UNIVERSITY OF TROMSØ UiT
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DEPARTMENT OF ARCTIC AND MARINE BIOLOGY

Site fidelity of Svalbard polar bears revealed by mark-recapture positions

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BIO-3910 Master`s thesis in Biology

May 2011

Front page photo: Young female polar bear captured and marked in Liefdefjorden, Svalbard in April 2011.

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Supervisors

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Tromsø, May 2011
Karen Lone

Abstract

The spring season is important to polar bears, since females with young cubs leave the maternity dens, ringed seal pupping creates a peak in prey availability, and it is the mating season. Understanding space- and resource use at this time is a key to understanding polar bear ecology. This study from Svalbard, Norway analyzed 348 measurements of spring-to-spring displacement from 220 polar bears obtained by mark-recapture sampling in the period 1987 – 2010 to assess whether the bears exhibit spring site fidelity. All age and sex classes of polar bears showed site fidelity when their movements were compared to a scenario of random movements between all capture locations. The median observed displacement for all bears was 43.0 km (bootstrapped 95% CI: 34.3 - 51.0 km), significantly smaller than the median potential displacement for random movements of 205.4 km (bootstrapped 95% CI: 205.1 - 205.6 km). Linear model analysis of all displacements showed that displacement length depended on both the age and sex of the individual. Subadult females had the longest displacements, followed by adult males and adult females. Consistent, precise site fidelity over time was only displayed by a subset of females. When only the first movement of each bear was included, the effects of age and sex in the linear model were less pronounced, and the difference between adult males (linear model estimate: 50.0 km) and adult females (40.7 km) was not significant. These findings support previous reports in the literature comparing movement patterns of males and females in other parts of the Arctic. Sufficient data to conclusively evaluate subadult movement patterns is still lacking. Overall similarities in site fidelity of adult males and females indicate that findings based on telemetry of females may be relatively representative of the whole adult Barents Sea population.

Key words: *Ursus maritimus*; movement; displacement; spring behavior; age and sex effects; Arctic

1. Introduction

Site fidelity, or philopatry, is the tendency to stay in, or return to, a previously occupied location (Greenwood 1980). This behavior is common in mammals, birds and amphibians and it contributes to the spatial structuring of a population – both in terms of population densities, social organization and patterns of relatedness. These factors, in turn, may shape the potential for inbreeding depression, kin competition and cooperation (Gandon 1999).

The evolution of site fidelity and dispersal patterns involves complex interaction of many factors, such as inbreeding avoidance, kin interaction, local mate and resource competition and spatial and temporal heterogeneity (Clobert et al. 2001, Lawson Handley and Perrin 2007). Predictability of habitat quality and resource distribution in heterogeneous environments influence the potential benefits from site fidelity (Switzer 1993). One cost of moving is loss of benefits of familiarity with an area that has been used (Switzer 1993). The common patterns of sex-biased site fidelity and juvenile-biased dispersal are thought to arise mainly from inbreeding avoidance (Pusey 1987) and mating systems (Greenwood 1980, Dobson 1982). In mammals, females generally show higher site fidelity than males (Greenwood 1980, Pusey 1987), and site fidelity is common both in gregarious and solitary mammals (Waser and Jones 1983). In the brown bear, the closest living relative of the polar bear (Talbot and Shields 1996), all adult bears show fidelity to a denning area within their respective home ranges, and subadult males move significantly longer distances between successive dens than females or adult males (Manchi and Swenson 2005).

The polar bear is a large solitary carnivore that depends on sea ice habitat for feeding, breeding and movement (Amstrup 2003). Although polar bears are highly mobile animals (Mauritzen et al. 2003a), site fidelity may be an important strategy in a largely heterogeneous and variable sea ice habitat that nonetheless has certain predictable features. Organisms that are strongly tied to a specific location or habitat may be particularly vulnerable in the face of changing resources and habitat availability (Laidre et al. 2008). For polar bears, such changes could take the form of large interannual variability in sea ice conditions or long term reduction in summer sea ice cover due to a warming climate (Serreze et al. 2007, Moline et al. 2008). More detailed knowledge of polar bear fidelity to areas used during the critical spring season is needed if we are to evaluate the vulnerability of polar bears to these scenarios. Spring is a critical time for females with young cubs who emerge from the maternity dens in March or early April (Hansson and Thomassen 1983, Larsen 1985). During late March and April, prey availability peaks with the pupping season of the polar bear's main prey item, the ringed seal (Lydersen and Gjertz 1986). Additionally, the mating season lasts from March to May (Lønø 1970).

Several approaches have been used to investigate the distribution and movements of polar bears in relatively inaccessible Arctic areas. Hunting statistics, trappers' knowledge, tracks and sightings of marked and unmarked animals were important in acquiring early knowledge of polar bear distribution (Lønø 1970, Larsen 1986, Taylor and Lee 1995). Mark-recapture and mark-recovery studies have shown that bears tend to return to the areas in which they have been tagged rather than venture into neighboring areas (Lentfer 1983, Larsen 1986). Delineation of the polar bear's circumpolar range into 19 currently recognized subpopulations (hereafter called populations, for simplicity) has for the most part been confirmed and refined using telemetry (Bethke et al. 1996, Taylor et al. 2001, Obbard et al. 2010) and genetic methods (Paetkau et al. 1995; 1999).

Argos- or GPS-based satellite telemetry is the most important modern tool for studying movement of polar bears, due to its ability to remotely collect large amounts of position data with high spatial and temporal resolution on an unlimited spatial scale. This has allowed fine-scale and large-scale analyses of movement and habitat selection (Ferguson et al. 1998; 2000, Mauritzen et al. 2003a; 2003b, Wiig et al. 2003, Andersen et al. 2008, Durner et al. 2009). The limitations of satellite telemetry include: the small number of tagged individuals, the length of battery life and the fact that telemetry collars are only fitted on adult females. Males readily shed collars (Mulcahy and Garner 1999) and collars fitted to young bears would become too tight when the bears reach mature size.

Genetic studies are also useful on the within-population level. By combining genetic methodology and capture positions, one can obtain a measure of natal dispersal distance and identify patterns of relatedness that arise as a consequence of site fidelity (Crompton et al. 2008, Zeyl et al. 2009a; 2010). The scale and integrative power are strengths of these studies, but also a weakness in that they generally provide little information on the individual level.

Polar bears relate actively to their environment. During sea ice formation and ablation, most polar bears track the sea ice edge (Larsen 1986, Mauritzen et al. 2001). Several studies have demonstrated that polar bears select sea ice habitat according to seasonally changing preferences (Ferguson et al. 2000, Mauritzen et al. 2003b, Durner et al. 2009). Habitat selection seems to be related to the prevalence of seals and hunting success (Stirling et al. 1993). Movements of female bears monitored by telemetry have been found to be near-random in the spring (Ferguson et al. 1998; 2000).

Large variation in annual home range size has been found in northern Canada, the Beaufort Sea and the Barents Sea (Wiig 1995, Ferguson et al. 1999, Amstrup et al. 2000, Mauritzen et al. 2002). This seems to be strongly related to geographic differences in sea ice conditions and -variability (Ferguson et al. 1999, Amstrup 2003). Differences in space use among individuals have also been demonstrated. Female bears in the Barents Sea tend to consistently use one of two strategies. ‘Pelagic’ bears utilize large home ranges, spending most of their time on the drift ice of the Barents Sea, whereas ‘nearshore’ bears have smaller home ranges and generally restrict their movements to some islands or fjords of the main islands of Svalbard (Mauritzen et al. 2001; 2002).

Distinguishing between site, area and regional fidelity is a matter of definition. Site fidelity may refer to a very specific location or area, such as a nesting site or a territory (Greenwood 1980). What some refer to as an area (Lentfer 1983) others might refer to as a region (Ferguson et al. 1997). Polar bears are non-territorial, and most of their activities relate to unbounded areas rather than to defined areas or single points in space, with the exception of maternal denning (Amstrup 2003). In the light of this behavior, this thesis assesses site fidelity in relation to a general area and evaluates its strength by the proximity of capture positions of individual polar bears in spring of different years.

