Oecologia (2020) 193:557–569
https://doi.org/10.1007/s00442-020-04696-8

POPULATION ECOLOGY – ORIGINAL RESEARCH

Pulsed food resources affect reproduction but not adult apparent survival in arctic foxes

Clément Chevallier[1] · Gilles Gauthier[2] · Sandra Lai[1] · Dominique Berteaux[1]

Received: 5 November 2019 / Accepted: 17 June 2020 / Published online: 28 June 2020

Abstract
As top or mesopredators, carnivores play a key role in food webs. Their survival and reproduction are usually thought to be influenced by prey availability. However, simultaneous monitoring of prey and predators is difficult, making it challenging to evaluate the impacts of prey on carnivores' demography. Using 13 years of field data on arctic foxes *Vulpes lagopus* in the Canadian High Arctic and a capture–recapture multi-event statistical approach, we investigated the hypothesis that increases in lemming abundance (a cyclic and unpredictable food source) and goose colony proximity (a stable but spatially and temporally limited food source) would be associated with increased apparent survival and reproduction probabilities of adults. Adult apparent survival varied greatly across years (0.13–1.00) but was neither affected by lemming nor goose variations in abundance. However, reproduction probabilities were strongly influenced by both lemming abundance and access to the goose colony. A fox breeding in the best conditions of food availability (year of high lemming density inside the goose colony) had a reproduction probability four times higher than one experiencing the worst conditions (year of low lemming density outside the goose colony). Breeding status of individuals also played a role, with breeders having a 10–20% higher probability of survival and 30% higher probability of reproduction the following year than non-breeders. As the Arctic ecosystem changes due to increased temperatures and species ranges, this study will allow better predictions of predator responses to management or environmental changes and a better understanding of ecosystem functioning.

Keywords Canid · Demography · Multi-event · Multi-source · *Vulpes lagopus*

Introduction

Carnivores are among the most threatened vertebrates which can play a keystone role as top or mesopredators, serve as umbrella species for the conservation of many other taxa, and generate formidable public interest (van de Kerk et al. 2013; Treves et al. 2017). As 25% of carnivore species are declared endangered (van de Kerk et al. 2013), obtaining detailed, high-quality data on their reproduction and survival as well as information on factors which influence demographic parameters is particularly pertinent and in high demand for fundamental research, ecosystem management, and conservation. However, carnivores often live at low densities, have large home ranges, and tend to be elusive and difficult to catch (Karanth and Chellam 2009). In addition, since all carnivores are predators, the dynamics of their populations should be influenced by their prey, either directly through bottom-up control (Fuller and Sievert 2001) or indirectly through interspecific competition, including intraguild predation (Martínez-García et al. 2010). Yet, studying the natural variation of vital rates in response to prey fluctuations is usually difficult since most monitored carnivore populations experience a heavy human-induced mortality related to hunting (e.g., collared leopard, *Panthera pardus,* Williams et al. 2017), road accidents (e.g., amur tiger, *Panthera tigris altaica,* Kerley et al. 2002) or population control

Communicated by Anders Angerbjörn.

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s00442-020-04696-8) contains supplementary material, which is available to authorized users.

✉ Dominique Berteaux
dominique_berteaux@uqar.ca

[1] Canada Research Chair on Northern Biodiversity and Centre d'Études Nordiques, Université du Québec à Rimouski, 300 Allée des Ursulines, Rimouski, QC G5L3A1, Canada

[2] Département de biologie and Centre d'Études Nordiques, Université Laval, 1045 avenue de la Médecine, Pavillon Vachon, Quebec City, QC G1V0A6, Canada

(e.g., free-ranging dogs, *Canis familiaris*, Belo et al. 2017). Conducting long-term and simultaneous monitoring of predator and prey populations is also logistically challenging. As a result, reliable estimates of vital rates, especially survival, are still relatively rare for wild carnivore populations exempt of anthropogenic pressure (Gorman et al. 2008).

In carnivores, it is much more difficult to estimate the effects of resource fluctuation on adult survival rates than on reproductive rates. Estimating adult survival requires the application of expensive or logistically challenging techniques such as telemetry (e.g., Mace et al. 2012; Loveridge et al. 2016), molecular tracking (e.g., Meijer et al. 2008), or resighting of a large number of marked or visually recognizable individuals (e.g., M'soka et al. 2016). Additionally, changes in food availability do not always result in changes in carnivore survival probability. For example, while in wolves (*Canis lupus*, Peterson et al. 1998) or lynx (*Lynx lynx*, O'Donoghue 1997), food shortage does increase mortality of adults through starvation or intraspecific strife, survival of spotted hyenas (*Crocuta crocuta*) in Zambia seems impacted neither by food density, interspecific competition, nor human proximity (M'soka et al. 2016). As such, the effects of food availability on survival remain unclear, especially because of potential time lags (Fryxell et al. 1999; Dennis and Otten 2000) or compensatory mechanisms (Sedinger et al. 2010; Chevallier et al. 2015a). In contrast, assessing reproductive success is facilitated by the dependence of many species on dens for breeding (e.g., Tannerfeldt and Angerbjörn 1996; Breitenmoser et al. 2007; Rauset et al. 2015), and positive effects of food abundance on reproduction parameters such as fecundity, litter size, and pup survival have been reported for several carnivore species (wolverines, *Gulo gulo*, Persson 2005; iberian lynx, *Lynx pardimus,* Lopez-Bao et al. 2010; arctic fox, *Vulpes lagopus,* Meijer et al. 2013; coyote, *Canis latrans*, Gese et al. 2016; see other examples in Fuller and Sievert 2001 and Rauset et al. 2015).

The arctic fox is a small circumpolar canid (Angerbjörn et al. 2004a) and one of the most important predators in the tundra food web (Legagneux et al. 2012, 2014). Arctic foxes rely on food sources that show contrasted patterns of temporal and spatial variability in abundance (Angerbjörn et al. 2004a). Due to the relatively simple structure of the tundra ecosystem, these fluctuations in food sources can be readily quantified. In most inland and some coastal tundra areas, two types of prey constitute the main food sources for arctic foxes: microtine rodents and migratory birds (Audet et al. 2002). Both are pulsed resources showing periodic superabundance, albeit on different time scales (Angerbjörn et al. 2004b; Samelius et al. 2007). Migratory birds, such as geese, represent an abundant allochthonous input to the ecosystem (Gauthier et al. 2011) available every year but only during summer months (Giroux et al. 2012), whereas lemming or vole populations usually exhibit 3–5-year cycles in abundance (Krebs 2013). Temporal fluctuations of microtines are key drivers of the population dynamics of many arctic predators (Angerbjörn et al. 1999; Therrien et al. 2014). Previous studies reported that some arctic fox populations exhibit cyclic dynamics and are resource dependent (Angerbjörn et al. 1999). In particular, strong resource dependence was linked to den occupancy, litter size and juvenile survival in Fennoscandian and Canadian fox populations (Tannerfeldt and Angerbjörn 1996; Tannerfeldt et al. 1998; Angerbjörn et al. 2004b; Eide et al. 2012; Giroux et al. 2012). This was confirmed through supplementary feeding experiments (Angerbjörn et al. 1991; Meijer et al. 2013). However, most estimates of adult survival for the species come from carcass analyses (Macpherson 1969; Hiruki and Stirling 1989; Fay and Rausch 1992; Eide et al. 2012) or recapture studies based on modest sample sizes (Tannerfeldt and Angerbjörn 1996; Meijer et al. 2008, but see Samelius and Alisauskas 2017).

Here, we report on 13 years of capture–mark–recaptures of arctic foxes involving live trapping, visual observations, camera trapping, and carcass recovery. We studied the predator within a multiple prey system that demonstrates different spatio-temporal dynamics (geese being seasonal migrants and spatially restricted in the study area, and lemmings being cyclic) and in an area where the population is neither heavily hunted nor managed. We used data to their full potential through multi-event analytical approaches combining data from both live and dead encounters (Pradel 2005). One assumption in several capture–mark–recapture models is that all marked individuals have the same probability of being sighted (Amstrup et al. 2005), which is rarely the case. In addition, long-term monitoring programs often include changes in protocols over time, such as the use of new technologies, an increase of the study area or temporal changes in sampling efforts. We, thus, incorporated such potential confounding effects in our analyses to minimize biases on parameter estimation. We predicted that in adult foxes, survival probabilities and reproduction probabilities would be higher during years of high lemming abundance and inside the goose colony.

