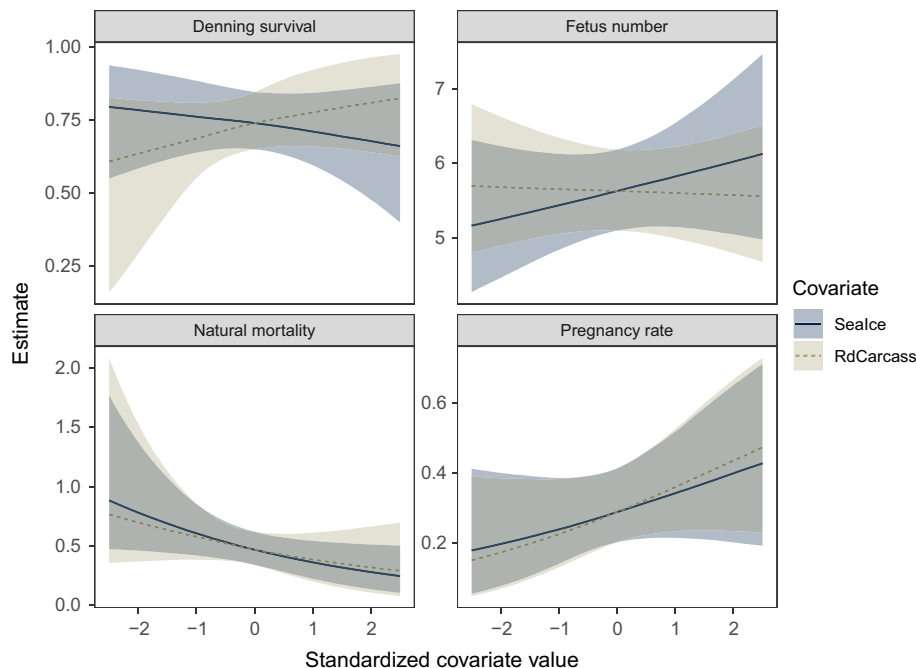
Fig. 2. Predicted effects of sea ice extent (solid, blue) and reindeer carcass availability (dotted, brown) on different arctic fox vital rates. x-Axes show standardized values of the relevant covariates. y-Axes show the posterior estimate for the effect slope (β_{cov}^{X}, where X = vital rate in panel title). Lines represent posterior medians, and ribbons mark the 90% credibility intervals.

effect of reindeer carcasses (50% CI overlapping 0), and random year variation could not be estimated reliably (Table 1, Fig. 2).

Time average denning survival was estimated at 0.74 [0.65, 0.85], with the model indicating a potential decrease over time (Appendix S1: Fig. S9) and a positive relationship with the number of reindeer carcasses available to parents in the previous winter (Table 1, Fig. 2). A potential sea ice effect on denning mortality/survival had a 50% CI overlapping 0, and random year variation was not estimated as clearly distinct from 0.

Finally, between 16 [3, 43] and 52 [28, 91] young females were predicted to immigrate into the population every year. Throughout the study period, the average number of female immigrants per year was 33 [19, 58] with a SD of 14 [6, 27], and thus fairly close to the number of locally produced female pups (Fig. 3).

A summary of the posterior distributions of all vital rates and associated parameters can be found in Appendix S1: Table S2.

Population dynamics during the study period

Population size in late summer (including all young of the year and prospective immigrants) was predicted as relatively stable throughout the study period (low year-to-year variability, no long-term trends), and averaged 98 [63, 125] females across the period 1997–2019 (Fig. 4). Population growth rates varied from a minimum of 0.68 [0.46, 0.99] in the interval 2000–2001 to a maximum of 1.49 [0.99, 2.11] in the interval 2018–2019, with an overall mean of 1.06 [1.02, 1.12] (SD = 0.32 [0.22, 0.45]). Population structure was also relatively stable over time with, on average, 59 [53, 67]%, 20 [16, 24]%, 10 [8, 11]%, 5 [4, 6]%, and 5 [4, 7]% of females in age classes 0 through to 4+, respectively (Appendix S1: Fig. S10). Estimated numbers of locally born female pups and of female immigrants were similar on average, but uncertainty was substantially higher for the latter (Fig. 3). Post hoc analyses revealed only a low degree of covariation among the two, with a correlation coefficient of −0.19 [−0.48, 0.15].