Seasonal site fidelity of polar bears has previously been reported in the spring (Schweinsburg et al. 1981; 1982, Lentfer 1983) and year-round (Mauritzen et al. 2001). Zeyl et al. (2009a) showed a population structure in Svalbard in which closely related polar bears were found closer together in space than other bears, indicating restricted movements of both males and females during the mating season. Site fidelity during different seasons may vary between regions. In southwestern Hudson Bay, fidelity to certain sections of coastline during the ice-free summer has been confirmed (Stirling et al. 2004). Ferguson et al. (1997) found low fidelity to area during the autumn in the Northwest Territories.

Females do not reuse exact denning sites, but are often faithful to a denning area (Ramsay and Stirling 1990, Zeyl et al. 2010) and to substrate in regions where denning on land, fast ice and drift ice occur (Amstrup and Gardner 1994). Zeyl et al (2010) found a matrilineal structure within main denning areas, indicating that daughters are highly philopatric to the area where they were born, given that autumn sea ice conditions allow them to reach the islands.

In contrast to the rather extensive knowledge of movement patterns of adult female polar bears, we have little information about movement and site fidelity in adult male polar bears and young polar bears of both sexes from Svalbard or any other part of the Arctic.

Studies based on satellite telemetry have wisely been careful about not generalizing or extrapolating findings from female polar bears uncritically to whole populations. In one study off the north coast of Alaska, seven male polar bears with surgically implanted satellite transmitters (Mulcahy and Garner 1999) showed movement patterns similar to the female polar bears in the same region (Amstrup et al. 2001). Site fidelity between years could not be investigated since all senders stopped working within six months of deployment (Amstrup et al. 2001). In addition to the previously mentioned study in Svalbard by Zeyl et al. (2009a), male-female comparisons in other Arctic regions have been undertaken using capture-recapture data. In northern Canada, Taylor et al. (2001) found small-scale between-sex differences in distance moved, but no large-scale differences. They therefore argued that telemetry data collected on female bears can be extrapolated to describe population boundaries. Furthermore, they found that subadults moved farther than adult bears (Taylor et al. 2001). An early study in Alaska did not find any age and sex differences, but used a much coarser measure, the likelihood of being recaptured in the same area (Lentfer 1983).

The aim of this study is to complement previous knowledge of the movements and space use of polar bears in the Svalbard area obtained from telemetry and genetics studies by analyzing mark-recapture positions collected between 1987 and 2010. One goal is to evaluate if results from telemetry studies may based on adult females may be valid for bears of all ages and both sexes. The focus will be spring-to-spring site fidelity of marked bears, since this is the core information obtained when analyzing distance between two capture positions in different years. This distance will hereafter be referred to as “displacement”. The study addresses the following questions: (1) Do Svalbard polar bears exhibit site fidelity in the spring? If so, can this be shown when taking into account that detection probability is a function of the sampling effort in time and space (Koenig et al. 1996), and (2) do the patterns of displacement differ according to sex, age and female reproductive status? If females exhibit stronger site fidelity, as in most mammals (Greenwood 1980), subadult and adult males should display the longest displacements.

2 Methods

2.1 Study site

Polar bears have been captured and marked all over the Svalbard archipelago (Fig.1) through the Norwegian Polar Institute's polar bear research program. The bears in Svalbard are part of the Barents Sea population, which extends east to Novaya Zemlya and north into the pack ice from Franz Josef Land in the east to the areas northwest of Svalbard (Obbard et al. 2010).

Figure 1: Map of the study area – the main islands of the Svalbard archipelago.

Most of Svalbard's islands are located between 76 – 81°N, and 10 – 30°E. They have a mild climate for their latitude due to the flux of heat brought in by the North Atlantic Current, a branch of which extends up along the west coast of Spitsbergen (Loeng 1991, Piechura and Walczowski 2009). The island group is influenced by cold arctic currents from the northeast and easterly winds that bring in drifting sea ice, creating north-south and east-west gradients in temperature and sea ice conditions. However, there is considerable interannual variation in sea ice cover, sea ice thickness, and time of sea ice arrival and disappearance, especially along the west coast of Spitsbergen and at Hopen (Vinje 1985, Gerland et al. 2008).

The sea ice is a heterogeneous, variable and unpredictable habitat (Durner et al. 2009). Polar bears utilize and occupy all areas with suitable sea ice and are potentially found anywhere on the islands or the surrounding sea ice, but are predominantly found in the eastern areas. Here the summer period with no sea ice is usually very short compared to that of the fjords on western Spitsbergen. Both ‘pelagic’ and ‘nearshore’ bears (Mauritzen et al. 2001; 2002) were sampled in the field, since the areas they use overlap geographically. Pelagic bears are more likely to be captured at Hopen and Kong Karls Land (Fig.1), while nearshore bears are predominantly found closer to the larger islands.

Constrained by weather, geography, costs and logistics at this high Arctic location, the sampling effort has necessarily been of an opportunistic nature. It has nonetheless produced an extensive capture-recapture dataset with more than 1800 capture events from 1967 to 2010. Polar bears have been captured every spring from 1987 to 2010, but spring captures were sporadic prior to 1987. Therefore, this analysis is limited to spring captures in the months of March, April and May from 1987 to 2010 (n = 1610).

The geographic distribution of the sampling (Fig.2) was influenced both by where bears were located and where the researchers went in search of them. The latter factor contributed strongly to between-year differences. Over the entire period, most of the Svalbard archipelago was sampled to some degree, but some areas received relatively more or less attention. For instance, Kong Karls Land, which has high densities of dens and bears (Larsen 1985; 1986), was strongly underrepresented due to logistic challenges. Most bears were captured near the shore, either on land or on land-fast ice in fjords or along the coast. In two years, 1997-98, a total of 69 bears were captured and tagged on drifting sea ice in the Central Barents Sea (74 – 76°N, 37 – 44°E).

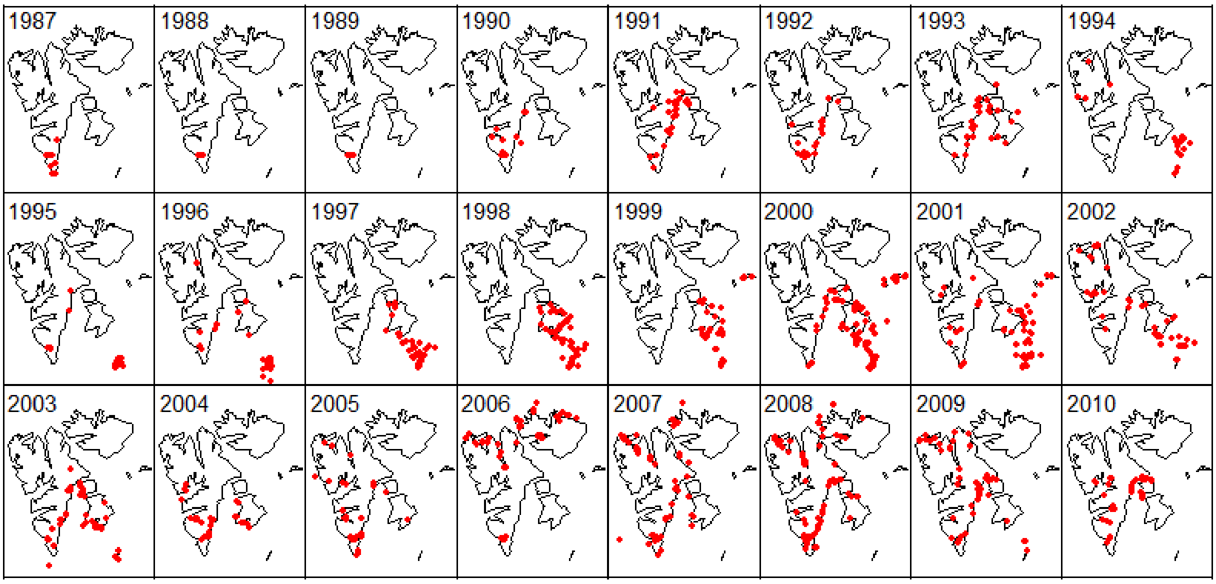

Figure 2: Map panels showing the spatial distribution of spring-time capture positions in the Svalbard archipelago between 1987 and 2010. Capture positions in the Central Barents Sea (74 – 76 °N, 37 – 44 °E) in 1997/98 are not shown.

