ARTICLE

Indirect effects of prey fluctuation on survival of juvenile arctic fox (*Vulpes lagopus*): a matter of maternal experience and litter attendance

R. Erlandsson, T. Meijer, S. Wagenius, and A. Angerbjörn

Abstract: Reproductive experience affects juvenile survival in a wide range of species with possible links to differences in foraging capacity and predation. Using supplementary feeding, we aimed to limit direct effect of prey abundance to investigate indirect effects of small-rodent availability and maternal experience on juvenile summer survival rates in an endangered population of arctic fox (*Vulpes lagopus* (L., 1758)). We used data spanning 7 years, included a complete small-rodent cycle, comprising 49 litters and 394 cubs. The effect of small-rodent abundance on juvenile survival depended on maternal breeding experience. Cubs born by first-time-breeding females had lower survival rate when small-rodent abundance was low compared with juveniles born to experienced mothers who remained unaffected. It was unlikely due to starvation, as physical condition was unrelated to survival. Instead, we favour the explanation that intraguild predation was an important cause of mortality. There was a negative relationship between survival and amount of time cubs were left unattended, suggesting that parental behaviour affected predation. We propose that a prey switch related to small-rodent abundance caused fluctuations in intraguild predation pressure and that inexperienced females were less able to cope with predation when small rodents were scarce.

Key words: arctic fox, *Vulpes lagopus*, juvenile survival, small rodents, cyclic, maternal experience, behaviour, intraguild predation.

Résumé : L'expérience de reproduction a une incidence sur la survie des juvéniles chez de nombreuses espèces, ce qui pourrait être relié à des variations de la capacité d'approvisionnement et de la prédation. En utilisant l'alimentation complémentaire, nous avons tenté de limiter l'effet direct de l'abondance des proies afin d'étudier les effets indirects de la disponibilité de petits rongeurs et de l'expérience maternelle sur les taux de survie estivale des juvéniles dans une population menacée de renards arctiques (*Vulpes lagopus* (L., 1758)). Nous avons utilisé des données sur 7 années, incluant un cycle complet de petits rongeurs, qui comprennent 49 portées et 394 renardeaux. L'effet de l'abondance des petits rongeurs sur la survie des juvéniles dépendait de l'expérience de reproduction maternelle. Les renardeaux nés de femelles qui se reproduisaient pour la première fois présentaient des taux de survie plus faibles, quand l'abondance de petits rongeurs était faible, que les jeunes nés de mères expérimentées dont le taux de survie ne changeait pas. Cela n'est probablement pas dû à la privation de nourriture, puisqu'il n'y a pas de relation entre l'embonpoint et la survie. Nous privilégions plutôt l'explication voulant que la prédation intraguilde ait été une importante cause de mortalité. Il y avait une relation négative entre la survie et le temps que les renardeaux passaient sans surveillance, ce qui donne à penser que le comportement parental avait une incidence sur la prédation. Nous proposons qu'un changement de proies associé à l'abondance de petits rongeurs a causé des fluctuations de la pression de prédation intraguilde et que les femelles inexpérimentées étaient moins en mesure de faire face à la prédation quand les petits rongeurs se faisaient rares. [Traduit par la Rédaction]

Mots-clés : renard arctique, *Vulpes lagopus*, survie des juvéniles, petits rongeurs, cyclique, expérience maternelle, comportement, prédation intraguilde.

Introduction

In a wide range of mammalian species, prior breeding experience has been linked to higher offspring survival (e.g., red deer (*Cervus elaphus* L., 1758), fallow deer (*Dama dama* (L., 1758)), mountain gorilla (*Gorilla beringei* Matschie, 1903), and arctic fox (*Vulpes lagopus* (L., 1758))) (Guinness et al. 1978; San José et al. 1999; Robbins et al. 2006; Meijer et al. 2011). Possible mechanisms behind lower performance by inexperienced parents include a reduced ability to provide food and protect offspring from predation. Such a difference would especially be expected in species with large parental investment.

Food availability is fundamental for both survival and growth. For mammalian juveniles, the mother provides the primary food during lactation, but parents often continue to provide food for their offspring after weaning (Pond 1977). For example, young carnivores generally rely on parental food provisioning long after weaning, as they are often incapable of hunting for their own food and need training before being able to survive on their own (Ewer 1973; Bekoff et al. 1984; Gittleman 1994). Food availability for juveniles might thus not only depend on food abundance in general, but can also be modified by parental foraging skill and effort (Lack 1954). One mechanism where lower juvenile survival rate has been associated with inexperienced parents is when inexperienced parents have lower hunting and feeding efficiency (Daunt et al. 2007). In species where juveniles often starve to death, the importance of foraging experience could be especially pronounced. For example, in lions (*Panthera leo* (L., 1758)) faced with substantial

R. Erlandsson, T. Meijer, S. Wagenius, and A. Angerbjörn. Department of Zoology, Stockholm University, SE-106 91 Stockholm, Sweden.
Corresponding author: Rasmus Erlandsson (email: rasmus.erlandsson@zoologi.su.se).

seasonality in prey abundance, cub mortality was higher in dry seasons, but the mortality of older individuals remained unaffected (Packer et al. 1988). Similarly, juvenile survival of arctic foxes was found to be lower during years with low small-rodent abundance (Tannerfeldt et al. 1994).

Young animals in general are more vulnerable to predation because of their smaller body size, undeveloped vigilance and senses, but also because of a lack of defence and experience (Lay 1974; Caro 1987; Longland and Jenkins 1987; Arenz and Leger 2000). A den or a burrow can reduce the risk of predation, but active protection, where parents prevent attacks by warning or fighting off intruders, may be necessary to achieve efficient protection (Doolan and Macdonald 1997). If parents are less efficient in defending their offspring against predators, then there can be considerable losses when predation pressure is high (Doolan and Macdonald 1997). Inexperienced parents can have a lower vigilance and capability to cope with predators of certain species (e.g., in cheetahs, *Acinonyx jubatus* (Schreber, 1775)) (Durant 2000). Therefore, predation could be an alternative explanation to lowered juvenile survival for inexperienced parents (Durant 2000; Meijer et al. 2011).

Food and protection are thus two basic requirements, but there could also be a trade-off between the two in which the need for hunting may keep parents from being vigilant at the rearing site. If hunting takes more time, due to a lower hunting efficiency, then juveniles could be left alone for longer periods of time. Inexperienced parents might thus leave juveniles unattended for longer. This could increase the risk of both predation and starvation.

