



# The mating strategy of female Svalbard reindeer (*Rangifer tarandus platyrhynchus*)



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## **Abstract**

The mating system of Svalbard reindeer was studied in detail on Nordenskiöld land, Svalbard during the mating season 2007. Little is known about the female mating systems of Svalbard reindeer. The aims of the study were to investigate the composition of harems in relation to male attractiveness, harem size and reproductive history and the associated behaviour of females. The movement patterns of marked females were studied in order to determine whether females stay in one harem throughout the rutting season.

Most of the females observed were in harems, i.e. in mating groups that included males. The majority of the harems were small compared to other reindeer populations. Harems usually consisted of 1-5 females, but up to 19 females were observed in a single harem, and up to five males were associated. With increasing number of females in the harem, the number of males increased, as did the maximum male antler size. This may indicate that antler size is an indirect sign of quality for Svalbard reindeer. Females with a calf at heel were uncommon in harems, suggesting they shortly visit harems to become fertilized. The number of males associated with the harem greatly increased the proportion of time the females spent on energy consuming activities such as running and walking. The frequency of mating behaviour (male-female and female-female interactions) directed towards females increased with increasing number of females in the harem, providing evidence for greater somatic cost for females being in harems.

The movement pattern of the observed females was mostly within the same valley, although some females were re-sighted in the adjacent valleys. The females were mostly re-sighted in harems, varying in size. Our results indicate that harems are dynamic entities in terms of the females attending them.





## 1 Introduction

In polygynous species where only the female performs parental care, or in species where one of the sexes has higher reproductive potential, different strategies to improve the reproductive success are evolved. The males should mate with as many females as possible, whilst females should be selective and choose the highest quality males as mates (Trivers, 1972). The reproductive success of the female is also influenced by breeding experience (Clutton-Brock et al., 1988), age, body condition and dominance status over conspecifics (Côté & Festa-Bianchet, 2001b; Holand, 2004). Social dominance over competing conspecifics is for ungulates correlated with features such as antler size (Espmark, 1964; Barrette & Vandal, 1986; Wolff, 1998), body size (Holand, 2004; Vervaecke et al., 2005) and age (Clutton-Brock et al., 1988; Côté, 2000; Côté & Festa-Bianchet, 2001b).

Adaptations to differing resource availabilities has resulted in development of different mating systems, such as lek breeding (male-dominance polygyny) (Stillman et al., 1996; Nefdt & Thirgood, 1997), resource-defence polygyny (Emlen & Oring, 1977; Carranza, 1995) and female-defence polygyny (Emlen & Oring, 1977). Lek-breeding is characterized by males defending a small territory using social signals to attract females. In resource-defence polygyny the males hold larger and more scattered territories and the breeding success of the male depends on the attractiveness of his territory to females. In female-defence polygyny, the females aggregate and the males compete for the right to mate with the female cluster. The strategy chosen in a species depends on the distribution of resources and females in time and space, the time and energy the male can afford to invest in mating behaviour, and the temporal availability of receptive females (Emlen and Oring, 1977; Clutton-Brock and Harvey, 1978; Wade, 1995). Mating behaviour includes male-female and female-female interactions that lead to reproductive success and causes stress and costs for females (Holand et al., 2006).

The aggregation of females found in some mating systems is known as “harem”. Espmark (1964) defines a harem as a group of females that a male has primary access to (hegemony). Harem systems are found in variety of mammals, including ungulates.

In large moving herds, bulls may defend and tend only one cow at a time (Lent, 1965), while in relatively stationary herds and in particular in populations with highly female biased sex ratios, harem sizes may be large and reach more than 100 females (Skogland, 1989). Females are motivated to join harems to avoid harassment by sub-dominant males (Carbone & Taborsky, 1996; Nefdt & Thirgood, 1997; Hirotani, 1989), predator safety (Clutton-Brock et al., 1996) and resources availability (Clutton-Brock et al., 1989). Although joining a harem may give negative effects of crowding in large harems (Wade, 1995).

Females often move between harems to allow evaluation of different breeding partners. This will possibly lead to increased fertilization success (Hirotani, 1989; Clutton-Brock et al., 1996; Nefdt & Thirgood, 1997). Female mating preferences may evolve when the cost of moving between harems in order to evaluate partners is low (Clutton-Brock, 1989; Komers et al., 1999). The ability of males to defend a harem is a sign of their quality (Hirotani, 1989; Wolff, 1998).

The harem size of reindeer is suggested to be influenced by sex ratio and distribution of resources and females in the area (Skogland, 1989). The Svalbard reindeer (*Rangifer tarandus platyrhynchus*) has a close to balanced sex ratio (ca 43:57 males:females) (Skogland, 1989), and the high frequency of males to females gives small harems due to high frequency of competition between males to monopolize females. Additionally, the small harem sizes predicted might be due to patchily dispersed resources in the area (Tyler & Øritsland, 1989), that causes females to be widely dispersed, and may reduce the opportunities to obtain large harems.

Compared to other ungulate populations, little is known about female mating systems for Svalbard reindeer (Skogland, 1989). This project describes the mating system of a natural population of Svalbard reindeer with focus on adult females. We give a general description of harem sizes in relation to the number of males associated with the harem, and the antler size of the dominant buck. As behavioural interactions with conspecifics and males may increase with increasing harem size we investigate whether females spend more time running and walking, and less time feeding and resting as harem sizes and the number of males

present increase. In addition we want to measure the time females are provoked to male-female interactions and female-female interactions with increasing harem size. Further we investigate whether a female's reproductive history influences participation in mating activities. Finally, using observations of individually marked female reindeer we evaluate whether the harems of Svalbard reindeer are stable entities throughout the mating season, or dynamic with females moving between the harems.