2.2 Mark-recapture dataset

Polar bears were darted with the tranquilizer Zoletil ® (Stirling et al. 1989) by researchers on snow scooter (1987-90) or in helicopter (1990 – 2010). The immobilized bears were marked with two ear tags, tattooed on each side of the upper lip, and from 1992 also implanted with a microchip transponder behind one ear. Bears were sexed and aged in the field. Researchers subjectively estimated age by visual impression of dental eruption, color and wear, but strove for consistency in age estimates between researchers and over time.

The latitude and longitude positions of captured bears were recorded in the field. For the bears that were captured from scooter, the positions were estimated from a map (1987-90). When bears were captured from helicopter (from 1990), GPS-positions were recorded while at the capture site (Ø Wiig, pers.comm.). In 130 cases, the positions were missing in the dataset, and place names were used to estimate a geographical position from a map.

All bears were categorized by age into the following groups: cub of the year (hereafter termed COY), yearling, 2 year old (yearling and 2 year old combine to category juvenile), subadult (3-4 years), adult (5+ years) based on estimated age. The estimation of age based on patterns of dental eruption is unambiguous for COYs and yearlings (Amstrup 2003). Both female and male subadults are generally significantly shorter than adults (Derocher and Wiig 2002), and their teeth are whiter and much less worn down. It is thus not likely that bears of age 2 – 4 years were misclassified by more than about one year. Age estimates from dental cementum layers were not used since they have been shown to be inaccurate in Svalbard polar bears, especially for bears up to six years of age (Christensen-Dalsgaard et al. 2010). Bears first captured as 0 – 2 year olds were considered to have known age on recapture. The age at recapture was corrected for a few other bears because the time lag of recapture combined with the estimated age on first recapture indicated that the bear must have been more than five years old, taking into account one year of uncertainty. Female bears with offspring, or females fitted with a telemetry collar, were also scored as adults. Bears for which none of the above information existed were assumed to be adults (two recapture bears only).

The dataset had a total of 1610 spring capture positions, including 348 recapture events of 220 unique bears. A total of 138 bears were recaptured only once, and the greatest number of recaptures of a single bear was six.

2.3 Statistical analyses of displacement

Displacement, the response variable, was defined as the great circle distance between a capture and the subsequent recapture position of an individual. In cases of multiple recaptures of the same bear, positions associated with each sequential time step were used and treated as independent displacements, if not mentioned otherwise. Great circle distance, i.e. the shortest distance between two points taking into account the curvature of the earth, was calculated using the spDists function of the package sp in the statistical software R (version 2.12.0, R Development Core Team 2010).

2.3.1 Testing for site fidelity

To evaluate the displacements observed relative to a null hypothesis of random movement over the sampled areas, the distribution of observed displacements was compared to the distribution of great circle distances between all the capture sites between different years. The latter makes up the potential displacements that we would be able to detect under the given sampling regime (Fig.2). A vector containing all potential displacements (n=1000771) was created based on all combinations of positions in a given year with all following years, excluding bears that died during capture (n=2) from the former because they could not have been captured again and COYs from the latter because they could not have been captured before. The medians of observed and potential distances were compared in a formal test using a bootstrap procedure. The datasets were resampled with replacement 10000 times to derive 95% confidence intervals for the medians. In addition to an overall comparison based on all displacements, each subgroup of observed displacement was compared to the entire set of potential displacements.

When the lag time between captures is long and/or highly variable, the outcomes of displacements may be impacted by the interaction of changing capture patterns and mortality. Lacking sufficient information to adjust for these effects, I used a simpler analysis that avoids them altogether, as a control. The simple analysis circumvents the issue by only including data with one year time lag between capture and recapture (from now referred to as “1 yr lag”). COYs recaptured as yearlings were excluded from the 1 yr lag analysis, since they depend on their mother during this time, and her movements were already included in the dataset. The 1 yr lag vector (n=78834) was therefore based only on combinations of positions in subsequent years and additionally excluded COY-to-yearling potential displacements.

2.3.2 Modeling the effect of demographic factors

Linear statistical modeling was used to determine the influence on the response variable displacement (y) of these demographic factors: 1) age at capture (*age.pre*), 2) age at recapture (*age.post*), and 3) *sex*. Time between captures (*years*) and the square of time between captures ($years^2$) were included as covariates in the linear model (Eqn.1).

$$\text{Eqn.1} \qquad y(\lambda) \sim age.pre*age.post*sex + years + years^2$$

To normalize the variance of the residuals, the response variable was transformed using the Box-Cox power transformation (Box and Cox 1964):

$$\text{Eqn.2} \qquad y(\lambda) = (y^\wedge\lambda - 1)/\lambda \qquad \text{if } \lambda \neq 0$$

$$\text{with the special case} \quad y(\lambda) = \log(y) \qquad \text{if } \lambda = 0$$

The unknown parameter λ can be chosen so as to optimize the log-likelihood of a given model. The transformation does not take non-positive values. Therefore, displacements measured to be exactly 0 km, which can be considered an artifact of the position resolution, were changed to 0.001 km.

Using Eqn. 1 as the starting point, the optimal model was chosen by a stepwise evaluation of Akaike's Information Criterion (AIC) using the stepAIC function from the library MASS in the R software (R Development Core Team 2010). Goodness of fit of the final model was evaluated by visual inspection of the residual plots. All model estimates were Box-Cox back-transformed to give the predicted displacements.

A mixed-effects modeling approach using individual bears as random effects would have been the preferred approach to take into account the lack of independence between multiple captures of the same bear. This method could not be pursued, however, because the high number of bears recaptured only one time creates non-convergence of the algorithm. Instead, two datasets were separately investigated within the linear model framework: the first consisting of the entire dataset including multiple recaptures and the second limited to the first recapture event (thus only one displacement) for each polar bear. The entire dataset utilizes all available information. The multiple recaptures are removed in the second to see if the pseudo-replication they represent has biased the results obtained using the entire dataset.

Another approach used to correct for possible bias arising from multiple recaptures, was to inversely weight the observations by the number of times the bear had been recaptured. This approach yielded estimates intermediate between the two other datasets (entire set and exclusion of multiple recaptures) and its results are not reported here. In addition, a linear model analysis parallel to the one described here was performed based on the 1 yr lag data, due to the concerns expressed in section 2.3.1. The outcome of that analysis is not included in the results due to small sample sizes, but can be found in Appendix A.

3 Results

3.1 Observed displacement and degree of site fidelity

A map of the observed polar bear displacements (Fig.3) reveals no long displacements between Northwestern Spitsbergen and the Storfjorden area, but both intermediate and short displacements within each area. Most of the long displacements were found in the southeast part of the Svalbard archipelago, with Hopen as a central hub. The two longest displacements observed were 444.1 km and 451.9 km, made by a female and a male bear, respectively. These bears were both captured in the Central Barents Sea and recaptured at Hopen Island three years later. The distribution of displacements was skewed towards very short distances, and the long displacements seen in the map (Fig.3) comprise a long right-hand tail on the distribution curve (Fig.4).