Fig. 3. Estimated number of female arctic fox pups produced within the study area (blue) and female immigrants entering the study are from elsewhere (green). Solid line represents the posterior medians, and ribbon marks the 90% credibility intervals.

Transient life table response experiments

Results from the random design LTRE revealed that variation in population growth rate was the outcome mostly of changes in annual mortality and pregnancy rate, and local population structure and immigration to a lesser degree (Fig. 5a). Variation in natural mortality contributed substantially more than variation in harvest mortality, and changes in juvenile mortality had been more influential than changes in adult mortality (Fig. 5b). Similarly, changes in the number of age class 0 individuals were responsible for more variation in population growth rate than changes in any other age class (Fig. 5e). For pregnancy rate, most change propagated to the population level via age class 2 (Fig. 5c), while no conclusions were possible for age dependence of contributions of changes in fetus number (likely because estimated variation was very limited, Fig. 5d).

The relative contributions of different vital rates and population structure (as calculated from the fixed design LTRE) varied over time (Fig. 6; Appendix S1: Fig. S11), but the pattern was mostly consistent with the ranking obtained from the random design LTRE (Fig. 5). Notably, periods with relatively low contributions from immigration were also characterized by

relatively higher contributions from pregnancy rate, in particular (Fig. 6).

DISCUSSION

Understanding and predicting the effects of ongoing rapid climate change on communities and ecosystems require in-depth knowledge about how key environmental drivers interact with demography and population dynamics of single species (Williams et al. 2002). Here, we elucidated demographic mechanisms and environmental drivers shaping population dynamics of an opportunistic apex predator, the Svalbard arctic fox, in a rapidly changing climate. Integrated analysis of several datasets allowed us to overcome a previously prohibitive sparsity of individual-based demographic data and revealed population dynamics stabilized by balanced contributions from survival, reproduction, and immigration, as well as inputs from terrestrial and marine food resources.

Stable population dynamics, local vital rates, and environmental drivers

Despite rapid changes in biotic and abiotic environmental factors and substantial alterations of harvest regulations, both population size and
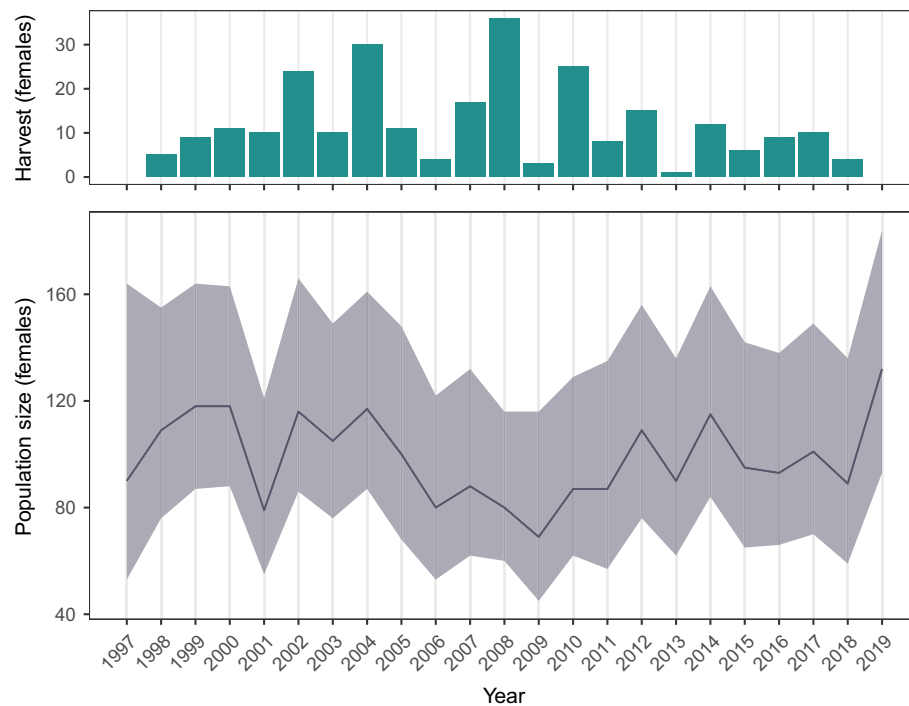
Fig. 4. Top panel: total number of female arctic foxes of all ages harvested in each trapping season (age-at-harvest data). Bottom panel: estimated arctic fox population size at the summer census (females only, including young of the year and all immigrants entering prior to/during the subsequent trapping season) over the course of the study period. Solid line represents the posterior median, and ribbon marks the 90% credibility interval.