Materials and methods

(a) Study area and studied species

We worked in the south plain of Bylot Island (73°N, 80°W), which is part of Sirmilik National Park, Nunavut, Canada. Our study area covered 600 km^2 and included more than 100 known denning sites visited at least twice every summer. The arctic fox is the main terrestrial predator in the ecosystem (Legagneux et al. 2012). Its diet is essentially composed of lemmings all year long, geese (mostly eggs and goslings) in summer and marine resources (mainly ringed seals, *Pusa hispida)* in winter (Tarroux et al. 2012; Giroux et al. 2012). The two species of lemmings on Bylot Island, the brown (*Lemmus trimucronatus*) and the collared lemming (*Dicrostonyx groenlandicus*), follow a 3–4-year cycle in abundance although the fluctuations in abundance are much stronger for brown lemmings (from <1 to 10 ind./ha for brown and remaining <1 ind./ha for collared lemmings; Gruyer et al. 2008; Gauthier et al. 2013; Fauteux et al. 2015). A large greater snow goose (*Chen caerulescens atlantica*) colony is present in this area, with over 20,000 nesting pairs mostly in a single colony (Reed et al. 2002). Adult geese arrive in early May and begin to lay eggs in mid-June, eggs hatch around the 9th of July, and all geese migrate to the south in late August (Gauthier et al. 2011, 2013). This nesting colony represents an abundant and predictable pulsed resource and foxes can cache an important quantity of eggs for later consumption (Samelius 2004; Careau et al. 2007b). Foxes also have access to seal carcasses left by polar bears (*Ursus maritimus*) during winter and seal pups in March–April (Gagnon and Berteaux 2009) though quantification of these resources was not part of this study.

(b) Collection of field data

From 2003 to 2015, we captured arctic foxes (adults and pups) every summer between mid-May and mid-August throughout the study area, often near known dens. Detailed trapping methods and techniques are described in Lai et al. (2015). We individually marked foxes using colored and numbered plastic ear tags (Rototags, Dalton Supplies). Starting in 2007, some of the adults were equipped with telemetry collars as part of a study of movement patterns, as described in Tarroux et al. (2010) and Lai et al. (2017). When trapping in an area, we also conducted visual observations at active dens to determine the identity of adults and the presence of pups. At least three observation sessions lasting 12 consecutive hours each were usually made for monitored dens (see details in Cameron et al. 2011). Weather permitting, observation sessions were conducted during three consecutive days; otherwise, they were suspended until the weather improved. We intensified our field monitoring in 2007, since the study area increased from 425 to 600 km^2 (89–111 known dens) and observers increased from two to four, improving our monitoring efficiency as well as capture and observation probabilities. Importantly, automated cameras were installed every summer on selected dens showing signs of fox activity, as described in Chevallier et al. (2015b).

Encounters of animals occurred in three ways. First, marked animals could be captured in traps ("capture"). Second, marked animals could be visually resighted in the field ("direct observation") or identified on pictures taken by cameras ("photographic observation") during the summer. Third, marked individuals could be found dead in the field opportunistically, or returned to us by local hunters who had trapped them ("recovery"). Trappers returning a collar received a $50 reward.

(c) Multi-event model design

We used a capture–recapture model based on the multi-event approach (Pradel 2005). As we monitor foxes only during the reproduction season in summer, young of the year have not yet reached adult size by the end of our field season (early August) and adults (≥ 1 year old) are easily recognizable by their larger body size and shape upon capture, visual or photography observations. We considered only adult individuals in the analyses. The capture events occurred during the summer season (between mid-May and mid-August) and included individuals encountered and identified as non-breeder (1), breeder (2), or uncertain (3). An individual was identified as breeder when observed (directly or through photography) providing care to pups at dens, or when found lactating upon capture. Foxes could also be recovered dead (4) or not encountered (0). Because recoveries could happen at any time of the year, an individual found or reported dead between occasions t and $t+1$ was coded at occasion $t+1$. We relied only on resightings in the field to determine the state of an individual (alive or dead) and did not use data from telemetry collars due to early battery failure of some collars during winter. Preliminary data (2006–2012) indicated that all breeding individuals and 84.6% of non-breeders with an actively transmitting collar within the study area are sighted during the field season (Lai 2017). We, however, included the presence of a collar (active or not) in the analyses to evaluate its potential effects on recovery and survival probabilities of individuals.

The events coded in the encounter histories are related to the biological states of individuals (Fig. 1). We considered the following states: Alive and Breeding (AB), Alive and Non-Breeding (ANB), Newly Dead (ND), and Dead (D). The Newly Dead state was used for recovery of individuals only in the year of death. The state Dead was for foxes that died during an earlier interval and were, thus, no longer available for recoveries. Three kinds of parameters are used in a multi-event approach: the initial state probabilities, the probabilities of transition between states, and the probabilities of the events conditional on the underlying states. Here, transition probabilities correspond to the annual apparent survival (s) and the annual probability of breeding (b). The combined transition matrix is defined as (see Online Appendix S1 for step-by-step matrices),

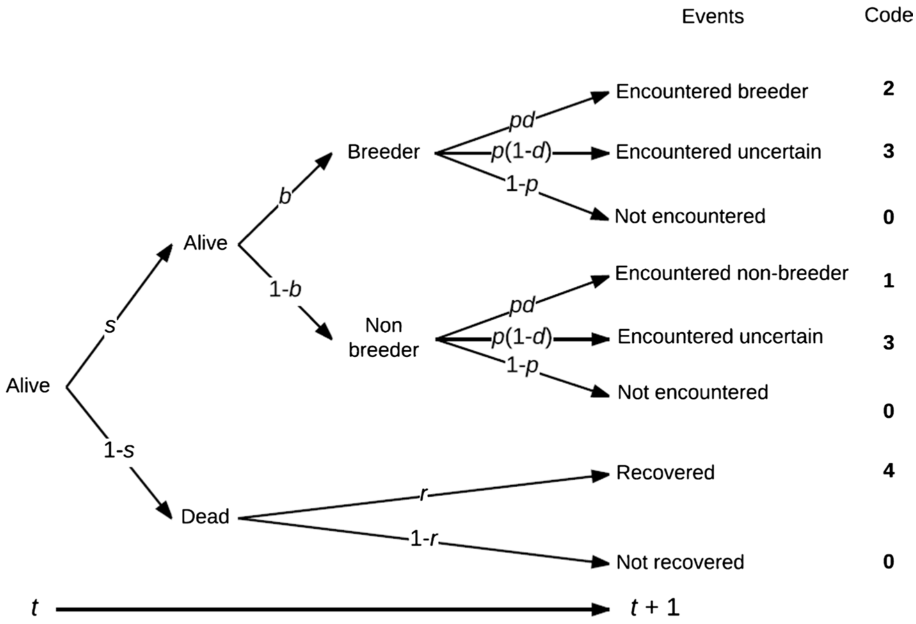

Fig. 1 Possible fates on summer season $t+1$ of adult arctic foxes marked on Bylot Island (Nunavut, Canada) during summer season t. The transition probabilities indicated within arrows correspond to the probabilities of surviving (s) and breeding (b). Event probabilities correspond to the probabilities of being encountered alive (p) and correctly identified as breeder or non-breeder (d), or of being recovered dead (r)

	AB	ANB	ND	D
AB	sb	$s(1-b)$	$1-s$	0
ANB	$s'b'$	$s'(1-b')$	$1-s'$	0
ND	0	0	0	1
D	0	0	0	1

where rows and columns represent, respectively, pre- and post-transition states. For example, the probability for a non-breeder to survive and become a breeder is $s'b'$.

The event probabilities correspond to the probabilities of being encountered alive during the breeding season (p), of correctly assigning the breeding status (uncertainty, d), or of being recovered dead (r). The event matrix relating events to states is, thus,

	“0”	“1”	“2”	“3”	“4”
AB	$1-p$	0	pd	$p(1-d)$	0
ANB	$1-p'$	$p'd'$	0	$p'(1-d')$	0
ND	$1-r$	0	0	0	r
D	1	0	0	0	0

where rows and columns relate biological states of individuals and events encountered in the field as described in the previous paragraph, respectively (see Online Appendix S1 for step by step matrices).

Our study design combined multiple sources of encounters (captures, direct or photographic observations, recoveries) that ran concurrently and which could have different detection rates. To minimize potential sources of heterogeneity related to these different sources, we separated recaptures from resightings (direct and photographic observations combined) using two encounter occasions each summer, one “dummy” and one real (Online Appendix S2), following Juillet et al. (2010). Direct and photographic observations were combined as resighting probabilities to improve the model ability to converge. Individuals observed or physically captured during the summer were coded in their corresponding occasion and probabilities of survival and reproduction were fixed at 1 for the time interval between these two occasions.

(d) Resource covariates

Annual lemming densities (both lemming species combined) were obtained in July from live-trapping capture–recapture estimates for 2004–2015 or from snap-trapping estimates converted to densities using known relationships for 2003 (see Gauthier et al. 2013 and Fauteux et al. 2015 for methods; Online Appendix S3). Lemmings reproduce in winter so that their spring densities are much better reflected by estimates obtained the following summer than by those obtained the preceding summer (Fauteux et al. 2015). The fates of foxes between summer season t and summer season $t+1$ can, thus, be influenced by lemming density as measured during both summer seasons. As in Millon and Bretagnolle (2008), this covariate was used in two ways. First, we compared annual arctic fox survival or breeding probabilities across the different phases of the lemming cycle: low (L) and high (H) during both summer season t and summer season $t+1$ (respectively, coded as “LH” and “LH + 1”). Second, we performed the same analyses using lemming density as a continuous variable (coded as “lem” for lemming density in summer season t and “lem + 1” for summer season $t+1$).