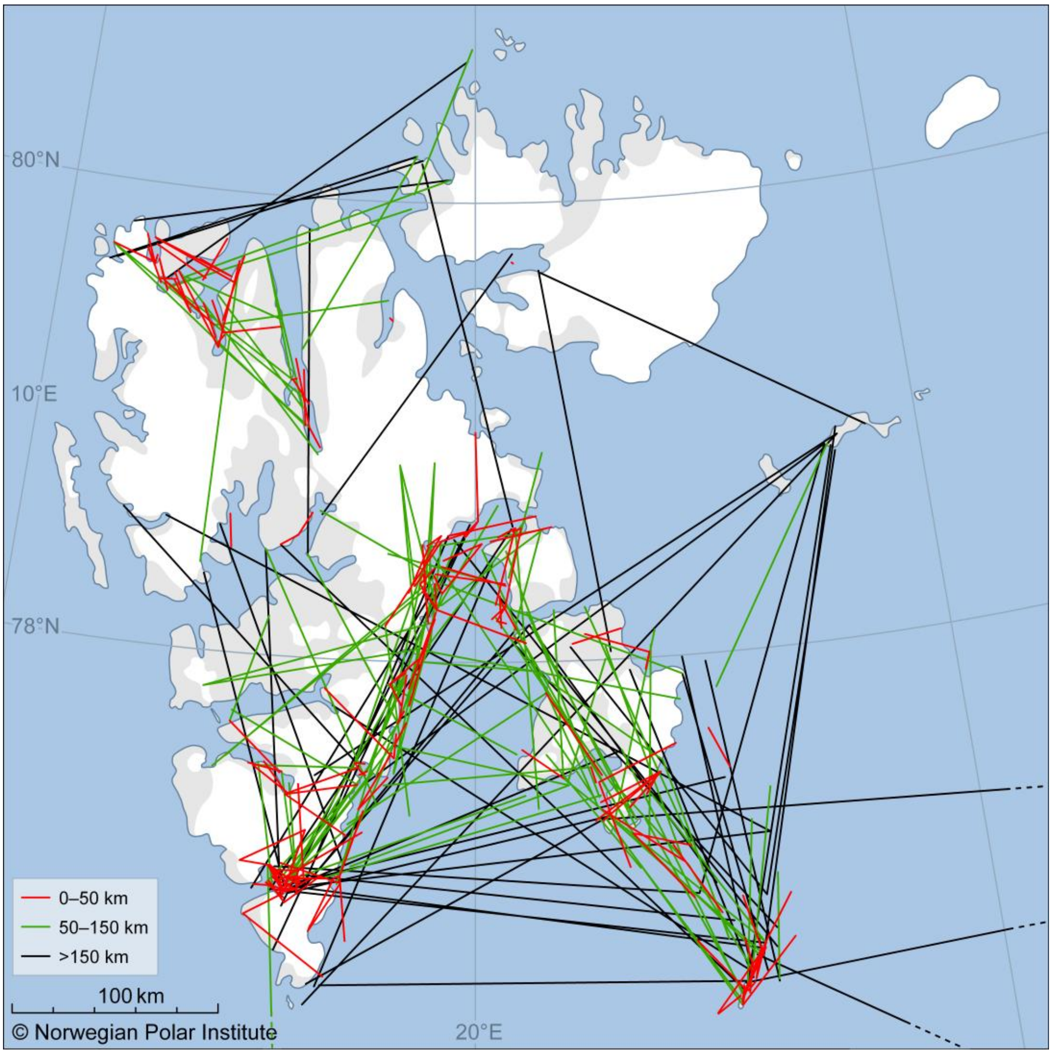

Figure 3: Map of all recorded displacements by marked individuals (n=348), color coded by the length of movement.

Figure 4 shows that the distribution of observed displacements had a different shape and was shifted left relative to the reference distribution of potentially observed displacements. This is a clear indication of site fidelity. The bears moved shorter distances than predicted in the null hypothesis scenario of moving randomly between the capture points between years, as evidenced by non-overlapping 95% confidence intervals of the median. When data from all years were included, the median observed displacement was 43.0 km (95% CI: 34.3 - 51.0 km) compared to a median potential displacement of 205.4 km (95% CI: 205.1 - 205.6 km). All age/sex groups showed site fidelity when compared to the potential displacements in this manner, and restricting the analysis to 1 yr lag does not affect the outcome of this analysis (Table 1).

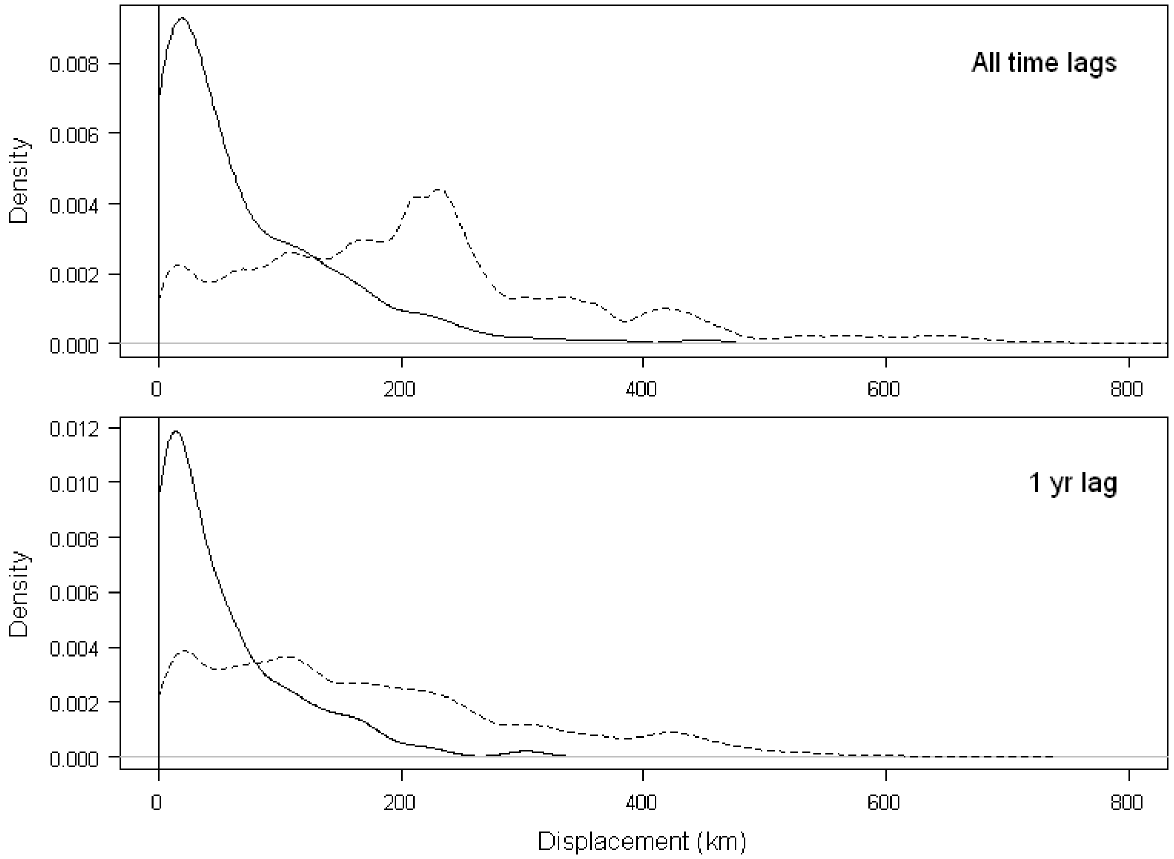

Figure 4: Density functions of the distributions of the observed (solid line) and potential (dotted line) displacements, based on the whole dataset and on the 1 yr lag dataset. The density functions were obtained by means of Gaussian kernel density estimate.

Table 1: Medians of potential and observed displacements (km), for the data based on all years, and restricted to 1 yr lag. The 95% confidence intervals are calculated by bootstrap.

