

# Testing five hypotheses of sexual segregation in an arctic ungulate

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## Summary

1. Sexual segregation occurs in most species of sexually dimorphic ungulates. At least five not mutually exclusive hypotheses have been formulated to explain patterns of social, habitat and spatial segregation; the indirect competition hypothesis (H1), the nutritional needs hypothesis (H2), the activity budget hypothesis (H3), the weather sensitivity hypothesis (H4), and the predation risk hypothesis (H5).

2. Each hypothesis has a unique set of predictions with respect to the occurrence of segregation, and how seasonality, density dependence and reproductive status affect sexual segregation.

3. We tested this set of predictions in order to separate the hypotheses H1–H5 for patterns of sexual segregation of the Svalbard reindeer based on 9 years data on seasonal estimates of spatial, habitat and social (i.e. grouping with their own sex) segregation in combination with resource selection functions.

4. Our results do not support that one single mechanism causes segregation. The activity budget hypothesis, the nutritional needs hypothesis and the weather sensitivity hypothesis were all partially supported, while the predation risk hypothesis was discarded for Svalbard reindeer because predators have been absent for at least 5000 years. Several mechanisms are thus interacting to explain the full-year pattern of sexual segregation and the combination of mechanisms varies among species and populations.

*Key-words:* activity budget hypothesis, climate, incisor arcade, population ecology, Svalbard reindeer.

*Journal of Animal Ecology* (2006) **75**, 485–496  
doi: 10.1111/j.1365-2656.2006.01069.x

## Introduction

Polygyny is the prevailing mating system in most species of ruminants (Clutton-Brock 1989; Shuster & Wade 2003). In polygynous mating systems, male reproductive success often depends on large body size, which is under sexual selection and leads to sexual body size dimorphism (e.g. Weckerly 1998). Males and females of dimorphic species almost universally live in

different groups outside the mating season (Ruckstuhl & Neuhaus 2002; Bowyer 2004). At the interspecific level, body size is regarded as a major factor in the nutritional ecology of large herbivores (Bell 1971; Jarman 1974; Clutton-Brock & Harvey 1983). There is some consensus that body size dimorphism at the intraspecific level is a main factor in the occurrence of sexual segregation (Mysterud 2000; Ruckstuhl & Neuhaus 2002; Bowyer 2004). There are at least four hypotheses that can explain sexual segregation induced by sexual body size dimorphism. These are based fundamentally on nutritional differences, but, operate through different mechanisms (H1–H4 below).

The basis of the indirect competition hypothesis (H1; Clutton-Brock & Harvey 1983; Illius & Gordon

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1987; Clutton-Brock, Iason & Guinness 1987; Gordon & Illius 1988) is that intake is limited by the incisor arcade breadth (scales as  $\text{Weight}^{0.33}$ ) when grass swards are grazed to short levels at high density, whereas intake is about isometric ( $\text{Weight}^{0.9}$ ) when grass swards are tall at low population density. When the scaling coefficient of intake is lower than requirements ( $\text{Weight}^{0.75}$ ), females (being smaller) have a competitive advantage as each bite will represent a larger fraction of the daily metabolic requirements. Thus as forage availability of a preferred sward declines, males are predicted to have a higher probability of leaving an area thus segregating from females.

The nutritional needs hypothesis (H2; Demment & Van Soest 1985) states that while high-quality forage is preferred by females, more fibrous forage is preferred by males. Males, being larger, can subsist on a lower quality diet than females (the Jarman–Bell principle; Bell 1971; Jarman 1974; Demment & Van Soest 1985). Males should accept lower diet and habitat quality than females, as there is often a negative relationship between abundance and quality. Recently, the gastrocentric hypothesis (Barboza & Bowyer 2000) has been presented and although based on the same principle, provides a more evolutionary explanation, suggesting males are physiologically poorly equipped to digest high-quality forage. Under H2, no competitive exclusion of males by females is required for segregation to take place as they simply do not prefer the same food.

The activity budget hypothesis (H3; Conrads 1998a; Ruckstuhl 1998; Ruckstuhl & Neuhaus 2002) suggests that sexual segregation arises from sexual differences in optimal activity patterns related to sexual body size dimorphism. Males, eating a lower quality diet, will need longer ruminating bouts and thus reducing synchrony in the grazing pattern between males and females (Conrads and Roper 2000). Sexes are therefore expected to stay in different groups, but no long-term segregation in space (including segregation into different habitat types) is expected as differential resource use is not implicit in this hypothesis (Myserud 2000; Bowyer & Kie 2004).

The weather sensitivity hypothesis (H4) argues that higher absolute heat losses relative to intake rates of larger individuals could lead to higher weather sensitivity resulting in males seeking shelter to a higher degree than females in cold, windy weather (Conrads, Clutton-Brock & Guinness 2000). This hypothesis relies on the assumption that exposed sites have higher nutritional quality and lower biomass than sheltered sites (Conrads *et al.* 2000). Hence, the larger males with higher absolute heat loss and energy needs (but more tolerant to lowered forage quality) will benefit from changing from exposed to sheltered sites earlier than females as the weather deteriorates (Conrads *et al.* 2000).

Finally, the predation risk hypothesis (H5; Main & Coblentz 1990; Miquelle, Peek & Van Ballenberghe 1992; Bleich, Bowyer & Wehausen 1997) states that females with calves will trade predator safe areas to good foraging

areas at the time of year when the offspring is the most sensitive to predation, most often directly after birth (Linnell, Aanes & Andersen 1995). Thus the prediction for this is that females prior to calving will move away from males to safer but nutritional suboptimal habitats.

