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# Age-dependent genetic structure of arctic foxes in Svalbard

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**Abstract** Arctic foxes are highly mobile arctic predators with a very weak population genetic structure over large parts of their range. Less is, however, known about the more local genetic structure within regions. Here, we analyze genotypes at 12 microsatellite loci for 561 arctic foxes trapped in the high-arctic archipelago Svalbard and investigate the genetic structure in three different age classes. Significant linkage disequilibrium, deficit of heterozygotes, genetic differentiation, and a decrease in relatedness with distance among animals trapped in their first winter suggested that some litter mates remain in proximity of each other during the first winter. This pattern was stronger for females than for males, indicating male-biased juvenile dispersal, and weaker for older animals. There was no genetic differentiation among adult foxes harvested in different hunting areas. The foxes from the protected area around Hornsund were however more differentiated than expected based on geographic distance alone, suggesting a possible disrupting effect of harvest on the spatial genetic structure in the rest of Svalbard. Our results also indicated a possible kin structure among adult females, suggesting natal philopatry, but further investigations will be needed to reach firm conclusions concerning kin structure in arctic foxes.

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## Introduction

Kin structure arises in a population when juveniles establish home ranges and reproduce in proximity to the home ranges of their parents. Given a behavioral attachment to the natal area, or a lack of necessity to leave it at maturity, a kin structure can exist also in highly mobile species. Thus, Zeyl et al. (2009) documented a kin structure in polar bears (*Ursus maritimus*) in the Svalbard and Barents Sea area. A kin structure at spatial scale well below the dispersal ability of the species has also been reported in the swift fox (*Vulpes velox*) in Colorado (Kitchen et al. 2005). The kin structure is expected to be stronger for the less dispersing sex, in mammals, generally females. This was the case in swift foxes, where the kin structure extended to a larger scale in females than in males (Kitchen et al. 2005), as well as in polar bears, where no kin structure was observed for males at the scale of the study (Zeyl et al. 2009). The existence of a kin structure within populations of arctic foxes (*Vulpes lagopus*), a medium-sized predator with impressive dispersal abilities (Sdobnikov 1940; Frafjord and Prestrud 1992; Pamperin et al. 2008; Tarroux et al. 2010), has not been previously studied by molecular genetic methods.

Although arctic foxes are able to move over very long distances, they are territorial during breeding. Adults may return to the same territory and use the same den over several years (up to 5 years have been observed; Ovsyanikov 1993; Angerbjörn et al. 2004a). In some populations, it has been shown that dispersal is male biased (Alaska et al. 1978; Mednyi Island, Goltsman et al. 2005)—a pattern typical for

mammals in general—but in other populations this was not the case (Angerbjörn et al. 2004a). Despite observations of natal philopatry from two populations at the margin of the arctic fox's range (central Norway, Strand et al. 2000; Mednyi Island, Goltsman et al. 2005), little is known about the total dispersal phase between the natal home range and the establishment of a reproductive territory, which would determine the formation of a genetically measurable kin structure. Dispersal of juveniles occurs either early in the autumn (August and September) or in mid-winter (December to March; Eberhardt et al. 1983; Frafjord and Prestrud 1992; Strand et al. 2000). Most young foxes leave their parents' territory during their first year of life, but some may not disperse until their second year (Angerbjörn et al. 2004b). Delayed dispersal of juveniles may result in a genetic structure where a correlation of relatedness with genetic distance is observed for juveniles, but not for adults.

Because of high migration rates involving long-distance movements, 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; Noren et al. 2010). Recently, sea ice has been shown to be a major determinant of gene flow between arctic islands and the mainland tundra (Geffen et al. 2007), and even relatively narrow stretches of open water can lead to significant genetic subdivision (Noren et al. 2009). On the contrary, differentiation is low among populations connected by sea ice in winter (Geffen et al. 2007). Analyzing the genetic structure of arctic foxes from the Canadian arctic and Svalbard, Carmichael et al. (2007) did not find any clear pattern, indicating generally high rates of gene flow over this part of the arctic. They showed, however, significant linkage disequilibrium for several pairs of loci in foxes from Svalbard, possibly indicating population substructure within this archipelago, but did not investigate this aspect any further.

In Svalbard, arctic foxes belong to the coastal ecotype (Braestrup 1941; Audet et al. 2002), as aside from a small, introduced population of sibling voles (*Microtus rossia-emeridionalis*, Henttonen et al. 2001), small mammals are absent from the archipelago. In addition to marine resources such as sea birds, ringed seal pups, or seal carcasses (*Phoca pusa*, *Erignathus barbatus*), the diet of Svalbard foxes consists of geese and their eggs, as well as reindeer carcasses (*Rangifer tarandus*) and rock ptarmigan (*Lagopus muta*), the latter two being the only terrestrial resources available year round (Prestrud 1992a; Frafjord 1993a; Eide et al. 2005). Eide et al. (2004) showed that the spatial behavior of arctic foxes in Svalbard in summer was related to the main resources available in the territory they occupied, leading to territorial specialization. Foxes inhabiting coastal territories relied on sea bird colonies and

had small, often overlapping territories, whereas foxes inhabiting less productive inland territories had larger and more exclusive home ranges. Foxes in rich inland areas with nesting geese occupied an intermediate position. If this resource specialization is transmitted from parents to offspring, as has been suggested for coastal versus inland foxes in Greenland (Pagh and Hersteinsson 2008), it might translate into genetic differentiation (e.g. Carmichael et al. 2001; Musiani et al. 2007). The percentage of occupied dens in Svalbard varies from year to year, but there are always dens suitable for reproduction, which are unoccupied (E. Fuglei, unpublished data). It is thus unlikely that dispersal is initiated directly by the need to find available dens.

