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Faculty of Environmental Sciences and Natural Resource Management

Effects of Resource Availability on Arctic Fox (*Vulpes lagopus*) Offspring Sex Ratios

Linn Marie Flølo

Natural Resource Management

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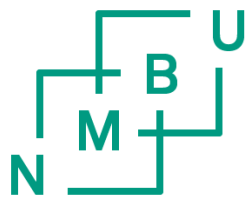
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Photo: Linn Marie Flølo

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Preface

This thesis marks the completion of my master's degree in Natural Resource Management at the Norwegian University of Life Sciences (NMBU). This 30 ECTS thesis within the topic of Arctic fox ecology is connected to the Faculty of Environmental Sciences and Natural Resource Management (MINA). It was done in cooperation with the Norwegian Institute for Nature Research (NINA) and is tied to the Norwegian Arctic Fox Captive Breeding Programme, which is funded by the Norwegian Environment Agency.

I would like to thank my supervisors for their guidance and helpful discussions, comments, and feedback along the way during this (rather) short but intensive MSc project period: my main supervisor Richard Bischof at MINA, and Craig Jackson, Kristine Ulvund, Lars Rød-Eriksen and Nina E. Eide at NINA. I would especially like to thank everyone at NINA for allowing me to use their data collected throughout the many years the Arctic Fox Captive Breeding Programme has been active, and for the opportunities they have given me to join their fieldwork and assist in data collection for the project.

Ås, 13th May 2022

Linn Marie Flølo

Linn Marie Flølo

Abstract

The sex ratio of animals at birth has long been a topic of genetic, evolutionary, and biological interest. In polygynous species, mothers in good condition are typically expected to produce more males, while mothers in poor condition are expected to produce more females.

The Fennoscandian Arctic fox (*Vulpes lagopus*) population was close to extinction a century ago but has started recovering in the last couple of decades thanks to conservation efforts, including supplemental feeding. This offers an opportunity to study the effects of resource availability, both from supplemental feeding and natural rodent population cycles, on offspring sex ratios in the Arctic fox.

I analysed data from 89 wild fox litters born in the Norwegian Snøhetta population from 2010-2020, and 81 litters born at a captive breeding station from 2006-2021. I compared empirical results on the effect of resource access on offspring sex ratios with predictions from theoretical models on sex ratio determination.

My results show a slight male skew in overall sex ratio. There was no significant effect of the rodent cycle in the wild population, however there was a significant positive correlation between offspring sex ratio (proportion of males) and distance from the den to the nearest active supplemental feeder. I found no significant difference in offspring sex ratios between the breeding station and wild population.

Given that males are the more dispersive sex and females the more philopatric sex, my results are most consistent with the predictions of Julliard's (2000) model, where mothers should favour the philopatric sex in high-quality habitats and the dispersing sex in poor-quality habitats. The local resource competition hypothesis, which predicts a bias towards the sex most likely to disperse, also supports my results to some extent, but does not account for the spatial variability of resources. Further studies are needed to compare the effects of resources on sex ratios between the wild-born and captive-bred litters.

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1. Introduction

The sex ratio of animals at birth has long been a topic of genetic, evolutionary, and biological interest (Trut, 1996). Attempts to explain drivers and mechanisms of sex allocation in a wide range of species have led to the formulation of several theoretical models and hypotheses. Darwin (1871) remarked in *The Descent of Man*: “I formerly thought that when a tendency to produce the two sexes in equal numbers was advantageous to the species it would follow from natural selection, but I now see that the whole problem is so intricate that it is safer to leave its solution to the future”. Later, Fisher (1930) developed a theory of how frequency-dependent reproductive advantage of the least abundant sex should balance average investment in males and females at the population level.

Several evolutionary theories explain the circumstances in which offspring sex ratio may deviate from parity. The Trivers and Willard hypothesis (TWH) suggests that in a polygynous species, given certain assumptions, mothers in good condition should invest more in male offspring because male offspring in good condition at the end of the period of parental investment are expected to have greater reproductive success than female offspring in similar condition. On the other hand, if they both are in poor condition, a female is expected to have higher reproductive success than a male, and hence mothers in poor condition should invest more in female offspring (Trivers & Willard, 1973).

Another model, the local resource competition (LRC) hypothesis, explains a skewed sex ratio through a difference between male and female offspring in their use of local, resource rich areas that are essential for female reproduction (Clark, 1978). Assuming that males are the dispersing sex while females establish in or near their natal range, related females may be forced to compete for resources if these resources are limited locally, while males will primarily compete with unrelated individuals in non-natal groups (Silk, 1984). Under such circumstances, the extent of competition among females could be reduced if females uniformly skew the sex ratio of their offspring in favour of males (Clark, 1978).