		All years			1 yr lag		
		Median (km)	n	95% CI (km)	Median (km)	n	95% CI (km)
Potential displacements		205.4	1000771	205.1 - 205.6	141.9	78834	140.4 - 143.5
All bears		43.0	348	34.3 - 51	31.8	117	19.3 - 43.0
COY (0 yrs)	F	20.8	12	4.6 - 33.7	-	-	-
COY (0 yrs)	M	19.0	15	2.6 - 71.2	-	-	-
Juvenile (1-2 yrs)	F	24.2	19	11.8 - 32.7	32.7	3	8.7 - 52.4
Juvenile (1-2 yrs)	M	43.0	19	16.1 - 85.3	16.1	7	9.4 - 43.0
Subadult (3-4 yrs)	F	89.0	13	18.3 - 158.4	41.3	6	11.4 - 123.7
Subadult (3-4 yrs)	M	19.5	12	7.5 - 45.1	21.9	5	4.7 - 43.1
Adult (5+ yrs)	F	33.7	135	22 - 50.5	19.0	48	9.4 - 31.0
Adult (5+ yrs)	M	62.5	123	50.9 - 94	53.9	48	41.9 - 76.8
Adult F w/COYs		19.7	12	9.7 - 36.2	-	-	-
Adult F w/o COYs		35.9	123	23.9 - 54.5	-	-	-

3.2 Displacement as a function of demographic factors

The stepAIC procedure arrived at different optimal models for the data when all recaptures (Eqn.3) or only the first recapture for each bear was included (Eqn.4). However, the model selection was ambiguous in the latter case, since several models that included the $years^2$ covariate (such as Eqn.3) and/or excluded the effect of sex altogether, achieved nearly as low AIC value as the optimal model (Table 2).

Eqn.3 $y(\lambda) \sim age.pre*sex + years + years^2$

Eqn.4 $y(\lambda) \sim age.pre*sex + years$

Investigating these models as well as the model used as the starting point, I found that optimal lambda was similar for each of them and used an intermediate value, $\lambda = 0.23$, in all analyses.

The optimal model for the dataset with all recaptures showed a significant interaction between *age.pre* (age group the individual belonged to at the first of the two captures used to measure the displacement) and *sex* (ANOVA, $F_{3,338} = 3.27$, $p = 0.021$). The optimal model for the dataset based on the first recapture displacement for each bear also had a significant interaction term between *age.pre* and *sex* (ANOVA, $F_{3,211} = 2.72$, $p = 0.046$), and an equally high adjusted R^2 of 0.84. Estimates of displacement for each age/sex combination based on the two datasets are given in Table 3. Here, Eqn.3 was used on both datasets to facilitate comparison.

Table 2: Summary of selected models fitted to displacement. Models with the lowest AIC value or within 1 unit of the lowest value are shown in bold type.

			AIC	
Covariates	Model	# of parameters	All recaptures per bear	First recapture per bear
years + years^2	age.pre*age.post*sex	20	1707.6	1105.6
	age.post*sex	9	1711.1	1106.6
	age.pre*sex	**11**	**1697.2**	**1094.1**
	age.pre + sex	8	1701.2	1095.6
	age.pre*age.post	12	1715.5	1100.9
	age.post	6	1714.5	1102.5
	age.pre	**7**	1708.6	**1093.9**
	sex	5	1713.1	1110.8
years	age.pre*age.post*sex	19	1717.1	1105.9
	age.post*sex	8	1718.5	1105.6
	age.pre*sex	**10**	1705.3	**1093.7**
	age.pre + sex	7	1710.5	1095.9
	age.pre*age.post	11	1725.4	1101.6
	age.post	5	1721.8	1101.6
	age.pre	**6**	1717.7	**1094.1**
	sex	4	1722.1	1111.0
none	age.pre*sex	9	1733.3	1109.3
	age.pre	5	1742.9	1107.8

Table 3: Estimated displacement (km), according to the Box-Cox transformed linear model. All estimates are evaluated using *years* = 1. Sample size n is given for each category in each analysis.

		All recaptures per bear[a]			First recapture per bear[a]		
		Estimate (km)	n	95% CI (km)	Estimate (km)	n	95% CI (km)
COY (0 yrs)	F	11.2	12	4.0 - 26	12.4	12	4.3 - 29
COY (0 yrs)	M	13.5	15	5.6 - 28	15.2	15	6.2 - 32
Juvenile (1-2 yrs)	F	16.0	19	7.6 - 30	20.3	14	8.5 - 42
Juvenile (1-2 yrs)	M	21.8	19	11 - 40	27.1	16	12 - 53
Subadult (3-4 yrs)	F	46.2	13	23 - 84	87.2	9	41 - 165
Subadult (3-4 yrs)	M	16.7	12	6.7 - 36	20.9	8	6.7 - 52
Adult (5+ yrs)	F	24.9	135	19 - 32	40.7	74	28 - 57
Adult (5+ yrs)	M	44.6	123	35 - 56	50.0	72	36 - 68

[a] Model structure used was $y(\lambda) \sim age.pre{*}sex + years + years^2$, the optimal model for the dataset based on all recaptures.

Although there is a high degree of overlap in the confidence intervals of the different age/sex categories due at least in part to the small sample sizes after categorization, some interesting trends can be seen. Older bears tended to have greater displacement than younger bears and adult males tended to move longer distances than females (Table 3, Fig.5). Looking first at the results of the analysis that included multiple recaptures, most estimates for the younger age groups were similar and within the range 11 – 22 km. An exception is subadult females, whose estimated displacement (46.2 km) was markedly higher. The estimates for the three youngest age categories increased when only the first recapture was used for each bear, but generally by only a few kilometers. Subadult females whose estimate nearly doubled to 87.2 km were again the exception. In this category, the four displacements that were removed were all among the six shortest movements. For adult bears, there was a pronounced difference between females and males when all recaptures were used, with estimated displacement of 24.9 km and 44.6 km, respectively. When only the first recaptures were included, the model produced higher displacement estimates (40.7 km for females and 50.0 km for males) but the difference between the sexes diminished.