## 2 Method

### 2.1 Study area

The study area was on Nordenskiöld land peninsula on Spitsbergen, the largest (37 673 km<sup>2</sup>) island in the high Arctic Archipelago of Svalbard (77° to 81° N). The study was carried out in the valley system of Colesdalen-Semmeldalen and lower parts of Reindalen and their adjacent side valleys, 6-30 km south of Longyearbyen (Figure 1).



*Figure 1: Nordenskiöld land peninsula on Spitsbergen, with the study area marked in yellow.*

The high arctic terrestrial ecosystems in the area are characterized by low primary production and a short plant growing season (ca 60-70 days) (Bengtson et al., 1999), and can be characterized as arctic desert due to low temperatures and little precipitation (Solberg et al., 2001). The high latitude implies a long dark season with 24 h darkness from 11 November-30 January, and the sun returning above the horizon in the end of February.

The mean air temperature for the area during the study period in September – October 2007 was -1.9 °C, with maximum and minimum temperatures -0.7°C and -5.3°C, respectively (eKlima, 2009). The mean precipitation for the study period was 1,02 mm per day, which fell as snow in the last part of the study period, disrupted by one day of rain.

## 2.2 Study species

The Svalbard reindeer (*Rangifer tarandus platyrhynchus*) is an arctic subspecies of reindeer (*Rangifer tarandus*), and is the northernmost large herbivore on earth. It is a small reindeer with a short nose and legs and a thick insulating fur that enable them to withstand air temperatures down to -40°C. The main limiting factor in their population dynamics are food, parasites and climatic conditions. In particular, extreme winter conditions with ice crust and ground ice formations may cause starvation (Solberg et al., 2001, Kohler & Aanes, 2004). Even though there are occasional records of adult Svalbard reindeer being taken by polar bears, and some neonatal mortality due to arctic fox predation (Prestrud, 1992), Svalbard reindeer are regarded as having no natural predators, nor do they suffer from severe insect harassment (Bjørkvoll et al., 2009). Human harvesting occurs at low intensities, in the years 1983-2008, 144 reindeer were on average harvested per year (Svalbard, 2009). The Svalbard reindeer contrasts with the mainland reindeer by having a sedentary, non migratory lifestyle (Tyler & Øritsland, 1989), and not occurring in large herds (Skogland, 1989). The rutting season for the reindeer in this area is in October (Skogland, 1989; Milner et al., 2003; Loe et al., 2006) and calving occurs during the two first weeks of June.

The reindeer population in the study area consists of approximately 1300 animals (Milner et al., 2003). In 1994 a monitoring project was started, each year since then a subset of female calves has been marked with numbered ear tags (allflex Europe (UK) Ltd., Hawick, UK) and neckmarker straps fitted with numbered sleeves (Dalton Supplies Limited, Henley-on Thames, UK). These animals are monitored in the summer when they are checked for presence of a calf, and in April when a subsample is caught and checked for pregnancy using ultra sound scanning and progesterone assay on blood samples (Albon et al. 2002).



*Figure 2: Svalbard reindeer (female cluster) in Semmeldalen. Notice the eartags on the animal to the left.*

### **2.3 Study design**

The study was conducted from 26 September to 29 October 2007. Observations were done daily between 11.00-16.00 hours, if weather and light conditions permitted. Initially the work was carried out on foot, and later in the season on skis. A tent was used for accommodation in Colesdalen, whilst available cabins were used when working in the rest of the study area. Priority was given to cover as much area as possible during the study period. Reindalen and Semmeldalen (the southern part of the study area) was covered three times, while Colesdalen with side valleys was only covered twice. The spatial distribution of the observation sites was determined by the distribution of reindeer. The field work was done in collaboration with Gro Vestues, who wrote her master thesis on the mating behaviour on the male part of the population (Vestues, 2009).

The reindeer were spotted at a distance of approximately 600 meters using Zeiss binoculars (10x40) and a Swarovski AT-80HD (60x80) spotting scope. From this distance the group size and demographic composition of groups were noted, and were distinguished for older animals, yearlings and calves. In addition, the identity tags of all marked animals were noted. The marked females were aged according to the known life history of the animal. Groups with female reindeer were classified as either female cluster, if the group contained females only, harems, if the group was a mixed sex group, or as single females. We define the harem size as the number of adult and yearling female reindeer in a harem. The location of the animals and their behaviour in the moment of observation was noted via GPS (WGS 84) (see Table 1 for behavioural categories). With the observer distance used, the reindeer showed no sign of observer effects on behaviour. A single female from a subset of groups were selected for focal watches.

### *2.3.1 Antler size*

The antler size of all the males observed was noted and categorized according to the size of the front part of the antlers (the brow tine) (Figure 3). The brow tine is an extra beam pointing forward above the nose. The categories used are no brow tine (1), small (2), medium (3) and full brow tine (4). The category “no brow tine” was used when the male had up to only a small sign of development of a brow tine. “Small brow tine” was used when the animal had a small development of a brow tine, showing only a simple beam. “Medium brow tine” was used for a simple beam with one extra spike, while the last category “full brow tine” was a beam with more than one spike and often a large flat surface on the brow tine.