age structure of arctic foxes in the study area on Svalbard have remained surprisingly stable over the last two decades (Fig. 4; Appendix S1: Fig. S10). This stability of population dynamics in a changing environment was linked to a balance in contributions from different demographic rates, as well as the ability to exploit resources from two ecosystems with diverging responses to climate change.

Several other populations of arctic foxes (Angerbjörn et al. 1995, Gruyer et al. 2008, Unnsteinsdóttir et al. 2016)—as well as other medium-sized carnivores, such as the red fox (Englund 1970)—feature dynamics that are strongly driven by direct impacts of resource availability on reproductive rates. Here, on the contrary, we found that variation in annual natural mortality, pregnancy rate, and immigration made roughly equal contributions to fluctuations in population size of arctic foxes on Svalbard (Fig. 5). In terms of local demography, natural mortality and pregnancy rate thus represent the

key drivers. We found both to depend on the availability of several food resources originating from terrestrial and marine ecosystems, in agreement with studies on diet diversity of coastal arctic foxes (Roth 2002, Carbonell Ellgutter et al. 2020). Reindeer carcasses constitute the main terrestrial food resource for arctic foxes during winter and early spring (Prestrud 1992, Eide et al. 2005), and the estimated increase in pregnancy rate following winters with more reindeer carcasses (Fig. 2) is consistent with previously reported positive relationships for the same population (Eide et al. 2012). This is likely mediated by female body condition improving with food availability in winter, and