Meijer et al. (2011) showed that juvenile survival in Scandinavian arctic foxes provided with supplementary food (dog food) was related to maternal experience and suggested that this was due to an increased risk of predation rather than starvation. The observations were based on a short-term study, with data from a single year. In a stable environment, such differences in reproductive performance between individuals could be expected to be consistent over time. However, when temporal fluctuations affect living conditions, a short-term study could give a biased view of a species ecology and evolutionary history. It could therefore be necessary to investigate how animals respond to different levels of fluctuation in variable environments.

At high latitudes in the northern hemisphere, many mammal and bird species (e.g., voles and ptarmigan) have fluctuating population dynamics. Small-rodent populations (e.g., voles and lemmings) can range from extremely low densities to being very abundant during peak years (increasing by 20–500 times) (Collett 1877; Elton 1924; Norrdahl 1995; Krebs 2013). This high variance in small-rodent abundance has a major impact on the reproduction of several predator species with a northern distribution (Korpimäki and Norrdahl 1989; Ims and Fuglei 2005; Meijer et al. 2013). Some predators such as the arctic fox and some birds of prey even abstain from breeding if small rodents are too scarce (Korpimäki and Norrdahl 1989; Meijer et al. 2013). During peak years of small-rodent abundance, all predation tends to be focused on this prey type. Even larger carnivores such as wolverines (*Gulo gulo* (L., 1758)) and Golden Eagles (*Aquila chrysaetos* (L., 1758)) can take advantage of the high small-rodent availability (Landa et al. 1997; Nyström et al. 2006). However, as rodent populations crash, predators could switch to alternative prey species (Murdoch 1969; Hellström et al. 2014), also including smaller carnivores (Korpimäki and Norrdahl 1989). Hersteinsson's hypothesis (Norén et al. 2012) predicts that intraguild predation pressure should increase with low basal prey abundance, drawing parallels between the situation of the arctic fox as a prey species and observations that many birds of prey switch from small rodents to mustelids when small rodents are declining (Korpimäki and Norrdahl 1989).

The arctic fox is a small canid and mesopredator living in arctic and subarctic tundra (Angerbjörn et al. 2004). Inland populations depend heavily on microtine rodents and both litter size and juvenile survival is closely related to small-rodent population cycles (Elmhagen et al. 2000; Meijer et al. 2013). Low arctic fox cub survival has been associated with starvation, as well as predation by other carnivores such as the larger red fox (*Vulpes vulpes* (L., 1758)), wolverine, and occasionally the brown bear (*Ursus arctos* L., 1758). Furthermore, birds of prey (e.g., Golden Eagle) are known to prey on arctic fox cubs (Angerbjörn et al. 2004).

For arctic foxes, offspring of first-time-breeding females showed lower summer survival during a single year with decreasing small-rodent abundance, which is suggested to be related to intraguild predation (Meijer et al. 2011). However, it remains unclear how general this effect would be throughout the small-rodent cycle. In a wild population, however, it is difficult to separate the effect of food limitation from that of intraguild predation, especially if they interact. Provision of supplementary food during the summer has been shown to reduce mortality in juvenile arctic foxes (Tannerfeldt et al. 1994) and improved physical condition of meagre cubs (C. Bergman, unpublished data). Providing supplementary food could thus work as an experimental treatment in identifying indirect effects of fluctuations in small-rodent abundance, such as variation in predation pressure, on juvenile survival by controlling for the direct effect (starvation).

As inland arctic foxes depend on small rodents, long-term data on small-rodent abundance, including all phases of a small-rodent cycle, is necessary to get a wider understanding of how juvenile survival and the population dynamics of the arctic fox are related to fluctuations in small-rodent abundance. In this study, we include and build upon the results of Meijer et al. (2011), putting them in to a more ecologically relevant setting. We expand the time scale, using juvenile survival estimates from a long-term (7 years) data set that span more than a whole small-rodent cycle and that comprise 49 arctic fox litters and 394 cubs that have been provided supplementary food.

We test the following hypotheses: (hypothesis 1) arctic fox juvenile summer survival increases with small-rodent abundance and (hypothesis 2) cubs of first-time-breeding females have a lower juvenile summer survival than cubs of females with breeding experience, but the difference is smaller during years when conditions are favourable. To provide a mechanistic explanation, we investigate if parental behaviour can account for differences in survival by testing the following hypotheses: (hypothesis 3) juvenile survival should increase with parental attendance of active cubs and (hypothesis 4) first-time breeders leave there cubs unattended more often.

Materials and methods

Study area

Data were collected from the arctic fox population located in the Helags area (63°00′N, 12°30′E), in the county of Jämtland, Sweden. The area is about 3400 km², consisting of low and high mountain tundra above the tree line (Borgström 1979). The area is generally snow covered for more than 225 days per year, from the beginning of October until the beginning of June (mean values for 1961–1990; SMHI 2016). Reindeer herding occurs in some parts of the area, as well as outdoor tourism.

Conservation measures as controlling factors

The Scandinavian arctic fox population was regarded as critically endangered during the time of the study (Angerbjörn et al. 2004) and is also a protected species in the European Union. Conservation measures in the form of supplementary food have been carried out at all known inhabited arctic fox dens in the research area since the late 1990s together with large-scale red fox culling (Tannerfeldt et al. 1994; Angerbjörn et al. 2013). Commercial dog food was provided in feeding stations located 50–100 m away from

dens. Food was refilled in March (75–100 kg) and refilled in June if needed (50–75 kg). During summer, feeding stations were checked in July and refilled in August (50–100 kg). In late December, another refill of 75–100 kg was carried out. All dens were treated equally with the same amount of food provisioned. Despite being provided with supplementary food, adults were still observed feeding juveniles prey such as small rodents and occasionally passerine birds. Carcasses of small rodents were found at den sites. Supplementary dog food tended to be left untouched in feeding stations when prey availability was high (R. Erlandsson, personal observation), suggesting that foxes preferred natural prey over dog food. No differences were apparent between experienced and inexperienced females with respect to their usage of supplementary food. A few juveniles started to use the feeding stations by themselves during the latter half of August.

Field method

Data were collected every year in July and August, from 2008 to 2014. All known arctic fox dens in the area ($n = 69$) were monitored and visited at least once in July after weaning to monitor the population and identify breeding (no reproduction occurred in 2009 and 2012, which coincided with low small-rodent abundance). Dens with cubs were observed for at least 24 h, as the high latitude provided daylight even at nighttime, and the number of cubs were recorded. Some dens were observed for up to 50 h, because of bad weather or low visibility, to ensure that the quality of observations was sufficient. Arctic foxes were trapped in baited live traps and tagged at occupied dens. Trapping was primarily carried out in July and less frequently in August, as older individuals are generally harder to trap. Captured individuals were ear tagged (Dalton rototags) to allow for remote identification, and their body mass (±5 g) and right hind-foot length (±1 mm) recorded. Identification by ear tags was used to keep track of individuals and allowed for determination of the experience levels of adult foxes. The experience levels of untagged adult individuals were estimated using the historical demography of the den. If the den was used for breeding in the previous year, then the female was classified as experienced the following year. Exceptions to this rule were made when it was clear that an untagged female was replaced by another (identified by different fur colour, for example). In unclear cases, the experience level was set to unknown ($n = 9$) and they were not included in the analyses.