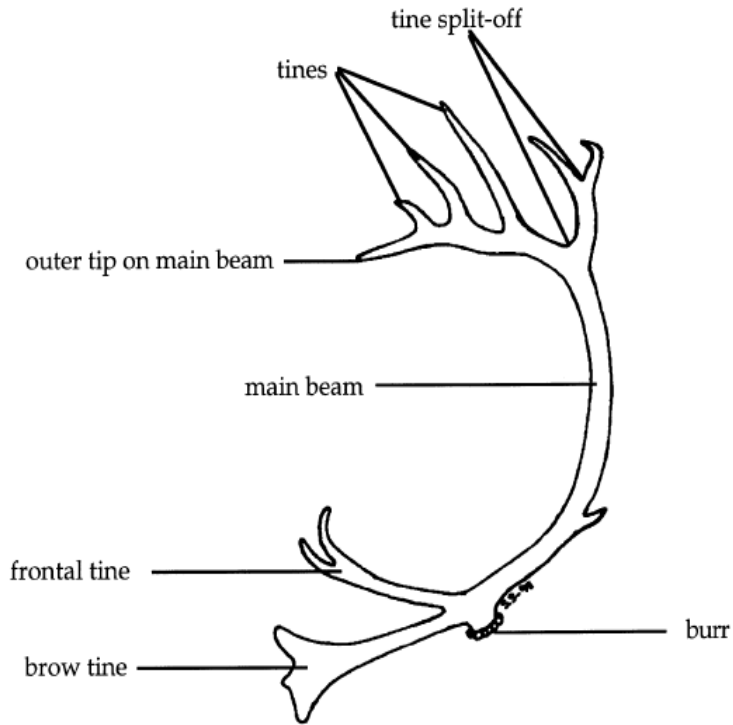


Figure 3: Antler of male reindeer (from Markusson & Folstad, 1997) showing a “full brow tine”

## 2.4 Observations of behaviour

During the study period sixty-nine 30 minute focal watches were carried out. During the focal watches one female was watched continuously, and every minute the behaviour was recorded giving 30 behavioural observations. One observation day consisted on average 1-5 focal watch periods depending on weather conditions and day length. Equal number of samples from large (>2 females) and small harems (1-2 females) was attempted, and marked individuals were selected if available. However, in cases with no marked females in a group, an unmarked female was randomly chosen for the focal watch. Efforts were made to choose groups for focal watches that were well spaced out, by systematically survey one area before moving on to the next.

The behavioural categories used included both non-reproductive behaviour and reproductive behaviour (Table 1). Female-female (FF) interactions were characterized by females chasing away other subdominant females. Male-female (MF) interactions were chasing and blocking of females. Male herding female (MHF) is the males action to avoid females to escape the harem. “Head low stretch” (HLS) is when the male approaches the female with his head low and stretched forward, he may produce grunting sounds, flick his tongue and show an O-shaped mouth (Skogland, 1989). Copulation was not observed during the study period.

*Table 1: Behavioural categories noted during the behavioural studies*

Behavioural categories	Reproductive behaviour	Non – reproductive behaviour
Standing		X
Walking		X
Running		X
Grazing		X
Lying		X
<b>HLS</b> = Head low stretched	X	
<b>FF</b> = female-female interaction	X	
<b>MF</b> = male - female interactions	X	
<b>M H F</b> = male herding female	X	

As most reproductive behaviour lasted only a few seconds and were relatively rarely observed at the 30 instantaneous observations, all reproductive behaviour events observed during the focal watches were also noted. This corresponds to the “all occurrence of some behaviours” design described by Altmann (1974). The reproductive behaviour noted was performed by or towards the female chosen for the focal watch. Among the non-reproductive behaviours observed, we interpreted standing, grazing and lying as neutral or positive behaviours, while running and walking was regarded as negative behaviours from an energy acquisition perspective.

## 2.5 Statistical analyses

The dataset collected during the rutting period consisted of 3 different types of data. These were demographic and position data from the survey of animal groups, behavioural observations from the focal watches, and the “all occurrence” sampling of reproductive behaviour during the half an hour of focal watches. A fourth data set was available from the previous and subsequent annual surveys of the population in April and August. This dataset included data on previous and subsequent reproductive success of the marked animals and population estimates of these parameters for the population as a whole. All statistical analyses were done using the statistical computing software R version 2.7.2.

### 2.5.1 *Composition of harems*

Generalized linear models (GLM) were used to test the association between male antler size and the harem size (i.e number of females associated), and the harem size and the number of males associated with the harems. A negative binomial error term was used to model the distribution of harem sizes, in addition, a log link function was used to ensure that predicted values based on the models were greater than zero (Crawley, 2007). The log link function provides a relationship between the linear predictor variable – antler size (x) and mean number of females in the harems (predicted variable y), giving  $\log(y)=a + bx$ . GLM was used to test if females with calf at heel had any influence on the harem size and number of males associated. Data of the demographic composition of all the reindeer groups observed during the study period was used in this investigation. The Likelihood ratio tests were used for statistical significance testing.

### 2.5.2 *Mating behaviour*

Behavioural patterns were investigated in relation to harem size (i.e number of females associated with the harem). The data from the focal watches were analysed by first calculating the proportion each behavioural category represented of the 30 focal watch observations. These proportions were analysed using generalised linear models (GLM) assuming a quasi binomial error term and a logit link function.

The logit link function constrains predicted values to be between 0 and 1, and it is a function that implies that the logit of predicted values ( $y$ ) are modeled as a linear function of the predictor variable  $x$ , giving  $\text{logit}(y/(1-y))=a + bx$ . ANOVA with F-ratios was used to assess the significance of the predictor variables (Crawley, 2007).

Due to small sample sizes in the focal watches mating behaviour were analysed using the frequency of male-female and female-female interactions in the “all occurrence” sampling of reproductive behaviour. The frequency of reproductive behaviour observations were also analyzed using generalized linear models (GLM) with harem size, number of females associated in the harem as predictor variables. The models were fitted assuming a quasipoisson error term, a log link function and statistical tests were performed using an ANOVA with F-ratios. General additive model (GAM) was used to check for potential seasonal trends in rutting period, where day since the start of the study was fitted using a flexible smoothing spline function. All statistical analyses were done with generalised linear (GLM) and generalized additive models (GAM) fitted using the base, MASS and mgcv packages available for the R-system. Additional base, gplots package was used for plots of tests with female with calf at heel.

### 2.5.3 *Movement pattern*

To investigate the movement patterns of the female during the rutting period we used the GPS (Global positioning system) recordings of the observed marked females. These recordings were downloaded to a GPS mapping Software; OziExplorer version: 3.95.4s on a map (UTM x 33, WGS 84). The marked animals were used to get accurate data on age in order to demonstrate if it has an effect on the movement pattern. The software enabled calculations of distance between the observations.