In contrast to the LRC, the local resource enhancement (LRE) hypothesis concerns species with sex-biased dispersal where the philopatric sex is more likely to remain in or near their natal group and act as helpers (Emlen et al., 1986). According to the LRE, helping behaviour *per se* is the driving force selecting for an imbalanced sex ratio, rather than vice versa (Emlen et al., 1986). According to the hypothesis, helpers repay part of the cost of their

production through their helping behaviour (Emlen et al., 1986). Assuming that males are the most philopatric sex, and therefore more likely than females to help their parents in later years, they would become the “cheaper” sex, and selection should favour females that skew the sex ratio of their offspring in favour of males (Emlen et al., 1986).

Aforementioned models do not consider the spatial heterogeneity of environments. Julliard (2000), on the other hand, connects offspring sex ratios with sex-biased dispersal and heterogeneity of resources (given that male and female dispersal behaviour differs, and that reproductive success differs between habitats). The model makes the simple prediction that parents should adjust the sex ratio of their offspring to the local habitat quality (Julliard, 2000). In a spatially heterogeneous environment, where some habitats are more favourable to reproduction than others, an individual should attempt to increase the number of offspring establishing in high-quality habitats (Julliard, 2000). Hence, in species with sex-biased dispersal, an individual may increase its fitness by producing a larger proportion of the more dispersing sex in low-quality habitats, since these offspring are more likely to disperse to another, higher quality patch, and by producing more offspring of the most philopatric sex in high-quality habitats, since these offspring are likely to remain in that patch (Julliard, 2000).

Theoretical frameworks have formed the basis for many empirical studies. Much is known about sex allocation in invertebrate taxa (Charnov, 1982; Godfray, 1994; Bourke & Franks, 1995; West et al., 2000), and in many of these taxa, sex ratios show a good fit to the predictions of simple models (Sheldon & West, 2004). Much less is known, however, about the mechanisms and drivers of sex allocation in mammals, and data from empirical studies are not always congruent with the predictions of models (Sheldon & West, 2004). Vertebrate sex ratios generally provide a poor fit to theoretical models (Cockburn et al., 2002; Uller, 2006).

The biggest source of sex ratio data in vertebrates has been polygynous mammals, especially ungulates (Clutton-Brock & Iason, 1986; Hewison & Gaillard, 1999; Sheldon & West, 2004). Most ungulates are sexually dimorphic, where male breeding success is dependent on their size and strength compared to other males. In addition, ungulates are generally polygynous, so variance in reproductive success may be greater among males than females. Reproductive success of males should be more influenced by body size, which in turn is dependent on early growth during maternal investment. Accordingly, Trivers and Willard (1973) used caribou (*Rangifer tarandus*), a highly sexually dimorphic, polygynous species, to

illustrate their argument (Hewison & Gaillard, 1999). However, empirical data demonstrate that the TWH is not applicable to all species, even among ungulates (Sheldon & West, 2004).

Among mammalian carnivores, it is known that, for example, brown bear (*Ursus arctos*) sex ratios are skewed in favour of females in core population areas and males in the peripheries of these areas (Swenson et al., 1998). In canids, a male-biased sex ratio is expected for the larger species (Moehlman, 1989; Geffen et al., 1996), and is typical of, e.g., grey wolf (*Canis lupus*) populations (Mech, 1970; Parker & Luttich, 1986) and African wild dogs (*Lycaon pictus*) (Malcolm & Marten, 1982). An equal sex ratio is expected for mid-sized canids (Moehlman, 1989; Geffen et al., 1996), e.g., black-backed jackal (*Lupulella mesomelas*) (Moehlman, 1986), while in small canids a female-biased sex ratio is expected (Moehlman, 1989; Geffen et al., 1996); e.g., red fox (*Vulpes vulpes*) (Macdonald, 1979). However, male-skewed sex ratios have been observed in, for example, wild (Ballard et al., 2000) and domestic Arctic foxes (*Vulpes lagopus*) (Beketov & Kashtanov, 2002).

Many aspects of Arctic fox ecology have been well studied, including the effects of resource availability on different population parameters. In general, abundant food leads to higher adult and juvenile survival (Eberhardt et al., 1983; Angerbjörn et al., 1991; Fay & Rausch, 1992; Tannerfeldt et al., 1994), higher pregnancy rates (Angerbjörn et al., 1991), larger litters (Tannerfeldt & Angerbjörn, 1998), and later dispersal (Frafjord, 1992). Sex ratio is also a population parameter that may be affected by spatial and temporal dispersion patterns of food resources (e.g., Geffen et al., 1996).