To assess if cubs were nourished above or below average, we calculated a physical condition index based on the relation between body mass and right hind-foot length following Tannerfeldt et al. (1994), using the relationship $W = aL^b$, where W is mass (kg), L is hind-foot length (mm), and calculated values $a = 0.19$ and $b = 1.92$. A model was fitted using data of body mass and right hind-foot length from all trapped foxes (the first record for each individual was used in case an individual was trapped several times). Mean residuals of physical condition index for each litter were used in statistical analyses.

To quantify juvenile summer survival, dens were revisited in August, approximately 40 days after the first visit. Juvenile summer survival rate was calculated for each litter using the following equation: juvenile summer survival rate = number of cubs in July/ number of cubs in August. If the number of cubs observed in a particular den was higher in August compared with July, then survival rate was set to 1 ($n = 6$). Survival rate for juveniles at each den was standardized to a month (30 days) to compensate for different time intervals between first and second visits, following Krebs (1989), and rounded to whole number of individuals.

Small-rodent trapping index was obtained from trapping lines placed in certain arctic fox territories within the research area in July (450–1440 trap nights per year). Trapping index indicates the number of trapped small rodents per 100 trap nights following the

same procedure as Hellström et al. (2014). Each year was classified as an increase, peak, or decrease phase of the small-rodent cycle, using the same classification method as Henden et al. (2009).

Behavioural observations at den sites were recorded in 2010 and 2011. The activity and number of cubs and adults were recorded every 5 min for about 48 h. Noninformative records during bad visibility (fog) were excluded from the records, resulting in a mean of 41 h of observations per den (data from one den was excluded, as too few observations were recorded due to bad visibility). Unattended cubs were considered to be more exposed to predation, so the total time that cubs were active at the den without an adult present was recorded. Field workers camped 80–150 m away from den sites during observations and trapping. Survival data from 2008 had previously been analysed and published by Meijer et al. (2011).

Permits and handling of animals

All trapping and handling of animals (foxes and small rodents) were carried out in accordance with Swedish law and approved by the Swedish Board of Agriculture (Jordbruksverket) and an ethical board (Umeå djurförsöksetiska nämnd; ethical permits A130-07, A131-07, A36-11, A18-14, and A19-14). As the Scandinavian arctic fox population is endangered, trapping had to be approved by the Swedish Environmental Protection Agency (Naturvårdsverket; permits 412-7884-07 Nv, NV-01959-14).

Statistical analyses

Two generalized mixed-effects models with binomial distributions were fitted using R (R Core Team 2014), RStudio version 0.98 (RStudio 2014), and the LME4 package (Bates et al. 2014). One extensive model, including data from all years, and one mechanistic model, limited to the 2 years with behavioural observations, were conducted. Proportion of juvenile summer survival (taking litter size into account) was used as a binomial response variable. Log-transformed values of small-rodent trapping indices were used in all analyses and maternal ID was used as a random factor to control for females that had several litters during the study period. In Fig. 1, 0.1 was added to trapping values of zero for plotting reasons.

In the extensive model, small-rodent abundance, maternal experience, and mean residual of physical condition of trapped individuals (assigned to the whole litter) were used as explanatory variables. An interaction between maternal experience and small-rodent abundance was included. The scaled values of small-rodent abundance and physical condition were used in the model. To assess if there were differences in physical condition, a random mixed-effects model was fitted with residual of the physical condition index as the response variable and date and maternal experience as explanatory variables. Litter was used as a grouping factor because siblings were included in the model.

The mechanistic model used juvenile summer survival as the response variable and included the significant explanatory variables of the general model (i.e., maternal experience and small-rodent abundance; however, the structure of the data did not allow an interaction term to be included) together with the proportion of the total time that cubs were active alone (i.e., unattended by an adult) on the den site as a scaled explanatory variable. Since behavioural data was recorded in 2010 and 2011, only data from these years could be included in the mechanistic model (13 litters). To test if litter attendance was related to maternal experience, a linear regression was fitted with litter attendance as the dependent variable and small-rodent abundance together with maternal experience as explanatory variables.

Results

Small rodents showed a clear cyclic dynamic with a period of 3–4 years. Small-rodent trap index varied substantially between years, ranging from 0.0 to 27 catches per 100 trap nights ($n = 5288$ trap

Table 1. Overview of reproduction and juvenile survival data for the arctic fox (*Vulpes lagopus*) covered in the study together with small-rodent abundance indices.

	Years							
	2008	2009	2010	2011	2012	2013	2014	Σ
Number of litters studied								
Experienced	8	NR	9	6	NR	2	8	33
First-time breeders	4	NR	—	7	NR	3	3	17
Unknown	—	NR	—	—	NR	7	2	9
Number of cubs								
Experienced	68	NR	58	91	NR	7	53	277
First-time breeders	23	NR	—	72	NR	14	14	123
Unknown	—	NR	—	—	NR	30	19	49
Mean juvenile survival (proportion)								
Experienced	0.90	NR	0.86	0.93	NR	0.38	0.87	
First-time breeders	0.43	NR	—	0.98	NR	0.44	0.79	
Unknown	—	NR	—	—	NR	0.58	0.69	
Mean	0.74	NR	0.86	0.96	NR	0.51	0.82	
Small-rodent abundance								
Small-rodent index	0.97	0	1.33	27.0	0	0.29	2.98	
Phase	↘	↓	↗	↑	↘	↗	↑	
n (trap nights)	826	≥500	450	510	1440	686	1376	≥5288

Note: NR, no reproduction. Small-rodent cycle was classified as an increase (↗), peak (↑), decrease (↘), or low (↓) phase.

nights). No arctic fox breeding occurred in years when no small rodents were trapped (i.e., 2009 and 2012, $n = 1950$ trap nights). In 2013 (0.29 catches per 100 trap nights), the mean juvenile survival rate was 0.51, which compare with 0.96 in 2011 when both arctic fox numbers and small-rodent abundance peaked (27 catches per 100 trap nights) (Table 1, Fig. 1). Thus, juvenile survival increased with increasing small-rodent abundance as predicted by hypothesis 1. However, the effect was also related to maternal experience (interaction between small-rodent abundance and maternal inexperience: likelihood ratio $\chi^2_{[1]} = 7.23$, $n_{obs} = 394$, $n_{litters} = 49$, $p = 0.007$; Table 2*a*). For a simulation of the statistical power of the interaction effect size see Supplementary Fig. S1.[1] But juvenile survival rate was unrelated to physiological condition (likelihood ratio $\chi^2_{[1]} = 1.18$, $p = 0.28$). The mean residual of the physical condition index was −0.0016 (95% confidence interval (CI): −0.001 to 0.005) for cubs of inexperienced females and −0.0009 (95% CI: −0.004 to 0.002) for cubs of experienced females. There was no effect of date ($n_{obs} = 226$, $n_{litters} = 42$, df = 1, $p = 0.20$) or maternal experience (df = 1, $p = 0.26$) on the residuals of the physiological condition index.