### 3 Results

#### 3.1 Composition of harems

In the survey of the study area, 685 reindeer were observed. Fifty two percent of the adult reindeer observed were female (Table 2). The demographic composition of the survey population differed significantly between what observed during the rutting period and what observed during the annual summer survey in August 2007 (Table 2,  $\chi^2 = 45.3$ ,  $df = 4$ ,  $p$ -value  $< 0.0001$ ). There were observed a much lower number of calves during the rutting period than in survey. During the rutting period survey 78 marked animals were observed, of which 53 were adult females and 14 were female yearlings.

*Table 2. The demographic composition (%) of the total survey population during the rutting period (September-October 2007), and the previous summer survey (August).*

Survey	Sample size	adult ♀	adult ♂	yearling ♀	yearling ♂	calves
September-October	682	52	28	5	1	14
August	850	45	21	5	4	25

Out of the 173 animal groups observed, 100 consisted of both male and female individuals (harems). The harem sizes varied between 1 and 19 females with mean number of females in the harems being 2.76 and only 3 harems with more than 10 females (Figure 4). Twenty-six groups were female clusters. Nineteen of these had only one adult or yearling female while the rest consisted of between 2 and 4 females.

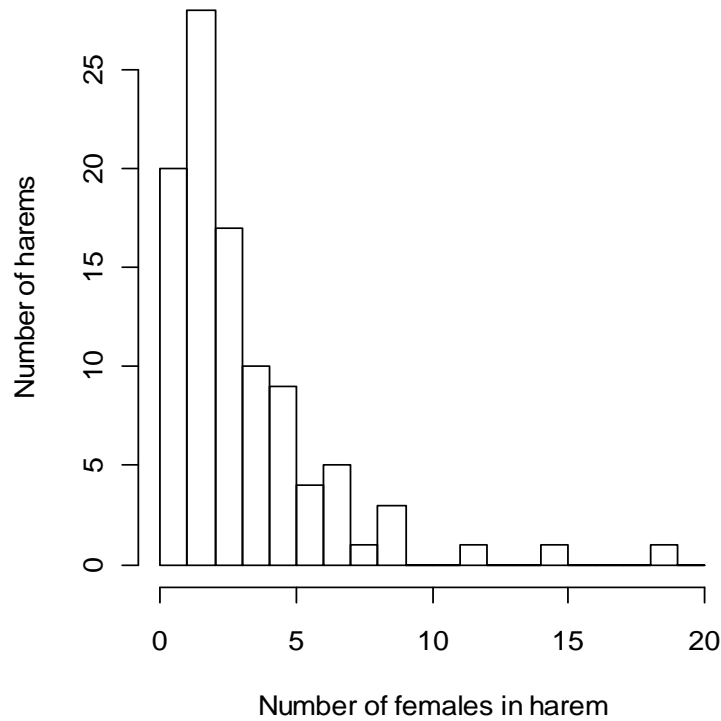


Figure 4: Observed frequency distribution of harems ( $n = 147$ ), excluding only female clusters.

There was a positive relationship between the antler size of the dominant male and average harem size (Figure 5a; Likelihood ratio test, Chi-square = 31.6,  $df = 145$ ,  $p$ -value < 0.001). The harem size of males with full sized antlers varied markedly (1-19 females, Figure 5a), while the three harem-holding males with no brow tine observed had only 1-2 females in their harems. Harem sizes of males with small or medium brow tine were intermediate. Also, there was a positive relationship between the number of males associated with a harem and harem size (i.e the number of females) (Figure 5b; Likelihood ratio test, Chi-square = 31.6,  $df = 145$ ,  $p$ -value < 0.001).

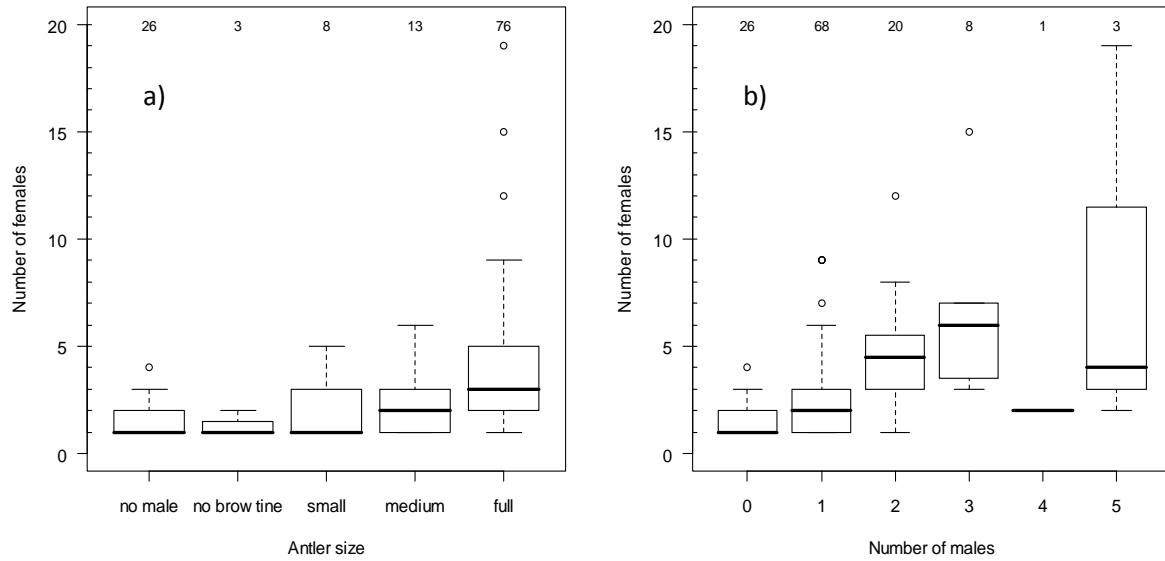


Figure 5: Number of females in groups in relation to a) the antler size of the dominant male of the harem and b) the number of males associated with the harem. Sample size is given in the upper row in the figure. The plot gives the medians (thick line), the interquartile range (box), approximate 95% confidence intervals of the medians (whiskers) and outliers (points).

