Does availability of resources influence grazing strategies in female Svalbard reindeer?

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Abstract: Foraging strategies and range use in wild female Svalbard reindeer (*Rangifer tarandus platyrhynchus*) were studied in two areas where the historical grazing pressure differed. We mapped vegetation where the reindeer were seen grazing, and related forage availability to characteristics such as home range size, activity budgets and reproductive status. There were significant differences in quantity of forage available between the two areas and the utilization of vegetation types differed between the sites. However, we found no difference in home range size between the two sites, and individual home range sizes were not related to forage quantity, possibly a result of a skewed and small sample size. Even though significant differences in availability of plant species and groups were found, no variation in home range size was found between reproductive and non-reproductive females on Brøggerhalvøya. Neither did we find any differences between areas or between reproductive groups within or between areas in how female reindeer allocated use of time, or in number of steps taken. However, a significant three way interaction indicated that some variance existed between reproductive groups within or between areas, but we do not conclude that this indicate different grazing strategies. Thus, even though variation in the duration of previous grazing has evidently resulted in rather different foraging conditions in our two areas, we detected no differences in present-day foraging behaviour. Thus, our analyses suggest no relationship or feedback between past grazing and current foraging behaviour in these reindeer.

Key words: home range, plant-herbivore, *Rangifer tarandus*, time budget.

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Introduction

Herbivores in the high Arctic live in an environment with large seasonal variations in grazing conditions and where food of high quality is available only for a short period of the year (Sørmo *et al.*, 1999). Because body weight influences fecundity (Albon *et al.*, 1986; Skogland, 1990; Cameron *et al.*, 1993; Sæther, 1997) and winter survival (Mitchell, 1984) of adult ungulates, a grazing strategy that maximizes weight gain during summer would be expected to improve fitness (Albon & Langvatn, 1992). Accordingly, the amount and quality of available food usually influences several aspects of ungulate biology such as behaviour, physiology and life-history traits (Hanley, 1997).

Several relationships have been proposed to exist between foraging strategy and food availability. The most common hypotheses to explain differences in grazing strategies are the forage abundance hypothesis (FAH) (MacArthur & Pianka, 1966), minimum area hypothesis (MAH) (Harestad & Bunell, 1979) and selective quality hypothesis (SQH) (Jarman & Sinclair, 1979).

According to FAH, herbivores are predicted to be selective at high resource levels, whereas they should graze opportunistically at low resource levels (MacArthur & Pianka, 1966; Skogland, 1984). A selective grazing strategy minimizes the cost of foraging because digestion time will decrease, thereby providing more time for searching (Lundberg & Åstrøm, 1990; Vivås *et al.*, 1991). An opportunistic grazing strategy enables herbivores to maximize net intake of energy or some nutrient per unit time by minimizing the time used to search for food (Sæther & Andersen, 1990). Hence, the level of forage abundance may be the major determinant influencing feeding strategies (Weckerly & Kennedy, 1992; van der Wal *et al.*, 2000). The increased searching effort as a consequence of improved grazing conditions can result in higher movement rates (Vivås & Sæther, 1987; Sæther & Andersen, 1990; Kohlmann & Risenhoover, 1994), which in turn may lead to a larger home range size (Predavec & Krebs, 2000). Thus, if the FAH applies to the Svalbard reindeer (*Rangifer tarandus platyrhynchus*), we would expect to see higher movement rates (*e.g.* take more steps) in the area with better foraging conditions.

The MAH predicts that the home range (*HR*) will be a result of the individual metabolic requirements of the animal (*R*), which may be caused by variation in number of offspring or body weight and the spatial variation in availability of nutrients (*N*) in the environment. Thus, $HR = RN^{-1}$ (Harestad & Bunell, 1979). Some studies have found that an improvement in the grazing conditions resulted in smaller home ranges (roe deer, *Capreolus capreolus*; Tufto *et al.*, 1996; arctic ground squirrels, *Spermophilus parryii*; Hubbs & Boonstra, 1998). Variation in home range size can to some extent be explained by differences in metabolic requirements due to differences in reproductive status as found *e.g.* in roe deer (Tufto *et al.*, 1996). Thus, for our reindeer, the MAH hypothesis predicts larger home ranges for reproductive reindeer because of their greater metabolic demands.

The selective quality hypothesis (SQH) predicts that herbivores are less selective at high resource levels when high quality resources are in greater supply and more homogeneously distributed (Weckerly & Kennedy, 1992). At low resource levels, a smaller amount of the food is palatable and consequently, high-quality food resources are the more important variable (Weckerly & Kennedy, 1992). Support for the SQH has been found in studies on white-tailed deer (*Odocoileus virginianus*) in a subtropical region where high quality food was available in sufficient amounts (Weckerly & Kennedy, 1992) and among topi (*Damaliscus korrigum*) in a tropical region (Jarman & Sinclair, 1979). The SQH predicts the same increase in home range size as the MAH for reindeer with greater metabolic demands (*i.e.* reproductive females), but it also predicts a reduction in selectivity with increased resource levels.

In the present study we examined the differences in grazing conditions, home range, movement pattern and time budget in two partially isolated populations of Svalbard reindeer. Due to historical differences in grazing conditions between the areas (see Material and methods), variation in grazing strategies was expected. The aim of the study was to investigate which of the three hypotheses; forage abundance hypothesis (FAH) (MacArthur & Pianka, 1966), minimum area hypothesis (MAH) (Harestad & Bunell, 1979) and selective quality hypothesis (SQH) (Jarman & Sinclair, 1979), best described the grazing strategies of female Svalbard reindeer facing varying grazing conditions. By answering these questions, we hoped to provide information on how a potential resource limitation (*i.e.* resulting from high densities of reindeer) may affect behavioural responses, leading to a better mechanistic understanding of density dependence as a process.