In some areas of Spitsbergen, the largest island in the Svalbard Archipelago, foxes are trapped for pelts. Fur trapping occurs annually from November 1–March 15, and a total of approximately 60–300 animals are harvested per year (E. Fuglei, unpublished data, http://mosj.npolar.no/). A juvenile survival rate of 26% was estimated in Svalbard, and in central Spitzbergen, 18% of tagged pups were trapped during the first winter. Adult survival was 68% (N. Eide, personal communication). This hunting pressure may impact the spatial structure of the population, potentially increasing turnover in territorial foxes and thus disrupting possible genetic structure (Haber 1996; Frati et al. 2000). In the southern part of Spitzbergen, around Hornsund (Fig. 1), trapping is not permitted. Assuming an enhancement of migration in the main fox population on Spitzbergen due to trapping, the genetic structure of foxes from Hornsund may be expected to be different from that further north on the island. Differences in genetic variation
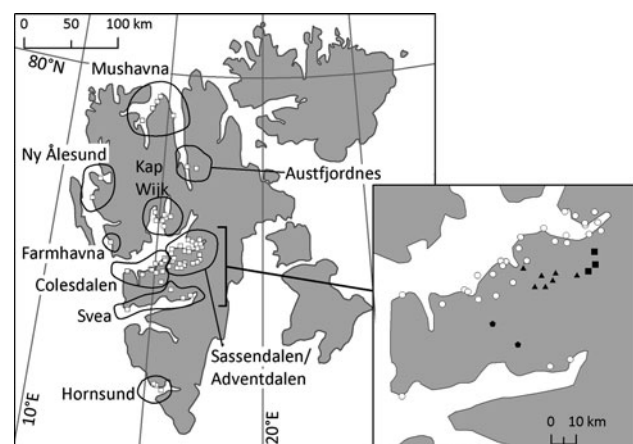


**Fig. 1** The study area on Spitzbergen, the largest island in the Svalbard archipelago. Trapping localities are shown, with samples grouped into hunting areas. The *insert* shows the region in central Spitzbergen where resource areas were defined by Eide et al. (2004): *black triangles* indicate rich inland, *black squares* poor inland, *black circles* inland, and *open circles* the coastal area

between hunted and protected populations have been observed in red foxes (Frati et al. 2000).

The objective of the present study is to characterize the genetic structure of arctic foxes within Svalbard both at the population and at the individual level. We first use several statistical methods to assess whether there is a genetic structure within the Svalbard population, as had been suggested by Carmichael et al. (2007), and in particular whether the protected population from Hornsund is different from the hunted population in the rest of Spitzbergen. Potential differences among foxes belonging to the described resource areas (coast versus inland, Eide et al. 2004) are also addressed. Second, we investigate whether there is a kin structure at the individual level and whether there was differences in genetic structure between juveniles and adult Svalbard foxes, which may provide information about the timing of juvenile dispersal in this population. We also address a possible male bias in dispersal.

## Materials and methods

### Study area, sample collection, and laboratory methods

The Svalbard Archipelago is located in the high arctic at 74°–81°N and 10°–30°E. Our study focuses on Spitsbergen, the largest island in the archipelago (Fig. 1). The island is characterized by several large fjords, which freeze in some winters, but not in all. Sixty percent of Svalbard's landmass is covered by permanent snow and glaciers, but since arctic foxes are known to travel over ice (e.g., Eberhardt and Hanson 1978; Andriashek et al. 1985; Frafjord and Prestrud 1992), physical barriers to dispersal are likely absent.

Carcasses of harvested foxes from different hunting areas within Spitzbergen (Fig. 1) were collected from trappers between 1997 and 2005 (harvest season from November 1 to March 15). In addition, four foxes were obtained from the 1995–1996 harvest season. We received special permission to trap foxes from Hornsund for the purpose of this study. Trapping location, date, and sex were recorded for each individual, and tissue samples were preserved frozen for DNA analysis. Age was estimated by counting annuli in the cementum of sectioned lower canine teeth (Grue and Jensen 1976).