we do indeed see positive associations between the number of reindeer carcasses and both body mass and body condition of harvested females (E. Fuglei, *unpublished data*). Furthermore, early pup survival, which may be influenced by maternal body condition (Cameron et al. 1993, Atkinson and Ramsay 1995, Ronget et al. 2018), was also higher
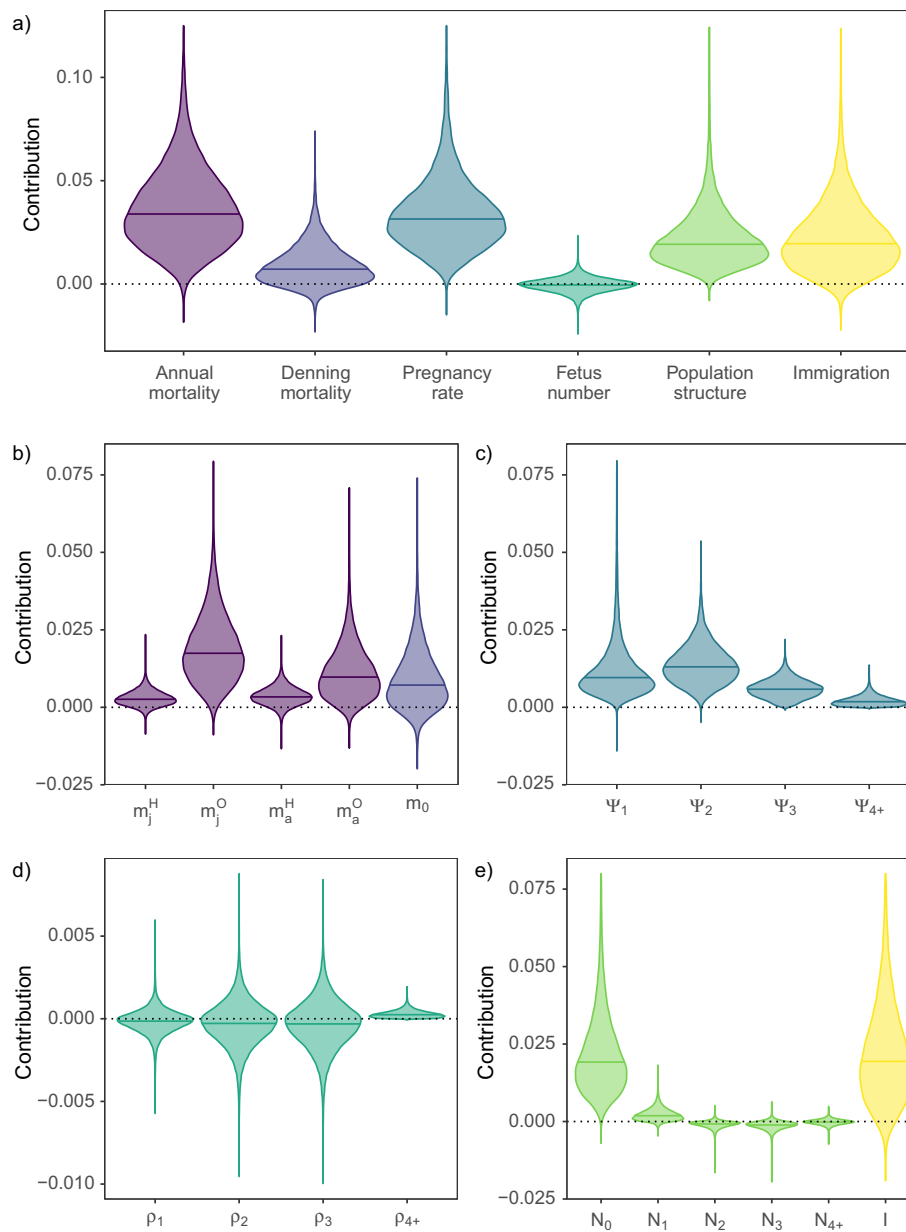
Fig. 5. Posterior distributions of the relative contributions of different demographic categories (a) and underlying age-specific vital rates and population structure (b–e) to changes in arctic fox population growth rate. Except for denning mortality and immigration, categories represent sums of several components: annual mortality (harvest and natural mortality of juveniles and adults, m_{Age}^{H} and m_{Age}^{O}), pregnancy rate (Ψ_{Age}, summed over all age classes), fetus number (ρ_{Age}, summed over all age classes), and population structure (N_{Age}, summed over all age classes). The solid line within each violin marks the posterior median.

following winters with plenty of reindeer carcasses (Fig. 2). Similar reproductive responses to carcass availability were found in wolverines (*Gulo gulo*, Rauset et al. 2015), illustrating the overall importance of carcass availability for mammalian carnivores (Pereira et al. 2014). Our model also revealed that natural mortality was lower (and survival therefore higher) in years
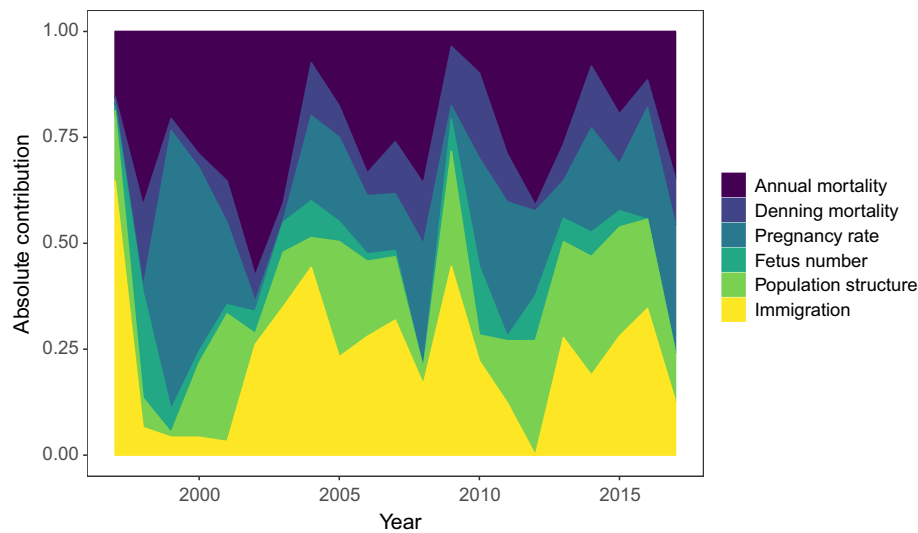
Fig. 6. Posterior medians of relative absolute contributions of different demographic components to changes in arctic fox population growth rate over the course of the study period. Absolute contributions are scaled to sum to 1 here.