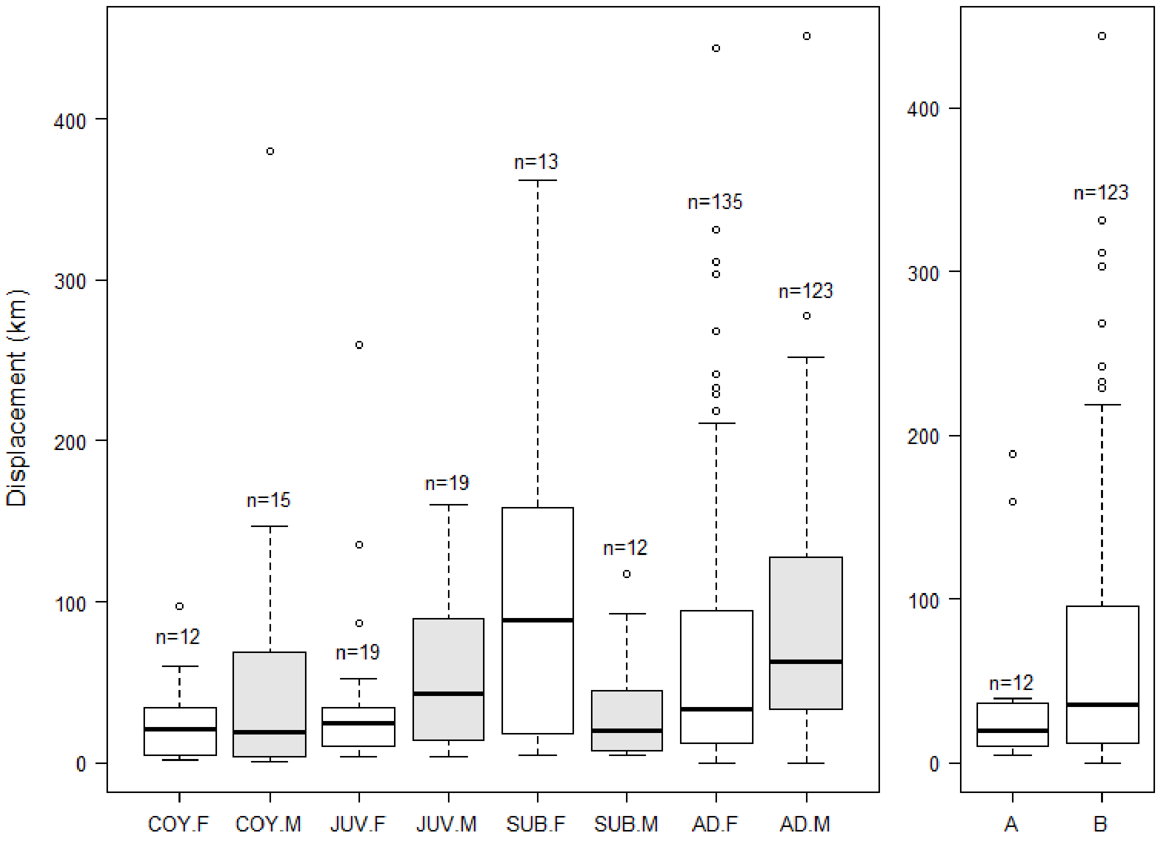

Figure 5: Observed displacement for all combinations of age at first recapture and sex (left panel) and adult females with COYs in both years (A) vs all other adult females (B) (right panel). Abbreviations: COY = cub of the year (0yr), JUV = juvenile (1-2 yrs), SUB = subadult (3-4yrs), AD = adult, F = female, M = male (shown in grey). The box-whisker plots show the interquartile range of the data (box) around the median (central horizontal line) with whiskers extending to the most extreme data point which is no more than 1.5 times the interquartile range of the box. Circles mark outlier datapoints.

The changing estimates reflect a difference between males and females when it comes to multiple recaptures. Nine females were recaptured four or more times, compared to only three males. In addition, females exhibited a strong negative correlation between mean displacement and the number of times the bear had been recaptured (Spearman rank correlation, ρ = -0.36, p = 0.0002 two-tailed). No such correlation was found for males (Spearman rank correlation, ρ = -0.028, p = 0.771 two-tailed); see Figure 6 for comparison.

The relatively large sample size for adult males and females allowed a more detailed comparison of these two groups. This comparison is of particular interest, as it is relevant to the question of whether female telemetry data can be extrapolated to the whole adult population. Female and male adult displacements differed markedly when all recaptures are considered (ANOVA, $F_{1,256} = 11.25$, p = 0.0009), but did not differ significantly when only one displacement for each bear was used in the comparison (ANOVA, $F_{1,167} = 1.31$, p = 0.2535). In both cases, a higher proportion of female recaptures takes place very close to the initial capture position, and displacements are shorter than for males (Fig.7).

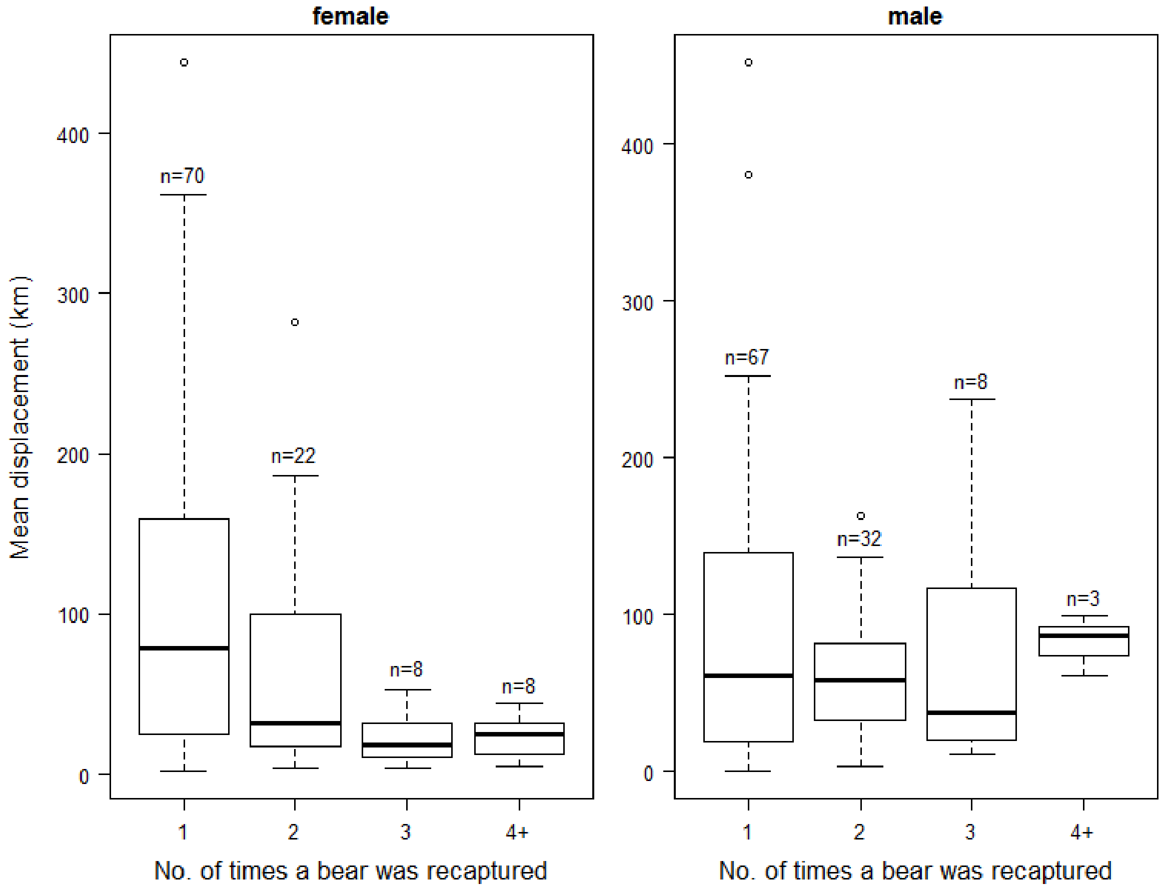

Figure 6: Plot showing the correlation between the number of times a bear was captured and its mean displacement for females and males, respectively. The given n is the number of bears in each category.

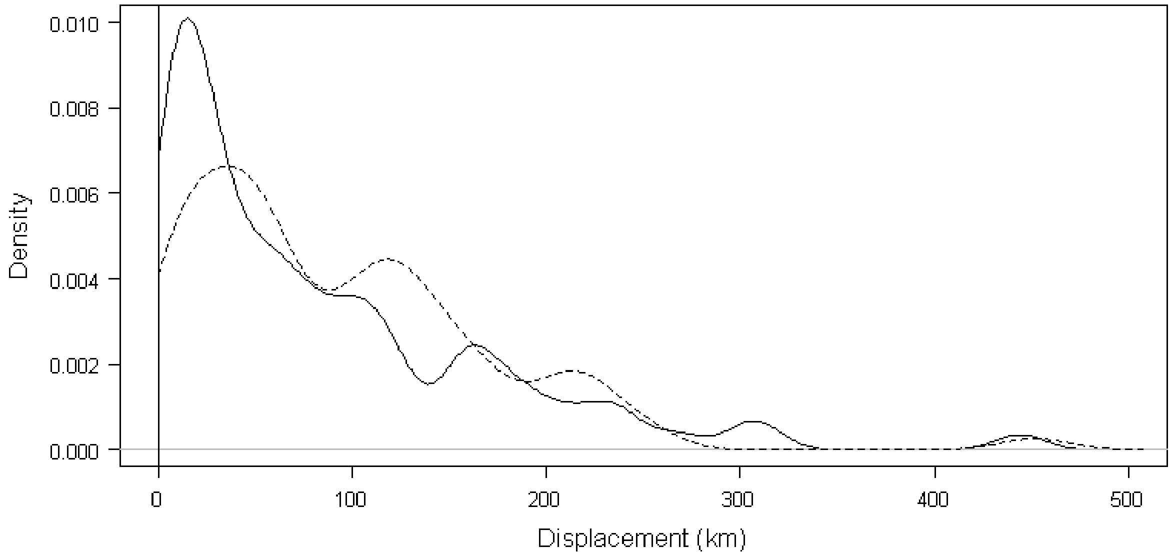

Figure 7: Density functions of the distributions of adult female (solid line, n = 87) and adult male (dotted line, n = 82) displacements, including only the first adult displacement for each bear.