Starting in 2007, we delimited the contour of the goose colony with a helicopter and a GPS receiver each year in late June. The shape of the goose colony may vary slightly between years; therefore, we averaged the colony extent over the course of the study (see Online Appendix S4 for details). Foxes were classified as "in" or "out" of the goose colony if the average location of their captures and observations was inside or outside the average extent of the colony plus a 1.75-km buffer zone beyond which the colony was not considered a significant food resource for foxes (1.75 km is approximately half the radius of an arctic fox home range in our study area; Rioux et al. 2017; see Online Appendix S4 for details).

(e) Goodness-of-fit test and model selection

Before analyzing the data, we performed a goodness-of-fit (GOF) test for multi-state models (Pradel et al. 2003) using U-CARE (version 2.3.2; Choquet et al. 2009a), which considers absorbing states (state that cannot be left) such as the dead state. This allowed us to test for potential effects of trap-shyness, trap-happiness, or heterogeneity in the dataset. The GOF tests were conducted on a 13-occasion dataset where the dummy occasions were merged with the real occasions each year. Tests were conducted on sub-groups based on sex, colony access, and presence/absence of a collar. The general assumptions of the model were met since the goodness-of-fit tests revealed no lack of fit (females: $\chi^2=3.76$, $df=23$, $p>0.9$; males: $\chi^2=8.31$, $df=22$, $p>0.9$; inside the colony: $\chi^2=6.93$, $df=20$, $p>0.9$; outside the colony: $\chi^2=8.48$, $df=23$, $p>0.9$; with collar: $\chi^2=7.98$, $df=26$, $p>0.9$; without collar: $\chi^2=3.29$, $df=11$, $p>0.9$) and thus no overdispersion, allowing us to proceed with the multi-state modeling.

We performed data analysis using E-SURGE (version 1.9.0; Choquet et al. 2009b). We followed a step-down approach for model selection starting by modeling only event (i.e., encounter type) probabilities and then event and transition probabilities (i.e., survival and reproduction; per matrices described in Appendices S1 and S2) combined (Lebreton et al. 1992). For encounter probabilities, we tested the effects of monitoring intensification in 2007, presence/absence of a collar, sex, and breeding status. Intensification of monitoring was tested using different resighting probabilities before and after 2007, but constant within each of these two periods (noted t7 in model selection tables). We also tested if the probability of correctly assigning the breeding status differed between sexes. For breeding and survival probabilities, we tested effects related to the individual (i.e., presence/absence of a collar, sex, breeding status), and food resources (lemming densities and access to the goose colony per our predictions). We cannot distinguish between mortality and permanent emigration for foxes that were not resighted, which is a common problem in studies of carnivore survival (Barthold et al. 2016) and may lead to an underestimation of survival. We believe this problem was limited for our study population since a satellite tracking study showed that our study population was mainly resident and that the risk of dying was 3.4 times higher for foxes quitting the island compared to the residents (Lai et al. 2017). An underestimation of survival due to uncertain fate was, thus, likely limited.

Model selection was based on the AIC corrected for small sample size (Akaike's Information Criterion; Burnham and Anderson 2002). If several models were within two points of the lowest AIC_c, the most parsimonious model was retained as the best supported model. Once we reached a best model at the end of our two-step approach, we re-examined some effects not retained on encounter probabilities during our initial model selection but nonetheless present in neighboring models. E-SURGE coding of effects retained in our preferred model is presented in Online Appendix S5. To assess the statistical significance of some covariates, we did an analysis of deviance (ANODEV) when relevant (Grosbois et al. 2008). Encounter probabilities are reported as mean ± SE; whereas, effects on breeding and survival probabilities are reported as beta values with their 95% confidence intervals.

Results

A total of 229 adult arctic foxes (116 M and 113 F) were captured and ear-tagged in this study, of which 134 were equipped with a collar. We recaptured 65 ear-tagged foxes at least once (for a total of 79 recaptures) and 119 were resighted at least once through direct or photographic observation (for a total of 193 resightings). We recorded 11 dead foxes (5 from hunters).

Encounter probabilities

When modeling encounter probabilities alone, the most parsimonious of the best supported models (model 15) retained an effect of breeding status on capture and observation probabilities, and an additive effect of monitoring intensification in 2007 on observations (Online Appendix S6). Capture probability was higher for breeders (0.33 ± 0.04) than for non-breeders (0.09 ± 0.03). Observation probabilities were also higher for breeders than for non-breeders and increased after monitoring intensification (breeders before 2007, 0.22 ± 0.06; breeders after 2007, 0.42 ± 0.03; non-breeders before 2007, 0.16 ± 0.05; non-breeders after 2007, 0.32 ± 0.04). Moreover, although a sex effect on the probability of correctly assigning the breeding status was retained (model 21), the model without sex effect fitted equally well ($\Delta AIC_c = 0.04$, see Online Appendix S6) and had one less parameter ($d = 0.94 \pm 0.01$). We thus pursued model selection on reproductive and survival parameters without this sex effect on d. When modeling encounter probabilities alongside survival and reproductive probabilities, there were similar effects of breeding status and monitoring intensity on encounters (Online Appendix S7). Additionally, there was no evidence that sex or presence of a collar affected capture or observation probabilities ($\Delta\mathrm{AIC_c}$ of models with such effects was > 25, see Online Appendix S7). Recovery probability was low (0.07 ± 0.02). Although the model with collar effect on recovery was not retained when modeling encounter probabilities alone (Online Appendix S6), this effect was retained in our preferred model once survival and reproductive probabilities were added (Online Appendix S7). Recovery probability for individuals wearing a collar was slightly higher (0.10 ± 0.03) than for those without a collar (0.03 ± 0.02).

Individual effects on survival and reproduction

When modeling survival or breeding probabilities with only collar presence, sex, and breeding status, we found no effect of the presence of a collar or sex (Table 1). However, both survival and breeding probabilities varied temporally and according to the breeding status (Table 1; in the best model, beta for survival probabilities = 1.08 [0.06, 2.1]; beta for breeding probabilities = 1.75 [0.52, 2.99]). Breeders experienced higher survival than non-breeders (Fig. 2a). Similarly, foxes had a higher probability to breed if they had bred in the previous year than if they had not (Fig. 2b). Both survival and reproduction probabilities appeared highly variable between years (Fig. 2).

Table 1 Top models in the model selection for the effects of time, sex, breeding state, and presence of a collar on probabilities (P) of survival (s) and breeding (b) of arctic foxes on Bylot Island, Nunavut, Canada. For each model, we present the number of estimated parameters (N_p), the deviance, and the difference in the corrected AIC with the preferred model ($\Delta\mathrm{AIC_c}$)

Model#	P_s	P_b	N_p	Deviance	$\Delta\mathrm{AIC_c}$
43	Breed + time	Breed + time	35	2015.68	0.00
56	Time	Breed + time	34	2020.17	2.70
42	Breed + time	Time	34	2023.84	5.88
45	Breed + time	Time + sex	35	2022.80	7.12
44	Breed + time	Time + collar	35	2023.47	7.79
31	Time	Breed*time	44	2010.65	16.00
36	Breed + time	Breed*time + collar	46	2006.18	16.31
33	Time + collar	Breed*time	45	2009.91	17.64
34	Time + sex	Breed*time	45	2010.60	18.33

Interactions are denoted by a ‘*’. For all models, we used the effects retained in the most parsimonious of the best supported models (model 15) of Online Appendix S6 for encounter probabilities

Breed breeding state, *collar* presence of a collar

Resource effects on survival and reproduction

We found no evidence that the presence of geese or lemming abundance affected survival. None of these covariates was retained among our preferred models (Table 2; Fig. 3a). Furthermore, the ANODEV test was not significant when using either lemming density (models 75 vs 67 vs 70, Table 2; $F_{1,10} = 1.1$, $p > 0.1$) or the phase of the lemming cycle (models 75 vs 68 vs 70, Table 2; $F_{1,10} = 2.2$, $p > 0.1$) as a covariate.

We found strong evidence that the presence of geese and lemming abundance affected breeding probability as all or most of our preferred models (i.e., $\Delta\mathrm{AIC_c} < 2$) retained those two variables (Table 2). Foxes located inside the goose colony had higher breeding probabilities than those outside (Fig. 3b; beta = 0.76 [0.04, 1.49]). The strong positive effect of lemming abundance on fox breeding probability was confirmed by the ANODEV test (models 79 vs 66 vs 64, Table 2; $F_{1,10} = 27.0$, $p < 0.001$). Regardless of the breeding status at time t, the probability to breed again at time $t + 1$ was strongly affected by lemming density at $t + 1$ (Fig. 3b; beta = 0.62 [0.43, 0.82]).