The Fennoscandian mainland Arctic foxes are heavily dependent on fluctuating populations of microtine rodents, especially Norway lemming (*Lemmus lemmus*) (Hersteinsson et al., 1989; Elmhagen et al., 2000; Angerbjörn & Tannerfeldt, 2014). Lemming abundance typically cycles with a peak every 3-5 years, and the Arctic fox population fluctuates widely in response to the abundance of their prey (Angerbjörn et al., 1999; Angerbjörn & Tannerfeldt, 2014). In years of increasing and peak lemming abundance, Arctic fox litters of up to 16-18 pups have been recorded (Tannerfeldt & Angerbjörn, 1998). In years of low rodent abundance, Arctic foxes produce small, or no litters (Tannerfeldt & Angerbjörn, 1998), and they rely on other food sources such as reindeer (*Rangifer tarandus*) carcasses, mountain hare (*Lepus timidus*), birds (*Aves* spp.), and vegetation (Strand et al., 1999; Elmhagen et al., 2000). The proportion of alternative food sources in their diet is higher during years of low rodent abundance (Strand et al., 1999).

Supplemental feeding in both summer and winter has proven to increase Arctic fox litter size (Angerbjörn et al., 1995). Feeding dispensers designed to exclusively feed the Arctic fox were developed as part of the Arctic Fox Captive Breeding Programme in Norway (Landa et al., 2017). Use of the customised food dispensers in the wild has reduced the impact of intraguild competition and decreased the variation in food availability for released Arctic foxes (Ertresvåg, 2014). Comparing reproductive output and survival between den sites with and without feeders, supplemental feeding has proven to impact number of litters, litter size and early pup survival (Tannerfeldt et al., 1994; Angerbjörn et al., 2013; Meijer et al., 2013). However, little is yet known about the impact of supplemental feeding and resource availability on Arctic fox offspring sex ratios.

In this thesis I explore the effects of resource availability on offspring sex ratio variation in the Arctic fox. The Norwegian Arctic fox population nearly went extinct a century ago but has started recovering in the past couple of decades thanks to conservation efforts, including captive breeding and subsequent supplemental feeding near dens at release sites (Landa et al., 2017). This offers an opportunity to study the effects of resource availability, both from supplemental feeding and natural rodent population cycles, on offspring sex ratios in the Arctic fox, comparing litters born in captivity at a breeding facility with litters born in the local wild population. I compare my findings on Arctic fox offspring sex ratios with the predictions of above-mentioned theoretical models.

2. Materials and Methods

2.1. Study species

The Arctic fox is classified as an endangered species in Norway (Eldegard et al., 2021), endangered in Sweden (SLU Artdatabanken, 2020) and critically endangered in Finland (Liukko et al., 2019). The species is classified as Least Concern on the IUCN Red List (Angerbjörn & Tannerfeldt, 2014) but was designated by the IUCN as one of ten flagship species indicating ongoing climate change impacts, due to shrinking alpine and Arctic habitats, red fox competition and range expansion, and changes in population cycles of their prey (IUCN, 2009a; IUCN, 2009b).

Historically, the Fennoscandian Arctic fox population size was likely in the range of 10 000–20 000 individuals but experienced a crash in the late 1800s and early 1900s (Collett, 1912; Tannerfeldt & Angerbjörn, 1998). The dramatic decline is generally believed to have been caused by overharvesting by the fur industry (Lönnerberg, 1927; Østbye et al., 1978; Linnell et al., 1999) (but see Selås and Vik (2008) for an alternative explanation). As a response to the decline, the Arctic fox was protected by law in 1928 in Sweden, 1930 in Norway and 1940 in Finland (Landa et al., 2017). However, there was still no indication of natural recovery of the population by the end of the 20th century, after 70 years of protection. On the contrary, the population decline had continued with several sub-populations going locally extinct (Herfindal et al., 2010).

At the turn of the millennium, there were as few as 40–60 adult individuals left in Scandinavia, separated into four relatively isolated sub-populations (Dalén et al., 2006; Angerbjörn et al., 2013). Due to being very small and fragmented, the population risked falling below viable population size over time (Herfindal et al., 2010). In addition, there was consensus that a lack of food resources in the form of interrupted rodent cycles (Loison et al., 2001; Henden et al., 2008), and range expansion and increase in population size of their superior competitor the red fox (Frafjord et al., 1989; Hersteinsson & Macdonald, 1992; Tannerfeldt et al., 2002), were the main threats challenging recovery and conservation of the Arctic fox population (Hersteinsson et al., 1989; Angerbjörn et al., 2013).

Several conservation measures were implemented to rescue the Scandinavian Arctic fox from regional extinction, including captive breeding and release, supplemental feeding to increase survival and reproduction, and red fox control to reduce intraguild interactions and

competition (Angerbjörn et al., 2013; Landa et al., 2017). There have been signs of population recovery in several regions during recent years (Ulvund et al., 2021). Population supplementation and reintroduction was considered necessary to restore connectivity and reduce the risks of inbreeding depression and Allee effects (Linnell et al., 1999). The Norwegian Environment Agency funded the Arctic Fox Captive Breeding Programme as a direct response, with the goal of strengthening existing populations and reintroducing the species to areas where it had gone locally extinct (Landa et al., 2017).