As a result of the interaction between small-rodent abundance and maternal experience, we made a separate model comprising only experienced females to investigate if small-rodent abundance had an effect on juvenile survival rate in experienced females. In contrast to first-time breeders, juvenile survival of experienced females was not affected by small-rodent abundance ($\chi^2_{[1]} = 1.47$, $n_{obs} = 227$, $n_{litters} = 33$, $p = 0.22$; Tables 2*b*, 2*c*), despite that the survival rates in the two groups were similar in 2013 (one experienced female failed entirely to rear a litter of two cubs; Fig. 1). Physical condition was again not related to survival ($\chi^2_{[1]} = 1.97$, $p = 0.16$; Tables 2*b*, 2*c*).

Hypothesis 2 predicted that juveniles of first-time-breeding females should have a lower probability of survival compared with those of experienced females, but that the difference would be smaller during years where conditions were favourable (i.e., high small-rodent abundance). This hypothesis was partly supported; however, juveniles of experienced females did not always perform better as shown by the overlap between the two groups when prey was more abundant (Fig. 2).

The proportion of total time observed in which cubs were left unattended (active at the den without an adult present) was 101 min per 24 h (bootstrapped 95% CI: 58 to 158) for litters of experienced females across both years, whereas cubs of first-time breeders in 2011 were unattended for 130 min per 24 h (bootstrapped 95% CI: 30 to 230). In the mechanistic model (comprising only 2010 and 2011), juvenile survival was negatively related to the time they were unattended (likelihood ratio $\chi^2_{[1]} = 5.26$, SE = 6.2, $n_{obs} = 151$, $n_{litters} = 13$, $p = 0.022$; Table 3), as predicted by hypothesis 3. There were no differences in survival between the two groups during years with available behavioural data because survival was unrelated to small-rodent abundance ($\chi^2_{[1]} = 0.12$, $p = 0.73$) and maternal experience ($\chi^2_{[1]} = 0.002$, $p = 0.97$). Hypothesis 4 was rejected because the time cubs were unattended was neither related to maternal experience ($n = 13$, df = 1, $p = 0.66$) nor to small-rodent abundance ($n = 13$, df = 1, $p = 0.90$).

Discussion

Arctic fox juvenile survival varied closely with small-rodent abundance, but the effect was related to maternal experience. As previously observed by Meijer et al. (2011), juveniles of first-time-breeding females had a lower chance of survival than those of females with prior breeding experience when food availability was low. However, overall juvenile survival was independent of prior breeding experience when small-rodent abundance was high (Fig. 2). Furthermore, survival was negatively correlated with the proportion of time cubs were unattended at the den.

Limited food availability, combined with the potentially lower capability of first-time-breeding females to provide for their offspring, could be expected mechanisms underlying the differences in juvenile survival when small rodents are scarce. However, cub physical condition index did not affect juvenile survival, indicating that the supplementary feeding that has been extensive in the research area since the late 1990s is likely to have substantially reduced the direct effects of food availability (Tannerfeldt et al. 1994; Angerbjörn et al. 2013). The positive effect of supplementary feeding is strengthened by the observation that juvenile survival among experienced breeders was unaffected by small-rodent

---

Fig. 1. Plot of mean survival of juvenile arctic fox (*Vulpes lagopus*) for litters included in the study in relation to small-rodent abundance and maternal reproductive experience. When small-rodent abundance was low, no litters were born (2009 and 2012). Values above error bars indicate the number of litters; error bars indicate the standard error. For plotting reasons, 0.1 was added to trapping values of zero (2009 and 2012). Figure appears in colour on the Web.
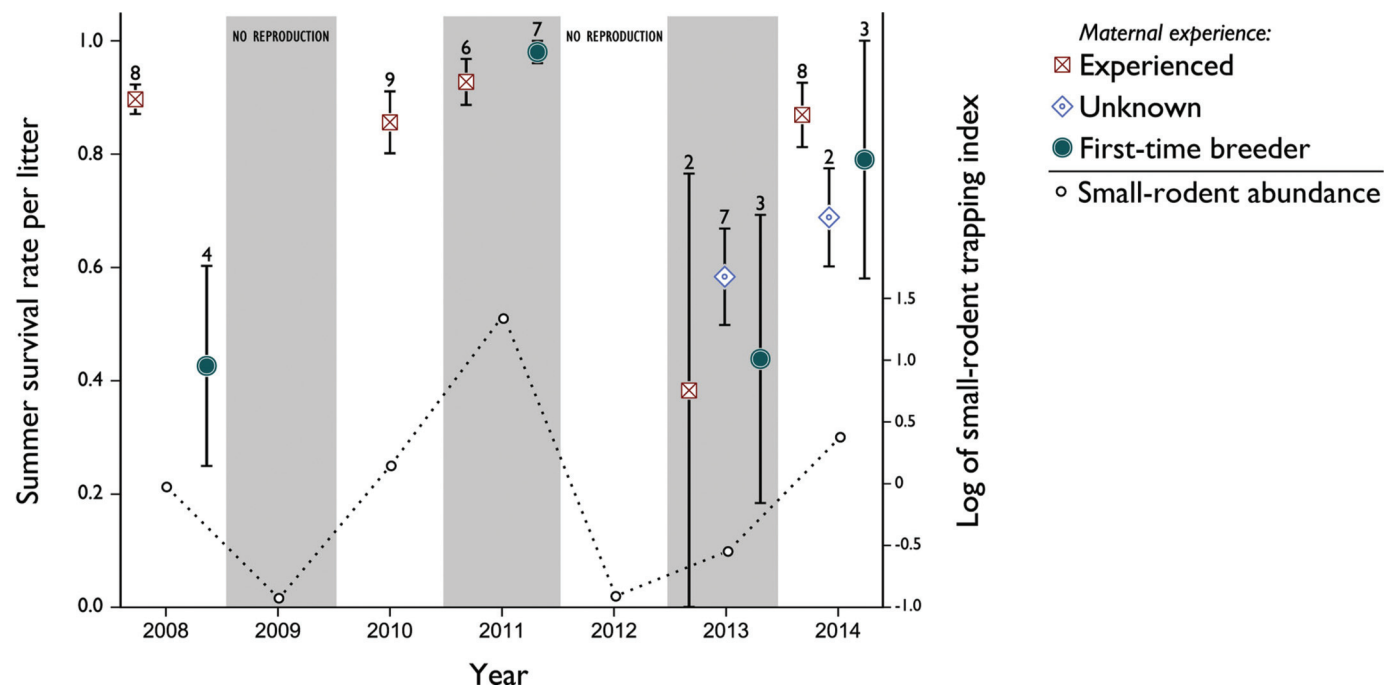