A total of 636 tissue samples were collected. These were included in Carmichael et al.'s (2007) large scale study of North American and Svalbard arctic fox populations, where genotyping with 12 microsatellite loci is described. For the present study, individuals not trapped on Spitzbergen or lacking precise harvest coordinates have been excluded. Our material therefore consists of 561 samples (Table 1). Age and sex were available for most of them,

**Table 1** Number of arctic foxes analyzed according to hunting area, age class, and sex

| Hunting area | Total | JUV1 | | JUV2 | | AD/SUBAD | | NA |
|---|---|---|---|---|---|---|---|---|
| | | F | M | F | M | F | M | |
| Mushavna | 43 | 5 | 7 | 6 | 11 | 5 | 9 | 0 |
| Austfjordnes | 84 | 21 | 22 | 4 | 5 | 7 | 11 | 14 |
| Ny Ålesund | 21 | 5 | 3 | 2 | 3 | 1 | 6 | 1 |
| Kapp Wijk | 129 | 33 | 37 | 11 | 12 | 11 | 15 | 10 |
| Farmhavna | 13 | 2 | 2 | 4 | 2 | 0 | 2 | 1 |
| Sassendalen/ Adventdalen | 132 | 27 | 28 | 9 | 18 | 9 | 22 | 19 |
| Colesdalen | 83 | 11 | 12 | 6 | 11 | 12 | 12 | 19 |
| Svea | 50 | 12 | 18 | 3 | 7 | 7 | 2 | 1 |
| Hornsund | 6 | 0 | 0 | 0 | 0 | 4 | 1 | 1 |
| Total | 561 | 116 | 129 | 45 | 69 | 56 | 80 | 66 |

*NA* indicates individuals for which information about age and sex was unavailable

but for a few individuals information was missing. These individuals were included in analyses of the total dataset, but excluded from analyses by age, class, or sex. Although arctic foxes are sexually mature at 1 year of age, in Svalbard most females start to reproduce when they are 3 years old (Prestrud 1992b). For males, the age at first reproduction in Svalbard is unknown, but it is likely that they also rarely reproduce as very young mature animals. We therefore separated the data into the following age classes: animals in their first winter (JUV1), animals in their second winter (JUV2), and older animals, including subadults and adults (AD/SUBAD). The reproductive status of 227 females could be determined during dissection. Some analyses could, therefore, be carried out for reproducing females only (48). A similar subdivision was not possible for males.

### Data analysis

Several approaches were used to investigate a possible genetic substructure of the population. First, as genetic subdivisions within a sample lead to a deficit of heterozygotes in the total sample (Wahlund effect, Wahlund 1928), we tested for deviations from Hardy–Weinberg (HW) equilibrium using a permutation test as implemented in the program FSTAT (Goudet 1995). Linkage disequilibrium could also indicate population subdivision; therefore, we tested the total dataset for deviations from linkage equilibrium using a randomization test in FSTAT. The significance of linkage disequilibrium was determined using the false discovery rate approach to account for multiple testing (implemented in the R library QVALUE; Storey 2002). Second, we subdivided the dataset into nine

geographic subsamples corresponding to different trapping areas (Fig. 1). Genetic differentiation among subsamples was estimated as $F_{ST}$ in FSTAT. Confidence intervals (CI) were estimated by bootstrapping across loci, and the significance of differentiation was tested with a permutation test (10,000 permutations), not assuming HW equilibrium within subsamples. Tests for HW equilibrium, linkage equilibrium, and differentiation among hunting areas were carried out for the total dataset, as well as for JUV1, JUV2, and AD/SUBAD separately. Third, we applied model-based clustering as implemented in the program Structure v. 2.3 (Pritchard et al. 2000). For a predefined number of groups ($K$), Structure allows simultaneous estimation of the probability of an individual belonging to each group and the allele frequencies in each group, using Markov Chain Monte Carlo (MCMC) estimation. We run an admixture model with correlated allele frequencies for $K = 1$–10 with a burnin period of 200,000 MCMC iterations followed by 1,000,000 iterations used for estimation. The calculations were carried out at the Bioportal of the University of Olso (http://www.bioportal.uio.no). The optimal number of groups was chosen as the $K$ with the highest likelihood, for which the algorithm converged on a single clustering solution. Similarity among the clustering solutions resulting from different runs was assessed with the similarity coefficient by Rosenberg et al. (2005; the R script Structure-sum used for the calculation is available at http://tiny.cc/dorothee_ehrich). As including an unknown number of closely related individuals may bias estimates of population allele frequencies, structure was run for AD/SUBAD only.

Estimates of pairwise differentiation among areas were used to assess whether foxes from Hornsund were more differentiated than foxes from the rest of Spitsbergen. The geographic structure of pairwise differentiation was visualized by plotting linearized pairwise $F_{ST}$ estimates (Slatkin 1995) between hunting areas against the natural logarithm (ln) of geographic distance. Separate trendlines were plotted for comparisons involving Hornsund and for comparisons among the other localities. We tested whether genetic differentiation was correlated with distance performing a Mantel test in FSTAT (10,000 permutations). As only adult foxes were captured in Hornsund, this analysis was carried out for AD/SUBAD only. The differentiation of the foxes from Hornsund was further assessed by an assignment test carried out with the program Geneclass2 (Piry et al. 2004). The probability of the genotype of each fox (AD/SUBAD only) in each area was estimated using a Bayesian assignment Criterion (Rannala and Mountain 1997) and a Monte Carlo resampling method simulating 1,000 individuals according to the procedure suggested by Paetkau et al. (2004).