Some of these hypotheses have been extensively debated. The debate is currently focused on whether or not sexual differences in optimal activity pattern (H3) alone are enough to explain the almost universal pattern of sexual segregation. It has been questioned if differences in activity is merely a correlate (Bowyer & Kie 2004) or a consequence (Mooring & Rominger 2004) – rather than the cause of segregation. There is still a search for one main mechanism for explaining the full-year pattern of segregation. However, segregation mechanisms may differ throughout the year (Bonenfant *et al.* 2004). As it is difficult to perform experiments, the seasonal pattern is indeed essential for pinpointing mechanisms (Bonenfant *et al.* 2004; Bowyer 2004). Conrads (1998b) developed indexes for social (grouping with their own sex), spatial and habitat segregation that are independent of sex ratio, population density and group size. These indexes are particularly useful as they can separate segregation mechanisms acting on the group level (the activity budget hypothesis H3) from all other segregation hypotheses that involve spatial segregation (Pérez-Barbería & Gordon 1998; Myserud 2000). Secondly, we need a set of tests that disentangles the remaining hypotheses for sexual segregation. The spatial component of sexual segregation is likely linked to differential resource selection (Bowyer 2004). To date, the role of resource selection functions (Manly 2002) has not been investigated in sexual segregation studies, although they are able to account for sexual differences in resource use.

We here analyse the pattern of sexual segregation based on a 9-year study of a Svalbard reindeer *Rangifer tarandus platyrhynchus* Vrolik population that underwent marked changes in population size due to the extreme climate at 78°N (Albon *et al.* 2002). Each of the above hypotheses has a unique set of predictions with respect to: (1) the degree of spatial and habitat segregation compared with social segregation (Conrads 1998b); and the effect of (2) density dependence; (3) seasonality (when segregation peaks); (4) reproductive status; and (5) weather (Table 1). The Svalbard reindeer have no competitors and have been predator free for at least 5000 years (van der Knaap 1989). This provides an ideal opportunity to test the social and nutritional based hypotheses as well as the effect of predation past on sexual segregation.

## Materials and methods

### STUDY AREA

The study area is located at Nordenskiöld land, Svalbard (77°54′–78°08′ N, 15°02′–15°50′ E), and covers a 123 km<sup>2</sup> area, including Colesdalen, Semmeldalen and parts of Reindalen, with adjacent side valleys. There

**Table 1.** Predictions from five different segregation hypotheses regarding density, climate and seasonal changes in spatial ( $SC_{Spatial}$ ), habitat ( $SC_{Habitat}$ ) and social ( $SC_{Social}$ ) segregation. The predictions that are supported are in **bold** and the rejected predictions are in *italic*. We predict segregation between different categories of reindeer (the first column), firstly between males and all females (sexual segregation), secondly we compare how reproducing (RF; females with calf) and nonreproducing females (NF; without calf) segregate from males (sexual segregation but females are divided in two reproductive categories), and thirdly within-sex segregation between the two reproductive categories of females (observed with and without calf)

