The effect of trapping on Arctic Foxes in Svalbard: demography and genetics

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Abstract

For hundreds of years arctic foxes on the Svalbard archipelago have been hunted and trapped for their warm and attractive fur. However, little is known about the effect that trapping has on this species population structure. Here I assess the effect of trapping on arctic foxes by comparing the demographic and genetic structure of foxes from the Austfjordnes area in Svalbard over three consecutive hunting seasons. The investigation focusses on changes to the demographic makeup of age structure, sex ratio, female reproduction and body weight from a population that had been low to moderately harvested (2008 – 2009) to those which had been intensively harvested (2009 – 2010 and 2010 – 2011). I also address whether there is a significant change in genetic diversity between the 2008 – 2009 and 2009 – 2010 trapping seasons and test for genetic subdivision within the population. Analyses of age structure revealed a breakdown in the usual population structure by a significant decrease of reproductive adults (especially females) and higher numbers of juveniles in the trapping area. Trapping did not seem to significantly alter the sex ratio or the proportion of females reproducing. However, the lack of reproductive females over three years old would influence future population numbers. Changes to body weight were thought to be related to reproduction and the effects of weather. Genetic analyses showed an increase in allelic richness and significant genetic differentiation between trapping seasons suggesting high immigration rates into the area.

Keywords: Hunting; Demography; Age structure; Sex Ratio; Reproduction; Body Weight; Genetics; Genetic diversity; Genetic subdivision.

1. Introduction

Since the archipelago of Svalbard was first discovered by Willem Barents in 1596 the local fauna including the arctic fox (*Vulpes lagopus*) have been hunted and trapped for their meat, skins and fur. Indeed the striking polar bear (*Ursus maritimus*) and arctic fox furs were an important incentive to the early trappers to stay during the harsh winter period. Although recent times have seen an increased awareness as to the effect that human exploitation can have on a species, recognition that exploitation can have consequences is not new. By the late 19th century, it had been noted in the fishing industry, and in hunting by the early 20th century (Allendorf and Hard, 2009). Concerns arising due to exploitation range from a direct negative impact on population size, to alterations in demography and genetics and even to evolutionary changes. These days, with fisheries and wildlife managers attempting to adopt management strategies for sustainable yield, studies are being carried out to investigate the repercussions of such consequences.

The warmth and attractiveness of the fox fur is the foremost reason for trapping this small carnivore and why it remains an important terrestrial game species in the Arctic. The high quality of the fur made the arctic fox an important source of income for the fur industry. The total harvest for North America between 1919 and 1984 was approximately 40 000 – 85 000 annually (Garrott and Eberhardt, 1987) whilst the total fur returns from Siberia reached more than 100 000 individuals in some years in the 1970's (Nasimovic and Isakov, 1985). Nevertheless, hunting has declined considerably over recent decades due to a decrease in demand and low fur prices as well as alternative sources of income. In the Yukon, the total value of all fur production decreased from $1.3 million in 1988 to less than $300 000 in 1994 (Angerbjörn *et al.* 2004). On Svalbard, the Svalbard reindeer (*Rangifer tarandus platyrhynchus*) being protected in 1925 to save it from extinction and the Polar bear becoming protected in 1973 eliminated the basis for profitable hunting and trapping. Whilst fox trapping still occurs, there are tight controls as to where they are taken from and the number of individuals removed. Registration of arctic fox trapping began in 1996-1997 with a total of approximately 60-300 foxes harvested per year (E. Fuglei, unpublished data, http://mosj.npolar.no/). All hunters follow strict guidelines (Box 1), which enable hunted species to be monitored.

Arctic foxes have a circumpolar distribution (Angerbjörn *et al.* 2008). They are found in tundra habitats throughout the Arctic (Audet *et al*. 2002) including Svalbard, Iceland, Greenland, North America, Siberia and Fennoscandia. Individual foxes are capable of long distance movements of >4500km and can therefore traverse extensive pack ice fields (Tarroux *et al*. 2010). Movements both on land and across the sea ice often occur in late autumn/early winter or during spring when individuals are searching for food (Roth, 2002; Tarroux *et al*. 2010).

The species is exceptionally well adapted to life in some of the coldest areas on earth. Their winter fur is highly insulating consisting of an extremely thick dense under hair and long guard hairs. In winter fur they can tolerate ambient temperatures below -40 $^{\circ}$C without having to increase their metabolic rate significantly to keep a constant body temperature (Scholander *et al.* 1950). Arctic foxes on average weigh between 2.5 and 4.0 kg and have a layer of fat which aids in keeping their body temperature constant. The layer of fat also acts as a food reserve so that when food is in short supply, they can survive starvation for longer and increase the likelihood of finding food again.

Arctic foxes live in two habitat types, with the foxes found in each often being referred to as different ecotypes: the "lemming" and the "coastal" fox. The two habitats differ in the availability of food resources giving rise to differences in arctic fox diets and life history characteristics (Braestrup, 1941; Herseinsson and Macdonald, 1996; Tannerfeldt and Angerbjörn, 1998; Prestrud, 1992a). On Svalbard, with a diet of eggs, birds and carrion from the marine system, as well as geese and their eggs, reindeer carrion and ptarmigan from the terrestrial food web, the foxes there are of the "coastal" ecotype (Braestrup, 1941; Fuglei *et al.* 2003). Unlike the lemming foxes who are dependent on fluctuating lemming cycles, the coastal foxes use of the marine food web provides a more constant food base, thereby enabling population dynamics to be relatively stable (Prestrud 1992a; Angerbjörn *et al.* 2004; Goltsman *et al.* 2005).

Summer home ranges vary widely in size and location on Svalbard from coastal (3-20 km^2) to inland (17-60 km^2) (Eide *et al*. 2005). The predictability of resources is a significant factor in determining the degree of overlap between ranges (Frafjord and Prestrud, 1992). However arctic foxes are territorial when breeding and natal dens are generally used by one family group. A fox pair will normally use the den as long as they live and the same den location is used over and over again for several generations (Prestrud, 1992b). Male home ranges generally include only one reproducing female (Prestrud, 1992b; Angerbjörn *et al*. 1997; Strand *et al*. 2000) however, male home ranges can include subordinate adult females in addition to the reproducing female (Strand *et al*. 2000, Eide *et al*. 2004).

Arctic foxes are sexually mature during their first year of life (~10 months old); however on Svalbard few vixens become pregnant in their first year of life (Eide *et al.* 2012). After the age of three is reached more than 90% of females give birth to 5 or 6 pups annually (Prestrud, 1992b; Angerbjörn *et al*. 2004) however maximum pregnancy rates are not obtained until they reach the age of four (Eide *et al.* 2012). The mortality rate during the first winter is higher than 75%, but then decreases and remains low until an age of six years. Average longevity is about three to four years, but a 16 year old individual has been recorded from Svalbard (E. Fuglei, unpublished data).

Dispersal of juveniles occurs either early in the autumn (August and September) or in mid-winter (December to March) (Frafjord and Prestrud, 1992; Strand *et al.* 2000), but the existence of kin structure within populations has been noted (Frafjord and Prestrud, 1992; Ehrich *et al.* 2012). The majority of young foxes leave their parents' territory during their first year of life, but some may not disperse until their second year (Angerbjörn *et al.* 2004).

In a population that is not harvested or only moderately harvested a higher and a more stable number of reproductive adults than in an intensively harvested population would be expected. The characteristic traits of the arctic fox such as home range and territorial behavior will result in this older age structure. In an intensively harvested area, an increase in juvenile number could be predicted. A study carried out by Whitman (2003) looked at American mink under light, moderate and heavy trapping regimes. It showed that a higher number of juveniles than adults were trapped in all harvest regimes. However, it is possible that juveniles enter traps more readily than adults, a phenomenon known to occur in mink (Ireland, 1990), thereby effectively reducing the probability of trapping adults in the post breeding season by occupying all the available traps (Bones *et al.* 2006). In an arctic fox population, removal of a breeding territorial pair may lead to free territories which may act as a dispersal "sink" thereby creating space for nomadic juveniles to move into.

The harvesting of a breeding pair could also modify the ratio of males to females found in the area. In a non-harvested area, the expected sex structure would be a breeding pair consisting of a male and female, with perhaps some young sub-adult females. Male biased juvenile dispersal has been reported for arctic foxes (Eberhardt and Hanson, 1978; Ehrich *et al.* 2012), therefore the majority of young males would likely have dispersed leaving a natal territory favoring females (Ehrich *et al.* 2012). However, often removal of the dominant males and the resulting low male densities in an area will tend to attract young males from neighboring regions as seen in red deer (*Cervus elaphus*) (Clutton-Brock *et al.* 2002). This may then see a shift either towards equal numbers of male to female juveniles' or towards higher numbers of young males.

Changes in the number of reproductive and mated females due to intensive harvesting will have an effect on the populations' reproductive success. By examining uteri for evidence of postpartum placental scars (Lindström, 1981) female reproductive success from the last breeding season can be studied. With a reduction in the number of adults due to intensive harvesting, one would expect an overall reduction in reproduction until the younger females came of age. However, as noted in red foxes (*Vulpes vulpes*) young females breeding for the first time often tend to produce smaller litters than older animals (Kolb and Hewson, 1980; Allen, 1983). If intensive harvesting of the population were to continue it is possible that the young females would be removed before they could reproduce.

This would see a dramatic decrease in population size and even higher immigration rates of non-breeding juveniles from neighboring areas.

The body condition of an animal is often related to its energetic state hence an animal in good condition has higher energy reserves (usually in the form of fat) than one in poor condition. Individuals with a larger fat layer may have better fasting endurance and higher survival (Millar and Hickling, 1990) as they can increase the time between successful searches for food. The amount of fat that an individual carries will increase the overall body weight. The foxes in a moderately harvested population with higher numbers of older more established individuals would likely have well-known food resource areas and stored food in caches within their territories. With the removal of these individuals, immigrants to the area may not have access to such food caches and body weight may therefore be expected to decrease.