Foxes trapped in different resource areas (coast, rich inland, poor inland, Eide et al. 2004) were compared with regard to genetic diversity (expected and observed heterozygosity, and allelic richness, estimated in FSTAT and compared by one-way ANOVA), and genetic differentiation among them was estimated as above. As resource areas were only described in the central part of Spitzbergen, only foxes trapped in this region were used here (Fig. 1).

In order to assess a possible kin structure within the population, we calculated maximum likelihood estimates of the coefficient of relatedness among all pairs of individuals using the program ML-Relate (Kalinowski et al. 2006). Relatedness was correlated with the geographic distance separating the trapping locations of the individuals, and the significance of the correlation was assessed by a permutation test randomly exchanging individuals among locations 1,000 times. In order to characterize a possible kin structure in the adult population, the correlation of relatedness and distance was estimated for all AD/SUBAD, for males and females separately, as well as for females which were classified as reproducing based on dissection results. With regard to the timing of dispersal of juveniles, we tested for a correlation of relatedness and distance within cohorts of foxes born in the same year (JUV1, JUV2, and AD/SUBAD). Here, only individuals born in the same year were permutated among trapping locations to keep the cohort structure of the data fixed.

In addition to relatedness, ML-RELATE determines which of four relationships (unrelated—U, half sibling—HS, Full sibling—FS, and parent–offspring—PO) has the highest likelihood. Often, however, the difference in likelihood between the most likely relationship and other relationships determined by this method is small, and the identification of relationships is not very accurate (Costello et al. 2008). Therefore, we used a simplified classification and considered pairs of FS and PO born in the same year as potential siblings, originating from the same litter. We compared geographic distances between the trapping locations of pairs of potential siblings harvested as JUV1, JUV2, or AD/SUBAD. As there were not many individuals involved in multiple pairs, the difference in distances was tested with an ANOVA. For AD/SUBAD, we also compared distances between trapping locations of closely related animals (FS and PO), HS, and U in order to test whether related individuals were trapped closer to each other, indicating a kin structure. This comparison was carried out for all AD/SUBAD and for males and females separately, excluding samples from Hornsund. The significance of differences in distance was estimated by a resampling approach taking into account the number of time each individual was involved in comparisons. If not stated otherwise, calculations were carried out in R v. 2.9.2 (R Development Core Team 2009).

# Results

There was a significant deficit of heterozygotes in the total dataset with $F_{IS} = 0.026$ ($P = 0.004$). When considering the three age classes separately, $F_{IS}$ was largest for JUV1 and smallest for AD/SUBAD (Table 2). For AD/SUBAD, the deviation from HW equilibrium was not significant. Linkage disequilibrium was significant for most pairs of loci in the total dataset (Table 2). Considering age classes separately, there was significant linkage disequilibrium among several pairs of loci for JUV1, but much less so for animals trapped later in life. As different loci were identified as linked in the different tests, we considered physical linkage a very unlikely cause for this result and interpret it as reflecting population substructure.

For the total dataset, genetic differentiation between the nine trapping areas was low, but significant, with an $F_{ST}$ of 0.013 ($P < 0.0001$). When comparing the three age classes, $F_{ST}$ between trapping areas was highest for JUV1 and lowest for AD/SUBAD (Table 3). Excluding Hornsund, AD/SUBAD foxes from the remaining localities were not differentiated as the 95% CI of $F_{ST}$ included 0 and single-locus estimates were significant only for one locus out of 12. Differentiation among JUV1 was significantly higher than for AD/SUBAD as the 95% CI excluded each other (Table 3). The value estimated for JUV2 was intermediate. The Structure runs for the AD/SUBAD foxes showed that $K = 1$ had the highest likelihood, thus indicating the absence of substructure within the population.

The plot of linearized $F_{ST}$ estimates against ln of geographic distance for AD/SUBAD showed an overall increase in differentiation with distance (slope = 0.013, $P = 0.035$). Farmhavna was excluded from this analysis, as only two AD/SUBAD samples were available from this area. The plot also revealed that pairwise comparisons involving Hornsund had higher differentiation estimates than comparisons among the other areas (Fig. 2). Plotting separate trendlines for the relationship of differentiation to distance for comparisons involving Hornsund and for comparisons among the other localities revealed that there

was no pattern of isolation by distance in either group. The overall increase in differentiation with distance is thus likely to be due to the fact that the population from Hornsund was more differentiated from the others and not to a general pattern of isolation by distance. Concerning comparisons involving Hornsund, the lowest differentiation estimate was obtained with Kap Wijk ($F_{ST} = 0.018$) and the highest with Ny Ålesund ($F_{ST} = 0.049$). The results of the assignment test were concordant with pairwise $F_{ST}$ estimates. The average probability of genotypes to originate from Hornsund was lower than the probability to belong to any other population for all areas except Mushavna, where Hornsund had the second lowest probability (Table 4).