### 3.2 Rutting period

The day of the rutting period was analysed against behaviour to check for potential seasonal change. Results show no significant relationship between the behaviour of females and the day of the rutting period, lying/grazing/standing;  $F_{1,138} = 0.02$ , p-value = 0.88. Running/walking;  $F_{1,138} = 0.21$ , p-value = 0.65. Mating behaviour;  $F_{1,138} = 1.32$ , p-value = 0.25.

### 3.3 Costs associated being apart of a harem

The focal watch observations show that the females spend less time on the neutral activities (lying, grazing and standing) with increasing number of males in the harem (Figure 6a;  $F_{1,62} = 6.42$ , p-value = 0.010). This did not apply for increasing harem size (i.e. increasing number of females associated with the harem) ( $F_{1,62} = 1.83$ , p-value = 0.18).

Results show that females in harems spent more time running and walking with increasing numbers of males in the harem (Figure 6b;  $F_{1,62} = 6.90$ ,  $p$ -value = 0.011). Significant increase in running and walking in relation to increasing harem size (i.e number of females associated with the harem) was not detected ( $F_{1,62} = 2.27$ ,  $p$ -value = 0.14). Increasing antler size of the dominant male did not show any influence on lying/grazing/standing and running/walking ( $F_{1,53} = 0.54$ ,  $p$ -value = 0.47,  $F_{1,53} = 0.43$ ,  $p$ -value = 0.51, respectively).

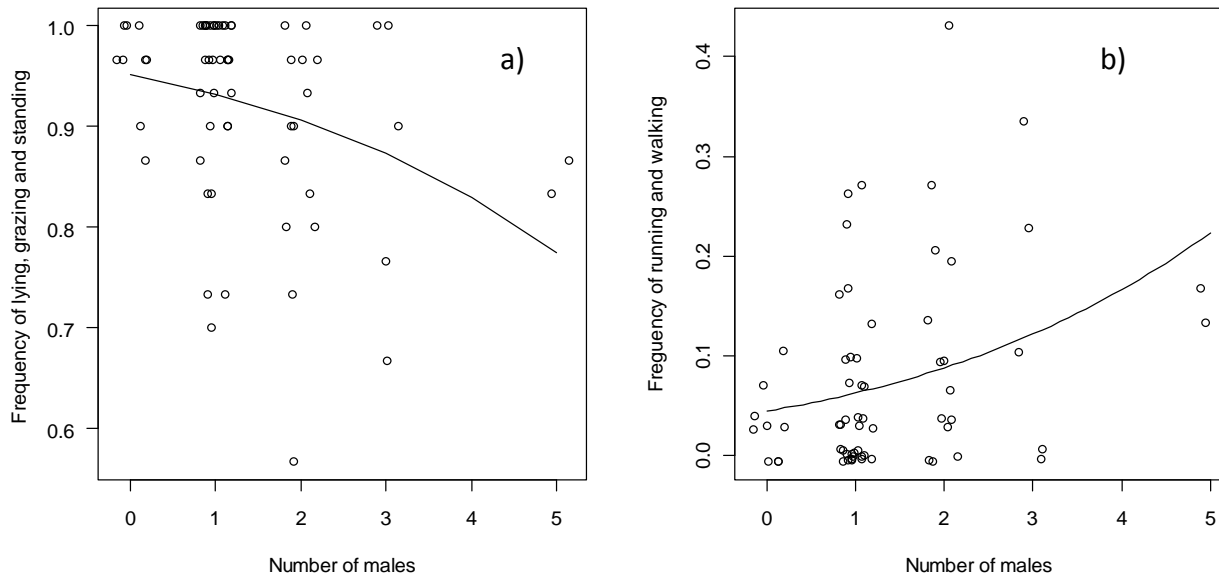


Figure 6: The relationship between time spent on the different behaviours a) three neutral behaviour types by the female in the harem compared to the number of males in the harem,  $\text{logit}(y) = -0.3462(\pm 0.1297)x + 2.9677(\pm 0.2729)$ . b) Running and walking by the female in the harem compared to the number of males in the harem,  $\text{logit}(y) = 0.3626(\pm 0.1307)x - 3.0621(\pm 0.2785)$ .

### 3.3.1 Mating behaviour

Mating behaviour towards or by the females in harems increased with increasing harem size (i.e number of females associated with the) (Figure 7;  $F_{1,62} = 6.67$ ,  $p$ -value = 0.012). This also applied to increasing antler size of the dominant male in the harem ( $F_{1,53} = 8.36$ ,  $p$ -value = 0.006). No copulation attempts were observed during the study period.



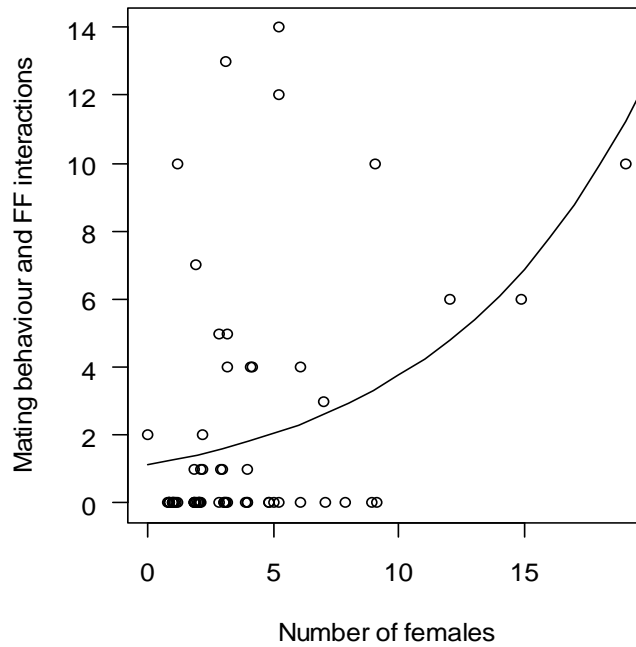


Figure 7: The relationship between mating behaviour (MF,HLS,MHF) and Female-female interactions (FF interactions) towards/of the observed female in the harem and the harem size (i.e number of females and the harem).  $\text{Logit}(y) = 0.14088(\pm 0.04101) - 3.85648(\pm 0.32502)x$ .