The changes to the genetic makeup of a population due to exploitation may be less obvious but have just as important an effect for managing the long term survival and health of a species. In a fox population genetic variability is dependent on the effective population size, on the frequency of replacement events in territories by nomadic individuals, and the relatedness of the replacing individual to the group (Frati *et al*. 2000). The replacement rate should increase in populations with a high mortality rate in the adult age class caused by predation or hunting. The effect on mortality rate on the proportion of reproducing individuals, litter size and dispersal "sinks" will all have a combined effect on the population.

Movement is often viewed as one of the most important processes determining the distribution of populations and therefore the genetic variation within and between populations (Slatkin, 1987). At a large scale, the genetic structure of arctic fox populations is characterized by very low differentiation over large parts of their circumpolar range (Dalen *et al*. 2005; Carmichael *et al*. 2007; Geffen *et al*. 2007). In game species, hunting may cause spatial differences in mortality which in turn may influence their population dynamics at a landscape scale. Intensively hunted populations with high dispersal ability may be able to persist due to immigration from areas that are not hunted (Little *et al.* 1993; Slough and Mowat, 1996). Results from two recent studies of the arctic foxes in Svalbard indicated that this may be the case for this population (Ehrich *et al*. 2012; Eide *et al*. 2012). Hunting potentially increases the turnover in territorial foxes and thus disrupting possible genetic structure.

Localised genetic differentiation has been documented for other hunted species including a relative of the arctic fox, the red fox (Frati *et al*. 2000). A study of territorial greywing francolin (*Francolinus africanus*) by Little *et al*. (1993) found no difference in expected heterozygosity (the probability of two alleles from the population being different) (Hartl and Clark, 1997) between populations that were

hunted and those that were not. However, they did find higher levels of inbreeding in the populations that were not hunted. They concluded that any reduction in heterozygosity caused by lower population size was compensated by greater gene flow within the hunted population. The net effect on heterozygosity was neutral (i.e., higher migration rates were balanced by fewer potential migrants), but hunting clearly had contributed to a breakdown in the usual territorial structure (Harris *et al.* 2002). Frati *et al*. (2000) reported lower genetic variability among non-hunted populations than hunted populations of red fox in Europe as reflecting changes in fox social structure following the loss of larger predators e.g. wolves (*Canis lupus*). Historically large predators kept fox social structure flexible and encouraged outbreeding. They suggested that human hunters took the place vacated by the predators increasing turnover and decreasing inbreeding, therefore partially mimicking the effects of predation pressure under which foxes had evolved (Harris *et al.* 2002). On Svalbard, the arctic fox has no natural enemies so its main predator over the last few hundred years has been mankind. Nevertheless, evidence would suggest that any removal of individuals, either naturally by predation or by hunting will have some level of social disruption. Intensive hunting could also reduce the size of a population to a level which would lead to loss of genetic diversity. Loss of genetic variation can reduce the productivity of exploited populations both by reducing individual fitness in the short term (primarily affected by heterozygosity) and by reducing the ability of subpopulations to evolve in the future (primarily affected by loss of allelic diversity) (Ryman *et al.* 1995).

Whilst trapping may be a cause of demographic and genetic changes in a population, it also provides the material to study possible alterations which have occurred. The objective of the present study is to assess the effect of hunting on arctic foxes in Svalbard by comparing the demographic and genetic structure of foxes from the Austfjordnes area over three consecutive hunting seasons. For several years the population had been low to moderately harvested (Fig. 4), however in 2008 -2009, the area was subjected to intensive harvesting over an expanding area which continued for the next two seasons, (2009 -2010 and 2010- 2011). In a low to moderately harvested population, the social structure of the arctic fox would be a key factor in determining the age and sex ratio of the individuals. We would expect the study area to be mainly divided into the home ranges and territories of established breeding pairs with an age range of three years and up. Relatively high numbers of reproductive adults would therefore be expected, with the majority of the juveniles likely being the young of the year for those breeding pairs and perhaps some of the previous year's females. Intensive hunting would increase the probability of one or both of the breeding pair being removed. We would therefore expect to see higher numbers of male and female juveniles as they move into the vacant territory. We address the changes to the demographic makeup of the population in the Austfjordnes area by looking at age, sex, female reproduction and body weight of the foxes trapped. Specifically, the objectives of demography part of the study were to: (i) test for differences in age structure between

the trapping seasons; (ii) test for differences in sex ratio between the seasons; (iii) estimate the proportion of reproducing females; and (iv) estimate the body condition of the foxes trapped by comparing body weight between seasons. Genetically, it is possible that trapping will cause a decrease in genetic diversity due to a reduction in population size; however on the other hand, this removal will cause space for immigrant individuals to move into the area which may then lead to an increase in gene diversity. For the genetic section of the study, the objectives were to investigate whether (v) there is a significant change in genetic diversity between the 2008 – 2009 and 2009 – 2010 trapping seasons using several statistical methods; and (vi) test for genetic subdivision within the population. This study will discuss, if any, the effect that trapping may have on the demography and genetics of the arctic fox population in the Austfjordnes area of Svalbard.

1.1 Box 1. Rules and regulations for trapping foxes on Svalbard – location, season and method

All hunting on Svalbard is subject to the provisions of the "Svalbard Environmental Protection Act". Only people who live in Svalbard (residents) are allowed to hunt and all hunters must follow the regulations relating to the harvesting of the fauna on Svalbard as detailed in the Act. Anyone wanting to hunt must pass a hunting license test, and pay a seasonal hunting fee which goes to the Svalbard Environmental Fund. The regulations provide the animals on Svalbard with protection by restricting hunting to specific areas (Fig. 1) and to particular seasonal timeframes. The hunting season for the arctic fox runs from the 1st November to 15th March. There is also a duty to report the results of the hunting/trapping season's activities to the Governor "not more than 10 days after the end of the period for which the hunting, trapping or fishing license or permit is valid".

Fig. 1. Map of Svalbard. Circled areas show where flora and fauna are protected and where hunting is banned. (Sysselmannen)

There are only a few people that make their living from the income gained from harvesting in Svalbard. They generally live in trapping stations quite a distance from Longyearbyen. The hunters that live in Longyearbyen are mostly recreational hunters and are restricted to allocated areas around the town.

Box 1. Continued

The method of trapping foxes is also subject to specific regulations and includes the statements "Arctic foxes may only be trapped using body-gripping traps and dead-fall traps", and "Traps shall function in such a way and with such force that foxes are killed immediately". A further regulation is that "as far as possible, the traps shall be inspected every week". These laws and regulations help with the management and monitoring of the Svalbard arctic fox population.

Fig. 2. Top left shows a Dead fall Trap not far from Austfjordnes (Photo by Eva Fuglei). Another example of a dead fall trap is shown above with bait and stuffed foxes (Photo taken in the Polar Museum, Tromsø). An example of the "Svalbard trap" is shown on the left (Photo by Eva Fuglei)

2. Materials and Methods

2.1 Study area and sample collection

Svalbard is an archipelago situated in the high Arctic between 74° and 81° north and between 10° and 35° east. Our study focused on Austfjordnes (Fig. 3) in the northern part of Spitsbergen. In this area, arctic foxes have been trapped with low intensity since 2000 (Fig. 4) However, in the 2008 – 2009 season, a large number of foxes were trapped and intensive trapping continued for the following two seasons (2009 – 2010 and 2010 – 2011). This resulted in a good opportunity to compare foxes from a low to moderately harvested population (2008 – 2009 foxes) to those subjected to intensive harvesting (from the two consecutive seasons).
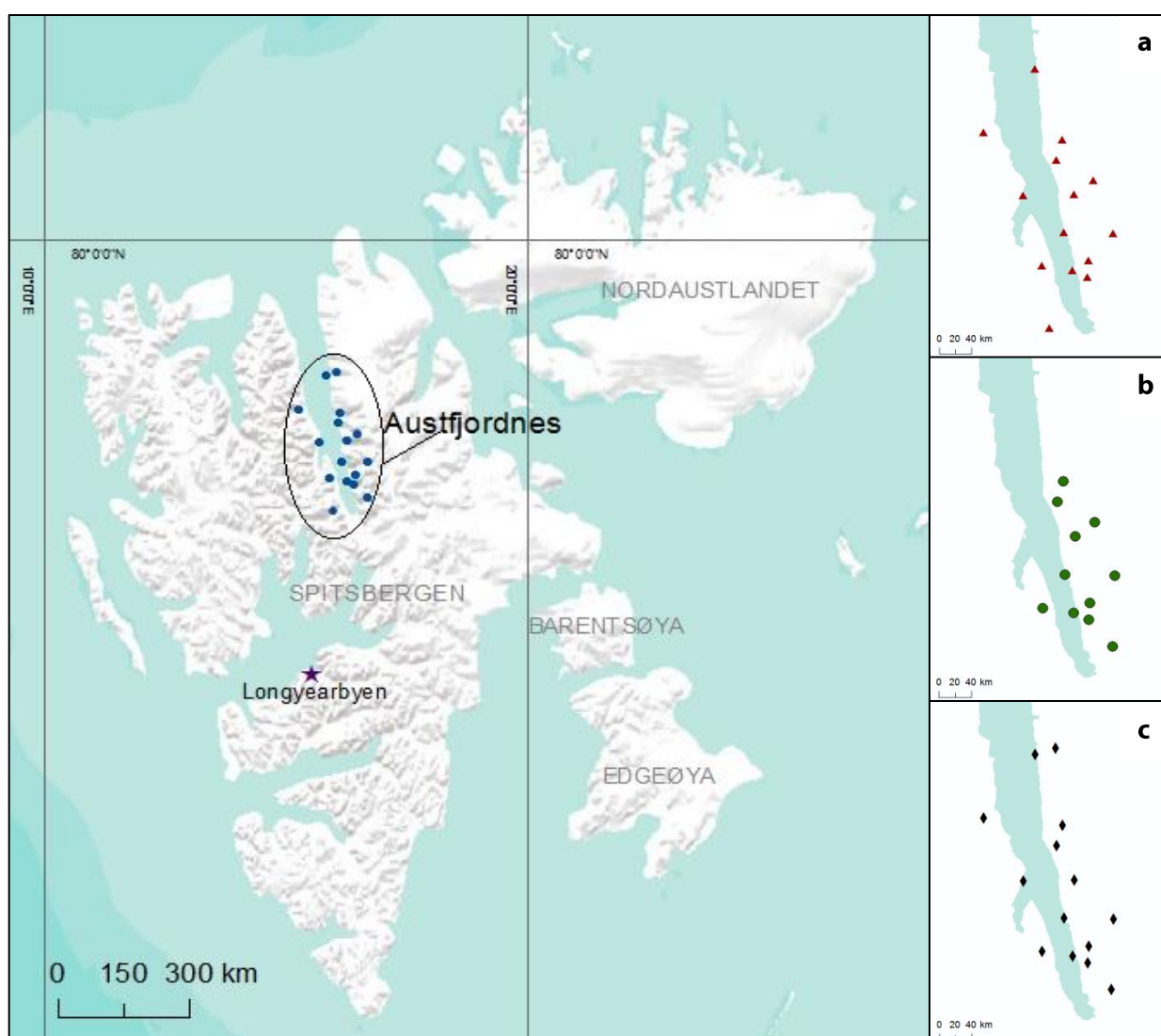