Discussion

We used a unique opportunity to test whether demographic parameters of an arctic carnivore can be affected by the availability of multiple preys. Our long-term data set combined with a robust multi-event capture–recapture model allowed us to integrate multiple sources of encounter (live captures, visual and photographic observations, carcass recoveries) to improve precision of our estimates. Our results do not indicate an effect of food resources on adult apparent survival, but confirm that reproduction probabilities are highly food dependent. Other key findings include the rather high inter-annual variability of both survival and reproduction probabilities, the strong influence of breeding status on both survival and reproduction, and the absence of an effect of sex or wear of a collar on survival and reproduction.

Encounter probabilities

We confirmed that several factors affected arctic fox encounter probabilities. Reporting these factors is important for a better optimization of monitoring or sampling designs and allows the inclusion of known heterogeneity in encounter probabilities in capture–mark–recapture models. As seen in other species (Clobert 1995; Grosbois and Thompson 2005), breeding status influenced detectability and catchability of

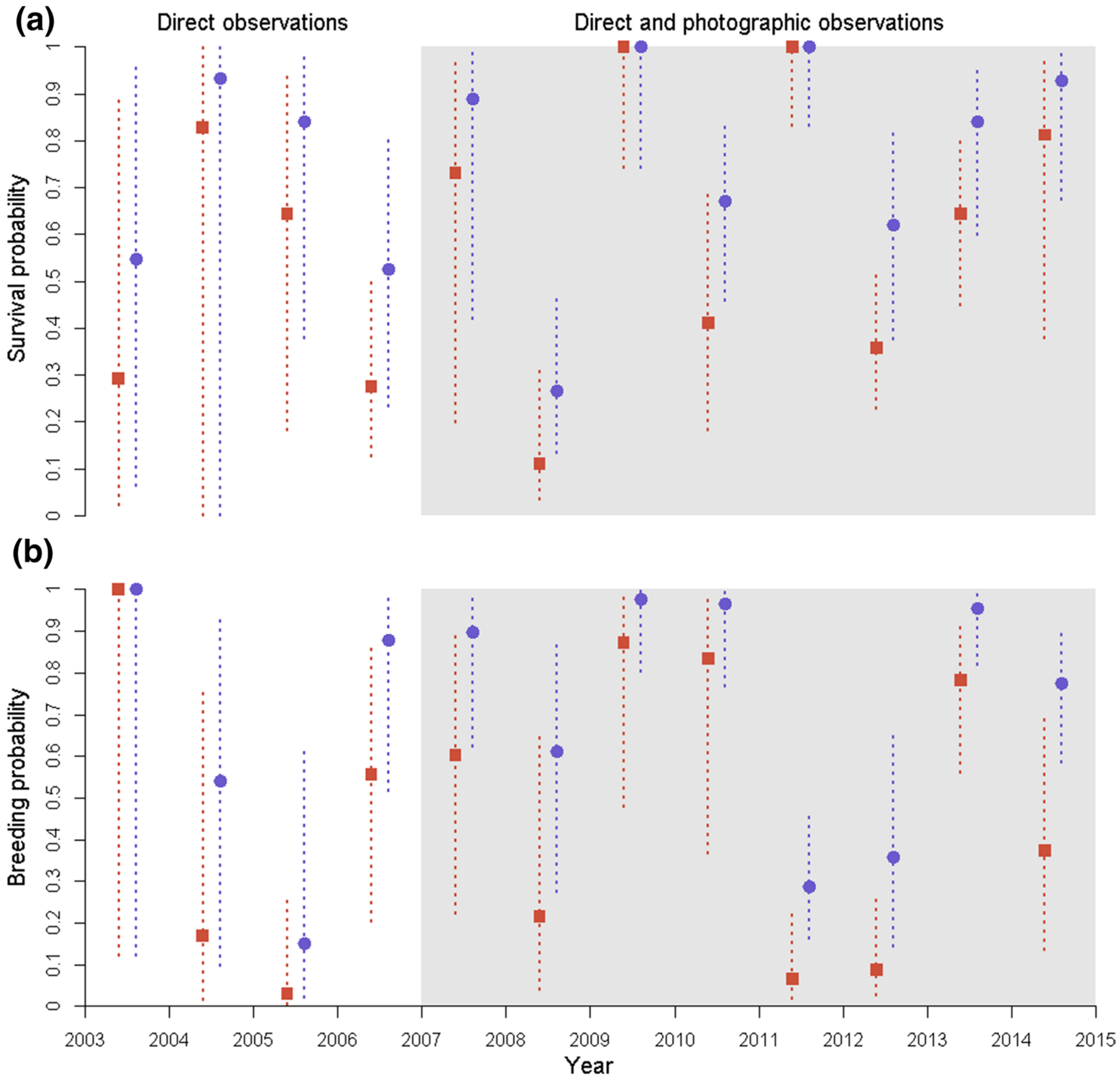

Fig. 2 Annual survival (**a**) and breeding (**b**) probabilities of arctic foxes that were breeders (blue circles) and non-breeders (red squares) in the previous year on Bylot Island, Nunavut, Canada (from model 43 Table 1). Error bars illustrate 95% confidence intervals

individuals, as the observation and especially capture probabilities were higher for breeders than for non-breeders (three times higher for capture probabilities), irrespective of sex. Arctic foxes may use their dens and remain in the same territory multiple years even if they do not produce pups during a breeding season (Eberhardt et al. 1982; Berteaux, unpublished data). However, the parental care provided by breeding foxes at dens, where most of our monitoring effort was concentrated, undoubtedly contributed to their higher encounter rate compared to non-breeders. The use of automated cameras doubled encounter probabilities. It is interesting to note that automated cameras increased the encounter rate of non-breeders considerably compared to live captures (0.32 vs 0.09), but less so for breeders (0.43 vs 0.32). Thus, automated cameras offer a great potential to increase the detection rate of non-breeders, which potentially solves the problem of underestimating survival of arctic foxes due to low detection probability during years with low rodent density (Meijer et al. 2008). The probability of correctly assigning the breeding status was very high and was not improved by cameras at dens.

Recovery rate was higher for individuals wearing a collar, which could be due to two reasons. First, the reward offered for the collar was indicated on the collar itself, which may have motivated hunters to report dead animals. Second, coordinates of immobile collars within the study area were used to locate carcasses. Although recovery was higher for collared foxes, survival rate did not differ between foxes with and without a collar, indicating that the presence of the collar and the reward did not increase their risk of dying.

Table 2 Top 20 models for individual (breeding status, collar presence, and sex) and resource covariates (annual lemming abundance and spatial location with respect to the goose colony) on probabilities (*P*) of survival (s), breeding (b), capture (c), resight (p), recovery (r), and of correctly assigning the breeding status (d) of arctic foxes on Bylot Island, Nunavut, Canada

Model#	P_s	P_b	P_c	P_p	P_r	P_d	N_p	Deviance	ΔAIC_c
117	Breed + time	Breed + [LH + 1] + goose	Breed	t7	Collar	*i*	25	2031.16	0.00
118	Breed + time	Breed + [LH + 1] + goose	Breed	Breed*t7	Collar	*i*	27	2027.47	0.73
104	Breed + time	Breed + time + goose	Breed	t7	Collar	*i*	35	2009.41	0.74
82	Breed + time	Breed + [lem + 1] + goose	Breed	Breed*t7	Collar	*i*	27	2027.65	0.91
94	Breed + time	Breed + time + goose	Breed	Breed*t7	Collar	*i*	37	2005.03	0.97
93	Breed + time	Breed + time + goose	Breed	t7	*i*	*i*	34	2012.24	1.28
114	Breed + time	Breed + [lem + 1] + goose	Breed	t7	Collar	*i*	25	2032.46	1.30
81	Breed + time	Breed + [lem + 1] + goose	Breed	t7	*i*	*i*	24	2035.30	1.93
79	Breed + time	Breed + time + goose	Breed	Breed + t7	*i*	*i*	36	2008.40	2.02
66	Breed + time	Breed + [lem + 1] + goose	Breed	Breed + t7	*i*	*i*	26	2031.19	2.24
75	Breed + time + goose	Breed + [lem + 1] + goose	Breed	Breed + t7	*i*	*i*	27	2029.00	2.26
61	Breed + time	Breed + [LH + 1]	Breed	Breed + t7	*i*	*i*	25	2036.07	4.91
43	Breed + time	Breed + time	Breed	Breed + t7	*i*	*i*	35	2015.68	7.01
116	Breed + time + goose	Breed + time	Breed	Breed + t7	*i*	*i*	36	2014.07	7.69
68	Breed + [LH + 1] + goose	Breed + [lem + 1] + goose	Breed	Breed + t7	*i*	*i*	17	2061.41	12.88
67	Breed + [lem + 1] + goose	Breed + [lem + 1] + goose	Breed	Breed + t7	*i*	*i*	17	2064.58	16.05
70	Breed + goose	Breed + [lem + 1] + goose	Breed	Breed + t7	*i*	*i*	16	2068.58	17.91
48	Breed + [LH + 1]	Breed + time	Breed	Breed + t7	*i*	*i*	25	2050.31	19.15
49	Breed + [lem + 1]	Breed + time	Breed	Breed + t7	*i*	*i*	25	2053.40	22.23
73	*i*	Breed + [lem + 1] + goose	Breed	Breed + t7	*i*	*i*	14	2082.90	28.00