### 3.4 Female reproductive history in harems

In the rutting period survey only 27 % of the adult females had a calf at heel, while 55 % were seen with a calf at heel in the summer ( $\chi^2 = 57.9$ ,  $df = 1$ ,  $p\text{-value} < 0.0001$ ). There were also some evidence for the ratio of male yearlings to adult females to be lower during the rutting period than in the summer survey ( $\chi^2 = 13.0$ ,  $df = 1$ ,  $p\text{-value} = 0.0003$ ), while the observed adult sex ratio (65 % and 68 % adult females,  $\chi^2 = 1.2$ ,  $df = 1$ ,  $p\text{-value} = 0.27$ ) and the ratio of yearlings to adult females ( $\chi^2 = 0.22$ ,  $df = 1$ ,  $p\text{-value} = 0.63$ ) were similar in the two surveys.

During the rutting period survey 78 marked animals were observed, of which 53 were adult females and 14 were female yearlings.

Only 19 of the marked adult female reindeer had also been observed during the summer survey in 2007. Of nine marked adult female reindeer seen with a calf at heel in the summer, only one was seen without the calf during the rutting period. This gives no evidence for the low frequency of calves seen during the rutting period being due to a loss of calves.

There was a weak tendency for marked adult females that had given birth to a calf to be underrepresented in the survey during the rutting period (47 % 95% C.I. = [ 27, 68]) when compared to the marked animals observed during the summer survey (53 %, 95% C.I. = [42, 64]), however the main difference between the two survey period seemed to be that among the marked females observed, nulliparous animals (yearling and 2 year olds) were more frequently observed in the survey during the rutting period (30 %, 95% C.I. = [20, 42]), than during the summer survey (13 %, 95% C.I. = [7, 22],  $\chi^2 = 5.4$ ,  $df = 1$ ,  $P = 0.010$ ). Also, marked female yearlings were misclassified as adults in 42 % of the field observations during the rutting period survey (95% C.I. = [23, 64]) while no adult females were misclassified as yearlings. This may suggest that many of the females recorded as adults may have been nulliparous yearlings.

The proportion of adult females with a calf at heel decreased with increasing harem size (i.e number of females associated with the harem) (Chi-square = 23.6,  $df = 1$ ,  $p$ -value < 0.0001), and with the number of males associated with the group (Chi-square = 15.4,  $df = 1$ ,  $p$ -value < 0.0001). However, there was no strong evidence for an effect of number of males after number of females had been controlled for (Chi-square = 1.7,  $df = 1$ ,  $p$ -value = 0.19). The pattern seen in the total dataset was supported in the dataset on marked females. The probability of an adult marked female to have a calf decreased with total number of females in the group (Figure 8a; Chi-square = 3.8,  $df = 1$ ,  $p$ -value = 0.05), and tended to decrease with the number of males in the group (Figure 8b; Chi-square = 3.0,  $df = 1$ ,  $p$ -value = 0.09).

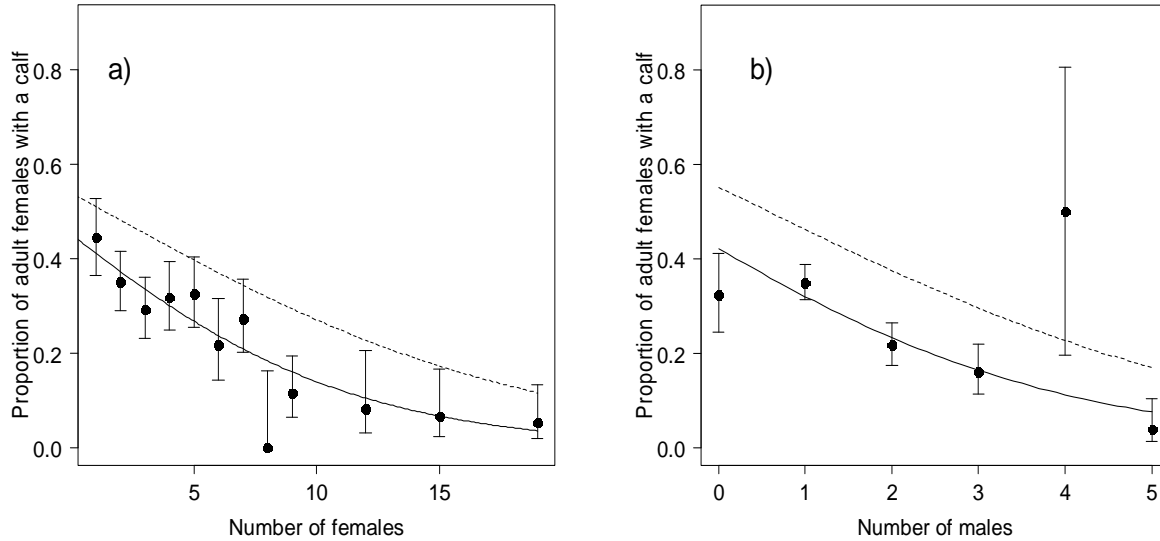


Figure 8: The proportion of adult female reindeer seen with calf relation to the a) harem size (i.e number of females associated with the harem) and b) the number of males associated with the group. Points gives point estimates for the different groups ( $\pm 1$  SE), the full line gives the fitted logistic regression line based on the counted number of calves and females, while the dotted line gives the estimated logistic regression line for the probability of the individually marked females to have a calf.