Segregation category	Indirect competition hypothesis (H1)	Nutritional needs hypothesis (H2)	Activity budget hypothesis (H3)	Climate hypothesis (H4)	Predation risk hypothesis (H5)
Males vs. females	$SC_{Social} = SC_{Spatial} = SC_{Habitat}$	$SC_{Social} = SC_{Spatial} = SC_{Habitat}$	$SC_{Social} >> SC_{Spatial} = SC_{Habitat}$	$SC_{Social} = SC_{Spatial} > SC_{Habitat}$	$SC_{Social} = SC_{Spatial} = SC_{Habitat}$
Males vs. females	<b><math>SC_{Spatial}</math> and <math>SC_{Habitat} &gt; 0</math></b>	<b><math>SC_{Spatial}</math> and <math>SC_{Habitat} &gt; 0</math></b>	$SC_{Spatial}$ and $SC_{Habitat} = 0$	<b><math>SC_{Spatial}</math> and <math>SC_{Habitat} &gt; 0</math></b>	<b><math>SC_{Spatial}</math> and <math>SC_{Habitat} &gt; 0</math></b>
Males vs. females	$SC_{Spatial} = SC_{Habitat}$	$SC_{Spatial} = SC_{Habitat}$	$SC_{Spatial} = SC_{Habitat} (= 0)$	$SC_{Spatial} > SC_{Habitat}$	<b><math>SC_{Spatial} &gt; SC_{Habitat}</math></b>
Males vs. females	$SC_{Social}$ calving = $SC_{Social}$ summer	$SC_{Social}$ calving < $SC_{Social}$ summer	$SC_{Social}$ calving ≠ $SC_{Social}$ summer?		$SC_{Social}$ calving > $SC_{Social}$ summer
Males vs. females	$SC_{Spatial}$ and $SC_{Habitat}$ calving = $SC_{Spatial}$ and $SC_{Habitat}$ summer > 0	<b><math>SC_{Spatial}</math> and <math>SC_{Habitat}</math> calving &lt; <math>SC_{Spatial}</math> and <math>SC_{Habitat}</math> summer</b>	$SC_{Spatial}$ and $SC_{Habitat}$ calving = $SC_{Spatial}$ and $SC_{Habitat}$ summer = 0	$SC_{Spatial}$ and $SC_{Habitat}$ calving > $SC_{Spatial}$ and $SC_{Habitat}$ summer	$SC_{Spatial}$ and $SC_{Habitat}$ calving > $SC_{Spatial}$ and $SC_{Habitat}$ summer
Males vs. females	$SC_{Social}$ strong wind = $SC_{Social}$ little wind	$SC_{Social}$ strong wind = $SC_{Social}$ little wind	$SC_{Social}$ strong wind = $SC_{Social}$ little wind	<b><math>SC_{Social}</math> strong wind &gt; <math>SC_{Social}</math> little wind</b>	$SC_{Social}$ strong wind = $SC_{Social}$ little wind
Males vs. females	$SC = f(N)$	<b><math>SC \neq f(N)</math></b>	<b><math>SC \neq f(N)</math></b>	<b><math>SC \neq f(N)</math></b>	<b><math>SC \neq f(N)</math></b>
Males vs. RF	$SC_{Social}$ RF =	<b><math>SC_{Social}</math> RF &gt;</b>	<b><math>SC_{Social}</math> RF &gt;</b>	$SC_{Social}$ RF =	<b><math>SC_{Social}</math> RF &gt;</b>
Males vs. NF	$SC_{Social}$ NF	<b><math>SC_{Social}</math> NF</b>	<b><math>SC_{Social}</math> NF</b>	$SC_{Social}$ NF > 0	<b><math>SC_{Social}</math> NF</b>
Males vs. RF	$SC_{Spatial}$ and $SC_{Habitat}$ RF = $SC_{Spatial}$ and $SC_{Habitat}$ NF > 0	<b><math>SC_{Spatial}</math> and <math>SC_{Habitat}</math> RF &gt; <math>SC_{Spatial}</math> and <math>SC_{Habitat}</math> NF</b>	$SC_{Spatial}$ and $SC_{Habitat}$ RF = $SC_{Spatial}$ and $SC_{Habitat}$ NF = 0	$SC_{Spatial}$ and $SC_{Habitat}$ RF = $SC_{Spatial}$ and $SC_{Habitat}$ NF > 0	<b><math>SC_{Spatial}</math> and <math>SC_{Habitat}</math> RF &gt; <math>SC_{Spatial}</math> and <math>SC_{Habitat}</math> NF</b>
RF vs. NF	$SC_{Social} = 0$	<b><math>SC_{Social} &gt; 0</math></b>	<b><math>SC_{Social} &gt; 0</math></b>	$SC_{Social} = 0$	<b><math>SC_{Social} &gt; 0</math></b>
RF vs. NF	$SC_{Spatial}$ and $SC_{Habitat} = 0$	<b><math>SC_{Spatial}</math> and <math>SC_{Habitat} &gt; 0</math></b>	$SC_{Spatial}$ and $SC_{Habitat} = 0$	$SC_{Spatial}$ and $SC_{Habitat} = 0$	<b><math>SC_{Spatial}</math> and <math>SC_{Habitat} &gt; 0</math></b>

are no roads in the area, and human presence is rare. The terrain within the study area is mountainous and moderately glaciated with peaks ranging from 500 to 1000 m above the sea level, but with wide and fairly even valley floors in between.

The climate on Svalbard is polar and snow covers the study area from October or November to mid-June. Annual precipitation is low (about 300 mm per year; <http://www.met.no>), but permafrost, which is present all over Svalbard keeps the water table high in summer by preventing drainage of melted water. In winter, ambient temperature often rises above freezing and a crust of ice is produced as a combination of cold capacity in frozen soil and drop in ambient temperature. This severely limits reindeer access to the already poor winter range.

#### THE REINDEER POPULATION

The Svalbard reindeer is the only large herbivore on Svalbard. The overall population of Svalbard reindeer in winter 1982/1983 was estimated to 11 000 animals (including 400 animals in Colesdalen and 250 in Semmeldalen, which compose the major parts of our study area; Øritsland & Alendal 1986). This species has one of the highest ratios of sexual size dimorphism in ungulates (Short & Balaban 1994) with adult females being at least 33% (vary with time of year) smaller than adult males (females: 40–50 kg in late winter; 60–70 kg in late summer (Tyler 1987); males: 70–80 kg in late winter;

100–120 kg in late summer; N. Tyler, pers. comm.). Reindeer face no natural enemies, except limited calf predation from the arctic fox *Alopex lagopus* L. (Tyler 1986) and the glaucous gull *Larus hyperboreus* Gundersen. The calving period in Svalbard reindeer is highly synchronized and 90% of the calves are born in the first 2–3 weeks of June (Tyler 1987). Calves are weaned approximately 3 months after birth. Median date of conception is about 24 October (earliest 13 October, latest 6 November) and the mating system is polygynous (Tyler 1987). Harvesting by humans is restricted to an annual cull of less than 200 reindeer (hunting statistics from the Governor of Svalbard).

#### SAMPLING PROCEDURE

A total number of 5534 groups ranging in size from 1 to 63 reindeer were registered between May and October from 1995 to 2003 (the 5th, 50th and 95th percentiles being group sizes of 1, 2 and 10, respectively). Snowmobiles were used in the field when snow was present (until early June). After that, field work was conducted on foot.