Table 2. Mixed-effects extensive model showing that the effect of small-rodent abundance on summer survival of juvenile arctic foxes (*Vulpes lagopus*) depended on maternal breeding experience (*a*). Two separate models for experience breeders and first-time breeders showed that juveniles of experienced breeders were unaffected by small-rodent abundance (*b*), whereas juveniles of first-time breeders were affected (*c*).

Explanatory factor	χ^2	df	P
(a) Both experienced and first-time-breeding females			
Small-rodent trapping index (scaled)	8.7145	1	0.003**
Maternal experience	1.7452	1	0.186
Condition index (scaled)	1.1846	1	0.276
Small-rodent index × maternal experience interaction	7.2344	1	0.007**
(b) Only experienced females			
Small-rodent trapping index (scaled)	1.4707	1	0.23
Condition index (scaled)	1.9657	1	0.16
(c) Only first-time-breeding females			
Small-rodent trapping index (scaled)	12.5059	1	<0.001***
Condition index (scaled)	0.3272	1	0.57

Note: The dependent factor is juvenile summer survival. **, $P < 0.01$; ***, $P < 0.001$.

numbers, although they still abstained from breeding in years when small-rodent abundance was low. Other physiological effects not related to the physical condition index are of course possible but were not testable with available data. However, our results suggest that mortality was not driven by food shortage or starvation because the low juvenile survival rates observed during periods when small-rodent abundance was in a phase of decline were uncoupled from the direct effects of food abundance.

Instead, variation between experienced and inexperienced parents in their capacity to cope with intraguild predation has been suggested as a major reason for differences in juvenile survival (Meijer et al. 2011). However, this was based on data from only a single year (2008) when small-rodent populations were in a phase of decline. The question then remains if intraguild predation pressure could be affected by the abundance of small rodents. Optimal foraging theory suggests that low numbers of small rodents

should cause a prey switch in generalist predators because they should, optimally, hunt for the most available prey (Murdoch 1969). Such a reaction could be expected in, e.g., Golden Eagle, red fox, and wolverine, which are generalist predators that prey on small rodents but are also capable of killing arctic foxes (Landa et al. 1997; Nyström et al. 2006; Elmhagen et al. 2014).

A numeric predatory response among such generalist predators could well be expected to follow a decline after a peak in small-rodent abundance (Solomon 1949; Taylor 1984). Increased reproductive output (i.e., more and larger litters) would imply a larger foraging effort for reproducing adults. During years when small-rodent abundance is in a phase of increase, or peaks, the effect of predation on alternative prey would likely be small or even negligible. However, during a phase when rodent populations decline, or suddenly crash, a mismatch between number of offspring and food availability would likely lead to a prey switch, resulting in

Fig. 2. Plot of the mixed-effects extensive model. Low small-rodent abundance affected the probability of survival for juvenile arctic fox (*Vulpes lagopus*) differently depending on maternal breeding experience (interaction term between small-rodent abundance and maternal breeding experience: $\chi^2_{[1]} = 9.73$, $n_{obs} = 394$, $n_{litters} = 49$, $p = 0.002$). Cubs born to first-time-breeding females had lower survival rates when small-rodent abundance was lower ($\chi^2_{[1]} = 12.5059$, $n_{obs} = 167$, $n_{litters} = 16$, $p < 0.001$). Juveniles born by experienced mothers remained unaffected ($\chi^2_{[1]} = 0.77$, $n_{obs} = 227$, $n_{litters} = 33$, $p = 0.38$). When small rodents were abundant, the probability of survival was generally high. Solid lines indicate empirical data, whereas broken lines indicate the theoretical extension of the functions.
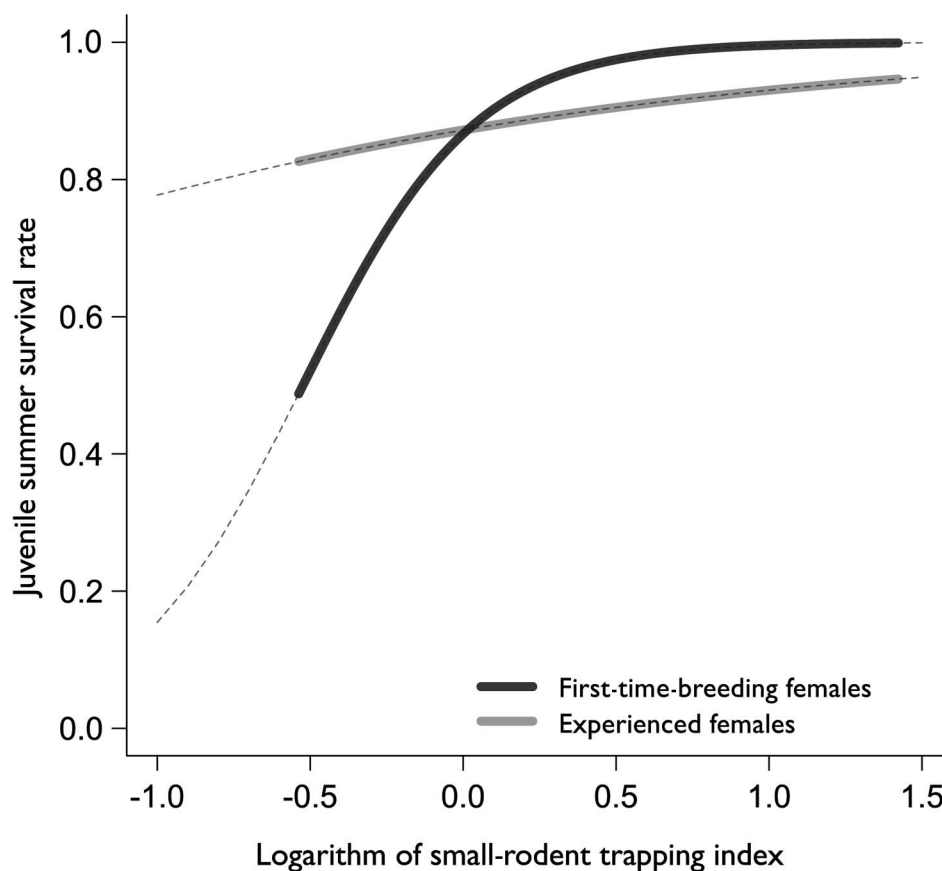