### 3.5 Movement pattern

The marked female and their GPS coordinates of observation site enabled us to determine whether harems were stable throughout the rutting period or whether females move between harems. Out of the marked females 20% were re-sighted 2-6 times (Table 3). All observations were done at a level less than 100 m above sea level.

Most repeated observations of females were close to each other, suggesting little movement (Table 3). Still harem sizes were usually variable between observations. The longest distance moved by one female was 17.7 km. The animal was first observed in Reindalen area (in the Southeast part of the study area) in the first week of the study period, and moved to the northern part in Colesdalen during the subsequent 5 observations visiting harems of different sizes on the way. Two similar incidents were observed (G61 and G45).

Non of these females that had traveled long distances had calf at heel. Age had no significant influence on the movement pattern (Table 3)

*Table 3: The distance (km pr day) the re-sighted females moved during the rutting period, including their age and mean harem size with harem range. N is total number of observations, D is the time span in days between the first observation and the last re-sight.*

<b>ID age</b>	<b>ID</b>	<b>N</b>	<b>Km total</b>	<b>D</b>	<b>Km/D</b>	<b>Mean harem size</b>	<b>Harem range</b>
1992	R240	4	4,66	1	4,66	6,75	15-2
1994	Y24	3	4,44	19	0,23	10	11-9
1999	Y71	2	3,57	8	0,45	5,5	9-2
2002	G45	6	16,97	10	1,7	3,8	11-2
2002	G61	3	16,86	21	0,8	10,3	15-8
2003	Y92	2	17,67	7	2,52	8	12-4
2004	B122	2	3,39	8	0,42	7,5	10-5
2004	B97	2	6,15	8	0,77	5	5
2005	W72	2	1,4	8	0,18	17	19-15
2005	W93	2	0,99	1	0,99	7	9-5
2006	G101	2	13,01	24	0,54	8	8
2006	G92	2	1,68	4	0,42	4,75	11-8
2006	R242	4	6,89	12	0,57	6,8	15-2

## 4 Discussion

### 4.1 Composition of harems

The observed number of females in the harems was relatively small (average 2.78 females), compared to other ungulates (e.g. red deer (*Cervus elaphus*) (Clutton-Brock et al., 1988; Bonenfant et al., 2004)). However, in other reindeer populations small harem sizes have been observed; Caribou in West Greenland (Roby & Thing, 1985) and Newfoundland (Bergerud, 1974). Harem sizes are expected to depend on the availability of females and competing males (Skogland, 1989). As the sex ratio approaches 1:1, as is the case in the study area, males are expected to switch from harem defence to more individual female defence (Bonenfant et al., 2004). The high proportion of adult males in the Svalbard reindeer population may give many males a reason to opt for the latter strategy. Additionally two aspects of the habitat may also restrict harem sizes. First, the low productivity of the habitat and patchily dispersed resources (Tyler & Øritsland, 1989) may make females want to avoid potential food competition associated with larger aggregations of animals. Second, the open landscape contains few natural obstacles that may limit female movement.

The majority of harems observed consisted of more than one male, and the number of males associated with a harem increased with harem size. In these multi male harems the competition to monopolize females increases, and the subdominant male has to make more effort than the dominant male to attract females. Young subdominant males are less sexually experienced than their dominant conspecifics, which may prolong their mating display and increases the frequency of harassment towards the females (Clutton-Brock et al., 1982; Holand et al., 2006). Thus the females may choose harems with high ranked males to avoid the additional costs. This adds to the cost for the males in guarding large harems through increased male-female and male-male interactions (Vestues, 2009).

Our results show that the harem size changed to more females where the dominant buck had fully grown antlers than in harems with a dominant male with poorly grown antlers. Thus males with full antler size were more likely to be found in harems. This is consistent with

previous findings for reindeer (Hirotani, 1989), caribou (Bergerud, 1974) and other ungulates (e.g. red deer (*Cervus elaphus*) (Kruuk et al. 2002; Bartos & Bahbouh, 2006), soay sheep (*Ovis aries*) (Preston et al., 2001; Preston et al., 2003)). Parallel to that which Darwin (1871) postulated, and supported by others (Clutton-Brock et al., 1980; Clutton-Brock et al., 1982; Andersson, 1994; Bro-Jørgensen, 2007), male antlers seem to be important secondary sexual characteristics. A larger antler size is both likely to give a better fighting ability and increased attractiveness to females. Reindeer antlers are regarded as an honest indicator of individual male quality (Markusson & Folstad, 1997; Lagesen & Folstad, 1998; Malo et al., 2005). On the other hand only using antler size represents a potential confounding effect on dominance (Bartos & Bahbouh, 2006). Body size and antler size are closely linked (Bergerud, 1974; Markusson & Folstad, 1997). Thus it is difficult to ascertain if it is the antler size itself that attracts the female, or if these two factors are in combination. Other factors that may also influence dominance are behaviour and age (Barrette & Vandal, 1986).

## 4.2 Rutting period

The timing of our study was matched to the main rutting period of the Svalbard reindeer. The mating behaviour coincides with the caribou in Alaska, starting in the end of September and lasting to the end of October (Lent, 1965). For the Scandinavian mainland reindeer, the rutting period starts earlier (beginning of September) (Espmark, 1964; Hirotani, 1989). The rutting period of ungulates living in seasonal environments is determined by the timing of births in the spring, which needs to coincide with the onset of the plant growth season (Skogland, 1989, Côté & Fest-Bianchet, 2001a; Mysterud et al., 2008). The female will during the energy demanding lactation be supplied with the greatest seasonal quality of forage. We did not detect any clear seasonal change in the rutting period behaviour over the study period as is reported of others. Bergerud (1974) and Skogland (1989) observed an increased frequency of the mating behaviour “head low stretched” in mid October.