Sex and age class (calf, yearling or adult) of each individual were registered. Coordinates of each reindeer group (in UTM with map datum European 1950) was recorded with a handheld GPS and the aspect (eight directions: N, NW, W, SW, S, SE, E, NE), slope (flat <5°, moderate 5–20°, steep >20°) and vegetation community was recorded (see below).

## DENSITY ESTIMATES

The Governor of Svalbard counts the number of observed reindeer by use of helicopter during 1–3 days in July along the same transects every year. The number of observers ranged between two and four and the sighting conditions ranged between medium to very good. Given the very open habitat and the highly visible pale reindeer against green or dark background, the obtained numbers likely correlate closely with the actual number of reindeer present (Noyes *et al.* 2000) and provide an index of density suitable for assessing year to year variation in reindeer numbers within each valley. The three main valleys were covered in the same day (limiting the possibilities for movements between valleys with subsequent multiple counts). The annual variation in total count between 1995 and 2003 varies by a factor of up to 3 (Reindalen, excluding Semmeldalen: min. = 138, mean = 260, max. = 441; Semmeldalen: min. = 92, mean = 187, max. = 325; Colesdalen: min. = 249, mean = 350, max. = 459). Carrying capacity likely differs between the three valleys. We therefore defined density as a valley-specific categorical variable; ‘High density’ and ‘Low density’ when the annual count was, respectively, above or below the mean of a given valley. A density estimate for each valley seems appropriate as Svalbard reindeer show site fidelity on a scale smaller than the full study area (R. Langvatn and S. Albon, unpublished data).

## VEGETATION AND VEGETATION TYPE CLASSIFICATION

The vegetation is open and without any high shrubs or trees. Vegetation is discontinuous with frequent intersections of gravel and rocky ground, and occurs mainly at altitudes below 100–150 m a.s.l. Hence, the spatial distribution of food resources for the Svalbard reindeer is rather two-dimensional compared with the situation in many temperate habitats, where the altitudinal component is more pronounced. *Luzula* DC.-heath was the most widely distributed vegetation type, together with patches with high densities of other graminoid species (e.g. *Poa* L. sp.) in hill sides and wetland vegetation with *Dupontia* R.Br./*Eriophorum* L. marshes at lower altitudes. Vegetation in the study area was classified according to eight vegetation types: (1) polar desert; (2) ridge vegetation; (3) *Luzula* heath; (4) graminoid sward; (5) *Alopecurus* L.–*Equisetum* L.–wet moss; (6) *Phippsia* R.Br.; (7) *Dupontia*/*Eriophorum* marshes; and (8) other types of vegetation (Van der Wal *et al.* 2000a). We registered vegetation types on sites occupied by reindeer groups.

## CLIMATIC DATA

We used daily mean values of precipitation, temperature and wind speed collected by the Norwegian Meteorological Institute (<http://met.no/index.shtml>).

The study area is situated between two weather stations; the airports at Longyearbyen and Svea (c.30 km N-NE and E-SE of the study area, respectively). We used the average values from the two weather stations as climatic variables in our analyses.

## STATISTICAL ANALYSES

*Sexual segregation*

We used the social, spatial and habitat segregation coefficients developed by Conratt (1998b). To detect aggregation patterns during the rut we did not use the modifications of the original index (Conratt 1999), which restricts the segregation coefficients between 1 (full segregation) and 0 (random associations between males and females). With the original index (Conratt 1998b), the segregation coefficient will be negative if sexes aggregate. While the degree of aggregation should not be quantified based on the segregation coefficients (then other measures should be used; L. Conratt pers. comm.) it is useful to detect timing of rut. We calculated social (eqn 1), habitat (eqn 2) and spatial (eqn 3) segregation following these equations.

$$SC_{social} = 1 - \frac{N}{X \cdot Y} \cdot \sum_{i=1}^k \frac{x_i \cdot y_i}{n_i - 1} \quad \text{eqn 1}$$

where  $x_i$  is the number of males in the  $i$ th group;  $y_i$  is the number of females in the  $i$ th group;  $n_i$  is the group size of the  $i$ th group ( $n_i = x_i + y_i$ );  $k$  is the number of groups with at least two animals;  $X$  is the total number of males sampled (excluding solitary animals);  $Y$  is the total number of females sampled (excluding solitary animals);  $N$  is the total number of males and females sampled (the sum of  $X$  and  $Y$ ).

$$SC_{habitat} = 1 - \frac{M}{Z \cdot W} \cdot \sum_{i=1}^l \frac{z_i \cdot w_i}{m_i - 1} \quad \text{eqn 2}$$

where  $z_i$  is the number of males in the  $i$ th habitat type;  $w_i$  is the number of females in the  $i$ th habitat type;  $m_i$  is the number of males and females in the  $i$ th habitat type ( $m_i = z_i + w_i$ );  $l$  is the number of habitat types that are used by at least two animals;  $Z$  is the total number of males sampled;  $W$  is the total number of females sampled; and  $M$  is the total number of males and females sampled. Contrary to social segregation, solitary individuals are included when calculating  $SC_{habitat}$ . When analysing seasonal change in social and habitat segregation, we divided the data into six time periods: winter (24 May–1 June), calving (2–19 June), early summer (20–30 June), mid-summer (1–31 July), late summer (1–31 August), pre-rut (1 September–15 October) and rut (16–19 October). The rut lasts longer but we have no systematic observations after this date). The periods were based on relevant seasons regarding reindeer biology and plant phenology, but comprised enough data in each time period (with a minimum of 35 groups;



