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The impact of maternal experience on post-weaning survival in an endangered arctic fox population

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Abstract Behavioural differences in parental care can influence offspring survival through variation in e.g. antipredator behaviour and ability to provide food. In a broad range of species, offspring survival has been found to be higher for experienced females compared to inexperienced first-time breeders. The increase in offspring survival for experienced females has mainly been explained by improved experience in providing food. In this paper, we have studied post-weaning juvenile survival in relation to maternal experience in an endangered population of arctic foxes (*Vulpes lagopus*) in Fennoscandia. For cubs raised by inexperienced and experienced females, the survival rate was 0.42 (CI 95%±0.31) and 0.87 (CI 95%±0.08), respectively. There was no difference in body condition between the cubs and no observations of starvation. We suggest that the difference in survival was due to lack of experience to one of the most common predators, the golden eagle (*Aquila chrysaetos*). Golden eagles were mainly observed on dens with litters where the females were inexperienced first-time breeders. From a conservation perspective, it is therefore important to increase adult survival through actions to enlarge the proportion of experienced breeders.

Keywords *Alopex lagopus* · Conservation · *Aquila chrysaetos* · Parental experience · Population dynamics · Body index · Juvenile survival

Introduction

Behavioural differences in parental care can influence offspring survival through variation in e.g. antipredator behaviour (Konttinen et al. 2009) and ability to provide food (Daunt et al. 2007). Such behaviours can be inherited (McCune 1995, Willsen and Sundgren 1998) or change with experience (Durant 2000). In a broad range of species, first-time breeding females not only give birth to fewer offspring than experienced females, but the survival of their offspring is lower (e.g. Sydeman et al. 1991; Daunt et al. 2007). The increase in offspring survival for experienced females has mainly been attributed to improved experience in food provisioning (Daunt et al. 2007). In addition to food provision, predation has been suggested to have a large impact on reproduction and juvenile survival (e.g. Watts and Holekamp 2008; Ralls and White 1995; Garrott and Eberhardt 1982). The risk of predation can be related to previous experience with specific predators and developed antipredator behaviour, where older individuals experience lower predation risk (Rohner and Krebs 1996). Conservation programmes that have released captive bred or translocated animals have often failed since the released individuals lacked previous experience of the local predators (Griffin et al. 2000). However, food abundance and predation are not independent factors and starving juveniles might be more exposed to predation due to less guarding by adults when the food resources are scarce (Tannerfeldt et al. 1994). From a conservation perspective it is thus important to understand how the age distribution of small and endangered populations can impact the reproductive success within a population.

The arctic fox (*Vulpes lagopus*) have one of the largest litter sizes in the order Carnivora with up to 18 cubs per litter during favourable food availability (Tannerfeldt and

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Angerbjörn 1998). Juvenile survival has been shown to be strongly linked to food availability. In populations depending upon highly fluctuating prey species, such as lemmings (*Lemmus lemmus*), almost all of the juveniles die due to starvation during years with low prey densities (Tannerfeldt et al. 1994; Angerbjörn et al. 2004a). In complement to food abundance, predation from red foxes (*Vulpes vulpes*) and avian predators such as golden eagle (*Aquila chrysaetos*) and snowy owl (*Bubo scandiaca*) has been suggested to lower the survival of arctic fox cubs in Fennoscandia (Frafjord et al. 1989; Tannerfeldt et al. 2002) and in northern Alaska (Garrott and Eberhardt 1982; Pamperin et al. 2006).

The Fennoscandian arctic fox population has gone through a severe demographic and genetic bottleneck during the twentieth century (Nyström et al. 2006) and has, despite legal protection since 1928 in Sweden, remained low. A conservation approach focusing on the two major factors affecting the population viability, food availability, and intraguild predation from the red fox, has showed to be an efficient method to increase the population viability and number of arctic fox litters (Angerbjörn et al. 2008). However, despite the intensive actions conducted, the annual survival of arctic foxes in Sweden is considerably lower compared to survival in other small canids (Ralls and White 1995; Cypher et al. 2000; Kitchen et al. 1999). In Fennoscandia, the annual juvenile survival in arctic foxes during a year with low small rodent abundance was found to be less than 10%, with 75% of the total mortality occurring during the first 6 months (Meijer et al. 2008).