Material and methods

Study area and species

The study was performed on Brøggerhalvøya and Sarsøyra, ("Brøgger" and "Sars") on the northwestern coast of Spitsbergen, Svalbard (78°55'N, 11°50'E) during July and August 1999 (Fig. 1). Brøgger is a peninsula characterised by a mountainous area along the centre, surrounded by areas of lowland plains (Aanes *et al.*, 2000). The total area is about 221 km^2, of which glaciers cover 25%.

In 1978, 15 Svalbard reindeer (*Rangifer tarandus platyrhynchus*) were introduced to Brøgger after more than 100 years of absence (Wollebæk, 1926; Lønø, 1959). The population increased exponentially and reached a maximum of nearly 400 animals during 1993 (Aanes *et al.*, 2000; 2002). Formation of crust ice as a consequence of temperatures above 0 °C and rainfall during winter 1993-94 made most of the forage inaccessible (Aanes *et al.*, 2002), and about 40 animals emigrated to a nearby area, Sars, which was previously uncolonized due to semi-restricted access. These animals constituted a partially isolated popu-

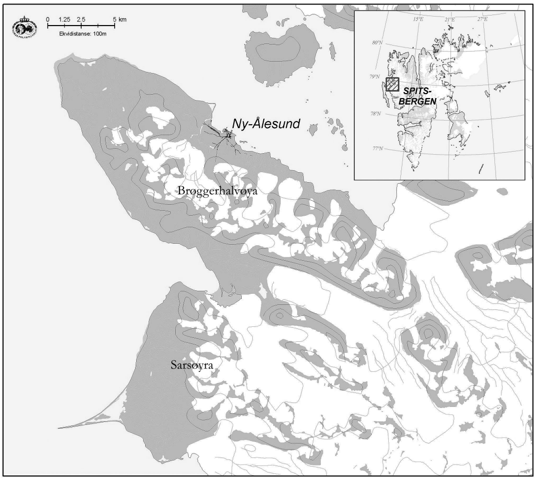

Fig. 1. The map shows Spitsbergen, Svalbard, and the study area situated on the nortwestern coast. Ny-Ålesund is situated at 78°55'N, 11°50'E.

lation of about 100 animals before calving in 1999 (R. Aanes, pers. obs.). The total population on Brøgger was about 200 animals prior to calving in 1999 (R. Aanes, pers. obs.). Generally, Svalbard reindeer are exposed to no harassment by insects, negligible predation, and no competition with other large herbivores and little or no hunting (none in the study area). Consequently, they show little or no apparent anti-predator behaviour, as scanning or predator-avoidance in choice of feeding sites. Contrary to other *Rangifer* subspecies, Svalbard reindeer are not nomadic within seasons and do not undertake long migrations but are rather sedentary (Tyler & Øritsland, 1989). They are not gregarious and usually occur in groups of less than five (Alendal *et al.*, 1979; Reimers, 1982). In 1975 and 1976, prior to the introduction of the reindeer, vegetation below the 200 m contour line was mapped (see Brattbakk, 1986). Areas with vegetation coverage greater than 5% constituted 93.5 km^2 and areas with more than 50% coverage were about 28 km^2 as estimated by using a 1 x 1 m^2 sampling frame (Brattbakk, 1986). Later studies (Persen *et al.*, 1983; Scheie & Grøndahl, 1990; Staaland *et al.*, 1993; Ødegård & Ranheim, 1996) revealed a significant reduction in coverage of vascular plants from 1979 to 1995 due to grazing and trampling. They also found a pronounced, but not significant, reduction in the coverage of mosses (Bryophyta) and lichens as well as total vegetation coverage. We summarised and recalculated these results and found a reduction in coverage of 58%, 11%, 50% and 25%, respectively for vascular plants, mosses, lichens and total coverage from 1979 to 1995. Two major bird cliffs are found on Brøgger, and as a result of manuring, there is very lush bird cliff- and moss tundra vegetation in a limited area in the vicinity of these. There are no bird cliffs on Sars and thus no similar areas with these highly fertilised vegetation types. There is no detailed vegetation map for Sars. From a 1:100.000 map, the total area below the 200 m contour line on Sars was estimated as 38.5 km^2, of which 33.4 km^2 was considered potential grazing land. Based on field observations, areas depicted as river plains on the map, containing little or no vegetation was not included in the estimate of potential grazing land. Sars is characterised by large plains where the lichens *Cetraria delisei* and *C. islandica* form mats covering large areas.

Monitoring routines

During April 1999, 21 adult females was caught and subsequently equipped with VHF-radiocollars. Seventeen of these females were located on Brøgger (11 reproductive) and four on Sars (two reproductive) when the present study was initiated. One of the non-reproductive females on Brøgger was excluded from the analyses because a broken hind leg restricted her mobility.