2.2. Study site

The data used in this study were collected in one Arctic fox core area, as well as at the Arctic fox captive breeding station in south-central Norway. The Arctic fox core area Snøhetta consists of Dovrefjell-Sunndalsfjella national park (located at 62°23'48"N 9°10'23"E, covering an area of 1830 km²), and some parts of Knutshø and Dalsida. The breeding station was established in 2005 and is located at Sæterfjellet in Oppdal municipality, Norway, in natural Arctic fox habitat (62°27'15"N 9°31'32"E; 1280 m a.s.l.) (Landa et al., 2017).

The data were collected at altitudes from 1080 to 1492 metres above sea level, and the study area is in the low and middle alpine bioclimatic zones and in the continental bioclimatic section. The climate is characterised by long winters and short summers, with snow cover for 150-225 days per year, normally from November to May, and a short growing season of 110-120 days (Moen et al., 1999). Microtine rodents such as Norway lemming, tundra vole (*Microtus oeconomus*), short-tailed field vole (*Microtus agrestis*), grey red-backed vole (*Myodes rufocanus*), and bank vole (*Myodes glareolus*) are found in the area (Frafjord, 1995). There are wild reindeer and muskox (*Ovibos moschatus*) in the Snøhetta area, and predators such as red fox, wolverine (*Gulo gulo*), least weasel (*Mustela nivalis*), stoat (*Mustela erminea*), golden eagle (*Aquila chrysaetos*), and white-tailed eagle (*Haliaeetus albicilla*) are found in the mountain tundra (Frafjord, 1995; Framstad, 2014).

2.3. Data Collection

I examined 11 years of data from 89 wild-born litters (born in the Snøhetta population between 2010-2020), and 16 years of data from 81 captive-bred litters (born at the Arctic fox captive breeding station between 2006-2021).

Breeding programme

In the Arctic fox captive breeding programme, Arctic foxes are bred in large enclosures in their natural habitat (Landa et al., 2017). The facility consists of eight large enclosures, in addition to one smaller enclosure used for soft release. Each of the main enclosures houses one adult male and one adult female and contains a minimum of two artificial dens made of fibreglass, in addition to several piles of small and large rocks serving as hiding and play areas (Landa et al., 2017). The foxes were fed standard fox food manufactured for the fox farming industry, as well as meat from roadkill of reindeer, muskox, moose (*Alces alces*), red deer (*Cervus elaphus*), and roe deer (*Capreolus capreolus*). The foxes were fed every day in summer and at least five times a week in winter. Each enclosure was also equipped with a feeding dispenser containing dry dog food. This ensured that the foxes had constant access to food in the event of long periods of severe weather preventing regular tending. The feeding dispensers also allowed the pups to get habituated to the type of artificial feeder they would later encounter in the wild after their release (Landa et al., 2017). Each animal in the programme was assigned a unique identification number. All events from birth, such as partner, breeding, and number of offspring, were recorded for every individual (Landa et al., 2017). The captive-born juveniles were released at sites with artificial dens and year-round supplemental feeding using custom-made food dispensers (Landa et al., 2017).

Captive-bred Arctic foxes were born in May/June at the breeding station and released during the following winter together with their siblings at historic den sites, or alternatively soft-released from the enclosure of the breeding station (Di Bernardi et al., 2021). Pups were released together with siblings as whole litters at each release site at eight months of age. Artificial dens of the same kind as used at the breeding station were placed at the release sites, which were prepared close to or on top of old unoccupied Arctic fox dens. Once reoccupation and regular use of the natural dens occurred, the artificial dens were removed (Landa et al., 2017). Released foxes were always supported with feeding dispensers near the release sites. Two feeding dispensers containing dry dog food were placed within 50-1000 m from the den to ensure a regular supply of food. The two dispensers were placed a minimum of 400 m apart to prevent monopolisation by a single individual (Landa et al., 2017). The foxes were already accustomed to the dispensers from the enclosures at the breeding station, and Thierry et al. (2020) observed that the dispensers were frequently used by both released and wild-born Arctic foxes, although less so in years when rodents were abundant.

Recorded breeding events in the wild where at least one parent originated from the captive breeding programme were followed up by trapping and marking of pups in July and August (Landa et al., 2017). Capture and marking procedures for wild-born pups were the same as for pups at the breeding station, except that wild-born pups did not receive ear tags (Landa et al., 2017). Captive-bred pups were marked with plastic ear tags in both ears, where number and colour combinations were unique for each individual and coordinated with Arctic fox tagging in Sweden. Pups also had a passive integrated responder (PIT) tag implanted under the skin of their neck. A DNA sample was taken from every individual (Landa et al., 2017). Wild-born pups descending from released individuals were trapped at the den sites during summer (July/August) and marked with PIT-tags only (Di Bernardi et al., 2021). Arctic fox pups, both at the breeding station and in the wild, were trapped when the pups were approximately two months old. The sex of all pups was recorded during trapping and sex ratios reported in this thesis thus represent the sex ratios of pups at approximately two months of age. For more details about the captive breeding programme, see Landa et al. (2017).