Foxes from the three different resource areas in the central part of Spitzbergen did not differ in genetic diversity (Table 5; ANOVA: all $P > 0.5$). There was no genetic differentiation between AD/SUBAD foxes trapped in different resource areas or between all foxes when divided into three different resource areas (Table 5). The significant differentiation estimate obtained when dividing all samples into two groups can most likely be explained by the presence of juveniles.

Relatedness coefficients estimated for the whole dataset were on average 0.055 and ranged from 0.000 to 0.895 (median = 0.005). Relatedness among adults decreased slightly with distance separating trapping locations, but the relationship was very weak (slope = −0.0037 per 100 km, $R^2 = 0.0007$, $P = 0.027$, Table 6). The slope of the regression was nearly the same when excluding the foxes from Hornsund. Considering sexes separately, there was a tendency for relatedness to decrease with distance in both males and females, but relationships were even weaker (Table 6). The same was the case when analyzing only females which had reproduced. Considering distances between pairs of animals with different levels of relatedness resulted in a clearer indication for a kin structure. Median distances were smaller between closely related AD/SUBAD (FS and PO) than between pairs of HS or U (Fig. 3). The difference was largest for females (median FS

**Table 2** Hardy–Weinberg (HW) equilibrium and linkage equilibrium for arctic foxes from Svalbard

| Data | Heterozygosity | | | | HW equilibrium | | Linkage equilibrium significant $q$ |
|---|---|---|---|---|---|---|---|
| | $H_e$ (SD) | $H_o$ (SD) | $F_{IS}$ | $P$ | Loc $P < 0.05$ | Loc $F_{IS} > 0$ | |
| Total dataset | 0.782 (0.027) | 0.762 (0.005) | 0.026 | 0.0042 | 4 | 10 | 65/66 |
| JUV1 | 0.780 (0.038) | 0.754 (0.008) | 0.032 | 0.0042 | 4 | 10 | 5/22 |
| JUV2 | 0.791 (0.026) | 0.774 (0.011) | 0.022 | 0.0417 | 1 | 9 | 0/3 |
| AD/SUBAD | 0.781 (0.031) | 0.779 (0.010) | 0.015 | 0.125 | 1 | 7 | 0/2 |

Expected and observed heterozygosities ($H_e$ and $H_o$) with standard deviations (SD), sample sizes, $F_{IS}$ estimates, and the results of significance tests are reported for the total dataset, as well as for first winter animals (JUV1), second winter animals (JUV2), and older animals (AD/SUBAD) separately

**Table 3** Differentiation among arctic foxes from different hunting areas in Svalbard

| Data | $F_{ST}$ | 95% CI | $P$ | Loc $P < 0.05$ | Loc $F_{ST} > 0$ |
|---|---|---|---|---|---|
| Total dataset | 0.013 | 0.009–0.017 | <0.0001 | 12 | 12 |
| JUV1 | 0.015 | 0.010–0.022 | <0.0001 | 9 | 12 |
| JUV2 | 0.010 | 0.002–0.018 | 0.0010 | 4 | 9 |
| AD/SUBAD | 0.008 | 0.003–0.014 | 0.0006 | 3 | 10 |
| AD/SUBAD—Horn. | 0.004 | 0.000–0.009 | 0.0075 | 1 | 9 |

$F_{ST}$ is reported with a confidence interval based on bootstrapping across loci (CI) and a $P$ value from a permutation test. The number of loci with positive or significantly positive $F_{ST}$ estimates is given. Trapping areas with less than 5 individuals for a particular age class were excluded
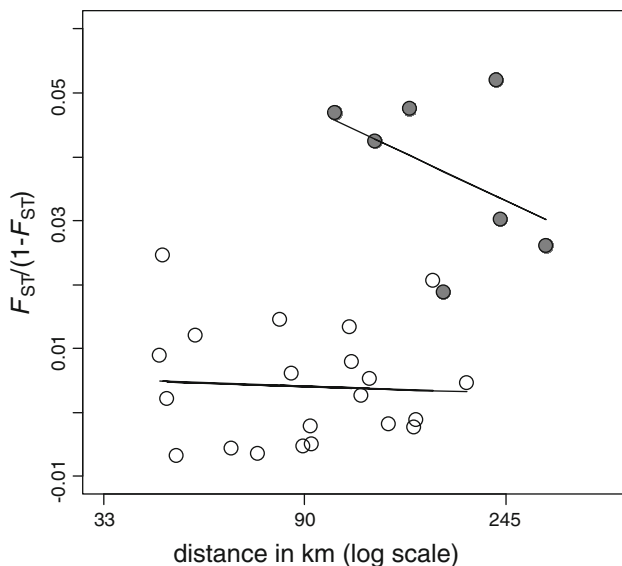


**Fig. 2** Relationship of linearized $F_{ST}$ among adult arctic foxes trapped in the different hunting areas with the ln of distance among areas (average coordinates of trapping locations; slope = 0.013, $P = 0.035$, $R^2 = 0.13$). The *filled circles* show comparisons with the protected area in Hornsund, whereas the *open circles* show comparisons between all other areas ($R^2 = 0.68$ for a linear model with only a factor with two levels "involving Hornsund" and "not involving Hornsund" as explanatory variable, and for a linear model with both this factor and distance as explanatory variables). Trendlines are plotted for comparisons with Hornsund and for comparisons between the other areas

and PO = 35.7 km, HS = 63.1 km and U = 56.1 km) and significant based on a resampling test.