with more reindeer carcasses (Fig. 2), suggesting that, in addition to increasing body condition, a higher number of reindeer carcasses may also directly reduce mortality due to starvation.

The effects of sea ice on demographic rates closely resembled those of reindeer carcasses, with fewer foxes dying and more breeding in years with relatively more sea ice (Fig. 2). In years with sufficient sea ice coverage, arctic foxes have ample opportunity to scavenge polar bears' seal kills and prey on ringed seal pups, which are born in late March to mid-April (Lydersen and Gjertz 1986). On the contrary, when there is little or no sea ice, access to seal carrion is more limited and seals hardly reproduce at all (Kovacs et al. 2011), resulting in reduced availability of marine resources for arctic foxes. Just as for reindeer carcasses, increased availability of seal pups and carrion (marine food resources) reduces the risk of starvation for arctic foxes during winter and leads to higher overall body condition (Roth 2003). This, in turn, would manifest as lower natural mortality, higher pregnancy rate, and a larger litter size at birth (Fig. 2). We note that due to the high correlation between sea ice extent and winter temperature, any effect of sea ice on arctic fox vital rates could also be interpreted as an effect of temperature more generally. However, effects via accessibility of marine resources seem

more likely here than direct effects of temperature, since in the latter case, we would expect to see opposite effects, that is, benefits (lower mortality, higher reproduction) in warmer winters due to reduced thermoregulatory costs.

Unlike reindeer and seals, which constitute primarily winter food resources for arctic foxes, breeding geese are available during the summer months (late May–September, Fox et al. 2009). As such, the availability of goose prey, and goslings in particular, is expected to influence body condition of foxes prior to winter (Fuglei et al. 2003, Eide et al. 2005). We did indeed find evidence that juvenile foxes experienced lower natural mortality during their first winter following summers with relatively high reproduction among pink-footed geese (Appendix S1: Fig. S6). This supports previous evidence from dietary studies that highlighted the potential importance of breeding geese for young arctic foxes (Giroux et al. 2012, Pálsson et al. 2016, but see also Carbonell Ellgutter et al. 2020). Notably, we found an effect of goose reproduction only on natural mortality of juveniles specifically, and not when extended to natural mortality of older females. This is consistent with other recent studies that failed to find a link between adult arctic fox survival and access to goose breeding colonies (Samelius and Alisauskas 2017, Chevallier et al.

2020) and supports the notion that the importance of different resources to arctic fox diet varies with age (Carbonell Ellgutter et al. 2020). Indeed, one reason for goose reproduction affecting juvenile but not adults foxes could be that adult territorial foxes can fall back on cached food during winter (Careau et al. 2008, Samelius and Alisauskas 2017), while juveniles need to rely more on reserves accumulated during summer and early autumn (e.g., via goose prey).