We present the number of estimated parameters (N_p), the deviance, and the difference in the corrected AIC with the preferred model (ΔAIC_c). Interactions are denoted by a '*'. For complete model list, see Online Appendix S7

Breed breeding state, *collar* presence of a collar, *t7* before/after monitoring intensification in 2007, *i* constant, *goose* inside or outside the goose colony, *lem/lem + 1* annual lemming abundance in current or next year (+1), *LH/LH + 1* lemming abundance reduced to years of high and low abundance in current or next year (+1)

Survival probabilities

Apparent adult survival was highly variable in this population, with annual estimates ranging from 0.13 to 1.00 and averaging 0.64 (SE = 0.03, 95% CI = 0.59–0.69, Model 73). Adult survival seems also variable across arctic fox populations, with estimates of 0.75 in Alaska (Fay and Rausch 1992), 0.68 in Norway (Eide et al. 2012), 0.52, 0.58 and 0.31–0.68 in Canada (Samelius and Alisauskas (2017), Hiruki and Stirling (1989) and Macpherson (1969), respectively), and 0.33–0.60 in Sweden (Tannerfeldt et al. 1994; Tannerfeldt and Angerbjörn 1996; Meijer et al. 2008). Comparisons across studies are difficult due to varying methodologies. Yet it is safe to conclude that adult survival is generally low for arctic foxes, especially compared to other carnivore populations where adult survival can be > 0.80 (e.g., 0.82 for adult female black bears, Beston 2011; > 0.90 spotted hyenas, M'soka et al. 2016). Our estimation of annual survival of arctic foxes appears, however, comparable with values reported for other canid species such as wolves (O'Neil et al. 2017), coyotes (Van Deelen and Gosselink 2006) or red foxes (*Vulpes vulpes*, Korytin 2002) for which estimations were, respectively, 0.75, 0.59 and 0.56. Sex and wear of a collar did not influence survival probabilities. The absence of sex effect is not surprising given that the species is highly monomorphic. On a more technical note, the absence of collar effect on survival is useful information given the growth of movement ecology.

While adult survival in arctic foxes is often suspected to be driven by resource variation (Hiruki and Stirling 1989), neither lemmings nor geese affected fox survival in our analysis. This is surprising considering the importance of lemmings (Angerbjörn et al. 1999) and cached goose eggs (Careau et al. 2007a) in the diet of foxes. Similarly, a recent study near Karrak Lake in Canada reported non-significant effects of small mammal abundance and goose abundance on apparent adult survival (Samelius and Alisauskas 2017). Contrary to our results, they found a constant apparent survival of adults (estimate of 0.52) over their 15 years of study. According to the authors, this may be attributed to the important subsidies provided by two large colonies of arctic geese in the area (about 1 million nesting geese). Given that arctic foxes are physiologically well adapted to food scarcity (Fuglei and Oritsland 1999), it may be possible that food

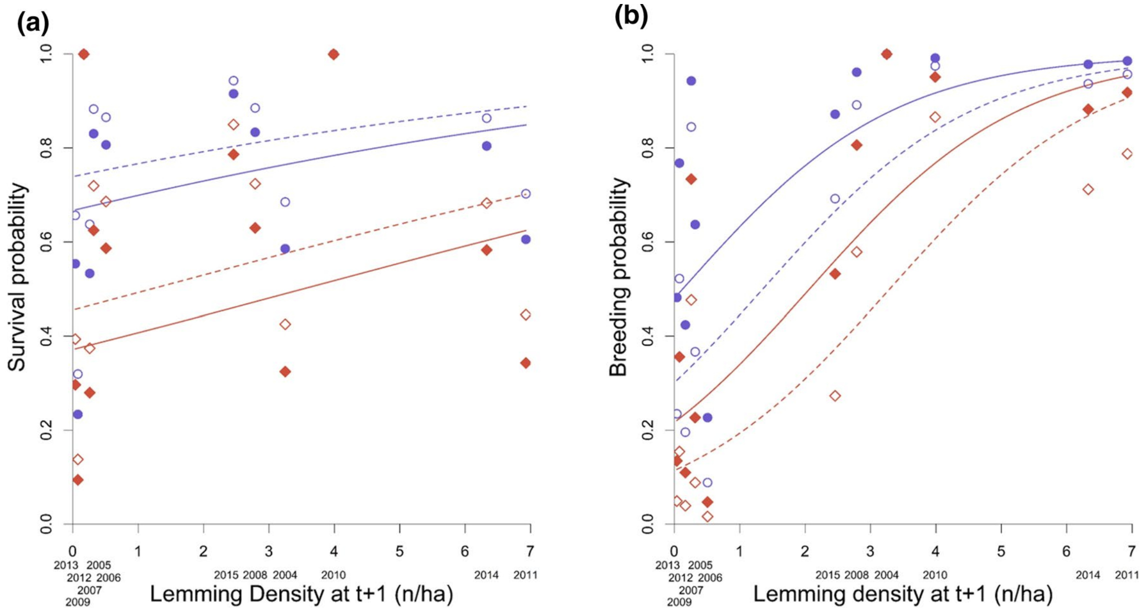

Fig. 3 Annual survival (**a**) and breeding (**b**) probabilities of arctic foxes that were breeders (blue dots) and non-breeders (red diamonds) in the previous year inside (filed symbols and plain lines) or outside (open symbols and dotted lines) a goose colony, in relation to next summer's lemming density on Bylot Island, Nunavut, Canada. In **a**, point estimates are from model 75 and predicted relationships are from model 67 in Table 1. In **b** point estimates are from model 94 and predicted relationships are from model 82 in Table 1 (see Online Appendix S8 for details)

availability in our study area never reached the threshold below which adult survival was compromised due to availability of goose-related resources.

Other potential factors enabling foxes to survive despite high fluctuations of terrestrial resources remain to be investigated thoroughly considering our dataset yielded survival estimates with large confidence intervals, especially prior to 2008. This imprecision may have affected our ability to detect biologically meaningful effects of resource availability. Bylot Island has the most intensive monitoring of a natural arctic fox population over a relatively large area and is one of the only six sites (out of 34 study areas) where capture–mark–recapture occurs extensively and annually (Berteaux et al. 2017b). This shows that despite massive field efforts, it is still not easy to obtain reliable estimates of vital rates for carnivores living in remote areas. Another limitation could be that we included terrestrial, but not marine, resources in our analysis. Foxes occasionally forage on sea ice during winter (Roth 2002, 2003; Lai et al. 2015). On Bylot Island, they do so especially when lemmings are scarce or if their territory is located far from the goose colony (Lai et al. 2017). The extent to which such access to allochthonous resources may have hidden survival costs of low terrestrial food availability is unknown. Finally, drivers of adult survival unrelated or indirectly related to food resources may also be at play. Positive effects of high food abundance could be weakened by an increase of predator density and then intraguild (Linnell and Strand 2000) and intraspecific competition (Rich et al. 2012). In carnivores, other parameters affecting adult survival are population density (e.g., wolverines, Brøseth et al. 2010), disease outbreaks (Prestrud et al. 1992), predation (e.g., spotted hyenas, Watts and Holekamp 2009), and climate variation (Grosbois et al. 2008) through direct effects on thermoregulation costs or indirect effects on food accessibility (Berteaux et al. 2017a). These clearly deserve further attention as well.

Maximum longevity in our study population is 8 years (Chevallier et al. 2017) but mean life expectancy as adult, calculated as − 1/ln(adult survival) (Munda and Hudnik 1991) is rather low, at only 2.2 years (− 1/ln 0.64). Complex trade-offs exist between reproduction, juvenile survival, and adult survival (Stearns 1989). Theory predicts that short-lived species should invest more in reproduction than survival and that reproduction could have a negative impact on subsequent survival (Stearns 1989). Our results indicating a higher impact of resource availability on reproduction than on survival suggests on the contrary that, when resources decrease, arctic foxes seem to be prioritizing their own survival. In addition, instead of non-breeders surviving better than breeders, survival probabilities of the latter were 10–20% higher than those of the former. This could be due to an apparently low cost of reproduction in arctic foxes (Tannerfeldt et al. 1998) or individual heterogeneity, with breeders being the highest-quality individuals, capable of sustaining both a higher survival and reproduction.