Table 3. Mixed-effect mechanistic model (comprising only 2010 and 2011) showing the effect of the explanatory factors small-rodent trapping abundance, litter attendance, and maternal experience on the dependent factor summer survival of juvenile arctic foxes (*Vulpes lagopus*).

Explanatory factor	χ^2	df	P
Small-rodent trapping index (scaled)	0.1208	1	0.73
Litter attendance	5.2676	1	0.022*
Maternal experience	0.0015	1	0.97

Note: Juvenile survival was negatively related to the time that juveniles where left unattended. In contrast with the extensive model, survival was unrelated to both small-rodent abundance and maternal experience during those 2 years. *, $P < 0.05$.

increased predation pressure on alternative prey including mesopredators (e.g., during 2008; Fig. 1). Nonetheless, if the decline in small-rodent abundance is too drastic, a higher predation pressure on mesopredator juveniles would not be expected for species that abstain from breeding when their prey is not sufficiently available (such as the arctic fox, e.g., as in 2009 and 2012; Fig. 1). The effect of a numerical response could, however, remain for several years in long-lived predators and could partly explain why arctic fox juvenile survival was so low in 2013 when small-rodent abundance was low but slightly increasing (Table 1, Fig. 1).

Therefore, it is conceivable that predation could account for a large proportion of the observed cub mortality when small-rodent abundance is low through prey switching by larger predators. The shortcomings of first-time-breeding females could thus be an in-

ability to deal with high predation pressure. These results are in accordance with observations by Durant (2000) who showed that more experienced female cheetahs were more successful in protecting their offspring from predators.

Given that a prey switch did occur as a consequence of fluctuations in small-rodent abundance, the crucial point would be to find a feasible mechanism that could explain a higher risk of predation on cubs of first-time-breeding arctic fox females. The negative relationship between cub survival and the time that they were left unattended could provide a feasible explanation. Unattended cubs that are active at the den site are likely more exposed to predation than if a vigilant adult is nearby. Reasons for cubs being left unattended could either be a result of parents being less present at the den site or cubs being more active when left unattended. If parents spend a lot of time away from the den, then it could indicate that they are inefficient hunters, that food is less abundant in the territory, or that they are unaware of the risks of leaving juveniles unattended. In the first two cases, supplementary feeding would likely have a positive effect on parental presence. If unattended cubs are more exposed to predation, parents would benefit from inducing a cautious behaviour in their offspring when they are unattended. Individual differences between parents in achieving this could have many possible explanations, but prior breeding experience would intuitively be expected to have an impact. Nevertheless, we could not find any relationship between maternal experience and litter attendance, suggesting that attendance affects juvenile survival no matter the level of maternal

experience and that individual differences between parents could be important (see discussion in Bjørnstad and Hansen 1994).

This could, however, be an effect of the data structure because behavioural data were only available for years when small-rodent abundance increased and peaked (2010 and 2011, respectively; Fig. 1). Small-rodent abundance affects reproduction and thus the population structure of arctic foxes. There were interyear differences in the number of litters and breeding experience of reproducing adults that could have obscured the processes involved. For example, we did not see any differences in reproductive performance between first-time breeders and experienced females during 2011 when juvenile summer survival was almost 100% and predation pressure, presumably, low. In contrast, during 2010, we would have expected a moderate level of predation pressure and a possible effect from differences in parental behaviour. Yet, no first-time-breeding females reared a litter in 2010 and hence we lack contrast to compare the effect of breeding experience on parental behaviour under different prey conditions. We can therefore only speculate that a difference in behaviour, related to maternal experience, would be expressed during years with low prey abundance. However, such a difference would be in accordance with a prey-switching explanation because a less cautious parent, or a less-effective hunter spending more time away from the den, could be expected to experience greater offspring losses if predation pressure is high, but perform equally well as a more vigilant parent if predation is low.

Norén et al. (2012) found that group living in arctic foxes was more common in ecosystems with higher predation pressure (Hersteinsson's model) and hypothesised that this behaviour could be a way to achieve increased guarding of juveniles. The observed relationship between litter attendance and juvenile survival provides some empirical support for this to be a likely mechanism behind increased group living.

Interspecific killing among canids is primarily connected to competition for food, territories, or other reasons rather than strict foraging (Polis et al. 1989; Palomares and Caro 1999; Kamler et al. 2003). Such competition could be expected to increase when food is scarce (Polis et al. 1989; Palomares and Caro 1999) and thus red fox killing of arctic foxes could be expected to increase during a phase of decline in small-rodent abundance (Frafjord et al. 1989), primarily due to increased competition and not as a means of foraging. Yet the red fox is unlikely to have been a major cause of death in this study because of the extensive red fox culling in the research area (Angerbjörn et al. 2013). Wolverine and bear presence is also limited, leaving Golden Eagles as a probable major predator (Meijer et al. 2011). Direct observations of predation are hard to record, especially in remote areas, because predation is often both instantaneous and irregular by nature.

The effects of maternal experience together with small-rodent fluctuations have implications for understanding the dynamics of the Scandinavian arctic fox population. Our results imply that the effect of prey fluctuations on population dynamics of predators is not limited to the direct effects of food availability. To better understand the role of predators in ecosystems with cyclic fluctuations in prey abundance, it is therefore necessary to incorporate indirect effects. This could apply to many species with northern distributions that experience fluctuations in prey abundance such as the red fox, wolverine, and Eurasian lynx (*Lynx lynx* (L., 1758)) in Eurasia (Lindström 1989; Persson et al. 2003; Andrén et al. 2006), as well as the Canadian lynx (*Lynx canadensis* Kerr, 1792) and coyote (*Canis latrans* Say, 1823) in North America (O'Donoghue et al. 1998). However, also in other ecosystems with fluctuating, but not necessarily cyclic, prey abundance (Saunders and Giles 1977; Fryxell 1987; Ogutu and Owen-Smith 2003), we would expect variation in predation pressure (Sinclair et al. 1990) where juvenile survival

would be affected by differences in breeding experience. When a factor that limits juvenile survival varies over time, there is a need for long-term studies to clarify what aspects are important for population dynamics.