Fig. 3. Location of the Austfjordnes study area and Longyearbyen, the largest settlement and administrative center of Svalbard. Both are situated on Spitsbergen, the largest island in the Svalbard archipelago. All trapping locations where foxes were trapped and used in the study are shown. Inserts a, b and c show trapping localities for each of the three hunting seasons in Austfjordnes respectively.
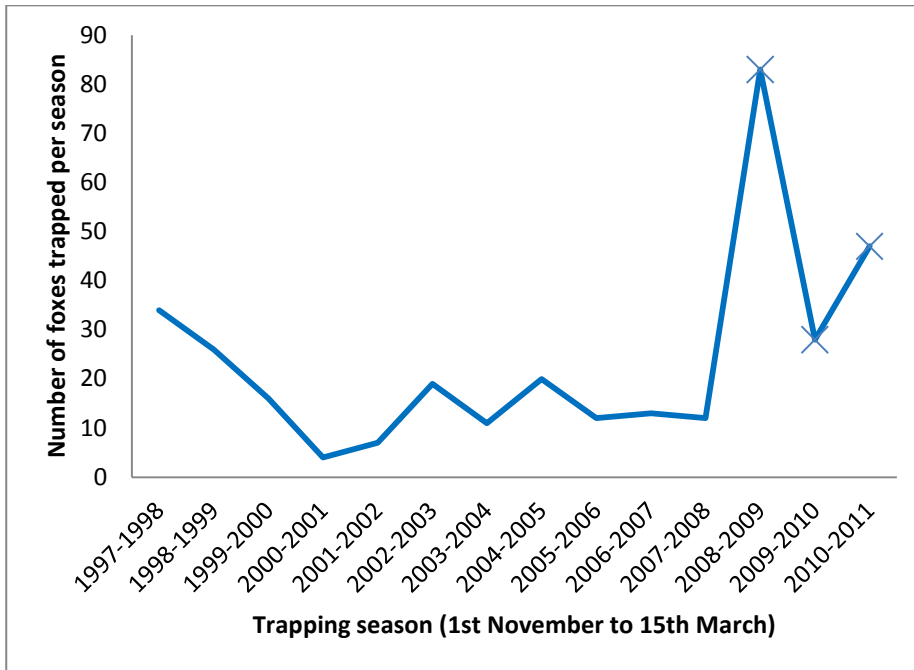
Fig. 4. The reported number of foxes trapped in Austfjordnes over the last 14 trapping seasons. Points highlighted by 'x' are the seasons examined in this study. The foxes removed in the 2008 -2009 trapping season are examples of a low to moderately harvested population but their removal, this "big take-out", signifies the first season of intensive trapping.

All of the studied fox samples came from the Austfjordnes hunting area and were collected by trapper Tommy Sandal. A total of 83 foxes were trapped in the 2008-2009 season. Of those collected 8 of the samples had been partially eaten, 7 of which were excluded as relevant data could not be collected. This left 76 individuals from the first season used in this study. 28 foxes were trapped in the next season 2009 – 2010 but one was partially eaten and lost in transit leaving 27 samples. All of the available samples from these two seasons were used for both the demographic and genetic analyses. Demographic data was collected for a third season (2010 -2011) with 47 foxes trapped. Of these samples 5, two females and three males could be sexed but not aged, and 2 could not be sexed as they were partially eaten and only the head remained. These 7 foxes were excluded from the analyses by age class or sex respectively.

The second trapping season (2009-2010) suffered from poor weather conditions (Fig. 5). Several days of rain followed by cold spells resulted in icing on the tundra during the winter. Combined with no sea ice in the Wijdefiorden, conditions were difficult for the trapper and he was unable to place the fox traps in all the same locations as the previous year (Fig. 3b insert). The weather conditions also created problems getting out and around with the traps. The lower number of foxes trapped can thus be attributed to a bad trapping season and is unlikely to be a direct consequence of the high numbers harvested the previous year. Trapping conditions improved the following year.
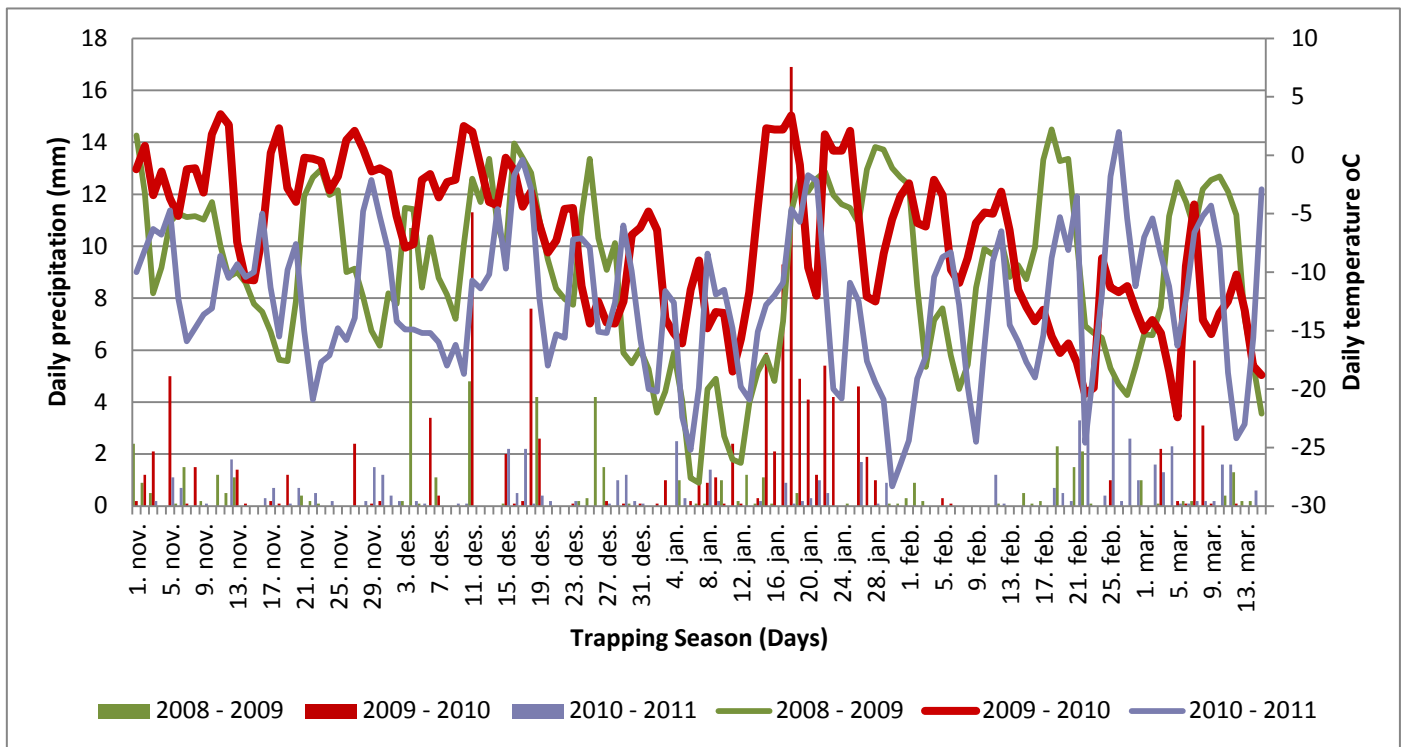
Fig.5. Comparative climate graph of daily meteorological data (precipitation (bars) and air temperature (lines)) from Svalbard airport during the 2008 – 2009, 2009 – 2010 and 2010 – 2011 hunting seasons. (Weather data from Met.no)

2.2   Demographic methodology

The trapping location (Fig. 3) and date was recorded for each individual removed from a trap. Once removed from the traps, the foxes were kept frozen to preserve the fur. Before removal of the fur the following measurements were taken: sex, body weight and back foot length (to the nearest mm from the bases of the claws to the rear side of *calcaneum*). At the end of the hunting season, the carcasses were transported to Longyearbyen by snow scooters where they were stored in freezers until shipped to the Norwegian Polar Institute, Tromsø. At the Veterinary Institute the carcasses were dissected. A tooth was taken for aging, the sex was documented and placental scars of the females investigated.

The reproductive status of the females could be determined at this point by studying placental scarring or fetuses in the uterus of each adult. The scars counted were of a dark colorization and assumed to be from the latest pregnancy. In cases where paler scars were also present, they were noted but not counted. The number of recent scars were assumed to be indicative of at least the number of young conceived in the latest pregnancy, although not necessarily the number of pups born (Lindstrom, 1981; Fay and Rausch, 1992)

Muscle tissue was frozen to preserve it for DNA analysis. Age was estimated by counting annuli in the cementum of sectioned lower canine teeth (Grue and Jensen, 1976). Whilst arctic foxes are generally sexually mature at 1 year old, Prestrud (1992a) and Eide *et al.* (2012) reported that in Svalbard most females start to reproduce when they are 3 years old. However as the animals are biologically capable and some do reproduce earlier than three years of age we therefore separated the data into two age classes (Table 1): Animals in their first winter aged up to one year old (JUV) and all older animals (2+ years) were considered adults (AD).