Conradt 1998b). Still, little data were available in the first and last periods (late winter and rut).

$$SC_{spatial} = 1 - \frac{C}{A \cdot B} \cdot \sum_{i=1}^r \frac{a_i \cdot b_i}{c_i - 1} \quad \text{eqn 3}$$

were  $a_i$  is the number of males in the  $i$ th grid square;  $b_i$  is the number of females in the  $i$ th grid square;  $c_i$  is the number of animals in the  $i$ th grid square ( $c_i = a_i + b_i$ );  $r$  is the number of grid squares with at least two individuals;  $A$  is the total number of males sampled (excluding males that are alone in a grid square);  $B$  is the number of females sampled (excluding females that are alone in a grid square); and  $C$  is the total number of males and females in the sample ( $C = A + B$ ). We assessed scale dependence in the spatial segregation coefficient by increasing the grid size (the area where we defined individuals to be together in space) from 100 m<sup>2</sup> (1213 grids) and up to 2 km<sup>2</sup> meters (85 grids).

If social segregation is just a by-product of habitat segregation, then  $SC_{social} = SC_{habitat} = SC_{spatial}$ . If social segregation is independent of habitat segregation, then  $SC_{social} \gg SC_{habitat}$  and  $SC_{spatial}$  (Conradt 1999). If sexes segregate because of spatial variation in other factors than habitat type,  $SC_{spatial} > SC_{habitat}$ .

Calculating spatial segregation on a fine scale is a problem due to data depletion (few groups will be left in each grid). In the extreme case one group will be left in each grid and social and spatial segregation will be completely confounded. To estimate if spatial segregation at small scale is real, or just an artefact of social segregation (i.e. that most individuals within a grid derive from the same group), we randomly reshuffled all reindeer groups (retaining the group composition) and spatial coordinates in the data set (keeping the real coordinates and not stimulating random coordinates within the study area). Thereafter, we calculated spatial segregation estimates at increasing scales from the randomized data (1000 randomizations for each analysis). As 'true' spatial segregation was removed in the randomization process, the remaining coefficients will quantify how much of the spatial segregation is due to social segregation at all scales. When it drops to zero, we have found the scale where this group effect is no longer acting.

For all coefficients, we computed standard errors by bootstrapping the segregation coefficient estimators (Efron & Tibshirani 1993; see Bonenfant *et al.* 2004 for the same approach) by replicating each analysis 10 000 times with randomly selected subsamples of the data (Efron & Tibshirani 1993).

#### Space use – kernel estimators

We assessed the spatial distribution of reindeer groups on the study area using kernel estimators (Worton 1989). The smoothing parameter ( $h$ ) was estimated by a least square cross-validation procedure (Worton 1995). We replicated the analyses for different group types by subsetting the data into female only, male only

and mixed groups to check for large-scale differences in space use at high and low density. We applied the same procedure but making the distinction between females with and without a calf at heel. We provide the 95% and 50% isoclines, which encompass the areas (in hectares) with 0.95 and 0.50 probabilities of observing a group of a given type.

#### Habitat utilization – resource selection functions

We investigated the pattern of habitat utilization using resource selection functions (Manly 2002). For each group observation, the response variable was binary (presence/absence). The coefficients of the logistic regression then provided us with a relative 'selection' or 'avoidance' for a given habitat characteristics. The factor sex was then entered in the model and differential space utilization according to sex tested through the second or third order interaction term between sex and habitat (seven levels), slope (covariable), wind (covariable) and aspect (eight levels). As we do not know the absolute availability of the different resources within our study area results show only the relative differences between the sexes. Standard logistic regression models were inadequate to model our data as we found evidence for overdispersion. Thus we modelled our data with Generalized Mixed Models and a logit link with year as a random factor. Because overdispersion came mainly from pseudo-replications within a year and from year to year, the use of mixed models corrected for the extra-binomial variation. Overall model goodness-of-fit (GOF) and predictive power were assessed using ROC (Response – Operating Curves; Boyce *et al.* 2003).