Similarly, adult females were pulled out as a subgroup and analyzed in terms of whether they were with COYs at both positions of capture or not. There was a non-significant trend (ANOVA, $F_{1,133} = 0.97$, $p = 0.327$) toward shorter displacement for females having COYs in both sampling years, compared to all other recorded displacements by adult females (Fig.5, right panel). Looking at the observations one by one, ten out of 12 displacements of the females with COYs at both capture events were less than 39 km, whereas the last two were 159.8 km and 188.3 km. The displacements are mapped in Figure 8.

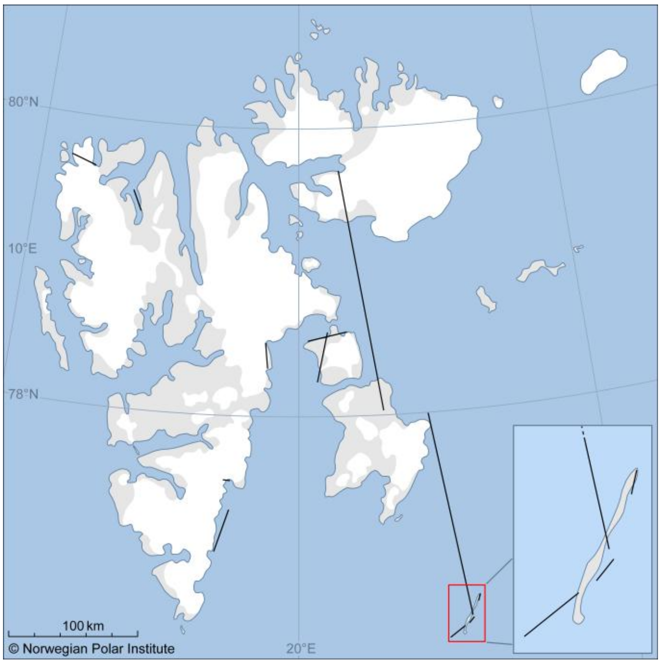

Figure 8: Map of displacements for adult females captured with COYs in both years (n = 12).

4. DISCUSSION

4.1 Site fidelity

Polar bears in the Svalbard area exhibit strong site fidelity, reflected in the short median spring-to-spring displacement found in this study (43.0 km, range 0 – 452 km). This is comparable to previously documented spring-to-spring displacements, based mainly on telemetry position, for females in this population (Wiig 1995), ranging from 5 to 512 km, with mean values of 149.3 km, 78.9 km, 51.1 km and 32.0 km after 1, 2, 3, and 4 years, respectively. Mauritzen et al. (2001) calculated the distance between telemetry positions of individual female polar bears separated by one year and found monthly mean values in the range 70 - 90 km in March, April and May with 95 % confidence intervals spanning *ca* 40 km. This study extends the documentation of site fidelity of Svalbard polar bears beyond that of female adults to include also males and bears of all ages.

Studies from other regions support the tenet that a certain degree of site fidelity and a large range of displacement values are characteristic of polar bears in general. Mean spring-to-spring displacement of 67 km was found for 15 marked polar bears in the Canadian Arctic (Schweinsburg et al. 1981), and average displacements of 116.5 km after one year and 85.4 km after two years were recorded in radio-collared bears in eastern Greenland showed (Born et al. 1997). Taylor et al (2001) reported from the Canadian Arctic a majority (59%) of displacement distances 100 km or less, and only 6.3% exceeding 400 km. By the same measures, Svalbard bears seem to exhibit stronger site-fidelity, since a much lower percentage of the displacements are greater than 400 km and about 75% of the recaptures are within 100 km. However, differences in probability of detection of displacements of various distances in different regions mandates care in making comparisons.

Koenig et al. (1996) pointed out that mark-recapture methods are unable to detect long movements out of the study area, and warned against faulty interpretation of dispersal rates decreasing to zero at the maximum diameter of the study area. In this study, frequency displacement rates are seen to drop to zero well before the distribution curve of potential distances dropped to zero. However, a long right-hand tail of the displacement curve indicates the likely existence of a few “long movers” who would never show up in the mark-recapture data likely exist. A case in point is the radio-collared female bear who moved across the polar basin from Alaska to Greenland, and seemingly undertook breeding in both locations (Durner and Amstrup 1995). Similarly, movements into or out of the Barents Sea population could be detected by telemetry, or by recovery of marked bears in another region. A few reports from the Greenland hunt have been registered (Larsen 1986, Wiig 1995), but these are rare events, and since 2003 there have been no such recoveries (J Aars, pers.comm.). Of all bears captured in the Barents Sea population, only two bears had previously been marked elsewhere. Both of them had been tagged in the spring in neighboring Novaya Zemlya and Franz Josef Land. Studies based on mark-recapture and telemetry have concluded that there may be some spatial overlap, but minor exchange of individuals, between the Barents Sea population and the East Greenland population to the west and the Kara Sea population to the east (Wiig 1995, Mauritzen et al. 2002). The paucity of long displacements observed in this study supports the current evidence that exchange may occur between these populations, but only very rarely.

4.2 Demographic differences

This study shows that in Svalbard, between-year displacement depends on age and sex of the individual bear. Taylor et al. (2001) reached a similar conclusion in Canada. Other studies have not been able to detect any effect of age or sex (Schweinsburg et al. 1981, Lentfer 1983). This may reflect real differences between the populations investigated, but could also relate to issues of sample size or methodology.

Of all age- and sex groups, the bears marked as subadult females were recaptured the farthest away from their initial position. The next longest displacements were found in adult bears, and the displacements were shorter for the remaining categories. Among adult bears, female polar bears had only slightly shorter displacements than males. My results have much in common with Taylor et al. (2001). They did not consider the interaction effects of age and sex, as this study did, but found that subadults tended to move longer distances than adults.

Since several measurements from the same bear are not independent, it was not unexpected that treatment of multiple recaptures proved to be critical to the outcome of the analysis. When the data could not be subjected to random effects models, the decision to include or exclude multiple recaptures involved a trade-off between removing bias and losing information. Estimates from several categories were shown to be robust to the potential bias of including multiple recaptures of the same bear. However, estimates of subadult female and adult female displacement were strongly affected by the removal of multiple recaptures. Estimates of displacement for both of these categories increased with the removal of multiple recaptures, with the greatest absolute and relative increase for the subadults. Small sample size may have affected the estimate for the subadult females, while the sample size for the adult female category remained large. Hence, the adult female category gave a considerably more reliable estimate after removal of multiple recaptures. Dependence on sex was less clear, and age and sex barely retained significance as an explanatory factor after removal of multiple recaptures, probably a combined result of smaller differences once the bias was removed, and the lower power of this conservative analysis.

The multiple recapture bias in this study involved a trend of decreasing displacement with increasing number of recaptures of an individual bear, for females only. The location of the bear affects the probability of capture (Nichols 1992, Bennetts et al. 2001) and the capture effort of this study included certain core areas repeatedly. If there is individual variation in degree of site fidelity and some bears are highly place-bound over several years, these bears would be expected to be recaptured multiple times. This would cause a trend of decreasing displacement with multiple recaptures. My interpretation is that very high between-year site fidelity is adopted as an individual strategy by some females, but not by any of the males.

The displacement of a female captured with COYs in both years is a measure of denning site fidelity. All observations of females with COYs were from late March or April. At this time, mother and cubs have recently emerged from their winter maternity den, and are likely to be close to the denning location (Hansson and Thomassen 1983, Garner et al. 1994, Zeyl et al. 2010).