In addition to investigating the effects of variation in resource availability, we also included time trends and residual among-year variation into our vital rate models. Since all other covariates were detrended, time trends in the present analysis encompass any effect of directional changes in the environment during the study period. This includes substantial increases in ambient temperature, increases in goose population density/reproductive output, decreases in sea ice extent (reduced access to marine resources), and other concurrent directional changes in the environment (e.g., rain-on-snow events, seabird abundance, Descamps et al. 2017). While there was no evidence for directional changes in natural mortality over the course of the study period (Appendix S1: Fig. S3), the model predicted notable changes in reproductive parameters. Breeding probability increased over time and seems to have stabilized at a higher level in the second half of the study period relative to the first (Appendix S1: Fig. S7). This resulted in relatively many breeding females (Appendix S1: Fig. S12) and high overall reproductive output (Appendix S3: Fig. S10) in the most recent years, which may be due to a variety of reasons: overall increased availability of (cached) terrestrial resources (Careau et al. 2008, Samelius and Alisauskas 2017), lower metabolic costs in milder winters (Prestrud 1991, Pálsson et al. 2016), and/or new opportunities for year-round foraging in the tidal zone of the now ice-free fjords (Hersteinsson and Macdonald 1996, Carlton and Hodder 2003). The latter could actually stabilize resource availability in winter, and thus allow for higher population densities of arctic foxes along the coast (Eide et al. 2004), something also seen in coastal coyotes (*Canis latrans*, Rose and Polis 1998).

As overall breeding probability increased, we estimated a concurrent decrease in the number of pups produced per breeding female (Appendix S3: Fig. S11), likely as a result of decreases in both fetus numbers (Appendix S1: Fig. S8) and the probability of fetuses to survive to emerge from the den (denning survival, Appendix S1: Fig. S9). While the former may be tied to the gradual decrease in sea ice, and therefore diminished access to important marine resources (seal pups and carrion) during a critical period for pregnant females, the latter may be a consequence of changes in the age structure of the breeding population: If pups of younger, less experienced mothers have lower early survival (Sydeman et al. 1991, Meijer et al. 2011), then higher proportions of young females in the breeding population (which our model indeed predicted, Appendix S1: Fig. S12) would inevitably result in lower estimates of population-average early survival.

Overall, increases in the number of breeding females were thus balanced by decreases in per-capita number of pups produced, and this ultimately resulted in a population-level reproductive output that did not differ substantially in the beginning and end of the study period (Appendix S3: Fig. S10). Taken together, these results suggest that the stability in population dynamics of arctic foxes in Svalbard arises from balanced contributions of different demographic rates and exploitation of resources from two ecosystems with contrasting changes. This may buffer arctic foxes, and possibly opportunistic carnivores more generally, against climate change.

The role of immigration

The observed fluctuations in arctic fox population size depended mostly on numerical changes in the youngest age class (Fig. 5). Over the course of the study period, this age class was composed of roughly equal numbers of locally produced and immigrated females (Fig. 3), highlighting the importance of immigration for the dynamics of this population. Since indirect estimation of immigration into wildlife populations became possible using IPMs (Abadi et al. 2010), many studies have documented crucial contributions of immigration to population dynamics (Millon et al. 2019). Nonetheless, with almost equal contributions of local reproduction and immigration, the percentage of immigrants in our study

population of arctic foxes appears to lie clearly above a recently reported mean for mammalian populations (26%, Millon et al. 2019). This could be a consequence of our definition of the study area, which is relatively small compared with movement ranges of arctic foxes (Tarroux et al. 2010, Fuglei and Tarroux 2019), but may also be related to immigration acting as a compensatory mechanism replacing individuals lost due to harvest.

The integrated analysis predicted the number of immigrants to vary up to over threefold between the year with the highest and lowest numbers (Fig. 3). Post hoc analyses suggested that there may have been fewer immigrants in years with high local reproductive output and (consequently) local population size. This hints at a possibility for negative density dependence and thus compensatory immigration (Loe et al. 2009, Schaub et al. 2010). Thorough investigations into potential drivers of immigration constitute an important venue for future research. The same is true for emigration, which may also play an important role for population dynamics but could not be separated from mortality in the present study. Ideally, further investigations should make use of additional data on individual movement, such as satellite telemetry data (which is currently being collected for arctic foxes elsewhere in Svalbard). This will allow to address problems with potential bias in estimation of immigration in IPMs (Schaub and Fletcher 2015, Riecke et al. 2019) and may make it possible to separate mortality and emigration.