2.4. Statistical analyses

All statistical analyses were carried out using R version 4.1.1 (R Core Team, 2021). In all cases a significance level of $P < 0.05$ was considered. I defined sex ratio as the proportion of males. To account for the binary structure of the sex ratio data (an individual is either male or female), I carried out logistic regression using generalised linear models (GLMs) defined with a binomial structure to test for effects of the rodent cycle and supplemental feeding on the sex ratios in wild-born litters, and to test for a difference in offspring sex ratios between the breeding station and the wild population. To account for variation in litter size, and to give more weight to observations from larger litters than from smaller litters in the analyses, I defined a matrix corresponding to the number of males and females in each litter: `sexes <- cbind(dfno_males, dfno_females)`. Then I used this matrix as the response variable in the GLMs.

Both a standardised numerical rodent index (number of rodents/100 trap nights) and a categorical variable with four phases of the rodent cycle (bottom; increasing; peak; and decreasing abundance) were tested against sex ratio in an initial analysis, but neither had any significant effect on sex ratio nor showed any specific patterns. Ultimately, the rodent phase was then used in subsequent analyses because the index showed large variations and because

of limited trap data; the phases were more general and divided into the four stages of the rodent cycle.

The effect of supplemental feeding was tested using the distance from each den to the nearest active feeding station as a predictor variable. This variable was severely right skewed and had many zeros and was therefore $\log(x+1)$ transformed to make the relationship between the response and the predictor more linear. For the analyses on 'distance to nearest active feeder', three observations with non-active feeders were removed, and two extreme observations of feeders > 6000 m from the den were removed by truncating the data at 2500 m, so that ultimately 84 of the original 89 observations were included in the models. The models compared for offspring sex ratio in the wild population can be seen in Table 1.

Table 1. Generalised linear models compared to test for the effects of resource availability on offspring sex ratios in the wild *Snøhetta* Arctic fox population. The distance variable was $\log(x+1)$ transformed.

Model name	Model structure
glm0	sexes ~ distance + rodent_phase + distance × rodent_phase
glm1	sexes ~ distance + rodent_phase
glm2	sexes ~ distance
glm3	sexes ~ rodent_phase
glm4	sexes ~ 1

Model selection was based on the Akaike Information Criterion corrected for small sample sizes (AICc; Burnham & Anderson, 2002). The best model was defined as the model with the lowest AICc ($\Delta\text{AICc} = 0$), but models with $\Delta\text{AICc} < 2$ were also considered competitive. The most parsimonious model was then defined as having $\Delta\text{AICc} < 2$ and the least degrees of freedom.

Not many variables in the dataset were comparable between the breeding station and the wild population. At the breeding station, all feeders were essentially 0 m from the dens with an unlimited supply of food, and the primary type of food also differed from the wild. Although rodents can easily pass through the enclosures (Landa et al., 2017), the rodent cycle is not expected to affect reproduction in captivity, due to the unlimited access to supplemental food. Therefore, I used a simple binomial GLM to test for a difference in offspring sex ratios between the breeding station and the wild, with the offspring sex ratio

matrix defined above as the response variable, and 'station' versus 'wild' as a two-level categorical predictor variable: $glm(\text{sexes} \sim \text{station_wild})$. For simplicity, the station was seen as a proxy for supplemental feeding/no rodent cycle and the wild as a proxy for rodent cycle/no supplemental feeding. The total number of observations for the station was $n = 81$ and for the wild $n = 89$ (no observations removed).

3. Results

3.1. Distance to nearest active feeder

The most parsimonious model explaining offspring sex ratios in the wild population included only distance to the nearest active feeder as a predictor variable (Table 2; Figure 1). Distance had a significant effect on the proportion of each sex ($p = 0.003$; Table 3). In other words, the proportion of males increased with increasing distance to the nearest active feeder. The model-predicted proportion of males was 0.35 (95% CI: 0.26–0.47) at 0 metres from the nearest feeder and increased to 0.61 (95% CI: 0.54–0.69) at 2500 metres.