In this paper, we have studied juvenile survival of arctic foxes in a population under intensive conservation actions. In order to increase the viability of the population, all inhabited dens were supplied with supplemental food and red foxes have continually been culled since 2001 (Angerbjörn et al. 2008). Since all litters were supplementary fed, we predicted that mortality due to starvation should be low and with no differences between experienced and inexperienced females. As the major cause of juvenile mortality, we predicted predation from either the red fox or golden eagle.

Method

Study area

The study was conducted on the sub-arctic tundra in Helagsfjällen (62.53 N 12.40 E), Jämtland county, Sweden (see Meijer et al. 2008). Since 2001, approximately 75% of all born cubs have been ear-tagged (Dalton Rototags) with unique colour combination which allows individual identification. When this study was carried out, in 2008, the

background of almost all adults was known. In 2006, the winter population size was estimated to 36–55 individuals (Meijer et al. 2008).

Field methods

In early July 2008, we found 14 arctic fox litters with a total of 107 cubs within our study area. Based on the ear-tags of the adults, we could determine the maternal and paternal age and breeding experience for 12 litters. Parents were classified as experienced if they had reared a litter during previous years (2001–2007). We found that eight of the females were experienced breeders while four females were breeding for the first time. Males were recorded on all dens that were included in the study, of which two males were recorded as first-time breeders, nine experienced and one unknown. A total of 91 cubs were included in the study, 64 of these were captured, ear-tagged and measured.

To record juvenile survival, all dens were revisited in mid-August approximately 30 days after the ear-tagging event. We monitored the den for 36 h with focal observations every 15 min to record the number of cubs present. Since all cubs were not ear-tagged in July, the number of untagged cubs was recorded at the same time to achieve an unbiased estimate of juvenile survival. In general, all cubs at a den were observed together at the same time during the first 12 h of observations and the remaining 24 h was used to confirm the number of cubs alive. If a cub was not observed during the 36 h observation period, it was considered dead. All observations were performed during good weather conditions; in case of bad weather (rain, strong winds) the observation time was prolonged to obtain 36 h of good conditions.

In order to quantify possible predators, we observed all dens during 4.5 days (3 days in July and 1.5 in August) and recorded all predatory species. In addition to visual observations, we used remote cameras (Prowler IR. Stealth Cam Inc.) at the dens to increase the number of observations. The cameras were placed on the most active part of the den, covering approximately 50% of the den area. The cameras were put out in the beginning of July and each camera was programmed to take a picture when triggered by motion after which it was put in sleeping mode for 3 min. The cameras recorded activity for 14 days after the cubs had been ear-tagged at each den. In total, 3,555 pictures from the remote cameras were analysed for presence of potential predators.

During the study, all dens with arctic fox litters had access to the same amount of supplementary food. Both experienced and inexperienced individuals were familiar with the supplementary feeding stations and have had earlier access to feeding stations with the commercial dog pellets provided (Dogman dinner).

Estimation of finite survival, body size index and statistical analyses

The finite juvenile survival rate for a period of 30 days was calculated following Krebs (1989). The finite survival rate is the number of surviving cubs divided by the number of cubs in the beginning of the time period. Since all dens with litters were not revisited after exactly 30 days, the survival rate and litter size was corrected for time differences (Keith et al. 1984). The confidence interval (CI 95%) for finite survival rate was calculated using the binominal confidence interval method (Krebs 1989). In order to test for differences in juvenile survival and body condition between inexperienced and experienced mothers we used logistic regression with logit as link factor. The litter size was log-transformed to obtain a normalised distribution and analysis of variance was used to test for differences. Fisher's exact test was used to test for occurrence of predators on dens with arctic fox litters. In order to test for differences in juvenile body condition, the regression of log weight on the log hind foot length was calculated following Tannerfeldt et al. (1994). Analysis of variance was used to test for differences in body condition between cubs reared by an inexperienced versus experienced female. All analysis were performed in Statistica 7.0 (Statsoft Inc., Tulsa, OK, USA).