Reproduction probabilities

We found that breeding probability could quadruple between the worst (year of low lemming density outside the goose colony) and best (year of high lemming density inside the goose colony) conditions of food availability. As in other studies of the same (e.g., Angerbjörn et al. 1991), or other species (e.g., wolverines, Persson 2005; iberian lynx, Lopez-Bao et al. 2010; coyotes, Gese et al. 2016), our results support the hypothesis that prey availability is crucial to sustain reproduction in carnivores.

The probability of becoming a breeder in the following summer was affected by lemming density in the following summer but not in the current summer. This can be easily explained given that regulation of reproduction by food limitation may occur through reduced ovulation rate during winter, prenatal loss during spring, and litter size reduction during summer (Tannerfeldt et al. 1998). Other studies have shown the reliance on lemmings in spring for fox reproductive output (number of litters produced) and pointed that supplemental food during the previous fall season (for example, fall migrating geese) or during winter (dog pellets and carcasses provided for a conservation program) did not counteract the influence of small rodent cycles (Meijer et al. 2013; McDonald et al. 2017). Additional food such as goose eggs, which are brought back to the den by adults, may, however, contribute to pup survival until emergence from natal dens (when we can observe them). Indeed, breeding probabilities were 20% higher for individuals with a significant access to the goose colony than for those without. This further confirms that a spatial heterogeneity in reproduction exists in this canid population (Giroux et al. 2012).

We also found that breeders had a 30% higher probability of breeding the following year compared to non-breeders. Along with the possibility of individual heterogeneity within the population previously discussed, parental experience may increase reproductive probability through enhanced pup survival (Meijer et al. 2011; Rauset et al. 2015; Erlandsson et al. 2017). At Karrak Lake, only a small proportion of foxes (27%) were able to maintain long residency times (3–7 years) and it was suggested that these individuals contributed the most to the local recruitment of the population (Samelius and Alisauskas 2017). The relative contribution of individual quality, parental experience, and overall experience of the territory (dens and prey availability) on reproductive success remains to be determined.

Carnivores demography

The arctic fox is intensively monitored at many sites throughout the Arctic (Berteaux et al. 2017b). Some populations are endangered and thus heavily managed to foster recovery (e.g., Angerbjörn et al. 2013); while others are subject to intensive harvesting aimed at reducing abundance (Hersteinsson 1992). A better knowledge of the species population dynamics is essential to improve arctic fox population management. Our system offered interesting opportunities to study demographic effects of both spatial and temporal heterogeneity in prey abundance within population. We concluded that measured resources explained variability in probabilities of reproduction but not adult apparent survival. Demographic studies are necessary to understand population dynamics of carnivores and, more generally, to shed light on some of the critical processes structuring ecosystems. As a general rule in vertebrate ecology, influence of body size on adult survival increases with generation length, which in turn increases with body size (Oli 2004; Bielby et al. 2007). Whether this pattern holds within the order Carnivora is unclear because data on adult survival are still rare for this group (see van de Kerk et al. 2013) and the majority of the studies on this order are made on populations threatened by human activities (hunting; e.g., collared leopard, Williams et al. 2017, road accidents; e.g., amur tiger, Kerley et al. 2002, population control; e.g., free-ranging dog, Belo et al. 2017). However, food shortage does increase mortality of adults in wolves (Peterson et al. 1998) or lynx (O'Donoghue 1997), but does not impact survival of spotted hyenas (M'soka et al. 2016). Also, other studies on predators found that experienced breeders had higher fecundity and survival rate than non experienced in a tawny owl population (*Strix aluco,* Karell et al. 2009) and that prey abundance had weak influence on survival of Montagu's harrier (*Circus pygargus*, Millon and Bretagnolle 2008). Our study shows that combining long-term field effort with state-of-the-art techniques of data collection and analysis does open productive avenues to understand life history traits in difficult-to-study species such as mammalian carnivores.

Acknowledgements We thank the many field workers who collected data on Bylot Island and Nicolas Casajus who provided statistical advice. We also thank Roger Pradel, Rémi Choquet and Guillaume Souchay for their advice on multi-event capture–recapture analysis with software ESurge. We are grateful to several reviewers who provided constructive comments. This study was supported by (alphabetical order): Canada Foundation for Innovation, Canada Research Chairs Program, Fonds de recherche du Québec—Nature et technologies (FRQNT), International Polar Year program of Indian and Northern Affairs Canada, Kenneth M Molson Foundation, Mittimatalik Hunters and Trappers Organization, Natural Sciences and Engineering Research Council of Canada (NSERC), Network of Centers of Excellence of Canada ArcticNet, Northern Ecosystem Initiative (Environment Canada), Northern Scientific Training Program (Indian and Northern Affairs Canada), Nunavut Wildlife Management Board, Parks Canada Agency, Polar Continental Shelf Program (Natural Resources Canada), and Université du Québec à Rimouski (UQAR).

Author contribution statement DB initiated the capture-recapture program while DB and CC designed the current study. DB, CC, GG, and SL planned the field work and carried out data collection. CC carried out the analyses in collaboration with GG. All authors contributed to the redaction of the manuscript and approved the publication.

Compliance with ethical standards

Data accessibility The long-term data used in this study will be archived at the Dryad Digital Repository.

References

Amstrup SC, Mcdonald TL, Manly BFJ (2005) Handbook of capture-recapture analysis. Princeton University Press, Princeton

Angerbjörn A, Arvidson B, Norén E, Strömgren L (1991) The effect of winter food on reproduction in the Artic fox, Alopex lagopus: a field experiment. J Anim Ecol 60:705–714

Angerbjörn A, Tannerfeldt M, Erlinge S (1999) Predator-prey relationships: arctic foxes and lemmings. J Anim Ecol 68:34–49. https://doi.org/10.1046/j.1365-2656.1999.00258.x

Angerbjörn A, Hersteinsson P, Tannerfeldt M (2004a) Arctic Fox (Alopex lagopus). In: Sillero-Zubiri C, Hoffmann M, David WM (eds) Canids: foxes, wolves, jackals and dogs. IUCN, Gland, pp 117–123

Angerbjörn A, Hersteinsson P, Tannerfeldt M (2004b) Arctic foxes: consequences of resource predictability in the Arctic fox—two lifehistory strategies. In: The biology and conservation of wild canids, pp 163–172

Angerbjörn A, Eide NE, Dalén L et al (2013) Carnivore conservation in practice: replicated management actions on a large spatial scale. J Appl Ecol 50:59–67. https://doi.org/10.1111/1365-2664.12033

Audet A, Robbins C, Larivière S (2002) Alopex lagopus. Mamm Species 1410:1–10

Barthold JA, Loveridge AJ, Macdonald DW et al (2016) Bayesian estimates of male and female African lion mortality for future use in population management. J Appl Ecol 53:295–304. https://doi.org/10.1111/1365-2664.12594

Belo VS, Struchiner CJ, Werneck GL et al (2017) Abundance, survival, recruitment and effectiveness of sterilization of free-roaming dogs: a capture and recapture study in Brazil. PLoS One 12:1–19. https://doi.org/10.1371/journal.pone.0187233

Berteaux D, Gauthier G, Domine F et al (2017a) Effects of changing permafrost and snow conditions on tundra wildlife: critical places and times. Arct Sci 3:65–90. https://doi.org/10.1139/as-2016-0023

Berteaux D, Thierry AM, Alisauskas R et al (2017b) Harmonizing circumpolar monitoring of Arctic fox: benefits, opportunities, challenges and recommendations. Polar Res 36:1–13. https://doi.org/10.1080/17518369.2017.1319602

Beston JA (2011) Variation in life history and demography of the American black bear. J Wildl Manage 75:1588–1596. https://doi.org/10.1002/jwmg.195

Bielby J, Mace GM, Bininda-Emonds ORP et al (2007) The fast-slow continuum in mammalian life history: an empirical reevaluation. Am Nat 169:748–757. https://doi.org/10.1086/516847

Breitenmoser U, Breitenmoser-Würsten C, Capt S et al (2007) Conservation of the lynx Lynx lynx in the Swiss Jura Mountains. Wildl Biol 13:340–355. https://doi.org/10.2981/0909-6396(2007)13%5b340:COTLLL%5d2.0.CO;2

Brøseth H, Flagstad Ø, Wärdig C et al (2010) Large-scale noninvasive genetic monitoring of wolverines using scats reveals density dependent adult survival. Biol Conserv 143:113–120. https://doi.org/10.1016/j.biocon.2009.09.012

Burnham K, Anderson D (2002) Model selection and multi-model inference: a practical information-theoretic approach, 2nd edn. Springer Verlag, New York

Cameron C, Berteaux D, Dufresne F (2011) Spatial variation in food availability predicts extrapair paternity in the arctic fox. Behav Ecol 22:1364–1373. https://doi.org/10.1093/beheco/arr158