References

Andrén, H., Linnell, J.D.C., Liberg, O., Andersen, R., Danell, A., Karlsson, J., Odden, J., Moa, P.F., Ahlqvist, P., Kvam, T., Franzén, R., and Segerström, P. 2006. Survival rates and causes of mortality in Eurasian lynx (*Lynx lynx*) in multi-use landscapes. Biol. Conserv. **131**: 23–32. doi:10.1016/j.biocon.2006.01.025.

Angerbjörn, A., Hersteinsson, P., and Tannerfeldt, M. 2004. Europe and North and Central Asia (Palearctic): arctic fox, *Alopex lagopus*. *In* Canids: foxes, wolves, jackals and dogs. Status survey and conservation action plan. *Edited by* C. Sillero-Zubiri, M. Hoffmann, and D.W. Macdonald. IUCN/SSC Canids Specialist Group, Gland, Switzerland. pp. 117–123.

Angerbjörn, A., Eide, N.E., Dalén, L., Elmhagen, B., Hellström, P., Ims, R.A., Killengreen, S., Landa, A., Meijer, T., Mela, M., Niemimaa, J., Norén, K., Tannerfeldt, M., Yoccoz, N.G., and Henttonen, H. 2013. Carnivore conservation in practice: replicated management actions on a large spatial scale. J. Appl. Ecol. **50**: 59–67. doi:10.1111/1365-2664.12033.

Arenz, C.L., and Leger, D.W. 2000. Antipredator vigilance of juvenile and adult thirteen-lined ground squirrels and the role of nutritional need. Anim. Behav. **59**: 535–541. doi:10.1006/anbe.1999.1345. PMID:10715175.

Bates, D., Mächler, M., Bolker, B.M., and Walker, S.C. 2014. Fitting linear mixed-effects models using lme4. J. Stat. Software, **67**(1): 1–48. doi:10.18637/jss.v067.i01.

Bekoff, M., Daniels, T.J., and Gittleman, J.L. 1984. Life history patterns and the comparative social ecology of carnivores. Annu. Rev. Ecol. Syst. **15**: 191–232. doi:10.1146/annurev.es.15.110184.001203.

Bjørnstad, O.N., and Hansen, T.F. 1994. Individual variation and population dynamics. Oikos, **69**(1): 167–171. doi:10.2307/3545298.

Borgström, I. 1979. Geomorphological map 18 C Sylarna: description and assessment of areas of geomorphological importance. Statens naturvårdsverk, Solna, Sweden.

Caro, T.M. 1987. Cheetah mothers' vigilance: looking out for prey or for predators? Behav. Ecol. Sociobiol. **20**: 351–361. doi:10.1007/BF00300681.

Collett, R. 1877. On *Myodes lemmus* in Norway. J. Linn. Soc. Zool. **13**(69): 327–334. doi:10.1111/j.1096-3642.1877.tb01388.x.

Daunt, F., Wanless, S., Harris, M.P., Money, L., and Monaghan, P. 2007. Older and wiser: improvements in breeding success are linked to better foraging performance in European shags. Funct. Ecol. **21**: 561–567. doi:10.1111/j.1365-2435.2007.01260.x.

Doolan, S.P., and Macdonald, D.W. 1997. Breeding and juvenile survival among slender-tailed meerkats (*Suricatu suricatta*) in the south-western Kalahari: ecological and social influences. J. Zool. **242**: 309–327. doi:10.1111/j.1469-7998.1997.tb05804.x.

Durant, S.M. 2000. Predator avoidance, breeding experience and reproductive success in endangered cheetahs, *Acinonyx jubatus*. Anim. Behav. **60**: 121–130. doi:10.1006/anbe.2000.1433. PMID:10924211.

Elmhagen, B., Tannerfeldt, M., Verucci, P., and Angerbjörn, A. 2000. The arctic fox (*Alopex lagopus*): an opportunistic specialist. J. Zool. **251**: 139–149. doi:10.1111/j.1469-7998.2000.tb00599.x.

Elmhagen, B., Hersteinsson, P., Norén, K., Unnsteinsdottir, E.R., and Angerbjörn, A. 2014. From breeding pairs to fox towns: the social organisation of arctic fox populations with stable and fluctuating availability of food. Polar Biol. **37**: 111–122. doi:10.1007/s00300-013-1416-3.

Elton, C.S. 1924. Periodic fluctuations in the numbers of animals: their causes and effects. J. Exp. Biol. **2**: 119–163.

Ewer, R.F. 1973. The carnivores. Weidenfeld and Nicolson, London.

Frafjord, K., Becker, D., and Angerbjörn, A. 1989. Interactions between arctic and red foxes in Scandinavia—predation and aggression. Arctic, **42**: 354–356. doi:10.14430/arctic1677.

Fryxell, J.M. 1987. Food limitation and demography of a migratory antelope, the white-eared kob. Oecologia, **72**: 83–91. doi:10.1007/BF00385049.

Gittleman, J.L. 1994. Female brain size and parental care in carnivores. Proc. Natl. Acad. Sci. **91**: 5495–5497. doi:10.1073/pnas.91.12.5495. PMID:8202515.

Guinness, F.E., Clutton-Brock, T.H., and Albon, S.D. 1978. Factors affecting calf mortality in red deer (*Cervus elaphus*). J. Anim. Ecol. **47**: 817–832. doi:10.2307/3673.

Hellström, P., Nyström, J., and Angerbjörn, A. 2014. Functional responses of the rough-legged buzzard in a multi-prey system. Oecologia, **174**: 1241–1254. doi:10.1007/s00442-013-2866-6. PMID:24448699.

Henden, J.A., Yoccoz, N.G., Ims, R.A., Bårdsen, B.J., and Angerbjörn, A. 2009. Phase-dependent effect of conservation efforts in cyclically fluctuating populations of Arctic fox (*Vulpes lagopus*). Biol. Conserv. **142**: 2586–2592. doi:10.1016/j.biocon.2009.06.005.

Ims, R.A., and Fuglei, E. 2005. Trophic interaction cycles in tundra ecosystems and the impact of climate change. Bioscience, **55**: 311–322. doi:10.1641/0006-3568(2005)055[0311:TICITE]2.0.CO;2.

Kamler, J.F., Ballard, W.B., Gilliland, R.L., and Mote, K. 2003. Spatial relationships between swift foxes and coyotes in northwestern Texas. Can. J. Zool. **81**(1): 168–172. doi:10.1139/z02-222.