#### Effect of wind on reindeer selection of aspect

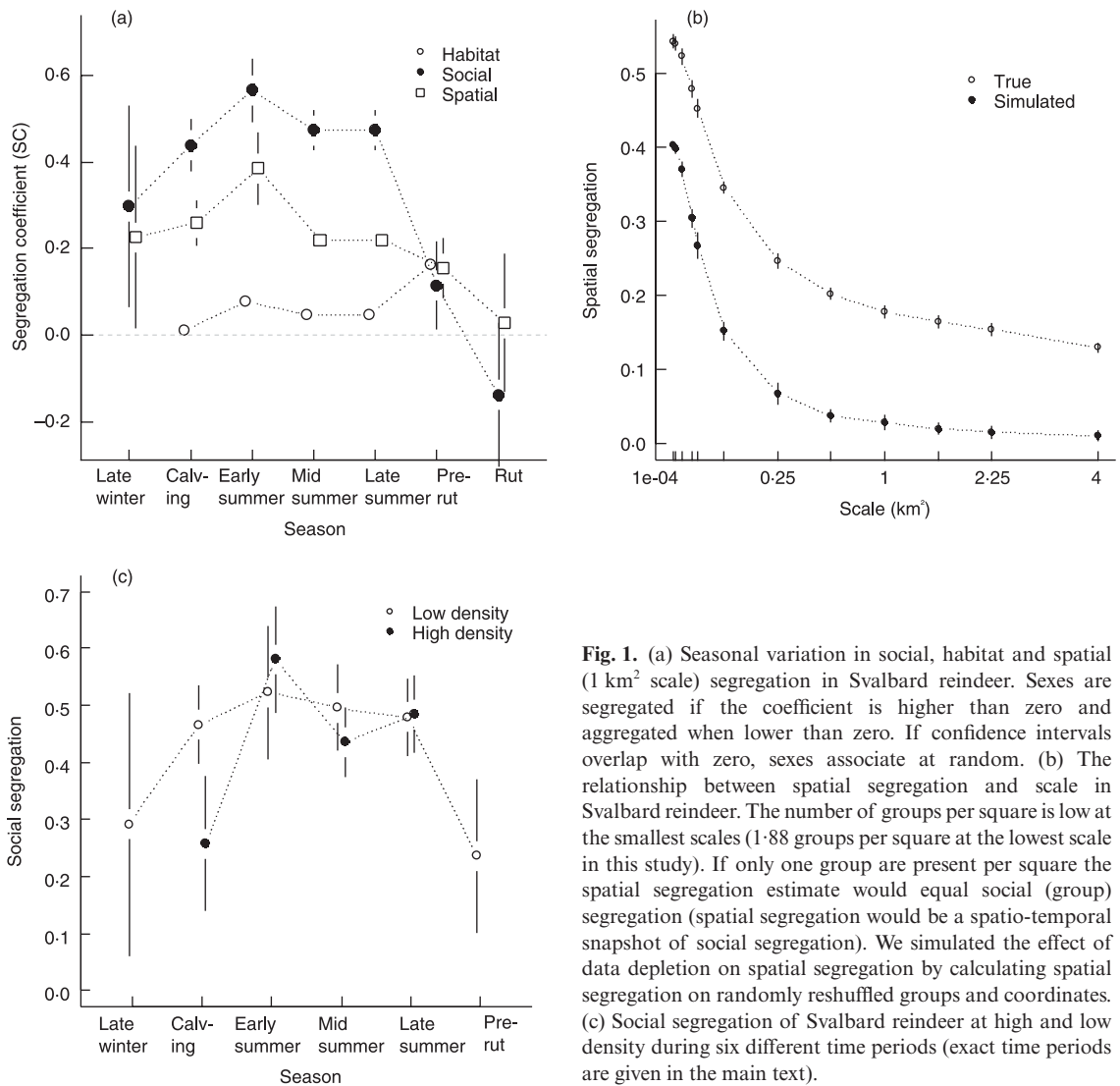
We transformed the average daily wind direction from the meteorological record into eight aspects (N, NE, E, SE, S, SW, W and NW) and matched it with the inverse of the observed aspect of individual reindeer or groups (the same eight aspect categories). A match indicate that the individual is sheltered (aspect against the wind direction), and no match indicate that the individual is exposed. To investigate the effect of wind direction on reindeer selection of aspect, we used (match/non-match) as the dependent variable in a logistic regression with sex and season as factors; and wind speed as continuous variable. We also addressed all possible two-way interactions.

All statistical analyses were performed using the statistical package R (R Development Core Team 2004).

## Results

### SOCIAL SEGREGATION VS. SPATIAL SEGREGATION

Social and spatial segregation took place all year except during the rut when males and females aggregated



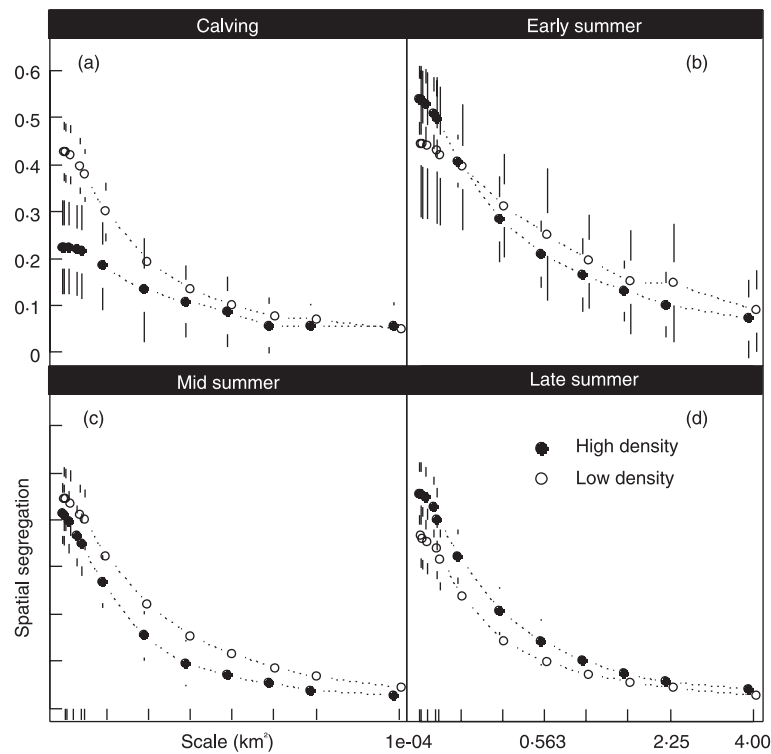
**Fig. 1.** (a) Seasonal variation in social, habitat and spatial (1 km<sup>2</sup> scale) segregation in Svalbard reindeer. Sexes are segregated if the coefficient is higher than zero and aggregated when lower than zero. If confidence intervals overlap with zero, sexes associate at random. (b) The relationship between spatial segregation and scale in Svalbard reindeer. The number of groups per square is low at the smallest scales (1.88 groups per square at the lowest scale in this study). If only one group are present per square the spatial segregation estimate would equal social (group) segregation (spatial segregation would be a spatio-temporal snapshot of social segregation). We simulated the effect of data depletion on spatial segregation by calculating spatial segregation on randomly reshuffled groups and coordinates. (c) Social segregation of Svalbard reindeer at high and low density during six different time periods (exact time periods are given in the main text).