Trapping season	Total	JUV		AD		N/A
		F	M	F	M	
2008 - 2009	76	12	18	22	23	1
2009 - 2010	27	8	3	2	13	1
2010 - 2011	45	8	20	4	8	5
Total	148	28	41	28	44	7
Total in each age class		69		72		

Table 1. Number of foxes per trapping season, age class and sex. N/A is individuals that could not be aged or sexed.

2.3   Genetic methodology

The muscle tissue samples were stored frozen. Following the manufacturer's protocol, DNeasy tissue kits (**QIAGEN ™**) were used to extract genomic DNA from samples from the first two trapping seasons (Table 1. 2008 -2009 and 2009 – 2010 with 103 samples in total). 10% of these samples were chosen at random to be repeated throughout the procedure in order to calculate the mean error rate. To decrease the risk of contamination, extractions were run in a laboratory expressly used for this purpose.

Microsatellite loci were amplified through polymerase chain reaction (PCR) using fluorescently labeled primers (Table 2). We used the same 12 loci as Carmichael *et al.* (2007): CPH5, CPH9, and CPH15 (Fredholm and Wintero, 1995); CXX140, CXX147, CXX173, and CXX250 (Ostrander *et al*. 1993); CXX671, CXX733, CXX745, CXX758, and CXX771 (Mellersh *et al*. 1997). Multiplex reactions were run as follows: CPH15/CXX758, CXX771/CPH9, CXX173/CXX147/CPH5/CXX671 and CXX250/CXX140/CXX733/CXX745. Each Pre-PCR mixture for the 4 multiplex reactions contained 6.25 μl QIAGEN, 1.25 μl of the primer mix (4% concentration of each primer), 2 μl RNase free water and 3 μl of approximately 20 ng/ μl DNA template.

Run	Multiplex reaction Mix	loci	Primer Colour
1	1	CPH15, CXX758	FAM
	2	CXX147, CXX173	NED
		CPH5, CXX671	VIC
2	3	CPH9, CXX771	FAM
	4	CXX733, CXX250	NED
		CXX745, CXX140	VIC

Table 2. Colour of fluorescently labeled primers and loci they were used on in multiplex reactions.

All PCR amplifications were conducted in Eppendorf Mastercycler ep thermocyclers (Eppendorf AG) following a touchdown protocol: 15 min at 95°C followed by 15 cycles of 30 s at 94°C and then 90s at 57-50.5°C and 60 s at 72°C. The annealing temperature decreased by 0.5°C each cycle. This was followed by 24 cycles of 35 s at 94°C before 90 s at 50°C, 60 s at 72°C; and 10 min at 4°C. Reaction products were diluted (FAM x20 and NED/VIC x30) and 1µl of each diluted PCR product was mixed with 9µlHiDi and 0.5µl Rox 350 size standard. Fragment analysis was carried out on one of the two machines available at the sequencing facility of UNN. A 3130xl Genetic Analyser or a 3500xl Genetic Analyser (made in Japan by Hitachi for Applied Biosystems) was used. Peak Scanner™ Software v1.0 (Applied Biosystems) was used to precisely calculate the fragment sizes. All fragment sizes for a locus were then plotted and binning to discrete alleles was carried out manually. Microsatellite toolkit version 3.1 for PC Microsoft Excel was used to check the data set for typographical errors

2.4   Data Analysis

Statistical analyses of the demographic data set were carried out in R v. 2.12.2 (R development Core Team 2011). Chi-square tests were used to evaluate the age structure of the foxes in relation to each of the three trapping seasons. The data was split into smaller age and sex classes (Table 1) to distinguish any effects that trapping may have had on the juvenile and adult populations. Chi-square tests were again used to evaluate the sex ratio as well as the reproductive activity of the vixens that were trapped in relation to season and age. When the data was split into age groups, the numbers of observations became small and were therefore evaluated using Fisher's exact test. Body condition of the foxes was assessed using a linear model to estimate the effect of season on body weight. Five candidate models (Appendix Table A1) were evaluated based on different combinations of the following explanatory variables: *Season* (1, 2 and 3), *BkFoot* (Back foot length) and *Sex* (M and F). *Season* is considered to be a focal variable in the analysis as it is this effect on body weight (*BW*) that we wish to examine. *BkFoot* was used as a proxy for total body size (Prestrud and Pond, 2003). To account for any differences the sex of the fox might have on its body weight and size, the variable *Sex*

was included. The simplest model contained only the additive effects of *Season* and *BkFoot.* The second model was similar but included a two-way interaction between *Season* and *BkFoot*. The additional three models all contained the additive effects of *Season* and *BkFoot*. However, one also had the additive effect of *Sex*, whilst another had a two-way interaction of *Season* and *Sex* and the third the two-way interaction of *BkFoot* and *Sex*. The best model was determined using Akaike's Information Criterion (AIC) and in accordance with Burnham and Anderson (2002), the model with the lowest AIC was chosen unless the differences were less than 2, in which case the most parsimonious model was selected. The chosen model was then plotted to ensure that the residuals did not deviate from a normal distribution.

For the genetic data Micro-checker (van Oosterhout *et al*. 2004) was used to identify any genotyping errors due to null alleles, short allele dominance (large allele dropout) and scoring errors due to stuttering. The mean error rate per locus was calculated according to Pompanon (2005).

We compared the genetic diversity of the foxes trapped in the two seasons to see if any changes could be detected. Gene Diversity per locus and population was calculated as expected heterozygosity using FSTAT v 2.9.3.2 (Goudet, 2002) and the means for each season were compared using pairwise t-tests in R. This type of analysis was carried out for the total dataset, as well as for each age class (Table 1). Another approach to measuring genetic diversity is to produce an estimate of allelic diversity or richness by measuring the number of different alleles per locus, corrected for sample size. Allelic richness per locus and population was calculated using FSTAT based on a minimum sample size of 27 diploid individuals. The means of the total dataset for the two seasons were compared by a pairwise t-test in R, as well as calculated for the two age classes.

We compared the observed genotype frequencies of the total dataset with those that are expected under the Hardy-Weinberg (H-W) equilibrium using FSTAT based on 2400 randomizations with an indicative adjusted nominal level of 5%. This was then repeated for the JUV and AD data sets. To evaluate population sub-structuring and inbreeding, F_{IS} was calculated for the total population in FSTAT using Bonferroni adjustment for multiple comparisons. Differentiation between the two seasons was calculated as F_{ST} and evaluated in FSTAT.

Linkage disequilibrium may also indicate population subdivision which could be important in regards to a hunted species due to drift or founder effects. To test the total dataset for deviations from linkage equilibrium a randomization test in FSTAT was used. This was again repeated for the different age classes.

3. Results and Analysis

3.1   Demography Results

3.1.1.   Age structure

The age structure in the sample of trapped arctic foxes from a low to moderately harvested population (2008-2009) showed individuals of all ages were present in the area. Following the "big take-out" of 2008 -2009 there was a decrease in ages being represented with the proportion of juveniles becoming higher in each of the successive seasons. (Chi-square test for two age classes, p=0.01). Fisher's exact test with all ages (of Fig. 6) was however not significant.
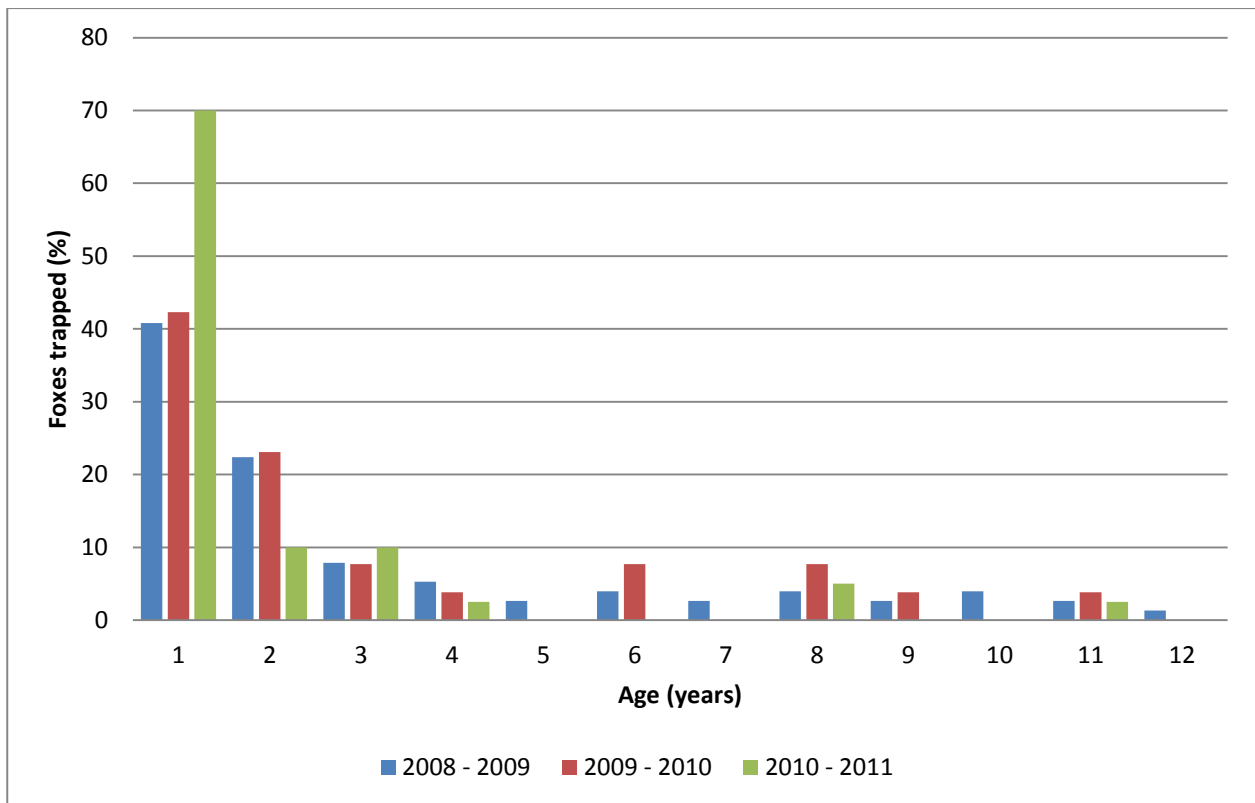