Summer range use by the reindeer was determined by plotting the position of each animal on an average of every third day (mean = 3.12 days, SD = ± 0.93) during the period 7 July to 1 September 1999. We used GPS (Global Position System) to obtain an accurate position of the animal. The Selective Availability (SA) was activated during field work, so the averaging function on the GPS was used to improve accuracy. The quoted accuracy from the GPS was ± 12.3 m (SD = ± 3.4 m). The first exact position where the animal was seen grazing (81% of the cases) or lying (19%) was used as the starting point for the vegetation analyses and the GPS position. Home range was defined as the area utilized by the individual females during the field period. The daily distances moved were calculated by dividing the distance between successive plots by the number of days between plots. Individual home ranges were calculated as 95% minimum convex polygons (MCP) using the RANGES V software (Kenward & Hodder, 1996) based on an average of 17.40 ± 1.35 (range 14-21) positions per individual on Brøgger and 17.50 ± 1.00 (range 16-18) positions on Sars. The MCP method was chosen because it is more robust than other methods when number of fixes is low (Harris *et al.*, 1990; Seaman *et al.*, 1999). Also the individual's pattern of space use does not have to confirm to a particular probability distribution (*e.g.*, bivariate or circular normal) and the non-statistical MCP method does not have as a basic assumption the independence of successive observations (see Harris *et al.*, 1990; Seaman & Powell, 1996). A harmonic mean estimator was used to calculate the centre of the 95% MCP home range. A linear regression revealed no relationship between home range size and number of plots per female (R^2 = 0.02, *df.* = 19, *P* = 0.59) indicating that the number of plots were sufficient.

Time budget

Time budget studies were conducted from 3-9 August 1999 from 10 a.m. to 10 p.m. in relatively uniform weather, on both collared and uncollared adult reproductive and non-reproductive females. The individuals were observed from a distance that had no visible affect on their natural behaviour, normally 35-120 m, using a 25-40x spotting scope. They also were allowed a period of minimum five minutes habituation. Each observation lasted for 15 minutes and the activity was recorded every 15 seconds, resulting in 61 observations per female. Distance moved was measured as number of steps: A "step" was each time the front left foot was lifted of the ground, and the count was doubled to account for steps of both feet. Eight observations were excluded from the analyses; seven individuals (three on Brøgger and four on Sars) laid down and one female on Brøgger moved out of sight during the observation period. We successfully observed 32 animals on Brøgger and 35 on Sars, of which 20 and 26, respectively, were reproductive. The observations were recorded for a variety of vegetation types throughout both Brøgger and Sars. Behaviour were grouped into five categories: (1) grazing, the mouth was seen moving, or the head or antlers were moved in a jerky manner as a consequence of grazing; (2) searching, the head moved slowly, about 10-15 cm. over the vegetation for a minimum of 0.5 second. The mouth was closed and/or the head was not moved jerkily; (3) walking, moving relatively slowly, normally not more than ten seconds. The head is held higher than during searching; (4) wandering, head held high and moving faster than during walking; (5) lying down, includes sleeping and rumination; (6) other, all activities not defined above, *e.g.*: standing, scratching or drinking.

Vegetation type

For 280 vegetation analyses on Brøgger and 72 on Sars there was an average of 17.5 ± 1.26 (range 15 – 21) and 18.0 ± 0.82 (range 17 – 19) plots per animal on Brøgger and Sars respectively, each plot consisting of three frames. We classified the vegetation into ten types as described by Elvebakk (1994): (1) Exposed ridge; (2) Mesic plain and slope; (3 a) Moderate snowbed; (3 b) *Saxifraga oppositifolia – Cetraria delisei* tundra (Rønning, 1996); (3 c) *Luzula* heath (Rønning, 1996); (4) Late snowbed; (5) Tundra mires; (6) Young moraine; (7) Bird cliff; (8) Erosion plains; (9) Moss tundra; (10) Polar desert. There was a large difference between the vegetation type "moderate snowbed" on Brøgger compared to Sars, because the lichens *C. delisei* and *C. islandica* formed large mats on Sars while on Brøgger, grazing and trampling by reindeer had almost totally removed these lichens. Consequently, the two additional categories: 3 b) and 3 c) were used (Rønning, 1996), to further classify the moderate snowbed community 3 a).

Food availability

Food availability was assessed where the reindeer were seen grazing, by noting the coverage and presence of selected plant species and groups within three 1 x 1 m^2 plots. The three 1 m^2 sampling frames, each divided with string into 100 10 x 10 cm^2 quadrats, were placed on the ground in an "L", each 1 m from the other with adjacent sides parallel. Compass orientation of the "L" was randomized. The triangle system provides a greater probability for analysing the actual place where the animals were grazing if an exact position could not be recorded.

This allowed us to estimate the relative amount of the available species in the area being grazed. We could not evaluate "diet selection" or "preference", because we did not know what was available in the study area, and we did not know which of the available species they were actually using. Based on previous histological analyses of faeces from Brøgger (Holand *et al.*, 1981; Scheie & Grøndahl, 1990; Ødegård & Ranheim, 1996), 13 plant species or groups of plants were selected for the analyses, including total coverage of living plants. Percent cover was estimated according to the number of 10 x 10 cm^2 quadrats with more than 50% cover (Nellemann & Thomsen, 1994). All living vascular plants, mosses and lichens, except the ubiquitous and minute *Stereocaulon*, were considered potential forage. Presence was estimated by counting all the 10 x 10 cm^2 quadrats where a particular species or group was observed. For several species of monocots such as grasses (Poaceae), sedges (Cyperaceae) and rushes (Juncaceae), leaves of the present year were intermixed with old and dead leaves. Herbivores would therefore in some cases have to eat dead leaves in order to access green parts. It was also difficult to distinguish dead from living tissue during the analyses, so dead leaves of monocots were included in the counts. Several species had a growth form that rarely or never resulted in recording of cover with our method. Recording presence therefore gave an alternate estimate of the amount of these species. Only percent cover and not presence was recorded for mosses since it was often difficult to distinguish dead moss from living and coverage gave a good estimate of what was available. The species/groups recorded in addition to total coverage were (1) brown lichens; (2) other lichens; (3) Equisetaceae; (4) mosses; (5) monocots; (6) *Dryas octopetala*; (7) *Oxyria digyna*; (8) *Polygonum viviparum*; (9) *Salix polaris*; (10) *Saxifraga oppositifolia*; (11) other herbs.