(Fig. 1a). Social segregation was twice as high as spatial segregation (Fig. 1a), supporting the activity budget hypothesis. Spatial segregation declined with scale (Fig. 1b). By comparing the observed spatial segregation with simulated spatial segregation (see Materials and methods), it was apparent that scale dependency is primarily caused by data depletion at small scale (one or few groups per square will confound spatial segregation with social segregation). Still, spatial segregation took place at all scales, and observed segregation was higher than simulated segregation [Fig. 1b; from 100 m<sup>2</sup> (average 1.88 groups per square) to 4 km<sup>2</sup>]. The scale where spatial segregation approaches independency from social segregation (i.e. where simulated values approach zero) was *c.* 1 km<sup>2</sup> in our study (Fig. 1b).

#### NO INCREASE IN SEGREGATION BY INCREASING DENSITY

Social segregation was lower at high than low population density during calving and did not depend on

density during summer (Fig. 1c), and there was thus no support for the indirect competition hypothesis. Moreover, there was no consistent effect of density on spatial segregation. While there was no significant effect during calving and early summer, the significant, small effect during mid- and late summer was in different directions (Fig. 2). The space use of single sex groups vs. mixed groups was similar – the spatial pattern cannot be visually separated at the two density regimes (Fig. S1a, electronic appendix), and kernel estimates were rather similar (95% estimates in hectares at high density: mixed group = 37 225, male groups = 42 938, female groups = 31 761; low density: mixed group = 39 771, male groups = 47 046, female groups = 34 237). Males and females grazed in more similar vegetation communities at high than at low density (Fig. S2, electronic appendix; significant third order sex × habitat–density interaction in Table 2) in all summer periods (no significant fourth order summer period × sex × habitat–density interaction;  $F_{3,2939} = 0.823$ ,  $P = 0.481$ ), again opposite to predicted from the indirect competition hypothesis.



**Fig. 2.** The relationship between spatial segregation of male and female Svalbard reindeer and spatial scale (in km<sup>2</sup>) at high and low density during (a) calving, and (b) early, (c) mid- and (d) late summer.

**Table 2.** Resource selection function, using presence–absence data for both males and females during summer

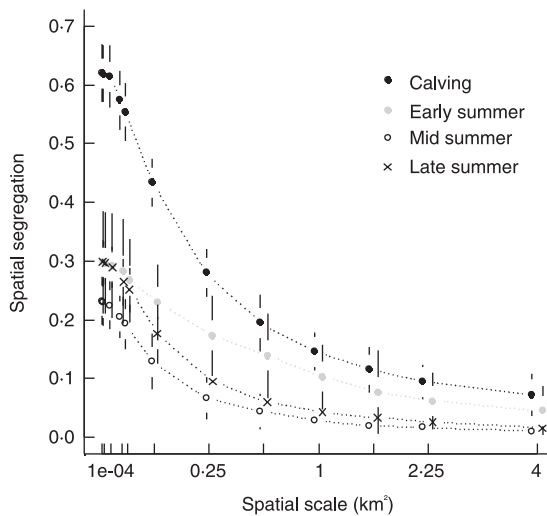
Variable	numDF	denDF	F-value	P-value
Slope × Density × Sex	1	3025	4.25678	0.0392
Vegetation type × Density × Sex	4	3025	4.29036	0.0018
Aspect × Sex	7	3025	4.5481	< 0.0001
Slope × Density	1	3025	1.09677	0.2951
Slope × Sex	1	3025	4.60045	0.032
Precipitation × Wind	1	3025	0.0381	0.8453
Temperature × Wind	1	3025	0.08743	0.7675
Sex × Density	1	3025	3.70629	0.0543
Vegetation type × Density	4	3025	0.13435	0.9697
Vegetation type × Sex	4	3025	19.71402	< 0.0001
Valley × Sex	3	3025	6.05871	0.0004
Aspect	7	3025	0.34707	0.9322
Slope	1	3025	0.65312	0.4191
Precipitation	1	3025	1.68669	0.1941
Wind	1	3025	1.27784	0.2584
Temperature	1	3025	0.02071	0.8856
Density	1	4	1.27715	0.3216
Vegetation type	4	3025	0.32191	0.8634
Sex	1	3025	108.09593	< 0.0001
Valley	3	3025	0.11457	0.9516

#### SEASONALITY AND EFFECT OF REPRODUCTIVE STATUS

Social and spatial segregation between males and females were highly seasonal. Estimates increased from late winter through calving season until early summer, where it culminated and was followed by a decrease into the rutting season (Fig. 1a). The higher social and spatial segregation during early summer than during calving is not expected from the predation risk hypo-

thesis (Table 1). The peak in social segregation during early summer is compatible with both the nutritional needs hypothesis and the activity budget hypothesis (if males and females differ maximally in activity budgets during this time period). However, the peak in spatial segregation during early summer (Fig. 1a) is only expected from the nutritional needs hypothesis.