Careau V, Giroux J-F, Berteaux D (2007a) Cache and carry: hoarding behavior of arctic fox. Behav Ecol Sociobiol 62:87–96. https://doi.org/10.1007/s00265-007-0441-z

Careau V, Lecomte N, Giroux JF, Berteaux D (2007b) Common ravens raid arctic fox food caches. J Ethol 25:79–82. https://doi.org/10.1007/s10164-006-0193-7

Chevallier C, Hernández-Matías A, Real J et al (2015a) Retrofitting of power lines effectively reduces mortality by electrocution in large birds: an example with the endangered Bonelli's eagle. J Appl Ecol 52:1465–1473. https://doi.org/10.1111/1365-2664.12476

Chevallier C, Lai S, Berteaux D (2015b) Predation of arctic fox (*Vulpes lagopus*) pups by common ravens (*Corvus corax*). Polar Biol 39:1335–1341. https://doi.org/10.1007/s00300-015-1843-4

Chevallier C, Gauthier G, Berteaux D (2017) Age estimation of live arctic foxes *Vulpes lagopus* based on teeth condition. Wildl Biol 17:wlb.00304. https://doi.org/10.2981/wlb.00304

Choquet R, Lebreton J-D, Gimenez O (2009a) U-CARE: utilities for performing goodness of fit tests and manipulating capture–recapture data. Ecography (Cop) 32:1071–1074. https://doi.org/10.1111/j.1600-0587.2009.05968.x

Choquet R, Rouan L, Pradel R (2009b) Program E-SURGE: a software application for fitting multievent models. In: Thomson DL (ed) Modeling demographic processes in marked populations. Springer Science + Business Media, pp 845–865

Clobert J (1995) Capture-recapture and evolutionary ecology: a difficult wedding? J Appl Stat 22:989–1008. https://doi.org/10.1080/02664769524757

Dennis B, Otten MRM (2000) Joint effects of density dependence and rainfall on abundance of San Joaquin Kit Fox. J Wildl Manage 64:388–400

Eberhardt LE, Hanson WC, Bengton JL et al (1982) Arctic fox home range characteristic in an oil-development area. J Wildl Manage 46:183

Eide NE, Stien A, Prestrud P et al (2012) Reproductive responses to spatial and temporal prey availability in a coastal Arctic fox population. J Anim Ecol 81:640–648. https://doi.org/10.1111/j.1365-2656.2011.01936.x

Erlandsson R, Meijer T, Wagenius S, Angerbjörn A (2017) Indirect effects of prey fluctuation on survival of juvenile arctic fox (*Vulpes lagopus*): a matter of maternal experience and litter attendance. Can J Zool 95:239–246. https://doi.org/10.1139/cjz-2016-0103

Fauteux D, Gauthier G, Berteaux D (2015) Seasonal demography of a cyclic lemming population in the Canadian Arctic. J Anim Ecol 84:1412–1422. https://doi.org/10.1111/1365-2656.12385

Fay F, Rausch R (1992) Dynamics of the arctic fox population on St. Lawrence Island, Bering Sea. Arctic 45:393–397

Fryxell JM, Falls B, Falls EA et al (1999) Density dependence, prey dependence, and population dynamics of marten in Ontario. Ecology 80:1311–1321. https://doi.org/10.1890/0012-9658(1999)080%5b1311:DDPDAP%5d2.0.CO;2

Fuglei E, Oritsland NA (1999) Seasonal trends in body mass, food intake and resting metabolic rate, and induction of metabolic depression in arctic foxes (Alopex lagopus) at Svalbard. J Comp Physiol B 169:361–369

Fuller TTK, Sievert P (2001) Carnivore demography and the consequences of changes in prey availability. In: Gittleman JL, Funk SM, Macdonald DW, Wayne RK (eds) Carnivore conservation. The University of Press, Cambridge, p 163

Gagnon CA, Berteaux D (2009) Integrating traditional ecological knowledge and ecological science: a question of scale. Ecol Soc 14:19

Gauthier G, Berteaux D, Bêty J et al (2011) The tundra food web of Bylot Island in a changing climate and the role of exchanges between ecosystems. Écoscience 18:223–235. https://doi.org/10.2980/18-3-3453

Gauthier G, Bêty J, Cadieux MC et al (2013) Long-term monitoring at multiple trophic levels suggests heterogeneity in responses to climate change in the Canadian Arctic tundra. Philos Trans R Soc Lond B Biol Sci 368:20120482. https://doi.org/10.1098/rstb.2012.0482

Gese EM, Roberts BM, Knowlton FF (2016) Nutritional effects on reproductive performance of captive adult female coyotes (Canis latrans). Anim Reprod Sci 165:69–75. https://doi.org/10.1016/j.anireprosci.2015.12.009

Giroux M-A, Berteaux D, Lecomte N et al (2012) Benefiting from a migratory prey: spatio-temporal patterns in allochthonous subsidization of an arctic predator. J Anim Ecol 81:533–542. https://doi.org/10.1111/j.1365-2656.2011.01944.x

Gorman TA, McMillan BR, Erb JD et al (2008) Survival and cause-specific mortality of a protected population of river otters in Minnesota. Am Midl Nat 159:98–109. https://doi.org/10.1674/0003-0031(2008)159

Grosbois V, Thompson PM (2005) North Atlantic climate variation influences survival in adult fulmars. Oikos 109:273–290. https://doi.org/10.1111/j.0030-1299.2005.13774.x

Grosbois V, Gimenez O, Gaillard J-M et al (2008) Assessing the impact of climate variation on survival in vertebrate populations. Biol Rev 83:357–399. https://doi.org/10.1111/j.1469-185X.2008.00047.x

Gruyer N, Gauthier G, Berteaux D (2008) Cyclic dynamics of sympatric lemming populations on Bylot Island, Nunavut, Canada. Can J Zool 86:910–917. https://doi.org/10.1139/Z08-059

Hersteinsson P (1992) Demography of the arctic fox (Alopex lagopus) population in Iceland. In: Mccullough DR, Barrett RH (eds) International conference on population dynamics and management of vertebrates—wildlife 2001: populations. Elsevier Appl Sci Publ Ltd., Barking Essex, pp 954–964

Hiruki L, Stirling I (1989) Population dynamics of the arctic fox, Alopex lagopus, on Banks Island, Norwest Territories. Can Field-Nat Ottawa 103:380–387

Juillet C, Choquet R, Gauthier G, Pradel R (2010) A capture-recapture model with double-marking, live and dead encounters, and heterogeneity of reporting due to auxiliary mark loss. J Agric Biol Environ Stat 16:88–104. https://doi.org/10.1007/s13253-010-0035-5

Karanth KU, Chellam R (2009) Carnivore conservation at the crossroads. Oryx 43:1. https://doi.org/10.1017/S003060530843106X

Karell P, Ahola K, Karstinen T et al (2009) Population dynamics in a cyclic environment: consequences of cyclic food abundance on tawny owl reproduction and survival. J Anim Ecol 78:1050–1062. https://doi.org/10.1111/j.1365-2656.2009.01563.x

Kerley LL, Goodrich JM, Miquelle DG et al (2002) Effects of roads and human disturbance on Amur tigers. Conserv Biol 16:97–108. https://doi.org/10.1046/j.1523-1739.2002.99290.x

Korytin N (2002) Analysis of survival of the red fox (*Vulpes vulpes* L.) at the phases of population growth and decline. Russ J Ecol 33:201–208. https://doi.org/10.1023/A:1015479507723

Krebs CJ (2013) Population fluctuations in rodents. The University of Chicago Press, Chicago

Lai S (2017) Organisation socio-spatiale et stratégie de mouvement d'une population de renards arctiques dans un contexte de fluctuations spatio-temporelles des ressources. Université du Québec à Montréal

Lai S, Bêty J, Berteaux D (2015) Spatio–temporal hotspots of satellite-tracked arctic foxes reveal a large detection range in a mammalian predator. Mov Ecol 3:1–10. https://doi.org/10.1186/s40462-015-0065-2

Lai S, Bêty J, Berteaux D (2017) Movement tactics of a mobile predator in a meta-ecosystem with fluctuating resources: the arctic fox in the High Arctic. Oikos 126:937–947. https://doi.org/10.1111/oik.03948

Lebreton JD, Burnham KP, Clobert J, Anderson DR (1992) Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecol Monogr 62:67–118. https://doi.org/10.2307/2937171

Legagneux P, Gauthier G, Berteaux D et al (2012) Disentangling trophic relationships in a High Arctic tundra ecosystem through food web modeling. Ecology 93:1707–1716. https://doi.org/10.1890/11-1973.1

Legagneux P, Gauthier G, Lecomte N et al (2014) Arctic ecosystem structure and functioning shaped by climate and herbivore body size. Nat Clim Chang E2168:1–5. https://doi.org/10.1038/NCLIMATE2168

Linnell JDC, Strand O (2000) Interference interactions, co-existence and conservation of mammalian carnivores. Biodivers Res 6:169–176. https://doi.org/10.1046/j.1472-4642.2000.00069.x