Results

For all litters, the mean survival rate for 30 days was 0.73 (CI 95%±0.16, $n=91$). However, the survival for cubs with an inexperienced mother was 0.42 (CI 95%±0.31), i.e. significantly lower than cubs with an experienced mother with a survival of 0.87 (CI 95%±0.08, $p=0.0007$). The paternal experience could not be tested in the study ($n=9$ experienced and 2 inexperienced) with one inexperienced male breeding with an experienced female and the other with an inexperienced one. The litter size in the beginning of July was slightly lower for inexperienced females ($5.7\pm SE, 1.7$ cubs) but could not be statistically separated from experienced females (7.5 ± 3.2 cubs, $p=0.33$). The mean body weight of cubs that were ear-tagged in the beginning of July ($n=49$) was 1,067 g (CI 95%±81 g) but the body weight differed between cubs with an inexperienced mother, 757 g (CI 95%±131 g) compared to cubs with experienced mothers, 1,125 g (CI 95%±70 g, $p<0.001$). However, the body condition index showed no difference related to the maternal experience with index 1.0 (CI 95%±0.014) for inexperienced and 0.99 (CI 95%±0.004) for experienced females ($p=0.44$). The survival was related to body weight ($p<0.001$) but not to body condition index ($p=0.44$).

Golden eagles were observed in close connection to five arctic fox dens, red fox at one den and wolverine at

one den. Two events of direct attacks from golden eagle were visually observed and one such event was recorded by a remote camera, all on dens with inexperienced females. In two of the attacks, a juvenile fox was consumed after killing, while in the third case the cub managed to survive and retreat into the den. On four dens, all with inexperienced females, golden eagles were observed three to four times. The appearance of golden eagles was significantly related to maternal experience (Fisher's exact test, $p=0.01$) with golden eagles recorded at all dens with an inexperienced female but only in one event with an experienced female. The wolverine was visually observed to interact with two inexperienced adult arctic foxes that managed to chase it away from the den. A red fox was captured by remote cameras only once and did not affect juvenile survival at that particular den since all cubs survived the summer. The female at this den was experienced while the background of the father was unknown.

Discussion

In our study, maternal experience was an important factor influencing juvenile survival where the survival of juveniles of inexperienced females was less than half compared to juveniles of experienced mothers. There was no difference in body condition index between the cubs, which might imply that inexperienced females gave birth later in the season, rather than that the cubs suffered of starvation. First-time breeders have been observed to give birth later in the season than experienced breeders in other mammal populations (Clutton-Brock et al. 1992; Hersteinsson P., personal communication). However, without supplementary feeding, it is possible that the effect of food abundance on juvenile survival would be more pronounced for inexperienced females. The results indicate that presence of golden eagles could be related to the level of maternal experience. The lower survival for cubs with an inexperienced female seems thus to be connected to a higher predation pressure rather than lower access to food. This could either be due to that inexperienced females have territories of poor quality with a higher risk of encountering golden eagles, or to a less efficient defence strategy against such predators. There is also a possibility that cubs that emerged from the den later in the summer suffered more from predation due to their smaller body size.

Golden eagles have large territories, ranging from 13 to 128 km² (McGrady et al. 2002). However, no breeding pair of golden eagles was found in the area during the eagle inventories 2008 (Lars Liljemark, personal communication), indicating that the observed eagles were non-breeders. Accordingly, the eagles were likely to be evenly

distributed in the area. Since most of the observed dens were situated in a small area, the risk of discovery by a golden eagle should be similar for all observed dens. A behavioural difference in predator defence between experienced and inexperienced breeders is therefore the most likely explanation for differences in golden eagle presence at the observed dens. A possible mechanism could be that inexperienced females spend less time at the den, leading to more opportunities for golden eagles to kill cubs. Further, intensive behavioural studies would be needed to test the background to our observations. Unfortunately, we could not test the effect the paternal experience due to a small sample size with only two inexperienced males. It is possible that the effect of paternal experience on predation is less pronounced since they are more involved in hunting than caring the cubs, especially in early summer (Angerbjörn et al. 2004b). If there is a paternal effect it might instead be more related to starvation during years with low food abundance and this would be more pronounced at dens without supplementary feeding.

Since juvenile arctic foxes with an inexperienced mother show a lower survival, possibly connected to predation, the impact on the population as a whole might be small in large populations with both experienced and inexperienced females breeding. However, in small endangered populations or in growing populations, the proportion of experienced breeders will be lower and predation can cause a negative population development or a slower recovery. From a conservation perspective, it is thus important to focus on conservation actions which improve both juvenile and adult survival to increase the population size and the number of experienced females. Especially in reintroduction programmes or recovery after a bottleneck, it might be necessary to take actions to decrease the impact of avian predators through e.g. eagle frightener or choose areas with low abundance of avian predators. However, to obtain a population with even age distribution, conservation actions must be upheld under several generations, which is of particular importance in inter-annually fluctuating populations.

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