The group brown lichens included *C. islandica* and *C. delisei* which were pooled because it was difficult to distinguish them readily in the field. The other lichens (mainly of the genus *Cladonia*) occurred in such small number that they were pooled. Cover and presence was recorded for *C. nivalis*, but combined with other lichens for statistical analysis due to small numbers. In the category "other herbs", two rarely encountered species of woody plants were also included; *Salix reticulata* and *Cassiope tetragona*. Nomenclature used was according to Rønning (1996).

We did not relate range use and activity budget to plant quality because of the difficulty with assessing quality, as it changes with phenological development and different plant parts have varying nutritional value.

Data analyses

One of the females on Brøgger represented an outlier because of her preference for the vegetation type "moss tundra" near a bird cliff. We present results from analyses where this outlier is both included and excluded. The range data were not normally distributed (Kolmogorov-Smirnov test, $P<0.05$). Thus, the non-parametric Mann-Whitney U test was performed to test if there were any differences with respect to home ranges and movement patterns between the two areas; and between reproductive females and non-reproductive females thereby statistically comparing selectivity. Two-tailed tests were used. The four females from Sars were not included in the home range analyses when differences between reproductive groups were examined.

Next we wanted to analyse whether the behaviour of adult females differed between the two study areas, and also if the behaviour differed among females due to the reproductive status of the female, that is, whether or not the female had calf. This way we could statistically compare how the time budget of different individuals vary between areas and reproductive groups. Initially we recorded 6 different behavioural categories. However, due to small sample sizes we pooled the behavioural categories: (3) walking, (4) wandering, (5) lying down and (6) remaining into the "remaining" category. Subsequently in the statistical analyses we distinguished between 3 behavioural categories; (i) grazing, (ii) searching and (iii) remaining. Thus, if we assume independence between each observation of behavioural outcomes the total number of observations of each behavioural category will follow a multinomial distribution. As demonstrated by Baker (1994), such data can adequately be analysed by using the so called "multinomial Poisson transformation" which is performed by analysing the data as if the counts of each behavioural category for each individual follow a Poisson distribution. Accordingly we applied Poisson regression analysis that fits a generalized linear model to the data by maximum likelihood techniques (Proc Genmod, log-link function, SAS Institute Inc. 1996). In the following "event" refers to the 3 behavioural categories while "femalenr" is used to separate the different females observed. "calf" refers to reproductive status of the females (*i.e.* reproductive or non-reproductive), whereas "site" refers to the two study areas Brøgger and Sars, respectively. The response variable is the frequency of observations within each of the behavioural categories for each female. The base model, corresponding to the 0-hypothesis, includes the main effects of the variables "events" to account for the average distribution among the 3 behaviour categories, while "femalenr" was included to account for the average differences in the frequencies of behavioural categories among females. Then to test the hypotheses that the behavioural pattern differed among study areas and reproductive status, respectively, we included the interaction terms between event*site, event*calf and the three way interaction between site*calf*event. Accordingly, the initial global model included the following terms: femalenr, event, event*site, event*calf, event*site*calf, where the model selection of the terms was based on stepwise exclusion of the least significant term by using likelihood ratio tests.

In order to select the most appropriate model according to the principle of parsimony, we applied the Akaike's Information Criterion, AIC (Akaike, 1973; Burnham & Anderson, 1998), on a set of candidate models, where the model with the lowest AIC was the one that best represented the data by using the smallest possible number of parameters.

The number of quadrats with vegetation cover and presence within each vegetation-category was summed for all animals and all vegetation analyses on each area, and χ^2 (chi-square) analyses were applied to determine whether significant differences in frequencies existed between the two study sites for each of the 11 groups and species. For statistical analyses, we summed those species and groups with average cover less than 1% within each area or reproductive group. The species and groups with average cover less than 1% were: (1) brown lichens; (2) other lichens; (3) Equisetaceae; (6) *D. octopetala*; (7) *O. digyna*; (8) *P. viviparum*; (9) *S. polaris* and (11) other herbs. For brown lichens the average cover was less than 1% only on Brøgger comparing reproductive groups.

The total number of quadrats with presence for all species and groups was calculated by summing the number of squares with presence for each single species or group. A chi-square test was used to test for differences between areas. When analysing differences in available forage between reproductive groups, we used only females from Brøgger. All statistical analyses, except from analyses of activity budget, were performed with SPSS for Windows, version 10.0. Numeric measures are given as mean ± one standard deviation (SD) unless otherwise stated. All tests of significance were two-tailed.