Table 2. GLMs fitted to test for the effect of supplemental feeding and rodent cycle phase on offspring sex ratios in the wild *Snøhetta* population of Arctic foxes. The models were ranked according to AICc. *df* = degrees of freedom, Δ AICc = the difference in AICc between the given model and the model with the lowest AICc value. ω_i = Akaike's weights, i.e., normalised likelihood of the models. The model with Δ AICc < 2 and the lowest *df* was the most parsimonious. The distance variable was $\log(x+1)$ transformed

Model name	Model structure	df	AICc	Δ AICc	ω_i
glm2	sexes ~ distance	2	261.3	0.00	0.910
glm1	sexes ~ distance + rodent_phase	5	266.8	5.43	0.060
glm4	sexes ~ 1	1	268.5	7.13	0.026
glm0	sexes ~ distance + rodent_phase + distance \times rodent_phase	8	273.0	11.71	0.003
glm3	sexes ~ rodent_phase	4	273.9	12.57	0.002

Table 3. Estimates for the most parsimonious GLM explaining offspring sex ratios in the wild *Snøhetta* population of Arctic foxes: sexes ~ $\log_{1p}(\text{distance})$. Estimates are given on the logit scale.

Coefficients	Estimate	SE	z value	P \leq
(Intercept)	-0.601	0.238	-2.522	0.012
$\log_{1p}(\text{distance})$	0.136	0.045	2.993	0.003

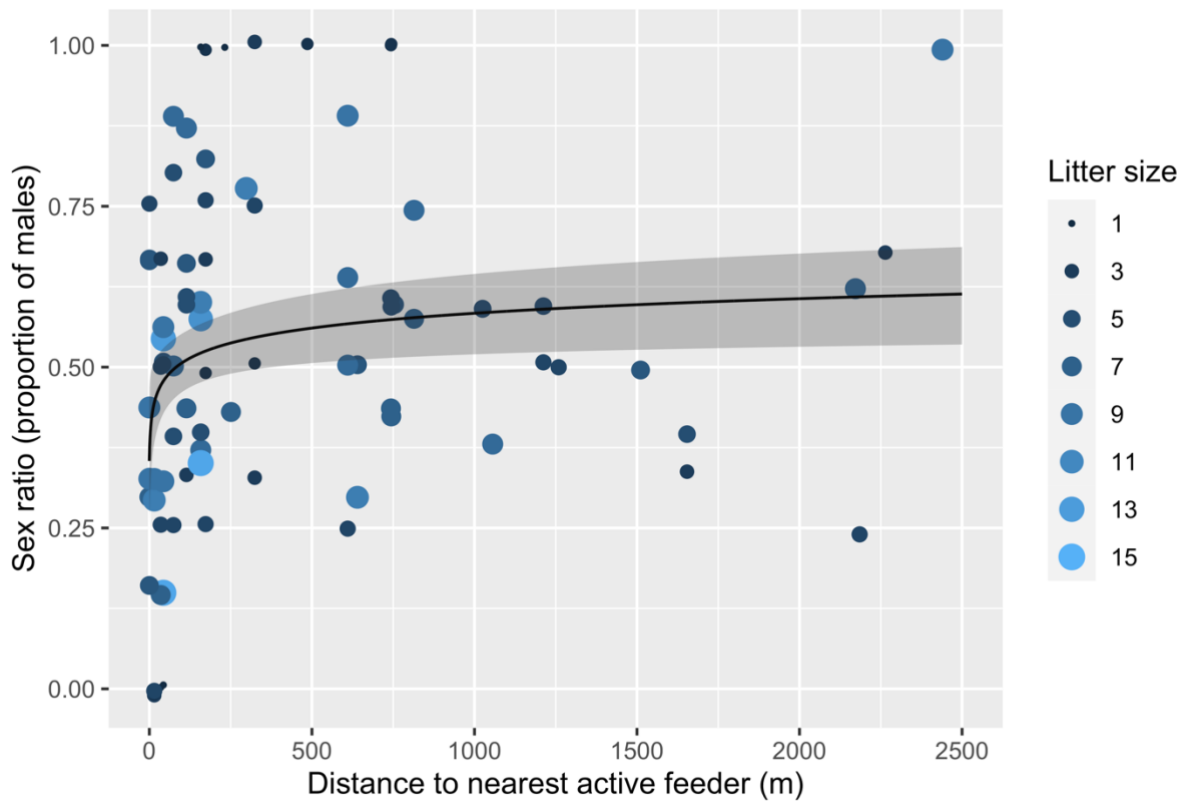


Figure 1. Results from the most parsimonious GLM from the AICc model selection, explaining offspring sex ratios in the wild Snøhetta population of Arctic foxes: $\text{sexes} \sim \log_{10}(\text{distance})$. The points represent the sex ratio (proportion of males) for each litter ($n = 84$) and are scaled and coloured according to litter size. The regression line is based on model-predicted values, and the shaded ribbon indicates the 95% CI of the predicted values.