Fig. 6. Comparison of percentage of foxes trapped in each age group over three trapping seasons (2008 – 2009, 2009 – 2010 and 2010 – 2011).
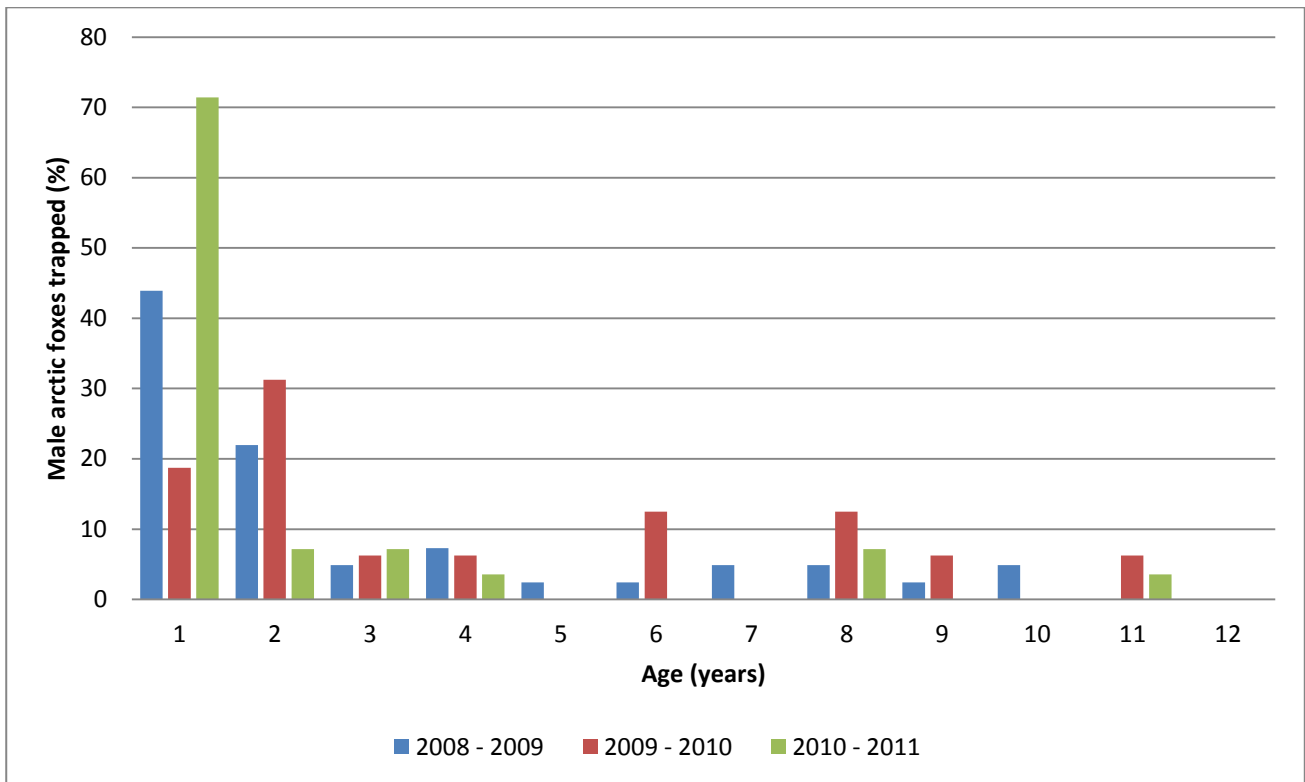
Fig. 7. Comparison of the percentage of male foxes of different ages trapped in each of the three hunting seasons.

The age structure of the males trapped show the greatest proportion to be aged between one and two (Fig. 7). The oldest animals were eleven year olds. In the low to moderately harvested population, over 40% of the males trapped were young of the year, 20% more than the nearest age group. The proportion of adults caught in this season was relatively well spread out across the age groups giving a juvenile (JUV) to adult (AD) ratio of 1:1. After the first year of intense harvesting, there was a decrease to only 18.75% of the males being young of the year resulting in a JUV: AD ratio of 1:4. Over 10% more second year males were however caught that season. The third season shows the greatest change with over 70% of the males caught that season being young of the year and changing the ratio of JUV: AD 2.5:1 in favor of male juveniles. The changes between the juvenile young of the year and the adult foxes show that there are significant differences in the structure of the age classes between seasons (Chi-square test for two age classes, p=0.007).

The greatest proportions of females trapped (Fig. 8) in each of the seasons were young of the year. The first season shows representatives from all but one age group (age seven) up to the oldest trapped fox aged twelve. The first season, had a JUV: AD ratio of 1:1.83, with over 40% of females trapped ranging from three to twelve years old. The second season age ratio changed to 4:1, with the majority of animals trapped being young of the year. The JUV: AD ratio for the third year was 2:1.

The female juvenile to adult ratio differed significantly between the seasons (Chi-square test for two age classes, p=0.01). The most notable observation for the 2009 -2010 and 2010 – 2011 seasons are that no female foxes older than 3 years old were trapped.
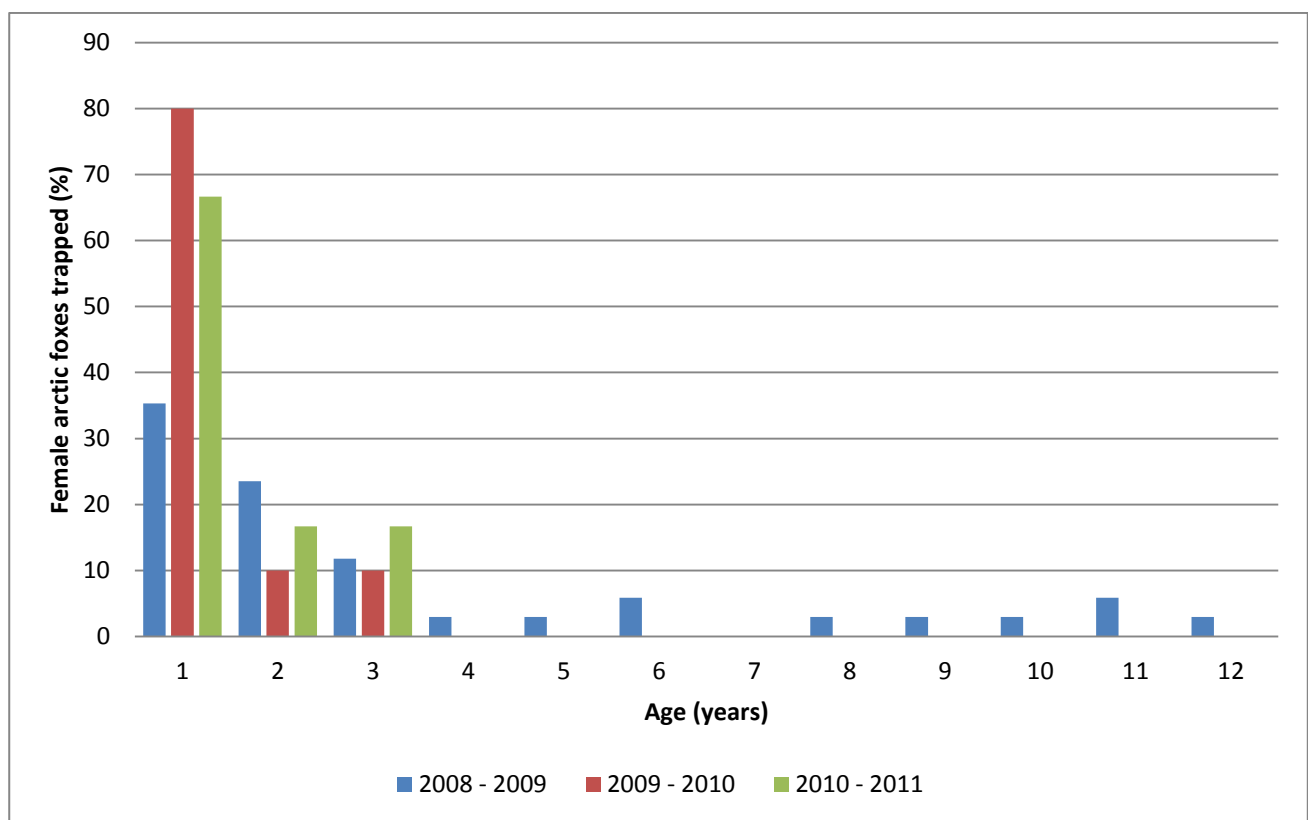

Fig. 8. Comparison of the percentage of female foxes of different ages trapped in each of the three hunting seasons.

3.1.2 Sex structure

The results of the sex structure of the trapped foxes showed that the highest proportion of foxes caught in each trapping season were male (Fig.9). In the first two seasons this was adult male foxes, but in the third trapping season, it was juvenile males. When considering the JUV age class, both the first and third years of trapping, revealed a greater percentage of males than females. This was different in year two, where a higher percentage of females than males (27%) were shown. The third year saw a similar difference in percentage but again more males (71%) than females.