Results

Vegetation type

Animals were found more often in moderate snowbed (3 a) on Brøgger than on Sars ($\chi^2 = 6.200$, *df.* = 1, $P < 0.013$) (Fig. 2) but significantly more in *Saxifraga oppositifolia – Cetraria delisei* tundra (3 b) ($\chi^2 = 86.763$, *df.* = 1, $P < 0.001$) and *Luzula* heath (3 c) on Sars (*df.* = 1, $P < 0.002$) (Fisher's exact test). Moss tundra (vegetation type 9) was utilized more on Brøgger than on Sars ($\chi^2 = 9.379$, *df.* = 1, $P < 0.002$).

Food availability

Both total plant cover and the calculated total number present for all plant species and groups recorded were significantly greater in the analysed areas on Sars (*i.e.* the less grazed area) than on Brøgger (Table 1). Vegetation analyses also revealed that there was significantly higher plant cover on Sars than on Brøgger for brown lichens, *S. oppositifolia* and summed cover of remaining species. Mosses and

Table 1. Mean percent cover and presence of recorded species and groups in plots used by the females on Brøgger and Sars. The chi-square refers to the total number of 10 cm x 10 cm on each site. The numbers presented for total count are the average total count of each square. Cover within areas was summed for: brown lichens; other lichens; Equisetaceae; *Dryas octopetala*; *Oxyria digyna*; *Polygonum viviparum*; *Salix polaris* and other herbs.

	Percent coverage			Number present		
	Brøgger	Sars	χ^2	Brøgger	Sars	χ^2
Total cover	33.9	43.7	684.0**	NR[c]	NR[c]	
Brown lichens[a]	0.3	20.2	16071.5**	8.5	47.4	17866.1**
Other lichens[b]				0.1	1.8	992.2**
Equisetaceae				4.3	3.4	42.3**
Mosses	21.2	6.2	2599.9**	NR[c]	NR[c]	
Monocots	1.5	1.2	10.9**	19.4	18.9	8.7**
Dryas octopetala				1.0	0.5	59.8**
Oxyria digyna				2.8	9.8	1952.4**
Polygonum viviparum				9.7	4.2	683.2**
Salix polaris				32.6	20.6	1351.9**
Saxifraga oppositifolia	1.9	4.0	341.5**	20.0	33.4	1516.9**
Other herbs				14.7	15.3	4.4**
Sum cover	1.2	1.6	422.4**			
Total count				113.1	154.1	2674.9**

[a] *C. delisei* and *C. islandica.*

[b] Including *Cetraria nivalis.*

[c] Not recorded.

* Significant at $P \le 0.05$.

** Significant at $P \le 0.005$.

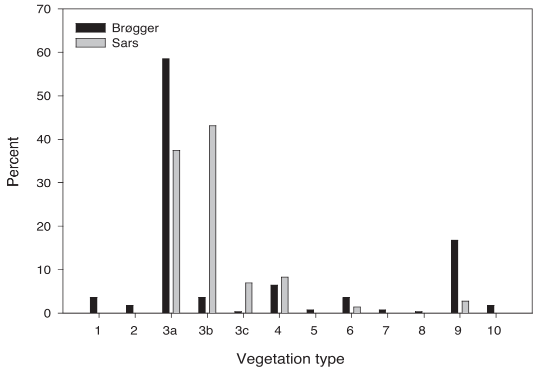

Fig. 2. Percentage of different vegetation types on Brøgger and Sars. Numbers refers to vegetation types: (1) Exposed ridge; (2) Mesic plain and slope; (3 a) Moderate snowbed; (3 b) *Saxifraga oppositifolia – Cetraria delisei* tundra (Rønning, 1996); (3 c) *Luzula* heath (Rønning, 1996); (4) Late snowbed; (5) Tundra mires; (6) Young moraine; (7) Bird cliff; (8) Erosion plains; (9) Moss tundra; (10) Polar desert.

monocots comprised more cover on Brøgger than on Sars. We found significantly higher numbers of plants on Sars for the species and groups: brown lichens, other lichens, *O. digyna*, *S. oppositifolia* and other herbs. The frequency of quadrats containing Equisetaceae, monocots, *D. octopetala*, *P. viviparum* and *S. polaris*, was significantly higher on Brøgger than on Sars.

On Brøgger, non-reproductive females accessed areas having a significantly greater total plant cover but reproductive females accessed areas with a greater calculated total frequency of species and groups (Table 2). The vegetation analyses also revealed that there was significantly higher plant coverage in the analysed area of the non-reproductive group regarding mosses. The reproductive group had more cover regarding *S. oppositifolia* and summed cover. We found significant higher number of plants present for the non-reproductive group on Brøgger for the species and groups: Equisetaceae, monocots, *D. octopetala* and other herbs. For the species and groups: brown lichens, other lichens, *O. digyna*, *P. viviparum* and *S. polaris*, the reproductive group had the highest numbers of 10 x 10 cm^2 quadrats with

Table 2. Mean percent cover and presence of recorded species and groups for area used by the reproductive and non-reproductive group on Brøgger. The chi-square refers to the total number of 10 cm x 10 cm. Cover within reproductive groups were summed for: brown lichens; other lichens; Equisetaceae; *Dryas octopetala*; *Oxyria digyna*; *Polygonum viviparum*; *Salix polaris* and other herbs. The numbers presented for total count are the average total count of each square.