Considering pairs of individuals born in the same year, and dividing the dataset into age classes, showed that there was a significant decrease in relatedness with distance for JUV1 (slope = −0.015 per 100 km, $P < 0.001$; Table 6). Among JUV1, relatedness decreased somewhat faster with distance in females than in males, but the 95% CI of the slopes overlapped (CIs were roughly estimated in a linear model and considered conservative as sample sizes were inflated by pairwise comparisons). Relatedness was also negatively correlated with distance for JUV2 born in the same year. The slope of the regression was, however, nearly half that for JUV1 (Table 6). There was a trend for a stronger relationship for JUV2 females as well. For animals born in the same year harvested as AD/SUBAD, relatedness coefficients were not correlated with distance. A comparison of distances between trapping locations of pairs of potential siblings identified on the basis of the results of ML-Relate supported this result. Potential siblings harvested as JUV1 were on average trapped at 25.6 km from each other, whereas distances between potential siblings trapped later in life were on average 65 km (mean difference = 39.4, 95% CI from 19.4 to 59.5, $P < 0.001$). JUV2 and AD/SUBAD were pooled for this test as only seven pairs of potential siblings were trapped as AD/SUBAD.

**Table 4** Probabilities of the genotypes of adult arctic foxes in each area as estimated by an assignment test are presented as averages per trapping area

| Probability in: individuals from | Colesdalen | Sassendalen/Adventdalen | Kapp Wijk | Austfjordnes | Ny Ålesund | Mushavna | Svea | Hornsund |
|---|---|---|---|---|---|---|---|---|
| Colesdalen | 0.417 | 0.478 | 0.564 | 0.378 | 0.202 | 0.180 | 0.163 | 0.106 |
| Sassendalen/Adventdalen | 0.268 | 0.375 | 0.538 | 0.356 | 0.167 | 0.238 | 0.206 | 0.067 |
| Kapp Wijk | 0.118 | 0.256 | 0.316 | 0.237 | 0.087 | 0.186 | 0.149 | 0.081 |
| Austfjordnes | 0.155 | 0.343 | 0.467 | 0.300 | 0.135 | 0.238 | 0.142 | 0.066 |
| Ny Ålesund | 0.213 | 0.314 | 0.349 | 0.251 | 0.198 | 0.414 | 0.148 | 0.066 |
| Mushavna | 0.073 | 0.285 | 0.425 | 0.217 | 0.184 | 0.309 | 0.136 | 0.097 |
| Svea | 0.200 | 0.494 | 0.603 | 0.353 | 0.220 | 0.357 | 0.194 | 0.098 |
| Hornsund | 0.049 | 0.153 | 0.435 | 0.196 | 0.101 | 0.144 | 0.097 | 0.213 |

**Table 5** Genetic diversity in arctic fox samples originating from different resource areas in the central part of Spitzbergen estimated as expected and observed heterozygosities ($H_e$ and $H_o$) and allelic richness (AR, standardized for the smallest sample size within one comparison) with standard deviations (SD), as well as samples sizes ($n$) and differentiation between resource areas

| | $n$ | Diversity | | | Differentiation | | $P$ |
|---|---|---|---|---|---|---|---|
| | | $H_e$ (SD) | $H_o$ (SD) | AR (SD) | $F_{ST}$ | 95% CI | |
| *Three areas* | | | | | | | |
| Coast | 230 | 0.77 (0.03) | 0.76 (0.01) | 6.97 (1.64) | | | |
| Poor inland | 17 | 0.76 (0.04) | 0.77 (0.03) | 7.35 (2.18) | | | |
| Rich inland | 15 | 0.74 (0.05) | 0.73 (0.03) | 6.58 (1.78) | 0.006 | −0.001–0.015 | 0.066 |
| *Two areas* | | | | | | | |
| Coast | 230 | 0.77 (0.03) | 0.76 (0.01) | 8.07 (2.08) | | | |
| Inland | 35 | 0.75 (0.04) | 0.74 (0.02) | 8.22 (2.47) | 0.007 | 0.001–0.015 | 0.005 |
| *AD/SUBAD* | | | | | | | |
| Coast | 56 | 0.77 (0.03) | 0.76 (0.02) | 6.60 (1.77) | | | |
| Inland | 12 | 0.75 (0.05) | 0.72 (0.04) | 6.58 (1.88) | −0.001 | −0.011–0.012 | 0.273 |