For the adult age class, the first trapping season (low to moderately harvested) provided a 1:1 sex ratio for the adult age class, with only a 2% difference in proportion of foxes of each sex trapped. This changed in the second and third seasons (intensively harvested), with a higher percentage of foxes trapped being male (87% and 67% respectively). The differences were however not significant (Chi-square test for sex, $p=0.29$).
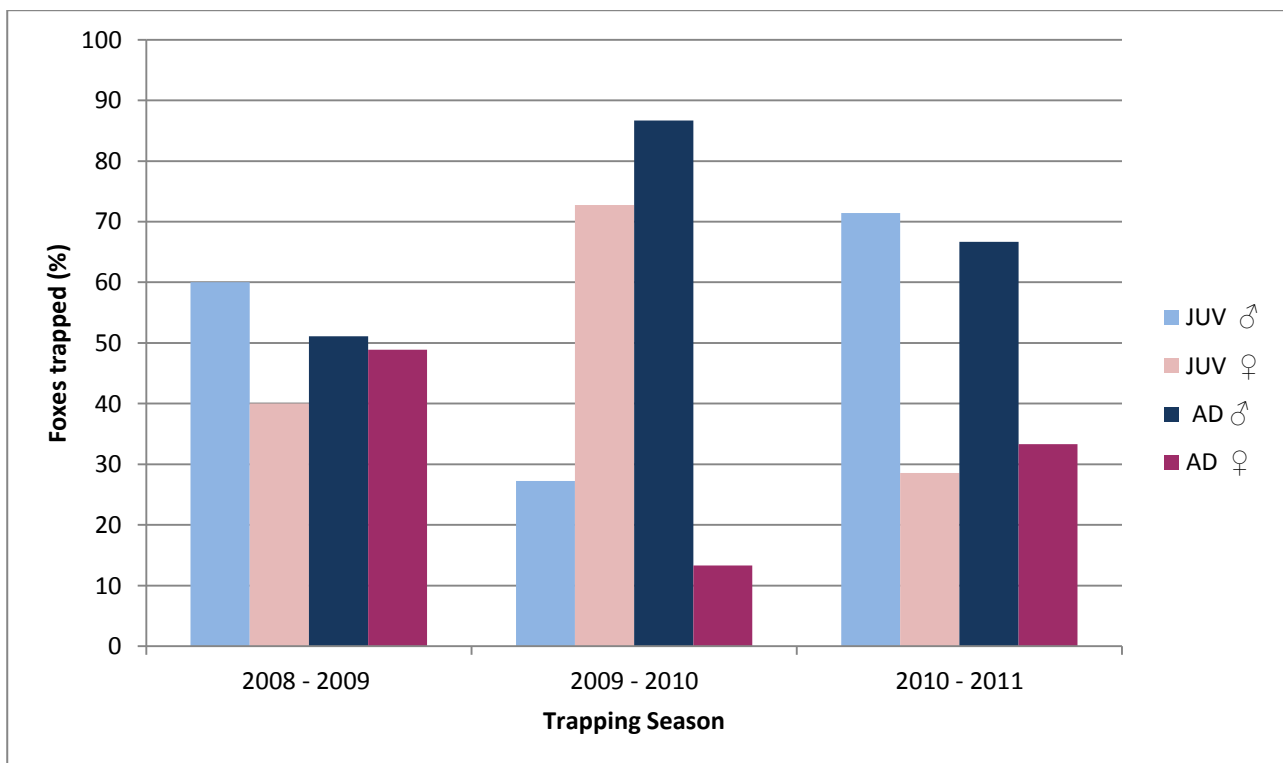

Fig. 9. Male to Female sex ratio percentages of foxes trapped divided by age class (Juvenile and Adult) and trapping season.

3.1.3 Female Reproduction

Of the 56 female foxes caught over the three trapping seasons, half were adults of reproductive age. Of these 28 vixens (57 %) did not show any signs of placental scars in uteri. The remaining 43 % (Fig. 10) showed evidence of having reproduced during the last summer. The majority of these foxes were trapped in the first season. Although there was a large decrease in the number of females trapped, the proportion of reproducing adult females did not change over the seasons.
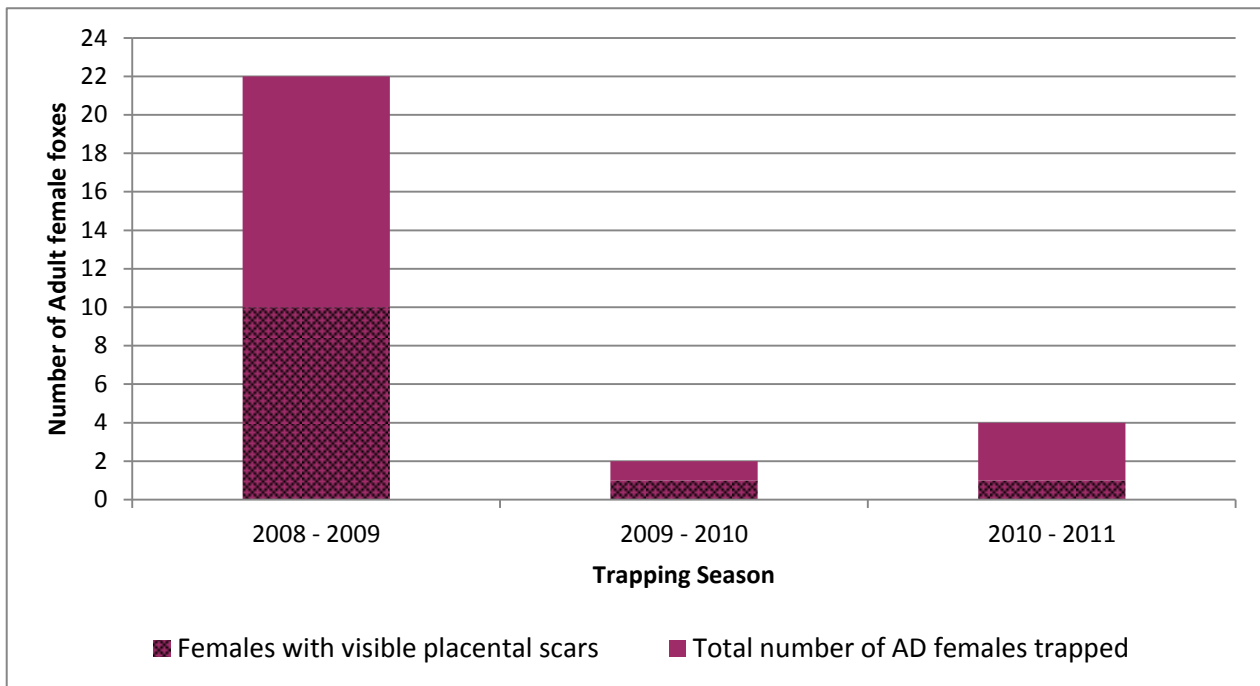

Fig. 10. The total number of female foxes of reproductive age (N=28) and the total number of individuals with visible placental scars in uteri (n=12) separated into the season in which they were trapped.

The age of the adult fox was seen to have a highly significant effect as to whether or not the vixen had reproduced during the most recent summer (Fisher's exact test for all adult ages $p<0.001$). The majority of adult foxes without any visible placental scars were young. 63 % of the foxes were aged two and a further 19 % aged three. 12 % were eight years or older.

Of the 12 vixens which did show signs of placental scarring in uteri in the study (Fig.11), only one individual under the age of three had placental scarring. This indicated that she had given birth to two pups. The other 11 foxes aged between three and twelve were found to have on average 5.6 visible placental scars. The age of the fox had no effect as to the number of visible placental scars i.e. the number of young conceived during the most recent summer (Fisher's exact test for all adult ages $p=0.62$).
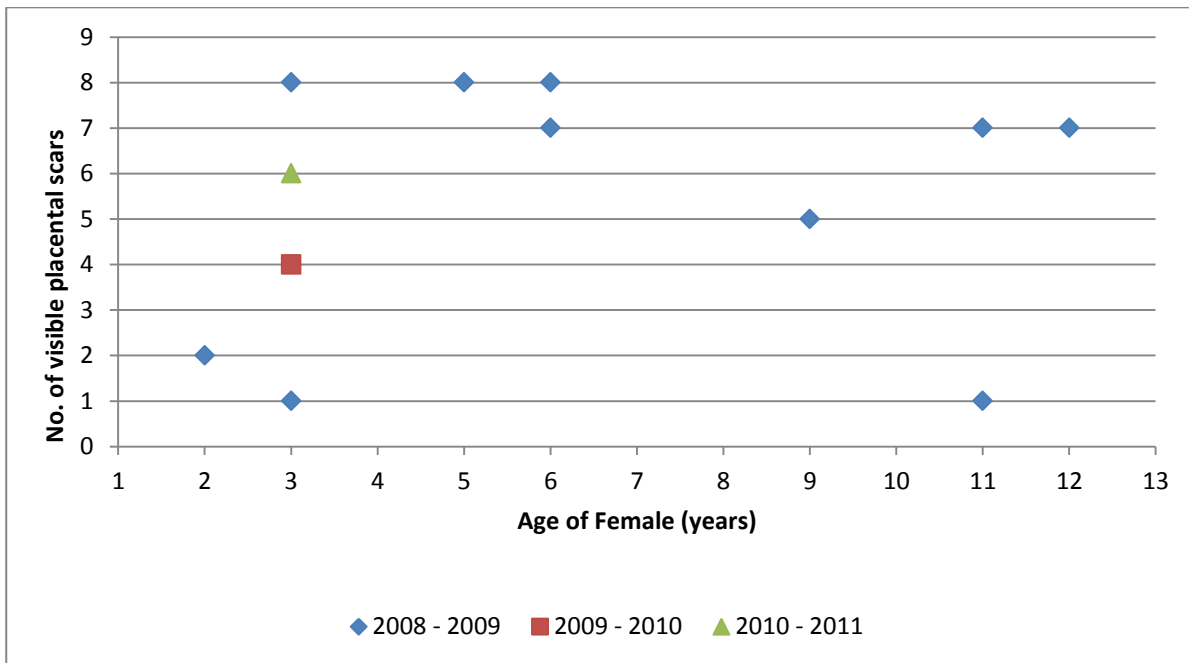
Fig. 11. Female foxes which had visible placental scarring in uteri. Their age, the number of visible scars seen during autopsy and the season in which they were trapped.