	Percent coverage			Number present		
	Non-repr.	Reprod.	χ^2	Non-repr.	Reprod.	χ^2
Total cover	38.9	31.7	413.1**	NR[c]	NR[c]	
Brown lichens[a]				6.8	9.7	185.9**
Other lichens[b]				0.0[d]	0.2	36.7**
Equisetaceae				6.0	3.7	217.4**
Mosses	28.4	18.0	1154.6**	NR[c]	NR[c]	
Monocots	1.5	1.5	0.4	19.2	17.5	32.7**
Dryas octopetala				1.6	0.8	110.1**
Oxyria digyna				1.1	3.7	451.3**
Polygonum viviparum				6.6	11.3	449.8**
Salix polaris				29.4	35.4	283.5**
Saxifraga oppositifolia	1.2	2.1	77.8**	20.5	21.0	2.4
Other herbs				20.7	10.4	1602.6**
Sum cover	1.4	1.6	5.6*			
Total count				111.7	113.7	6.5*

[a] *Cetraria delisei* and *C. islandica.*

[b] Including *Cetraria nivalis.*

[c] Not recorded.

[d] Frequency is < 0.1.

* Significant at $P \leq 0.05$,

** Significant at $P \leq 0.005$.

these species present. By removing the female with a preference for moss tundra, differences in cover and presence were reduced, but still significant ($\chi^2 > 4.959$, *df.* = 1, $P < 0.05$), for most species and groups, including total cover. However, for monocots, *D. octopetala*, *S. oppositifolia* and summed count, the difference in the frequency of plants present increased ($\chi^2 > 29.898$, *df.* = 1, $P < 0.01$). The difference were inverted ($\chi^2 > 29.898$, *df.* = 1, $P < 0.01$) for some species and groups, *i.e.* the reproductive group now had highest total cover (31.7% *vs.* 27.8%), frequency of monocots (17.5 *vs.* 13.7 numbers present) and summed count (113.7 *vs.* 109.2 numbers present), while non-reproductive had more *S. oppositifolia* (23.1 *vs.* 21.0 numbers present).

Home range size, movement patterns and time budgets of female reindeer

No significant difference in home range size was found between Brøgger (736 ha ± 697) and Sars (764 ha ± 452) when the outlier was included ($Z = -0.85$, $n = 20$, $P = 0.40$). Excluding the outlier did not cause any differences ($Z = -0.70$, $n = 19$, $P = 0.48$) between, Brøgger (782 ha ± 696) and Sars (764 ha ± 452.3). We found no difference in the daily distance moved ($Z = -0.09$, $n = 20$, $P = 0.93$) between females on Brøgger (533 m ± 201) compared to those on Sars (540 m ± 120). Excluding one female having a high preference for the rare moss tundra did not change this pattern ($Z = -0.30$, n = 19, $P = 0.76$). There was no relationship between the females' individual home range size and forage quantity available, when outliers were included ($F < 0.78$, *df.* = 1, $P > 0.39$) or excluded ($F < 0.01$, *df.* = 1, $P > 0.93$). Total cover and average number of all species present within plots was used as measures of availability.

There were no significant difference in home range size between the reproductive group (800 ha ± 656) and the non-reproductive group (596 ha ± 844) when the outlier was included ($Z = -1.64$, $n = 16$, $P = 0.10$). Removing the outlier reduced the differences between reproductive females (800 ha ± 656) and non-reproductive females (733 ha ± 907) ($Z = -1.175$, $n = 15$, $P = 0.24$). There was no statistical significant difference in mean daily distance moved ($Z = -1.64$, $n = 16$, $P = 0.10$) between the reproductive group (mean = 597 m, SD = ± 155) and the non-reproductive group (mean = 394 m, SD = ± 239). Excluding the outlier from the non-reproductive group (mean = 453 m, SD = ± 230) reduced the difference ($Z = -1.18$, $n = 15$, $P = 0.24$).

Activity budgets revealed no significant difference ($F_{1,67} = 2.46$, $P = 0.12$) in number of steps between females on Brøgger (315 steps, SD = ± 103) and Sars (353 steps, SD = ± 99). Results from the two areas were combined when investigating differences in number of steps between reproductive groups: no significant difference ($F_{1,67} = 0.52$, P > 0.48) was found between non-reproductive (318 steps, SD = ± 102) and reproductive (342 steps, SD = ± 102) females. The investigation of what factors influenced the behavioural pattern revealed that the final model included a significant three-way interaction in the global model including the terms: site*calf*event ($\chi^2 = 7.62$, *df.* = 2, $P = 0.022$), this was also the most appropriate model according to the AIC-criteria (see model 1, Table 3). The model including only the effects of femalenr ($P > 0.1$) and event ($\chi^2 = 862.24$, *df.* = 2, $P < 0.001$) (see model 2, Table 3) was not the most parsimonious according to the AIC-criteria. In this analysis femalenr + event actually represents the 0-hypothesis, *i.e.* no difference in behavioural pattern of females between areas and no effect of female reproductive status.

Individual preference and variation in range use

There were large individual differences in home range area, especially on Brøgger, where the smallest HR was 46 ha and the largest 2202 ha (calculated from 95% of fixes and based on 18 and 21 positions respectively). We evaluated whether some of this variation could be explained by individual variation in forage preference. The female with the smallest home range had a preference for the vegetation types moss

Table 3. Models tested to examine the effect of location and reproductive status on activity budget. The most parsimonious was determined by use of AIC. The candidate models are ranked according to the AIC value. Interaction between variables are indicated by an asterisk. See Material and methods for further description.