Denning site fidelity was stronger than fidelity of females to general areas used in spring, although the difference was not statistically significant. Fidelity to denning areas in Svalbard was demonstrated by Zeyl et al. (2010), but has not previously been compared to fidelity of non-denning females. Females may show greater fidelity to denning areas because they have specific denning habitat requirements (Durner et al. 2003). In Svalbard, these are only fulfilled in specific areas on some islands where enough snow accumulates in autumn (Larsen 1985). Familiarity with the area may be especially advantageous during the critical first period after leaving the den, and be a second factor promoting differentiation.

Evidence that female polar bears can switch denning area has been interpreted as plasticity of behavior rather than lack of site fidelity (Zeyl et al. 2010). Such plasticity can be viewed as an advantageous response to insufficient sea ice cover to reach the islands with preferred denning habitat. Sea ice cover has been shown to affect the number of dens on Hopen (Wiig et al. 2008).

One interpretation of the long displacements by subadult females is that they roam, or spend some years exhibiting less site fidelity, before returning to their natal areas. This idea is supported by non-significant observations from Canada that young females dominate the long displacements observed (Schweinsburg et al. 1981). Roaming could potentially benefit young females by allowing them to become familiar with several different potential denning areas, which would later facilitate a plastic denning strategy. Evidence for this behavior is rather weak, however. Had there been a particular age class with marked roaming behavior or a certain age at which dispersal occurred, it would be best described by a model including age at both capture and recapture. That age at recapture was categorically excluded by the model selection procedure is a signal that such behavior is at least not very pronounced.

Difference in displacement between groups can reflect difference in the size of activity area or difference in how far the center of activity has shifted. Females with COYs are known to have more restricted activity ranges (Amstrup et al. 2001), rates of movement (Garner et al. 1994) and mobility (Messier et al. 1992) than other groups of females, and this must also be part of the explanation of the difference in displacement between these groups. Brown bears intentionally restrict their home range to protect their cubs from infanticide by adult males (Dahle and Swenson 2003). Although it is possible that polar bears also benefit from reduced infanticide (Taylor et al. 1985), the mobility of COYs is probably the limiting factor for these family groups (Jonkel et al. 1972). Seasonal area use by females with yearlings, females with two year olds, solitary females, and males are similar (Amstrup et al. 2000; 2001, Mauritzen et al. 2001), and hence not thought to represent a major source of differences exhibited by these groups.

The observed patterns of displacement according to age and sex must be understood in the light of factors that govern polar bear behavior and distribution during the spring. During the mating season, March to May (Lønø 1970), male and female distribution is thought to be shaped by separate primary factors. While females are distributed according to prey resources, access to estrous females is the top priority for males (Sandell 1989). Polar bears have a promiscuous mating system (Zeyl et al. 2009b) and males rove widely in search of estrous females (Ramsay and Stirling 1986), as predicted for species in which females are widely and unpredictably distributed (Clutton-Brock 1989). If some dominant males start to rove, it becomes the optimal strategy for all males, both dominant and subordinate (Sandell 1989). The findings of this study could indicate that most males end up using a similar strategy. Females may be freer than males to choose their own strategy under this mating system, and some clearly opt to return to the same location year after year.

Similar levels of male and female philopatry, as I observed for polar bears, is atypical among polygynous or promiscuous mammals (Greenwood 1980, Dobson 1982). The polar bear is a highly mobile species living in an unstable environment for which predictability of resources may be the key factor explaining site fidelity. The similarity between males and females may thus indicate that prey resources and estrous females are predictable on a similar scale.

My data document a mechanism that contributes to the male and female kin structure and the slight male bias of gene flow (Zeyl et al. 2009a) that is known to exists in the Barents Sea population. Both sexes show relatively high fidelity, and the slight sex bias is too weak to be a mechanism that could prevent close relatives from getting the chance to inbreed. Nonetheless, inbreeding events are evidently infrequent. When charting the pedigree of the Svalbard polar bears, Zeyl et al. (2009a) genotyped 583 animals and only identified one incestuous mating event. Many mechanisms other than dispersal exist that can prevent inbreeding, for example kin recognition, hence levels of inbreeding in wild populations are generally low (Pusey and Wolf 1996).

Some of the limitations of the mark-recapture data used in this thesis have already been treated in detail, such as the lack of independence between subsequent measurements based on the same bear. That obtaining a location for bears is dependent upon capture is a shortcoming compared to telemetry studies, and means that nothing is known about the path and location of bears in the years between capture and recapture. The overall bias due to this factor was nevertheless shown to be minor, based on the comparison of my results with Mauritzen et al. (2001) and Wiig et al. (1995). The sampling of the study area will necessarily be biased regarding displacements of the pelagic bears, by mainly detecting spring positions in the Svalbard area, and missing displacements between Svalbard and the central Barents Sea or the pack ice further north and northeast. My estimates of site fidelity are representative of site fidelity in use of areas in the immediate vicinity of the main Svalbard islands. The large variance in displacement estimates reflected large variability within the population, an important characteristic of polar bear movement. However, large variance also means that either the differences in displacement or the sample sizes have to be relatively large for statistical significance to be found. Thus, the small sample sizes for all categories of non-adult bears made it difficult to make conclusive remarks about their behavior.

The result from this analysis from Svalbard supports the practice of using telemetry measurements to delineate population boundaries (Taylor et al. 2001). Even though adult females tended to have shorter displacements than adult males, the longest displacements of males and females were found to be quite similar. I conclude, in agreement with Taylor et al. (2001) that there are “small-scale sex differences” in displacement, and that in the absence of large-scale sex differences, it is justifiable to use telemetry data from females only to assess population boundaries.

In conclusion, polar bears of all ages and both sexes exhibited high site fidelity in the spring. There are clearly some differences in site fidelity between the sexes and between age groups, and subadult females stood out as the group of bears that were recaptured the farthest from their original capture point, while adult females with COYs showed the highest site fidelity. The differences found likely reflect different priorities and limitations and accordingly, optimal behavior according to age, sex and reproductive status.

Differences found here in spring-to-spring displacement point to an array of ways in which subadults, males and females could potentially be found to differ in an analysis using high-resolution data. A thorough investigation of age and sex differences would require instrumentation of males and subadults of the population, but that has proved challenging.

This study has identified only one marked difference that warrants some caution in extrapolation of telemetry studies. That very high site fidelity over time is only found in a few female individuals has been linked to the special circumstances that prevail during the mating season. However, it does raise the question of whether the inter-individual variations in overall space use strategy and annual home range size of males are as large as those identified for females using telemetry (Mauritzen et al. 2001).

Age- and sex-related differences in displacement were small relative to the variance, indicating that estimates and variability based on telemetry on females can in many circumstances be considered relatively representative for males also. The same can be claimed for young bears, although with less certainty. The continuation of the mark-recapture effort and the resulting long-term datasets will nonetheless continue to be a valuable resource for observing the movement and behavior of males and young bears.

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Appendix A

Estimated displacement (km), according to the Box-Cox transformed linear model based only displacements with 1 yr lag. Sample size n is given for each category in each analysis.

		All recaptures per bear			First recapture per bear [a]		
		Estimate (km)	n	95% CI (km)	Estimate (km)	n	95% CI (km)
Juvenile (1-2 yrs)	F	26.3	3	4.4 - 93	26.3	3	3.8 - 100
Juvenile (1-2 yrs)	M	18.6	7	5.6 - 47	20.5	6	5.3 - 58
Subadult (3-4 yrs)	F	39.2	6	13 - 92	39.2	6	12 - 97
Subadult (3-4 yrs)	M	16.3	5	3.6 - 50	16.3	5	3.2 - 53
Adult (5+ yrs)	F	21.5	48	14 - 31	32.7	32	20 - 50
Adult (5+ yrs)	M	49.3	48	35 - 67	50.0	34	33 - 73

[a] Optimal model (lowest AIC) for "first recapture" was a constant, but the dataset is analyzed here with $y(\lambda) \sim age.pre*sex$.