3.1.4. Body Weight

The body weight of the arctic foxes was significantly correlated with back foot length increasing by 41.90 (± 5.46 SE) grams per mm ($p<0.001$). Taking back foot length into account, the body weight of trapped vixens was shown to differ significantly between consecutive seasons (Fig. 12a). There was a significant increase of 569 ± 170 grams ($p=0.001$) in the second season. However, there was only a slight difference in weight (126 ± 154 grams) ($p=0.41$) between the first and third trapping season in the study. Weights predicted by the model are shown together with the observed data in Fig. 12.

Male foxes were significantly heavier than females (268 ± 114 grams) ($p=0.02$) therefore the average body weight in season 1 was 3147 grams (Fig. 12b). The significant interaction between season and sex ($p=0.02$) indicates that contrary to the females, the body weight of males did not differ greatly between the seasons (Appendix Table 2).
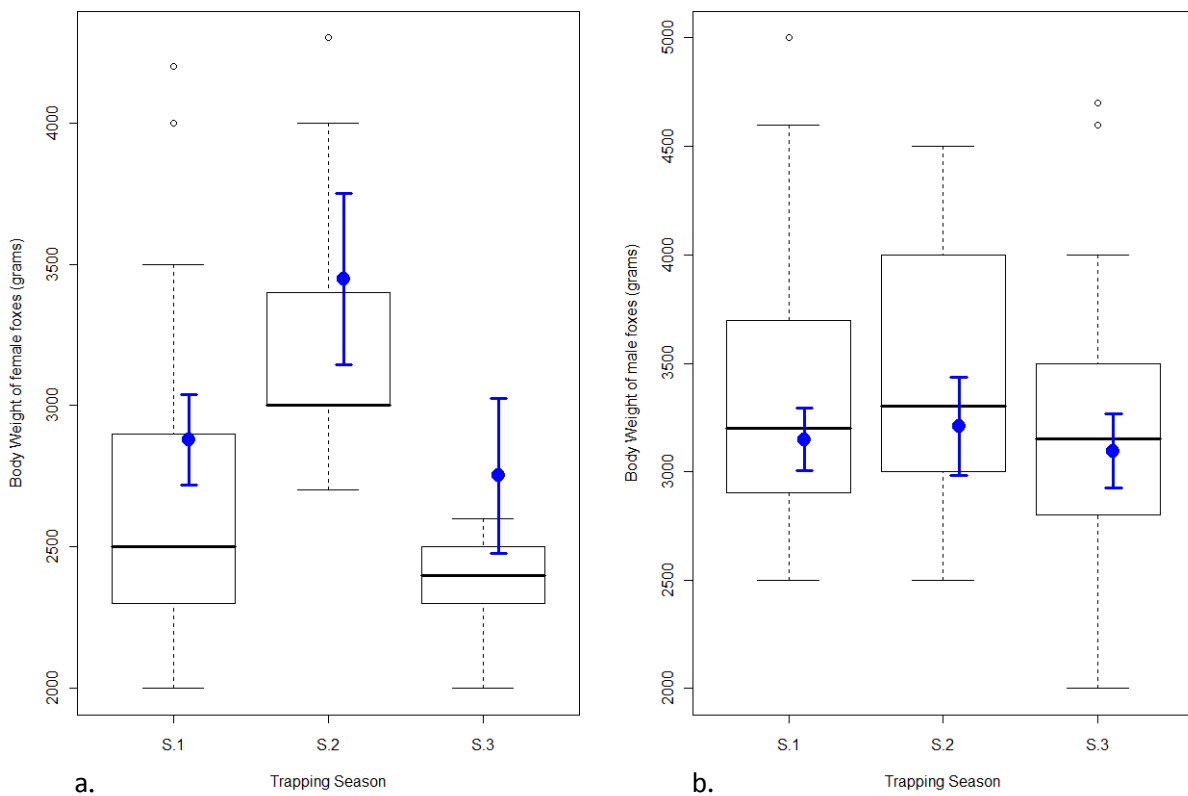
Fig. 12. Body weights of female (a.) and male (b.) arctic foxes in each of the three trapping seasons (S.1 = 2008 – 2009, S.2 =2009 - 2010 and S.3 = 2010 – 2011). Boxplots show observed sample minimum, lower quartile, median, upper quartile, sample maximum and outlier values. Predicted values for the chosen model standardized with an average back foot length of 125 mm and 95% Confidence Intervals are shown in blue.

3.2 Genetic Results

The genotyping error rate in the data set was calculated and estimated to be 0.76% (mean error rate per locus) due to the fact that one of the repeated genotypes did not show any alleles. As the only two recorded errors were cases where the genotypes were blank, we calculated a further error rate minus the obvious missing data. This resulted in an estimate of < 0.61% (mean error rate per locus).

The gene diversity for each of the two trapping seasons (2008 – 2009 and 2009 – 2010) was calculated for the total dataset with the mean gene diversity for season 1 being 0.78 (± SD 0.08) and 0.80 (± SD 0.08) for season 2 (Table 3). The single locus estimates were checked for normality using the Shapiro-Wilk normality test and were found not to deviate from a normal distribution (p=0.63). There was no significant difference in gene diversity between the two seasons (paired t-test resulted in a p-value= 0.14). Individual analysis of the two age classes (Adult and Juvenile) also agreed with these results and

did not show any differences in genetic diversity. The mean allelic richness in the first season was 7.98 (± SD 1.92) and there was a significant increase to a mean 8.58 (± SD 2.27) in the second season (p=0.03). When separated into age classes, neither the adults (p=0.31) nor the juveniles (p=0.55) showed any significant change in allele number, but there was a slight increase in allelic richness in both age classes.

Data	Season 1			Season 2			p values	
	N	GD (± SD)	AR (± SD)	N	GD (± SD)	AR (± SD)	p_{GD}	p_{AR}
Total dataset	76	0.78 (0.07)	7.98 (1.98)	27	0.80 (0.07)	8.58 (2.27)	0.14	0.03
AD	45	0.78 (0.08)	7.14(1.87)	16	0.79(0.09)	7.41(1.62)	0.70	0.30
JUV	31	0.78 (0.08)	6.57 (1.23)	11	0.81 (0.07)	6.75 (1.60)	0.19	0.55

Table 3. Number of individuals trapped (N), Mean Genetic Diversity (GD) and mean Allelic Richness (AR) with standard deviation (SD) for seasons 1 and 2 with corresponding p values (p_{GD}) (p_{AR}) respectively for the total dataset as well as for first winter animals (JUV) and adults (AD).

Most loci were in H-W equilibrium, however, loci 173 and loci 5 showing signs of a null allele. When the seasons were analysed separately with Micro-Checker, only the second trapping season had a locus showing signs of a null allele (loci 250). As the loci that show the null alleles are different, it would be likely that this is not due to technical problems but deviations from the H-W equilibrium.

When the total dataset for the two seasons was tested for deviation from H-W equilibrium, the first year showed a significant overall deficit of heterozygotes (p=0.03). Season 2 showed no significance (p= 0.23). Of the 12 loci in the study, only loci 5 in the 2008 - 2009 season showed a significant deficit of heterozygotes (p = 0.001). Analysis of the adult data set showed no significant deviations for either season (p=0.26 and 0.81 respectively). However, the juveniles showed an overall significant deficit of heterozygotes both in the first (p=0.03) and second (p=0.04) trapping season. For the total dataset, genetic differentiation between the two trapping seasons was low, but significant, with an F_{ST} of 0.007 and with a 95% confidence interval of 0.002-0.012.

Linkage disequilibrium tests show that out of the 66 tests run, 11 are shown to be significant (p<0.05). When separated into the age classes, the data for the Adults show 9 tests to be significant (p<0.05), and juveniles 8 tests. Of the tests that were shown to be significant for adults, two were also significant in the juveniles. These test were between loci 173 and 140 (AD p=0.01 and JUV p= 0.02) and between loci 250 and 733 (AD p= 0.02 and JUV p=0.004).

4. Discussion

4.1   Demography

The results of the study demonstrate that intensive trapping has an effect on the age structure of the arctic fox population in Austfjordnes. The foxes trapped in 2008 – 2009 show the age structure of a low to moderately harvested population in this area comprising of animals from all age groups, from young of the year to aged twelve. On the assumption that the trapping data represents a random sample and can be used to assess demographic changes to the population structure as a whole, then the population before the first year of intensive trapping was a well-established one with over 60% of the foxes of possible breeding age (two years and up). These individuals would likely have had established territories and in the case of the individuals over three, have started to reproduce (Prestrud, 1992a; Angerbjörn *et al*. 2004; Eide *et al.* 2012). However the data from the second and third trapping seasons of the study (2009 – 2010 and 2010 – 2011) show changes in the age structure. An increase in foxes under the age of three is seen, with the greatest increase shown in the young of the year. The percentage of young of the year trapped increased slightly between the first and second season, and then showed an increase of over 20% by the third season. At the same time there was a decrease in the number of adult foxes trapped, with gaps now shown in several age groups. It is probable that the first year of intensive trapping resulted in the removal of several of the established territorial breeding pairs, allowing larger numbers of juvenile foxes to either remain in their parents' territory as likely seen during the 2009 – 2010 season or to move into the Austfjordnes area from further afield.

Demographic analysis carried out by the Norwegian Polar Institute (E. Fuglei, unpublished data) revealed possible differences between the foxes harvested in a core trapping area around Longyearbyen, and those trapped in new areas where hunting had not previously been conducted. For example in the 2007-2008 hunting season, 92% of the trapped foxes from the core area were juveniles whilst in areas with less hunting pressure there were higher numbers of adults. This seems to follow the same trend as noted in this study.