3.2. Station vs. wild

The mean sex ratio across all litters was 0.52 ± 0.03 (1.08 males per female; $n = 89$) in the wild population and 0.56 ± 0.03 (1.27 males per female; $n = 81$) at the breeding station. However, the difference (0.19 males per female) was not significant ($p = 0.176$; Table 4).

Table 4. Estimates for the GLM tested for Arctic fox offspring sex ratios at the breeding station compared to the wild population; $\text{sexes} \sim \text{station_wild}$. Estimates are given on the logit scale.

Coefficients	Estimate	SE	z value	P ≤
(Intercept)	0.208	0.090	2.317	0.021
station_wildwild	-0.172	0.127	-1.353	0.176

4. Discussion

My results show that offspring sex ratios of Arctic foxes in the wild Snøhetta population are significantly affected by resource availability in the form of supplemental feeding, but not by the population cycle of small rodents. For all recorded litters born across the 11 years of data collection, the proportion of males at two months of age was increasingly higher the further the dens were from supplemental feeders. When comparing offspring sex ratios between the wild population and the Arctic fox captive breeding station, I found no significant difference.

4.1. Distance to nearest active feeder

My analyses revealed a positive correlation between the proportion of males in wild-born Arctic fox litters and distance from the natal den to the nearest active supplemental feeder. In other words, there was a stronger male bias in “resource poor” ranges than in “resource rich” ranges. Similarly, Goltsman et al. (2005) found that the proportion of male pups at emergence from the den was consistently lower at resource rich sites than resource poor sites in the Mednyi Arctic fox (*V. lagopus semenovi*).

A possible explanation for the observed sex ratio pattern is sex-biased natal dispersal, where males are the dispersing sex, and so mothers in “resource poor” ranges, i.e., in dens at a greater distance from the nearest active feeder, produce more male offspring to reduce competition for resources in the natal range. This is consistent with the LRC hypothesis (Clark, 1978), and Julliard’s (2000) model where the more dispersing sex is favoured in poor habitats. In support of this, dispersal of juvenile Arctic foxes on Mednyi Island was found to be strongly sex-biased: approximately 91% of juvenile males dispersed from their natal range within one year after birth, compared to only 40% of the females (Goltsman et al., 2005). This is typical for many species of mammals (Greenwood, 1980; Pusey, 1987; Wolff, 1993; Wolff & Plissner, 1998) and especially for small canids (Creel & Macdonald, 1995; Macdonald et al., 2004). The dispersal pattern on Mednyi was the same between resource rich and resource poor ranges (Goltsman et al., 2005). It is, however, important to note that the mobility of Arctic foxes on Mednyi is limited by the size of the island (187 km²) and by social constraints, as they live in small home ranges and raise small litters (Goltsman et al., 2005), and therefore cannot be directly compared to the Arctic fox population in my study.

On the other hand, Tannerfeldt and Angerbjörn (1996) and Hersteinsson (1984) found no indication of a sex bias in Arctic fox dispersal patterns. There were no strictly philopatric animals in the Arctic fox population studied by Tannerfeldt and Angerbjörn (1996), and strict philopatry appears to be rare in the Swedish Arctic fox population (Angerbjörn et al., 1995). However, moving to a vacant home range might not be associated with higher risks than staying at home in a population of low density, especially with the parents as neighbours. Therefore, Tannerfeldt and Angerbjörn (1996) considered the strategy of short-range dispersers observed in their study as equivalent to a strictly philopatric strategy in a population of high density.

An alternative explanation for the correlation between sex ratio and distance to the nearest active feeder, given that females are the more philopatric sex, is that mothers favour female offspring in “resource rich” ranges because they may remain in or near the natal den as helpers. This is in congruence with the LRE hypothesis (Emlen et al., 1986), as well as Julliard’s (2000) model where the more philopatric sex is favoured in good habitats. In Arctic foxes, typically one reproducing female lives together with a male (Eberhardt et al., 1982; Prestrud, 1992; Angerbjörn et al., 1997; Anthony, 1997; Strand et al., 2000). However, in some cases, multiple adult females are found within the home range of an adult male; Usually this is a reproducing female and one or more subordinate females (Hersteinsson & Macdonald, 1982; Frafjord, 1991; Strand et al., 2000), but sometimes more than one reproducing female may share a den (Frafjord, 1991; Strand et al., 2000). In some populations, adult offspring may remain in the parents’ home range and act as helpers (Hersteinsson, 1984). On Mednyi Island, most females spend their life in their natal range, or in an immediately adjacent range (Goltsman et al., 2005). Alloparental care by non-breeding adults is a widespread trait of the canid family (Macdonald et al., 2004), and it is likely that philopatric female Arctic foxes help their mothers raise the next litter, which has been observed in the Mednyi population (Goltsman et al., 2005). However, evidence for cooperative rearing of pups is scarce in most populations (Strand et al., 2000) (but see Hersteinsson & Macdonald, 1982; Angerbjörn et al., 2004).