### 4.3 Cost associated being part of a harem

The average time used by females for neutral activities (lying/grazing/standing) decreased with increasing number of males in the harem. Consequently the time spent on running and walking increased with increasing number of males in the harems. These findings suggest that females experience energetic costs with joining harems (Holand et al., 2006). The small number of pure female groups observed may indicate that females choose to associate in harems, in spite of the related costs. The benefits given females to join harems are harassment avoidance by non harem holding males (Clutton-Brock, 1989; Carbone & Taborsky, 1996; Nefdt & Thirgood, 1997) and to enhance their reproductive success by comparing the different harem holding males (Clutton-Brock, 1989). Both benefits may act together, and it becomes difficult to disentangle them (Carbone & Taborsky, 1996). On the other hand predator avoidance is also suggested as one reason why females should join harems, but the non existence of predators in the study area rules out this explanation.

#### 4.3.1 Mating behaviour

The frequency of mating behaviour (male-female and female-female interactions) increased with increasing harem size (i.e number of females associated the harems), adding more stress to the females (i.e less time spent on neutral activities). In big group males are not able to prevent other males to intrude the harem (Hirovani, 1989), thus the existence of more males in the harem will increase the mating behaviour in total due to competition for females (Skogland, 1989). Additionally with more females present the antagonistic behaviour towards conspecifics increases due to feeding competition (Sánchez-Prieto et al., 2004). The decrease in feeding and resting in course of the rut due to increased mating behaviour reduces the post rut condition of female, as is reported for bucks of reindeer (Skogland, 1989; Mysterud et al., 2003), red deer (Yoccoz et al., 2002), Kafue lechwe antelope (*Kobus lechwe kafuensis*) (Nefdt & Thirgood, 1997) and American bison (*Bison bison*) (Wolff, 1998), but in lower rates. Holand et al. (2006) found a loss of body weight of Scandinavian mainland reindeer counting on average only one sixth of the loss of bucks'.

Therefore the female's participation in mating activities will be a compromise between winter survival and enhanced reproductive success. The post rut condition of the female is influenced by the condition the female enters the rut, good condition females are more able to cope with the cost related mating activities than the females in poor condition (Holand et al., 2006).

No copulation was observed during the study period although a few mounting attempts were seen. This may indicate that mating occur irregularly, and may be related to the time of the day these events normally occurs. According to Espmark (1964) and Bergerud (1974) observations, most of ungulate mating occurs at dusk (14.00-18.00). Because of the limitations due to decreasing sunlight, we might have missed these events.

#### *4.3.2 Mating system of Svalbard reindeer*

The mating system existing in the study population may be a combination of resource-defence polygyny and female-defence polygyny (Emlen & Oring, 1977). This study found evidence to support both theories. Our GPS recordings show that most of the marked animals were observed at an elevation of less than 100m above sea level, assuming that when the rutting period approached and the snow cover increased (Solberg et al., 2001) the animals moved down from the adjacent small valleys to the lower wide valley bottoms, with less snow and available resources. They seemed to stay here the whole rutting period, indicating a seasonal sedentary behaviour (Tyler & Øritsland, 1989). This movement pattern may support a resource-defence polygyny where the males defend an area, not fixed, that is attractive for the females (Clutton-Brock et al., 1981; Carranza, 1995), and thereby giving the females the possibility to choose the territory that enhances their reproductive success. On the other hand, giving the short availability of resources in the study area in early winter (rutting period), harems size might be determined by the males' ability to defend the females in clusters, hence the vigorous mating behaviour observed.



#### **4.4 Female reproductive history in harems**

Females with a calf at heel seemed to avoid large harems and harems with many associated males, suggesting that females with calves preferred small groups with few males. The larger harems consisted therefore predominantly of females that had no calf. The reason for this is most likely to be that they avoid the disturbance caused by the males and the high density of females, which may lead to increased somatic costs. Holand et al. (2006) showed that females with calves at heel lost more body mass during the rut than females without. The avoidance of harems by females with a calf at heel also seemed to affect the demographic structure of the survey population in that few calves and an elevated number of nulliparous animals were observed. Data on the marked animals supported the interpretation that the low number of calves observed during the rutting period was not due to a loss of calves, but rather a result of a biased subsample of animals having been observed. The survey data suggest that adult females with a calf at heel stay away from the main valleys and harems during most of the time during the rutting period, and probably enter the harems just for short periods of time to become fertilised. We can only speculate on where the females with calves stayed during our survey, the high plateaus above the valleys were less intensively searched during the survey due to the snow cover that reduced accessibility.

#### **4.5 Movement pattern**

During the rutting period, females moved predominantly within the same valley. The females were mostly re-sighted in harems that varied in size. This pattern agrees with the previous observations on reindeer and caribou where composition of harems is constantly changing (Lent, 1965; Bergerud, 1974), and they seem to move short distances during the rut (Hirotani, 1989).

The reindeer were clustered in the valley bottoms during the rutting period, where there is an open landscape with high visibility. Open landscape is reported by Bergerud (1974) to simplify the formation of harems and therefore facilitates the mating.

The distances between harems were often short, and may make it easy for females to join and leave harems. This dynamics of receptive females that constantly change harems, could allow the females to evaluate a larger number of males before mating, and thus increase reproductive success. Additionally will she be protected from lower ranked males who are not able to defend harems through male-male interactions to get access to females (Hirota, 1989).

## **5 Conclusion**

The harem sizes of Svalbard reindeer are relatively small compared to other reindeer and caribou populations. The results of this study suggest that Svalbard reindeer harems are unstable entities in that they vary substantially in size and composition during the rutting period. Females seem to move between harems, and females with a calf at heel appear to avoid the larger harems. The harem size and the number of males associated with the harem showed a positive relationship, and an increasing number of males associated with the harem seemed to cause more disturbances in that females were walking and running more and spend less time grazing and resting. This disturbance is likely to be the main reason why females with a calf at heel avoid staying in the large harems for prolonged periods of time.



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## Appendix 1