$F_{ST}$ is reported with a confidence interval based on bootstrapping across loci (CI) and a $P$ value from a permutation test. For comparing coast and inland, samples from rich and poor inland were pooled, and three additional samples from unspecified inland were used

**Table 6** Relationship of relatedness between pairs of individual arctic foxes and distance between their trapping locations for different age and sex classes

| Data | Slope per 100 km | $P$ | Pairs | Inds |
|---|---|---|---|---|
| AD/SUBAD | −0.00371 | 0.027 | 9,316 | 137 |
| AD/SUBAD—Horn. | −0.00410 | 0.026 | 8,515 | 131 |
| AD/SUBAD ♀ | −0.00046 | 0.438 | 1,596 | 57 |
| Reproducing ♀ | −0.00033 | 0.265 | 1,128 | 48 |
| AD/SUBAD ♂ | −0.00457 | 0.075 | 3,160 | 79 |
| *Cohorts* | | | | |
| JUV1 | −0.01528 | <0.001 | 4,224 | 245 |
| JUV1 ♀ | −0.02388 | <0.001 | 900 | 116 |
| JUV1 ♂ | −0.01185 | 0.003 | 1,180 | 129 |
| JUV2 | −0.00823 | 0.037 | 1,064 | 114 |
| JUV2 ♀ | −0.02538 | 0.068 | 154 | 43 |
| JUV2 ♂ | −0.00571 | 0.127 | 363 | 69 |
| AD/SUBAD | −0.00003 | 0.284 | 900 | 136 |
| AD/SUBAD ♀ | 0.00402 | 0.575 | 150 | 55 |
| AD/SUBAD ♂ | −0.01130 | 0.105 | 276 | 78 |

*AD/SUBAD—Horn* indicates that foxes from Hornsund were excluded. Significance was assessed with 1,000 permutations ($P$). For tests carried out by cohorts, only animals born in the same year were considered. The number of pairwise comparisons (pairs) and individuals involved (inds) is given

## Discussion

In accordance with the high mobility of arctic foxes and the absence of dispersal barriers within Spitzbergen, our results showed that there was no genetic subdivision within the AD/SUBAD foxes, except to a certain degree for foxes of the southernmost sampling locality in Hornsund. There was no deficit in heterozygotes and nearly no linkage disequilibrium, supporting the absence of a cryptic population substructure. Moreover, the model-based clustering analysis carried out with Structure resulted in no subdivision being most likely. Estimates of genetic differentiation were very low and only statistically different from 0 when including the foxes from Hornsund. The observed absence of genetic structure is in agreement with the very low levels of genetic differentiation among arctic fox populations at a much larger scale documented by Geffen et al. (2007), Carmichael et al. (2007), and Noren et al. (2010).

The significance of linkage disequilibrium, leading Carmichael et al. (2007) to hypothesize a substructure within the Svalbard fox population, could be explained by the occurrence of a large number of potentially related juveniles in the dataset. Linkage disequilibrium, deficit of heterozygotes as well as genetic differentiation was most evident among animals harvested in their first winter and decreased for older animals (Tables 2 and 3). As arctic foxes have relatively large litters (averaging 5.5 in Svalbard, Prestrud 1992b; Frafjord 1993b), it is likely that several individuals from a group of siblings were trapped and could thus be included in the dataset. Immigration might also have contributed somewhat to the observed linkage disequilibrium. Indeed, Noren et al. (2011) recently presented genetic evidence for immigration into the Svalbard population following a lemming population crash, and they identified two individuals as likely originating from Siberia.

The explanation of linkage disequilibrium as resulting primarily from the presence of related juveniles was supported by the relatedness analysis. Considering only individuals born in the same year, relatedness was negatively
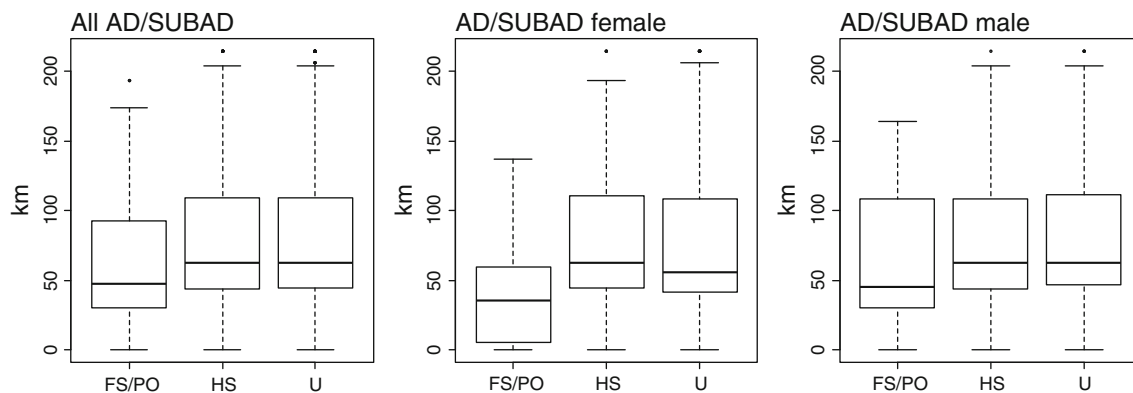
**Fig. 3** Geographic distances among pairs of arctic foxes with different degrees of relatedness: *PO* parent–offspring, *FS* full siblings, *HS* half siblings, *U* unrelated. The lines show the median value, the box indicates the middle 50% of the data, the whiskers show 1.5 times the interquartile range, and values outside this range are represented with points