Benefits of integrating data

While integrated data analysis has quickly become an important tool in population ecology (Zipkin and Saunders 2018, Plard et al. 2019), the core of any IPM—long-term data from marked individuals—is still costly and hard to obtain (Clutton-Brock and Sheldon 2010). In the present analysis, we demonstrated that not just estimates of vital rates and population size, but also important insights into demographic mechanisms and environmental drivers, can be obtained from innovative integration of commonly collected harvest and population survey data in combination with just a minimal amount of data from marked individuals (142 individuals marked in only the 7 first years of a 22-yr study period, in

this case). The former are readily available for many animal populations that are under substantial human management. This opens the possibility to use IPM approaches to investigate the potential impacts of different harvest strategies, conservation actions, or measures for population control, while fully accounting for uncertainty in predictions (Arnold et al. 2018, Zipkin and Saunders 2018). The IPM developed here could, for example, be used to assess potential future impacts of ongoing environmental change on arctic foxes in Svalbard and contribute to the development of sustainable harvest strategies in a changing climate.

Model limitations and the way forward

Data limitations do, however, affect the confidence with which certain types of inference can be made. For the arctic foxes in Svalbard, data on marked individuals were sparse and the study period relatively short compared with the time scale of environmental variation. This manifested as substantial uncertainty in estimates, particularly of environmental effects (Fig. 2), partial failure to quantify residual environmental variation (Table 1), and resulting limited ability to quantify contributions of (1) environmental drivers to vital rate variation (Appendix S1: Fig. S13) and (2) vital rates to population dynamics (Table 2, Fig. 5). As a result, population projections from this IPM will have a large degree of uncertainty and forecasts of environmental impacts in particular need to be interpreted with caution. Assessing model performance and updating the model with new data over time in an adaptive management framework will therefore be important (Nichols et al. 2007).

We also note that obtaining reliable population projections requires models accounting for all of the most important population processes (Benton et al. 2006). The model we present here ignores three potentially important aspects of arctic fox demography: spatiotemporal variation in resource distribution, density dependence, and sex differences. First, resource availability is not homogenous across the study area. Some arctic fox territories provide better access to certain resource types (i.e., geese, sea birds, reindeer carcasses), and this spatial heterogeneity in prey abundance affects social organization (Eide et al. 2004) and reproductive

Table 2. Overview of the temporal variance of all arctic fox vital rate and population structure parameters estimated by the integrated population model, and the corresponding calculated life table response experiment (LTRE) contributions.

Abbreviation	Parameter	Estimated variance	LTRE contribution
m_j^H	Juvenile harvest mortality	0.03 [0.01, 0.06]	0.003 [0, 0.007]
m_j^O	Juvenile natural mortality	0.17 [0.05, 0.37]	0.018 [0.004, 0.039]
m_a^H	Adult harvest mortality	0.02 [0.01, 0.04]	0.003 [0, 0.009]
m_a^O	Adult natural mortality	0.04 [0.01, 0.13]	0.010 [0.001, 0.027]
m_0	Denning mortality	0.02 [0.01, 0.07]	0.007 [0.001, 0.027]
Ψ_1	Age 1 pregnancy rate	0.00 [0.00, 0.01]	0.010 [0.003, 0.031]
Ψ_2	Age 2 pregnancy rate	0.03 [0.01, 0.05]	0.013 [0.005, 0.025]
Ψ_3	Age 3 pregnancy rate	0.02 [0.00, 0.04]	0.006 [0.001, 0.011]
Ψ_{4+}	Age 4+ pregnancy rate	<0.01 [0.00, 0.01]	0.002 [0, 0.005]
ρ_1	Age 1 fetus number	0.34 [0.09, 0.93]	<0.001 [0.000, 0.002]
ρ_2	Age 2 fetus number	0.40 [0.11, 1.05]	0.001 [0, 0.003]
ρ_3	Age 3 fetus number	0.47 [0.13, 1.21]	0.001 [0, 0.003]
ρ_{4+}	Age 4+ fetus number	<0.01 [0.00, 0.01]	<0.001 [0, 0.001]
N_0	Number of age 0	292.96 [136.94, 701.16]	0.019 [0.006, 0.049]
N_1	Number of age 1	110.06 [62.26, 204.31]	0.002 [0.000, 0.006]
N_2	Number of age 2	27.67 [14.63, 56.71]	0.001 [0.000, 0.003]
N_3	Number of age 3	8.89 [4.73, 18.79]	0.001 [0.000, 0.004]
N_{4+}	Number of age 4+	5.90 [3.02, 11.60]	0.001 [0.000, 0.002]
I	Number of immigrants	227.37 [66.85, 612.98]	0.020 [0.002, 0.053]