Korpimäki, E., and Norrdahl, K. 1989. Avian predation on mustelids in Europe 1: Occurrence and effects on body size variation and life traits. Oikos, **55**: 205. doi:10.2307/3565424.

Krebs, C.J. 1989. Ecological methodology. Harper and Row, New York.

Krebs, C.J. 2013. Population fluctuations in rodents. The University of Chicago Press, Chicago, Ill.

Lack, D. 1954. The natural regulation of animal numbers. Clarendon, Oxford.

Landa, A., Strand, O., Swenson, J.E., and Skogland, T. 1997. Wolverines and their prey in southern Norway. Can. J. Zool. **75**(8): 1292–1299. doi:10.1139/z97-153.

Lay, D.M. 1974. Differential predation on gerbils (*Meriones*) by the little owl, *Athene brahma*. J. Mammal. **55**: 608–614. doi:10.2307/1379549.

Lindström, E. 1989. Food limitation and social regulation in a red fox population. Ecography, **12**: 70–79. doi:10.1111/j.1600-0587.1989.tb00824.x.

Longland, W.S., and Jenkins, S.H. 1987. Sex and age affect vulnerability of desert rodents to owl predation. J. Mammal. **68**: 746–754. doi:10.2307/1381551.

Meijer, T., Norén, K., and 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. doi:10.1007/s10344-010-0463-0.

Meijer, T., Elmhagen, B., Eide, N.E., and Angerbjörn, A. 2013. Life history traits in a cyclic ecosystem: a field experiment on the arctic fox. Oecologia, **173**: 439–447. doi:10.1007/s00442-013-2641-8. PMID:23512202.

Murdoch, W.W. 1969. Switching in general predators: experiments on predator specificity and stability of prey populations. Ecol. Monogr. **39**: 335–354. doi:10.2307/1942352.

Norén, K., Hersteinsson, P., Samelius, G., Eide, N.E., Fuglei, E., Elmhagen, B., Dalén, L., Meijer, T., and Angerbjörn, A. 2012. From monogamy to complexity: social organization of arctic foxes (*Vulpes lagopus*) in contrasting ecosystems. Can. J. Zool. **90**(9): 1102–1116. doi:10.1139/z2012-077.

Norrdahl, K. 1995. Population cycles in northern small mammals. Biol. Rev. **70**: 621–637. doi:10.1111/j.1469-185X.1995.tb01654.x. PMID:8527608.

Nyström, J., Ekenstedt, J., Angerbjörn, A., Thulin, L., Hellström, P., and Dalén, L. 2006. Golden Eagles on the Swedish mountain tundra — diet and breeding success in relation to prey fluctuations. Ornis Fenn. **83**: 145–152.

O'Donoghue, M., Boutin, S., Krebs, C.J., Zuleta, G., Murray, D.L., and Hofer, E.J. 1998. Functional responses of coyotes and lynx to the snowshoe hare cycle. Ecology, **79**: 1193–1208. doi:10.2307/176736.

Ogutu, J.O., and Owen-Smith, N. 2003. ENSO, rainfall and temperature influences on extreme population declines among African savanna ungulates. Ecol. Lett. **6**: 412–419. doi:10.1046/j.1461-0248.2003.00447.x.

Packer, C., Herbst, L., Pusey, A.E., Bygott, J.D., Hanby, J.P., Cairns, S.J., and Borgerhoff Mulder, M. 1988. Reproductive success of lions. *In* Reproductive success: studies of individual variation in contrasting breeding systems. *Edited by* T.H. Clutton-Brock. The University of Chicago Press, Chicago, Ill.

Palomares, F., and Caro, T.M. 1999. Interspecific killing among mammalian carnivores. Am. Nat. **153**: 492–508. doi:10.1086/303189.

Persson, J., Willebrand, T., Landa, A., Andersen, R., and Segerström, P. 2003. The role of intraspecific predation in the survival of juvenile wolverines *Gulo gulo*. Wildl. Biol. **9**: 21–28.

Polis, G.A., Myers, C.A., and Holt, R.D. 1989. The ecology and evolution of intra-guild predation: potential competitors that eat each other. Annu. Rev. Ecol. Syst. **20**: 297–330. doi:10.1146/annurev.es.20.110189.001501.

Pond, C.M. 1977. The significance of lactation in the evolution of mammals. Evolution, **31**: 177–199. doi:10.2307/2407556.

R Core Team. 2014. R: a language and environment for statistical computing. Versions 3.0.2 and 3.1.0 [computer program]. R Foundation for Statistical Computing, Vienna, Austria. Available from https://www.r-project.org/.

Robbins, A.M., Robbins, M.M., Gerald-Steklis, N., and Steklis, H.D. 2006. Age-related patterns of reproductive success among female mountain gorillas. Am. J. Phys. Anthropol. **131**: 511–521. doi:10.1002/ajpa.20474. PMID:16941601.

RStudio. 2014. RStudio. Version 0.98 [computer program]. RStudio, Boston, Mass. Available from https://www.rstudio.com/products/rstudio/.

San José, C., Braza, F., and Aragón, S. 1999. The effect of age and experience on the reproductive performance and prenatal expenditure of resources in female fallow deer (*Dama dama*). Can. J. Zool. **77**(11): 1717–1722. doi:10.1139/z99-149.

Saunders, G.R., and Giles, J.R. 1977. A relationship between plagues of the house mouse, *Mus musculus* (Rodentia: Muridae) and prolonged periods of dry weather in south-eastern Australia. Wildl. Res. **4**: 241–247. doi:10.1071/WR9770241.

Sinclair, A.R.E., Olsen, P.D., and Redhead, T.D. 1990. Can predators regulate small mammal populations? Evidence from house mouse outbreaks in Australia. Oikos, **59**: 382. doi:10.2307/3545150.

Solomon, M.E. 1949. The natural control of animal populations. J. Anim. Ecol. **18**: 1. doi:10.2307/1578.

Swedish Meteorological and Hydrological Institute (SMHI). 2016. Snötäckets utbredning och varaktighet. Available from http://www.smhi.se/kunskapsbanken/meteorologi/snotackets-utbredning-och-varaktighet-1.6323 [accessed 17 October 2016].

Tannerfeldt, M., Angerbjörn, A., and ArvidSon, B. 1994. The effect of summer feeding on juvenile arctic fox survival — a field experiment. Ecography, **17**: 88–96. doi:10.1111/j.1600-0587.1994.tb00080.x.

Taylor, R.J. 1984. Predation. Chapman and Hall, London.