Interestingly, although no significant effects of trapping on the sex ratio in the Austfjordnes fox population were detected, increasingly higher percentages of males than females were trapped across the consecutive three seasons of the study (55%, 62% and 70% respectively). In regards to juveniles, the majority of young foxes leave their parents' territory during their first year of life (Angerbjörn *et al*. 2004). The arctic fox population in Svalbard is a saturated population with few vacant territories available for yearlings and young animals (Eide *et al.* 2012), therefore with a 20% decrease in adult foxes present in the 2010 -2011 season and high juvenile immigration rates (Ehrich *et al.* 2012) an increase to over 60% of juveniles (44% being young males) could be seen.

A key point highlighted by this study was the lack of adult females aged between four and twelve after the first year of intensive trapping. If intensive harvesting were to continue to remove these older females, in time it could influence several demographic factors including the adult sex ratio. In the low to moderately harvested population (2008 -2009), there were only a slightly higher percentage of adult males to females (51%) (Fig.9). As monogamy is a main part of the family structure of the arctic foxes (Garrott and Eberhardt, 1987), an equal number of male and female adults could be expected to be observed as breeding pairs in an established population. However, one year after the "big take out" of 2008 – 2009 which saw the removal of the largest number of individuals in the study, the data shows more adult males (87%) than females. Adults still made up 60% of foxes trapped, but the majority was male, with the only adult females' trapped being under the age of three. The third season in the study saw a shift from an adult dominated population to a juvenile population. Adults trapped in this season comprised of 39% of the total trapped and of these there were 34% more males than females. This could have serious knock-on effects for finding a monogamous mate in order to reproduce in the coming summer.

With a decrease in reproductive females being present in the population, a decrease in female reproduction across the three trapping seasons was noted. On Svalbard, maximum pregnancy rates are not obtained until the vixens are four years old (Eide *et al*. 2012). After the age of three, more than 90% of females give birth to 5 or 6 pups (Prestrud 1992b; Eide *et al*. 2012). However, due to variation in availability of food resources such as reindeer carcasses, female foxes do not necessarily reproduce every year (Fuglei *et al.* 2003; Eide *et al.* 2012). Of the females trapped in Austfjordnes which were over three years old 64 % had visible placental scars and had given birth to an average of 5.6 pups the previous summer (Fig. 11). This relates to studies by Prestrud (1992a), Frafjord (1993) and Eide *et al*. (2012) who reported that arctic foxes on Svalbard have litters averaging 5.5 pups. However, after the first intense harvest (2008 – 2009), the only females that showed placental scarring were three years old. With no older foxes present in the population, maximum pregnancy rates would not be reached.

The intensive long term removal of breeding females from a population may lead to a decrease in population (Heydon and Reynolds, 2000) or a shift in life history strategy to reproduction at a younger age. Arctic foxes are sexually mature during their first year of life (~10 months old) and more could reproduce at this younger age in Svalbard as they do in Iceland (Hersteinsson, 1992). However, the study area had not been heavily trapped for several years (Fig 4.), and the area would need to be studied for a longer period of time before any shifts in reproductive age may be noted in Austfjordnes.

The results revealed that the body weight of females showed large variation between seasons but that male body weight did not. The body weight of the females from the low to moderately harvested population may have been due to the cost of reproduction. 65% of the females trapped in this first

season (2008 – 2009) were adults with 45% showing signs of having given birth during the most recent summer. Reproduction has high energy costs for the females (Sand, 1998; Bårdsen *et al*. 2008) resulting in decreased body weight and therefore body condition. This could explain the lower body weight of the females in the first trapping season compared to the second season as well as the difference in body mass between the sexes.

Being able to access sufficient food resources during the winter period is key to survival. Eide *et al* (2004) writes that arctic fox food caching behaviour suggests that they are dependent on cached food stores for winter survival. Access to fresh food resources from either the marine or terrestrial food webs, is often dependent on weather conditions which vary greatly across and between the trapping seasons. Levels of competition for these resources may also influence the body weight of the foxes. The weather conditions during the 2008 – 2009 trapping season were ideal for the foxes to gain access to food items from the marine food web due to the fjord icing over. This meant that polar bears could have been present and hunting in the study area, thereby providing seal carcasses for the foxes to scavenge (Hiruki and Stirling, 1989; Audet *et al.* 2002; Geffen *et al*. 2007). However, the conditions on the tundra were different. There was not a lot of ground ice which whilst good for the reindeer, meant fewer reindeer carcasses were available as winter food for the foxes. With high numbers of adults with years of experience in searching for food, there may have been high competition for the available food resources between individuals thus keeping body weight at a lower level than seen the following season. The second seasons weather conditions were extremely mild (Fig. 4) resulting in an unstable winter with poor sea ice conditions and heavy ground ice on the tundra. Although the lack of sea ice removed many marine based food items from the fox's diet (Roth, 2002) the icing of the tundra likely increased availability of reindeer carcasses. The trapper Tommy Sandal reported seeing seven young of the year calves together, with no sign of their mothers by the end of January. Unlikely to survive for long, these calves would then provide the foxes with food (Frafjord, 1993; Prestrud, 1992c; Fuglei *et al.* 2003). After the removal of many of the adults in the first intensive harvest (2008 - 2009), competition for food resources may have decreased. With better food resource availability in the area, an increase in body weight as seen in both sexes of fox trapped during the 2009 – 2010 season could have occurred. The third season (2010 – 2011), had similar weather conditions to the first with sea ice in late December and very low icing on the tundra. Similar weather conditions, resulted in a similar body weight to that recorded in 2008 – 2009. The lack of carcasses on the tundra due to no icing on the lower slopes, increased competition from the foxes which had moved into the area as well as the new comers not having their own food cashes may be an explanation for the decrease in body weight recorded for this trapping season.

4.2   Genetics

An objective of the study was to investigate whether there was a significant change in genetic diversity between the 2008 – 2009 and 2009 – 2010 trapping seasons. Hunting potentially increases the turnover in territorial foxes as seen by the removal of high numbers of adult foxes during the 2008 – 2009 trapping season. However, studies have shown that intensively hunted populations with high dispersal ability may be able to persist due to immigration from areas that are not hunted (Little *et al.* 1993; Ehrich *et al*. 2012; Eide *et al*. 2012). The results showed that whilst there was only a slight and non-significant increase from a mean genetic diversity of 0.78 in the first season to 0.80 in the second for the total dataset, there was a significant increase in allelic richness (Table 3). This supports the theory that immigration rates in the Austfjordnes area rose between the first and second seasons, with the individuals replacing those that had been removed being the cause of an increased number of alleles per locus in the population.

The foxes from the low to moderately harvested population which were caught during the 2008 – 2009 trapping season showed a significant deficit of heterozygotes suggesting either inbreeding or subdivision within the population. When separated by age class, the adult foxes showed no significant deviations from the H-W equilibrium in either season. The juvenile foxes however, did show a significant deficit of heterozygotes in both trapping seasons. Previous studies have described a similar result within the arctic fox population on Svalbard and explained this by the occurrence of a large number of potentially related juveniles (Carmichael *et al.* 2007; Ehrich *et al.* 2012). Arctic foxes on Svalbard have larger average litter sizes (Prestrud and Nilssen, 1992) (average 5.6 pups, Fig. 11) compared to other coastal fox populations (Iceland: average 4.2 pups (Hersteinsson, 1992) and on Mednyi Island: average 4.6 pups (Goltsman *et al.* 2005b)), therefore it is likely that in each season several individuals from a group of siblings were trapped thereby being included in the dataset (Ehrich *et al.* 2012).

The results show the estimate of genetic differentiation between the low to moderately harvested population (2008 – 2009) and the intensively harvested one (2009 – 2010) as being weak but significant. The "big take out" of the first trapping season in the study therefore significantly changed the allele frequencies in the Ausfjordnes population by the removal of such a large number of individuals and subsequent increase in immigration to the area. Several pairs of loci showed significant linkage disequilibrium which could be explained by subdivision between the two seasons as indicated by F_{ST}. Low levels of differentiation among arctic fox populations on Svalbard have been documented by Ehrich *et al*. (2012) and on a larger scale by Dalen *et al*. (2005), Carmichael *et al*. (2007), and Geffen *et al*. (2007).

4.3   Conclusion

This study indicates that intensive trapping can have serious short term effects on both the demographic and genetic structure of the arctic fox population as seen in the Austfjordnes area of Svalbard. Both the demographic and genetic analyses show that trapping causes changes to the population structure by the removal of high numbers of territorial, reproductive adults thereby encouraging high numbers of juveniles to immigrate into the area. Whilst a rise in immigration may result in increased allelic richness, trapping clearly contributed to a breakdown in the usual territorial structure similarly noted in studies by Harris *et al.* (2002) and Frati *et al.* (2000). Significant changes to age structure especially amongst females was discovered which in turn had a negative effect on the numbers of females available to reproduce. Further studies could examine some of the other trapping areas on Svalbard, especially if total population numbers are known, in order to determine whether trapping has an additive effect on the mortality of the arctic foxes during the winter, and assess more long term effects of trapping on the population.

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7. Appendix

Model	df	AIC
BW ~ Season + BkFoot	5	2123.962
BW ~ Season * BkFoot	7	2125.282
BW ~ Season + BkFoot + Sex	6	2121.699
BW ~ Season * Sex + BkFoot	**8**	**2118.871**
BW ~ Season + BkFoot * Sex	7	2123.537

Table A1. Selection table for fox Body Weight linear models. The best model according to AIC is highlighted in bold type. Season refers to trapping season and BkFoot is the back foot length in mm.

	Estimated Std.	Error	t value	Pr(>|t|)
Intercept	-2359.774	662.184	-3.564	0.000509
Season 2	569.457	170.002	3.350	0.001053
Season 3	-126.635	154.139	-0.822	0.412795
Sex Male	268.095	114.230	2.347	0.020402
Back foot length	41.909	5.463	7.672	3.21e-12
Season 2 x Sex (M)	-507.989	216.263	-2.349	0.020300
Season 3 x Sex (M)	73.222	189.311	0.387	0.699538

Table A2. R output from chosen model.