correlated with geographic distance for JUV1, revealing a spatial grouping of related animals of this age class. Moreover, the distance among trapping locations of genetically identified pairs of siblings was shorter for JUV1 than for older foxes. Such a pattern indicates that not all juveniles disperse far during their first fall, but that in some cases litter mates remain in proximity of each other during the first winter and thus probably in proximity of the territory of their parents. This is in agreement with the observations from Sweden and Iceland, where not all juvenile foxes left their parents' territory in fall (Anger-björn et al. 2004b). A similar, though weaker, pattern was observed for JUV2, but not for older animals, suggesting that some spatial associations of litter mates could be maintained until the second winter. Some foxes may thus delay dispersal by more than one and a half years. For both JUV1 and JUV2, relatedness decreased faster with genetic distance for females than for males, consistent with male-biased juvenile dispersal as reported for arctic foxes from Alaska (Eberhardt and Hanson 1978) and Mednyi Island (Goltsman et al. 2005).

Analyzing relatedness among AD/SUBAD individuals sampled over all years resulted in a very weak negative correlation with distance. Although the relationship was significant for both sexes together, this was the case neither for males or females alone. Contrary to this result, the comparison of distances between pairs of individuals with different degrees of relatedness revealed a clear tendency for closely related females to be closer to each other than randomly chosen females, indicating philopatry. This trend was weaker for males, in accordance with the general mammalian pattern of male-biased dispersal. As our samples were not collected during the breeding season, some year-round fidelity to a certain area in addition to philopatry is required for a kin structure to be clearly measurable. Assuming that certain foxes leave their breeding area during winter, but return in the next season (Tarroux et al. 2010), it is possible that samples collected in spring or summer would reveal a stronger pattern. Natal philopatry has previously been documented in foxes from Mednyi Island, a highly isolated population which differs from other arctic foxes in both ecology and behavior (Goltsman et al. 2005). Also, in a small alpine population in Norway, some pups have been documented to return to their natal range (Strand et al. 2000). Foxes inhabiting coastal ecosystems, where resource availability is more predictable than for tundra foxes specialized on lemmings, could be expected to have a more stable population structure over seasons, years, and generations. All together, our results indicate that a kin structure is likely for female arctic foxes in Svalbard but would require further research to confirm.

We did not observe any genetic differences between foxes trapped in the different resource areas in central Spitzbergen, except for a weak but significant differentiation between coastal and inland foxes when including all samples. As for differentiation among trapping areas, this result can most likely be explained by the presence of related juveniles in the sample. Resource areas were described in summer (Eide et al. 2004), and it is not clear to what extent resource specialization extends to other seasons. In a radio-telemetry study, in Svalbard, about half of the followed foxes were relocated in the same area in several seasons (Frafjord and Prestrud 1992). Assuming that foxes shift home ranges seasonally, it is possible that we did not detect a genetic structure which might exist in summer. Considering the small spatial scale of the resource areas, it is, however, unlikely that habitat specialization could lead to measurable levels of genetic differentiation.

Contrary to the samples obtained from hunting areas, the foxes analyzed from the protected area in Hornsund were significantly differentiated from other areas based on allele frequencies. Despite being clear, this differentiation was

weak as it did not lead to any detection of subdivision of the total adult sample neither in the structure results nor as deviation from HW or linkage equilibrium. Although Hornsund was the most distant sampling area, it is unlikely that the observed pattern is due solely to geographical distance (Fig. 2) The topography of Svalbard does not indicate that there could be any barriers to dispersal in this area, which would differ from those in the northern part of Spitzbergen. Although this result has to be considered preliminary due to the small sample size in Hornsund ($n = 6$), the differentiation of the adult foxes from Hornsund may thus be interpreted as resulting from a more stable population structure in this undisturbed area (Haber 1996; Frati et al. 2000). In contrast, in northern and central Spitzbergen, the regular removal of territorial individuals may lead to higher rates of replacement and dispersal, thus contributing to the absence of population substructure among hunting areas. A possible kin structure among adults may also have been weakened by hunting pressure and might be clearer in undisturbed populations of arctic foxes. Although our results indicated a kin structure in female arctic foxes in the core of their range, they were not clear enough to reach any firm conclusions about philopatry. In further research, data from the breeding season should be obtained and it would also be interesting to investigate the kin structure of a lemming fox population for comparison.

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