4.2. Station vs. wild

The proportion of males in the captive-bred litters was marginally higher than in the wild-born litters, which is contrary to the findings discussed above. However, this difference was not

significant, and therefore there is no evidence for a difference in overall offspring sex ratios between the breeding station and the wild population, despite the experimental conditions being different. There was a limited amount of data available, with a relatively small sample size, and the number of variables that were comparable between the breeding station and the wild population was extremely limited. For example, I cannot say much about the influence of the rodent cycle on the offspring sex ratios, and how it compares between the breeding station and the wild, due to lack of data and the rodent population cycle being extremely variable. Therefore, I cannot really exclude the effect of small rodent abundance, not even at the breeding station.

In future studies it would be worth exploring further why there was no difference in overall offspring sex ratios between the station and the wild. More potential explanatory variables would be needed, including more data on small rodent abundance and population cycles, and detailed data on the differences in food resources. Perhaps the offspring sex ratios are not so flexible after all? But this would be speculation at this point. Future analyses should also compare captive-born litters to only the wild-born litters from dens very close to feeding dispensers, as this would be more directly comparable to the conditions in the breeding enclosures.

4.3. Theoretical model predictions

Although the TWH is the classic hypothesis used to predict offspring sex ratio allocation, directly applying it to the reproductive strategy of small canids would lead to the prediction that “limited food resources may select for female-biased litters” (Geffen et al., 1996). In other words, if this hypothesis explained the demography of the wild population of Arctic foxes in this study, I would expect female-biased sex ratios in “poor ranges” (dens far away from an active feeder) and male-biased sex ratios in “rich ranges” (dens close to an active feeder). In contrast, the LRC hypothesis predicts a male bias when there is competition for a resource locally because males are generally the dispersing sex, the LRE predicts a female bias if philopatric offspring remain as helpers because females are generally the philopatric sex, and Julliard’s (2000) model predicts a female bias in rich ranges and a male bias in poor ranges, because mothers should favour the philopatric sex in high-quality habitats and the dispersing sex in poor-quality habitats. Based on these predictions, my results are most consistent with Julliard’s (2000) model, because it considers the spatial variation in habitat quality. In part the

results are also consistent with the LRC, at least more so than with the LRE, since Arctic foxes are generally non-cooperative breeders, and females in Fennoscandian populations are more likely to disperse to nearby vacant home ranges than to stay in their natal range and help their parents. Most evidence of helping behaviour is from a small, isolated island population (Goltsman et al., 2005). Male offspring, being the more dispersive sex, give less competition for resources locally and should therefore be favoured when local resources are limited. However, neither the LRE nor the LRC consider the heterogeneity of environments like Julliard (2000).

It is difficult to directly compare my results with the predictions of Julliard's (2000) model, because I have not explicitly categorised the home ranges as either resource poor or resource rich. I have only looked at the proportion of males in relation to the distance to the nearest feeder, which is a continuous variable with no defined cut-off point between rich and poor habitats. But, in support of my findings, the observations of Goltsman et al. (2005) were also most consistent with the predictions of Julliard's (2000) model. Similarly, Silk and Brown (2008) examined the effects of LRC and LRE on birth sex ratios in 102 primate species. They found that birth sex ratios were skewed in favour of the dispersing sex in species that do not breed cooperatively, as predicted by the LRC model (Silk & Brown, 2008). In accordance with the LRE model, birth sex ratios were generally skewed in favour of the more beneficial sex in cooperatively breeding primate species (Silk & Brown, 2008). Arctic foxes are, across much of their geographical range, non-cooperative breeders, and therefore the LRC hypothesis should also be a better fit than the LRE.

5. Conclusion

The results of my study show a correlation between Arctic fox offspring sex ratios and food access, suggesting that resources do have an impact on Arctic fox sex allocation. This may have implications for conservation actions, such as supplemental feeding of released captive-bred foxes, intended to support the recovering Scandinavian population. It is therefore important to take potential indirect population effects into consideration, not just direct effects such as increased survival and reproduction. I show that the combined monitoring of both direct and indirect demographic parameters to assess the effect of conservation efforts on an

endangered species can offer a more complete insight into the success or failure of attempts to re-establish previously extirpated wildlife populations.

I did not find evidence for a difference in offspring sex ratios between the captive breeding station and wild Arctic fox population. Therefore, future studies should focus on the effects of food resources on sex ratios of captive-bred compared to wild-born litters, and consider the differential experimental conditions, as well as the effects of potential confounding factors such as mother age (in relation to peak fecundity), litter size, and differential mortality of the sexes, and the relationship between them.

6. References

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Norges miljø- og biovitenskapelige universitet
Noregs miljø- og biovitenskapelige universitet
Norwegian University of Life Sciences

Postboks 5003
NO-1432 Ås
Norway