Note: All results are given as median [90% credibility interval] and are based on 45,000 samples from the joint posterior distribution.

output (Eide et al. 2012). Furthermore, access to some resources is highly seasonal (Giroux et al. 2012, McDonald et al. 2017), and seasonality in resource access itself may change as the Arctic continues to warm (Descamps et al. 2017). Second, some vital rates may be subject to density-dependent feedbacks, and post hoc analyses of our model estimates did indeed provide evidence for correlations between population size and population growth rate ($r = -0.63$ [-0.78, -0.48]). Similar evidence for density dependence was also found for arctic foxes in Iceland, where population size is strongly constrained by the number of breeding territories (Pálsson et al. 2016, Unnsteinsdóttir et al. 2016). However, while density dependence in Icelandic arctic foxes appears to be mediated primarily by breeding probability (Unnsteinsdóttir et al. 2016), we found that for arctic foxes in Svalbard the signal for density dependence was strongest for natural mortality ($r = 0.42$ [0.11, 0.65] for juveniles, $r = 0.34$ [0.01, 0.60] for adults). The underlying mechanism may be linked to competition affecting density dependence in either local mortality or emigration rate, a distinction not accounted for by our model. Finally, the model we presented here focused only on the female segment of the population, primarily because of difficulties determining reproductive output of males. However, males can have substantial impacts on population size and structure, particularly in harvested populations (Milner et al. 2007, Rankin and Kokko 2007), and there is evidence for sex differences in physiology, behavior, and vital rates of some populations of arctic foxes (Hersteinsson 1984, Goltsman et al. 2005, Friesen et al. 2015). Other studies failed to find differences in key vital rates between males and females (Tannerfeldt and Angerbörn 1996, Samelius and Alisauskas 2017, Chevallier et al. 2020), but for arctic foxes in Svalbard, potential sex differences have not yet been investigated in detail. Spatiotemporal and seasonal heterogeneity in resource availability, density dependence in vital rates, and the dynamics of males may thus have substantial impacts on how the population responds to changes in environment and management practices and should be investigated in future studies.

Conclusion

In this study, we combined commonly collected harvest and population survey data with rarer and much more costly mark-recovery data in an integrated analysis to elucidate the mechanisms underlying population dynamics of an opportunistic apex predator, the arctic fox on Svalbard. We have shown that population size has been relatively stable over the last two decades despite concurrent climate change and a shift toward stricter harvest regulation. This stability was linked to balanced contributions of several vital rates (natural mortality, pregnancy rate, and immigration) and to compensatory resource inputs from both marine and terrestrial systems. Both of these mechanisms may ultimately increase resilience of populations of opportunistic predators, such as arctic foxes on Svalbard, to climate change. We obtained a wealth of important insights into the drivers of population dynamics from and IPM despite a sparsity of data from marked individuals. We thus underline the large potential of such approaches to inform management and conservation of wildlife populations also when resources for marking individuals are limited.

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Chloé R. Nater, Eva Fuglei, and Nigel G. Yoccoz conceived the ideas and designed methodology. Eva Fuglei, Nina E. Eide, and Åshild Ø. Pedersen collected the data. Chloé R. Nater ran the analyses and visualized the results. Chloé R. Nater and Eva Fuglei led the writing of the manuscript. All authors contributed critically to drafts and gave final approval for publication.

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Data Availability

Parts of the data (up to 2001) are summarized in Eide et al. (2012). Posterior samples from the fitted IPM are provided in Data S1. Code for formulating the model (ArcticFox_IPM.R) and for implementing the transient LTRE analyses (ArcticFox_randomLTRE.R, ArcticFox_fixedLTRE.R) is provided in Data S1.

Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3546/full