Lopez-Bao JV, Palomares F, Rodriguez A, Delibes M (2010) Effects of food supplementation on home-range size, reproductive success, productivity and recruitment in a small population of Iberian lynx. Anim Conserv 13:35–42. https://doi.org/10.1111/j.1469-1795.2009.00300.x

Loveridge AJ, Valeix M, Chapron G et al (2016) Conservation of large predator populations: demographic and spatial responses of African lions to the intensity of trophy hunting. Biol Conserv 204:247–254. https://doi.org/10.1016/j.biocon.2016.10.024

M'soka J, Creel S, Becker MS, Droge E (2016) Spotted hyaena survival and density in a lion depleted ecosystem: the effects of prey availability, humans and competition between large carnivores in African savannahs. Biol Conserv 201:348–355. https://doi.org/10.1016/j.biocon.2016.07.011

Mace RD, Carney DW, Chilton-Radandt T et al (2012) Grizzly bear population vital rates and trend in the northern continental divide ecosystem, Montana. J Wildl Manage 76:119–128. https://doi.org/10.1002/jwmg.250

Macpherson AH (1969) The dynamics of Canadian arctic fox populations. Can Wildl Serv Rep Ser 8:1–50

Martínez-García M, Lorda-Sanchez I, García-Hoyos M et al (2010) Síndrome de Holt-Oram: descripción de 7 casos. Med Clin (Barc) 135:653–657. https://doi.org/10.1016/j.medcli.2010.04.013

McDonald RS, Roth JD, Baldwin FB (2017) Goose persistence in fall strongly influences Arctic fox diet, but not reproductive success, in the southern Arctic. Polar Res. https://doi.org/10.1080/17518369.2017.1324652

Meijer T, Norén K, Hellström P et al (2008) Estimating population parameters in a threatened arctic fox population using molecular tracking and traditional field methods. Anim Conserv 11:330–338. https://doi.org/10.1111/j.1469-1795.2008.00188.x

Meijer T, Norén K, Angerbjörn A (2011) The impact of maternal experience on post-weaning survival in an endangered arctic fox population. Eur J Wildl Res 57:549–553. https://doi.org/10.1007/s10344-010-0463-0

Meijer T, Elmhagen B, Eide NE, Angerbjörn A (2013) Life history traits in a cyclic ecosystem: a field experiment on the arctic fox. Oecologia 173:439–447. https://doi.org/10.1007/s00442-013-2641-8

Millon A, Bretagnolle V (2008) Predator population dynamics under a cyclic prey regime: numerical responses, demographic parameters and growth rates. Oikos 117:1500–1510. https://doi.org/10.1111/j.0030-1299.2008.16458.x

Munda IM, Hudnik V (1991) Trace metal content in some seaweeds from the Northern Adriatic. Bot Mar 34:241–250

O'Donoghue M (1997) Numerical responses of Coyotes and Lynx to the snowshoe hare cycle. Oikos 80:150–162

O'Neil ST, Bump JK, Beyer DE (2017) Spatially varying density dependence drives a shifting mosaic of survival in a recovering apex predator (Canis lupus). Ecol Evol 7:9518–9530. https://doi.org/10.1002/ece3.3463

Oli MK (2004) The fast–slow continuum and mammalian life-history patterns: an empirical evaluation. Basic Appl Ecol 5:449–463. https://doi.org/10.1016/j.baae.2004.06.002

Persson J (2005) Female wolverine (Gulo gulo) reproduction: reproductive costs and winter food availability. Can J Zool 83:1453–1459. https://doi.org/10.1139/z05-143

Peterson RO, Thomas NJ, Thurber JM et al (1998) Population limitation and the wolves of Isle Royale. J Mammal 79:828. https://doi.org/10.2307/1383091

Pradel R (2005) Multievent: an extension of multistate capture-recapture models to uncertain states. Biometrics 61:442–447. https://doi.org/10.1111/j.1541-0420.2005.00318.x

Pradel R, Wintrebert CM, Gimenez O (2003) A proposal for a goodness-of-fit test to the Arnason-Schwarz multisite capture-recapture model. Biometrics 59:43–53

Prestrud P, Krogsrud J, Gjertz I (1992) The occurrence of rabies in the Svalbard Islands of Norway. J Wildl Dis 28:57–63. https://doi.org/10.7589/0090-3558-28.1.57

Rauset GR, Low M, Persson J (2015) Reproductive patterns result from age-related sensitivity to resources and reproductive costs in a mammalian carnivore. Ecology 96:3153–3164. https://doi.org/10.1890/15-0262.1

Reed A, Hughes R, Boyd H (2002) Patterns of distribution and abundance of greater snow geese on Bylot Island, Nunavut, Canada 1983–1998. Wildfowl 53:53–65

Rich LN, Mitchell MS, Gude JA, Sime CA (2012) Anthropogenic mortality, intraspecific competition, and prey availability influence territory sizes of wolves in Montana. J Mammal 93:722–731. https://doi.org/10.1644/11-mamm-a-079.2

Rioux M-J, Lai S, Casajus N et al (2017) Winter home range fidelity and extraterritorial movements of Arctic fox pairs in the Canadian High Arctic. Polar Res 36:11. https://doi.org/10.1080/17518369.2017.1316930

Roth JD (2002) Temporal variability in the diet of artic foxes as reflected in stable-carbon isotopes; the importance of sea ice. Oecologia 133:70–77

Roth JD (2003) Variability in marine resources affects arctic fox population dynamics. J Anim Ecol 72:668–676. https://doi.org/10.1046/j.1365-2656.2003.00739.x

Samelius G (2004) Foraging behaviours and population dynamics of arctic foxes. Arctic 57:441–443. https://doi.org/10.14430/arctic521

Samelius G, Alisauskas RT (2017) Components of population growth for Arctic foxes at a large Arctic goose colony: the relative contributions of adult survival and recruitment. Polar Res 36:6. https://doi.org/10.1080/17518369.2017.1332948

Samelius G, Alisauskas RT, Hobson KA, Larivière S (2007) Prolonging the arctic pulse: long-term exploitation of cached eggs by arctic foxes when lemmings are scarce. J Anim Ecol 76:873–880. https://doi.org/10.1111/j.1365-2656.2007.01278.x

Sedinger JS, White GC, Espinosa S et al (2010) Assessing compensatory versus additive harvest mortality: an example using greater Sage-Grouse. J Wildl Manage 74:326–332. https://doi.org/10.2193/2009-071

Stearns S (1989) Trade-offs in life-history evolution. Funct Ecol 3:259–268

Tannerfeldt M, Angerbjörn A (1996) Life history strategies in a fluctuating environment: establishment and reproductive success in the arctic fox. Ecography (Cop) 19:209–220

Tannerfeldt M, Angerbjorn A, Arvidson B et al (1994) The effect of summer feeding on juvenile arctic fox survival-a field experiment. Ecography (Cop) 17:88–96. https://doi.org/10.1111/j.1600-0587.1994.tb00080.x

Tannerfeldt M, Angerbjörn A, Angerbjorn A (1998) Fluctuating resources and the evolution of litter size in the arctic fox. Oikos 83:545–559. https://doi.org/10.2307/3546681

Tarroux A, Berteaux D, Bêty J (2010) Northern nomads: ability for extensive movements in adult arctic foxes. Polar Biol 33:1021–1026. https://doi.org/10.1007/s00300-010-0780-5

Tarroux A, Bêty J, Gauthier G, Berteaux D (2012) The marine side of a terrestrial carnivore: intra-population variation in use of allochthonous resources by arctic foxes. PLoS One 7:e42427. https://doi.org/10.1371/journal.pone.0042427

Therrien J, Gauthier G, Korpimäki E, Bêty J (2014) Predation pressure by avian predators suggests summer limitation of small-mammal populations in the Canadian Arctic. Ecology 95:56–67

Treves A, Chapron G, López-Bao JV et al (2017) Predators and the public trust. Biol Rev 92:248–270. https://doi.org/10.1111/brv.12227

van de Kerk M, de Kroon H, Conde DA, Jongejans E (2013) Carnivora population dynamics are as slow and as fast as those of other mammals: implications for their conservation. PLoS One 8:e70354. https://doi.org/10.1371/journal.pone.0070354

Van Deelen TR, Gosselink TE (2006) Coyote survival in a row-crop agricultural landscape. Can J Zool 84:1630–1636. https://doi.org/10.1139/Z06-170

Watts HE, Holekamp KKE (2009) Ecological determinants of survival and reproduction in the spotted Hyena. J Mammal 90:461–471. https://doi.org/10.1644/08-MAMM-A-136.1

Williams ST, Williams KS, Lewis BP, Hill RA (2017) Population dynamics and threats to an apex predator outside protected areas: implications for carnivore management. R Soc Open Sci. https://doi.org/10.1098/rsos.161090