Mode l	Explanatory variables in model	AIC	AIC-dev
1	femalenr, event, event*site, event*calf, event*site*calf	5105.0	
2	femalenr, event	5007.1	-97.9
3	femalenr, event, event*calf	4957.9	-147.1
4	femalenr, event, event*site	4934.6	-170.4
5	femalenr, event, event*site, event*calf	4884.4	-220.6

tundra and bird cliff. Seventeen out of 18 observations of this female were in these two vegetation types close to a bird cliff on Brøgger. The bird cliff vegetation and moss tundra related to the bird cliffs constituted about 1% of the productive area on Brøgger (Brattbakk, 1986).

Discussion

The present study showed that reindeer females in the less grazed area at Sars had better foraging conditions than females on Brøgger, which had a longer grazing history. This was evident through a higher total vegetation cover and more cover of *e.g.* brown lichens and *S. oppositifolia* in the plots on Sars compared with Brøgger (Table 1). Females on Sars also had higher presence frequencies of *e.g.* lichens, *O. digyna*, *S. oppositifolia*, and other herbs, in addition to total frequency of all species. Females on Brøgger had higher cover percentages of *e.g.* moss and monocots and greater frequencies of *e.g.* monocots, *P. viviparum* and *S. polaris*. However, we were not able to detect any effect of food availability on home range size, even though the utilization of some vegetation types (*e.g.* moderate snowbed and moss tundra) differed between the two areas. Home range size was not dependent on whether females on Brøgger had a calf or not. Neither did we find any differences in how female reindeer allocated use of time in the two areas or between reproductive groups within or between areas, or in number of steps taken. However, a significant three way interaction indicated that some variance existed between reproductive groups within or between areas. However, the differences in probability within each behavioural category were small (Fig. 3). Therefor we do not conclude that this indicates different grazing strategies. The amount of available forage did not relate to individual home range size of the females, although large variations in home range size and grazing conditions were found. Recently Aanes *et al.* (2000) showed that population dynamics on Brøgger was influenced by a combination of density dependence and climatic variability. Accordingly, we found that Brøgger had less available resources compared to the less grazed Sars suggesting competition for resources. As expected, differences in available forage were less between reproductive and non-reproductive females on Brøgger than between the two areas, Brøgger and Sars (Table 2). Non-reproductive females had *e.g.* larger total cover, cover of mosses and frequency of other herbs, possibly a result of one female's preference for moss tundra. Reproductive females on the other hand, had *e.g.* larger cover of *S. oppositifolia* and higher frequency of brown lichens and *S. polaris* present. By removing the female with a preference for moss tundra from the analyses the differences were further reduced for most species and groups.

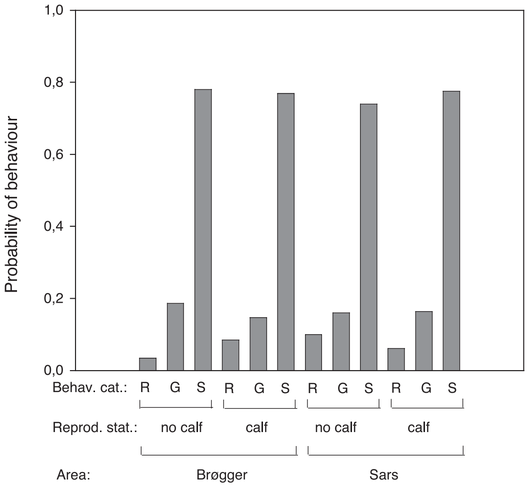

Fig. 3. Probability of the three behavioural categories within reproductive categories in each area as predicted by the initial multinomial model. Letters R, G and S indicates behavioural category remaining, searching and grazing respectively.

Several studies in temperate regions have shown a reduction in home range size, with improved grazing conditions within the home range, that is consistent with the minimum area hypothesis (MAH), (Wahlström & Kjellander, 1995; Tufto *et al.*, 1996; Hubbs & Boonstra, 1998). However, moose (*Alces alces*) and white-tailed deer, which lived on a diet of low quality and low species diversity, increased the movement rates when the quantity of available forage increased (Vivås & Sæther, 1987; Sæther & Andersen, 1990; Kohlmann & Risenhoover, 1994). The increased resource level enabled animals to be more selective in grazing and thereby increased the quality of their diet (Vivås & Sæther, 1987; Sæther & Andersen, 1990; Kohlmann & Risenhoover, 1994). These studies on moose and white-tailed deer lend support to the forage abundance hypothesis (FAH), because of the increased selectivity observed with increased forage quantity. Increased movement rates were also found among the reindeer on Brøgger, shortly after their introduction in 1978. They grew heavier and roamed more than reindeer in the source population in Adventdalen, Spitsbergen, where the grazing conditions were less favourable (Øritsland & Alendal, 1986). The increased movement rates reported in the study of Svalbard reindeer could also be a result of increased selectivity. The variation in amount of grazing resources observed in this study was therefore expected to result in different grazing strategies and thereby in a different range use. However, we were not able to find any significant difference in home range size or movement pattern that could have been caused by differences in the amount of available forage between the areas. Neither were we able to find any relation between individual home range size and quantity of forage available; thus there was little support for any of the hypotheses. This may have been because the original hypotheses were not applicable to this particular case. Our sample size was small and skewed, which in connection with differences in individual experience and preference could prevent us from detecting existing differences caused by variation in grazing conditions. White-tailed deer feeding in agricultural – deciduous forest habitat in Tennessee on the other hand, were less selective when forage abundance was high (Weckerly & Kennedy, 1992). In these ranges, fibre content in forages, and not forage abundance as in arctic ranges (van der Wal *et al.*, 2000), was the important factor affecting feeding strategies.

Variation in reproductive status was expected to cause variation in home range size due to different metabolic requirements caused by the extra cost imposed by pregnancy and lactation (Gerhart *et al.*, 1996). Thus, we would expect larger home ranges for the reproductive group, as predicted by the MAH (Harestad & Bunell, 1979; Tufto *et al.*, 1996). However, the calf could also place movement restriction on the mother. We found large variations in cover and presence between reproductive and non-reproductive females on Brøgger (Table 2). However, no clear pattern emerged of which reproductive group accessed areas with most forage. The large difference in total cover was largely caused by the non-reproductive group accessing areas with more moss cover. When the female with a preference for moss tundra was removed from the analyses, the overall difference between the groups was reduced for the majority of species and groups, even though the difference increased for some species and groups (*e.g.* cover and presence of monocots). For total cover and moss cover, presence of monocots and summed count the reproductive group now had highest frequencies while non-reproductive females had highest frequency of *S. oppositifolia* present. Even though we found that reproductive females occupied the largest home ranges, this was not statistically significant, indicating that the variation in forage may have been too small to allow variation in foraging strategy. By removing the outlier the differences in home range sizes and available forage were reduced, supporting this view. The spatial scale at which we measured selectivity may not have been appropriate to detect actual differences. Also the small sample size (*i.e.* five non-reproductive females on Brøgger) may be the reason why no difference in home range size between reproductive groups were found. Variation in home range observed might have been caused by patchy distribution of resources within home ranges, but without knowledge about resources available we can not correct for patchiness. Roe deer with fawns have been found to have the largest home ranges, supporting the MAH, but also that heavier animals tended to have smaller home ranges than expected (Tufto *et al.*, 1996), suggesting that other mechanisms than purely metabolic requirements influence home range size.

The investigation of what factors influenced the behavioural pattern revealed that the most appropriate model according to the AIC-criteria, included a three way interaction in the global model (model 1, Table 3). This indicates that there were no differences between females on Brøgger and Sars or reproductive groups, but when these variables were held constant, the probability for a certain event in one of the categories (*e.g.* non-reproductive females on Brøgger) was not random (see Fig. 3). This can probably to some extent be explained by a smaller probability for non-reproductive females on Brøgger to perform other activities than grazing and searching (*i.e.* remaining) than other females on Brøgger and Sars (Fig. 3). However, the difference was small and we do not conclude that this is an indication of an alternative foraging strategy since no difference was found between locations and reproductive groups as predicted by the hypotheses, and the significant three way interaction may therefor only explain a small part of the overall variation in the global model. The second most parsimonious model according to AIC was the model including femalenr + event, which actually represents the 0-hypothesis. This indicates that differences in foraging conditions between females on Brøgger and Sars and differences in their reproductive status had no effect on the behavioural patterns (model 2, Table 3). Because of time deficiency the time budget studies were performed over a limited period of time relatively late in season when variation in forage quality is small (van der Wal *et al.*, 2000). However, both moose (Vivås & Sæther, 1987; Sæther & Andersen, 1990) and white-tailed deer (Kohlmann & Risenhoover, 1994) responded to forage depletion by foraging less selectively. Similar relationships have been found among reindeer (Skogland, 1984; White *et al.*, 1981). White-tailed deer in a subtropical region showed the opposite pattern, *i.e.* being less selective when forage abundance was high (Weckerly & Kennedy, 1992). Even though past browsing has reduced food quantity on Brøgger, reindeer browsing may also have caused a slight increase in the food quality that compensates for the reduction in quantity (Skarpe & van der Wal, 2002). Behavioural adjustments, such as altered bite size, could compensate for different resource levels. However, this is not very likely due to the spread out growth characteristics (Hanley 1997) of the majority of food plants utulized (with exception of some grasses and mosses). The level of selectivity is expected to change throughout the season due to phenological changes in the plants and changing nutritional demands in the herbivore (van der Wal *et al.*, 2000). Unfortunately we were not able to test this.

Analysis of space use and foraging behaviour revealed large individual variations among the animals. This may suggest that home range size is unsuitable as an indicator of resource availability in these arctic ranges because individual preferences resulted in different patterns of space use. Some animals preference for specific vegetation types illustrating that learning and experience may also be an important component of the foraging process (Hanley, 1997).

The utilization of vegetation types by reindeer on Brøgger (see Ødegård & Ranheim, 1996) changed from grazing a few highly preferred vegetation types, to utilizing a wider range of types as the grazing resources were depleted and the number of animals in the area increased (Ødegård & Ranheim, 1996; Aanes *et al.*, 2000). The present study confirmed this pattern because, reindeer females on Brøgger utilized a wider range of vegetation types than females on Sars (Fig. 2). This was most likely a result of reduced variance among vegetation types as the resources were being depleted.

Future research should focus on quantitative analysis of forage quality in preferred food plants. Also, more effort should be focused on individual strategies as females in the same area (Brøgger) showed large variation in range use. If different individual strategies exist this could possibly be related to reproductive success. Further effort should also be put into investigating whether the level of selectivity changes between reproductive groups as the nutritional value of different forage plants becomes more equal due to phenological development (see van der Wal *et al.*, 2000). Also a more intensive radiotracking regime could provide additional information on movement patterns on such a short time scale as two intense summer months. This should be followed up by an analysis of how well the measure of daily distance moved corresponds with actual distance walked.

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