Females with calves were more socially segregated from males than females without a calf in the most intensive lactation period (early and mid part of



**Fig. 3.** Spatial segregation between females with and without calf at increasing spatial scale during the four time periods calving (2–19 June), early summer (20–30 June), mid-summer (1–31 July), late summer (1–31 August).

summer) than during the calving season (Fig. S3a, electronic appendix). There was also social (Fig. S3b, electronic appendix) and spatial segregation (Fig. 3) within the female segment. The significant spatial segregation between reproducing and nonreproducing females during calving and early summer at scales higher than  $1 \text{ km}^2$  (where spatial segregation is independent of social segregation, see above), suggests that segregation between these two groups is not only due to different activity budgets (Fig. 3). At scales higher than  $1 \text{ km}^2$  females with and without calf tended to be more segregated during calving than during early summer (Fig. 3). Females used only a limited part of the full study area to calve both at high and low density (95% kernel estimates in hectares for groups with calf: high density = 12 975, low density = 16 365; for groups without calf: high density = 29 532; low density = 39 692) as expected from predation risk hypothesis, but the core area for calving is within an area preferred also by other groups (Fig. S1b in the electronic appendix). Surprisingly, although females with calf segregated socially from females without calf (predicted from both hypotheses), the degree of segregation did not differ between calving and lactation periods (Fig. S3b in the electronic appendix).

#### SPATIAL SEGREGATION IS NOT ONLY CAUSED BY HABITAT SEGREGATION

Habitat segregation (with respect to our seven habitat types) is significantly different from 0 (Fig. 1a). Indeed, males selected different vegetation types than females (resource selection analysis; significant vegetation–sex interaction; Table 2). However, spatial segregation coefficients are much higher than habitat segregation coefficients (Fig. 1a;  $SC_{\text{habitat}} < 20\%$  of  $SC_{\text{spatial}}$  in all periods except during pre-rut when they are similar).

Some of the difference between spatial and habitat segregation may be explained by sexual differences in choice of aspect (males more often in southern aspects; Table 2, Fig. S4 in the electronic appendix) and slope (males less often in steep slopes; Table 2). This provides some support to the nutritional needs hypothesis (Table 1), as the aspect may also influence plant quality. However, the AUC value (estimate of the area under the ROC curve) from the Resource Selection Function was 0.66 (Fig. S2 in the electronic appendix), which is relatively poor (maximum is 1 and minimum is 0.5), implying that a large part of spatial variation in site choice remains unexplained.

#### SEGREGATION AND WEATHER

Sexes were slightly more segregated during late winter and during pre-rut when there was strong wind (Fig. S5a, electronic appendix). Correspondingly, there is roughly one deer less per group in windy weather in these two periods (Fig. S5b, electronic appendix). During calving and the rest of the summer there was no clear and systematic effect of wind speed on neither segregation nor group size (Fig. S5a,b). Wind did not affect the degree of sexual aggregation during rut, but group size tended to be smaller in windy weather (Fig. S5a,b). There was no evidence from the resource selection function that one sex chose more wind-sheltered sites than the other sex (the best model for shelter seeking includes only wind speed and period (time of year) and their interaction; including the factor sex increased AIC value by 1.089; the parameter estimate  $[-0.085 \pm \text{SE } 0.089]$  goes in the direction of males seeking more shelter than females).

#### Discussion

##### PARTIAL SUPPORT FOR THE ACTIVITY BUDGET HYPOTHESIS

Our analysis provides some support for the activity budget hypothesis confirming findings in some recent studies (Ruckstuhl & Neuhaus 2002; Neuhaus & Ruckstuhl 2004). However, other studies do not support this hypothesis as the single mechanism for segregation in ungulates (Bonenfant *et al.* 2004; Mooring & Rominger 2004; Yearsley & Pérez-Barbería 2005). If sexual segregation derives from the activity budget hypothesis alone, no long-term spatial or habitat segregation is expected. In Svalbard reindeer, social segregation was twice as high as spatial segregation. Thus, the activity budget hypothesis likely contributes to, but is not enough to explain fully sexual segregation in Svalbard reindeer.

The maximum values in Svalbard reindeer segregation coefficients ( $SC_{\text{social}} = 0.56$  during early summer;  $SC_{\text{habitat}} = 0.18$  during pre-rut) is intermediate compared with the huge variation in red deer between populations at different latitudes (Bonenfant *et al.* 2004). The maximum segregation values in Svalbard reindeer



are lower than for red deer in France ( $SC_{social} = 0.75$  and  $SC_{habitat} = 0.30$  during calving; Bonenfant *et al.* 2004) and Scotland ( $SC_{social} > 0.90$  during winter;  $SC_{habitat} = 0.40$  during April; Conradt 1999), but higher than for red deer in Norway ( $SC_{social} = 0.30$  and  $SC_{habitat} = 0.15$  during calving; Bonenfant *et al.* 2004). Body size dimorphism in Svalbard reindeer (females are 33% smaller than males) is also within the large range of variation for red deer (females are *c.*40%, 35% and 25% smaller than males in Rum [Table 2.1 in Clutton-Brock, Guinness & Albon (1982), Norway (Post *et al.* 1999) and France (Bonenfant *et al.* 2002), respectively]. The fact that the degree of segregation among red deer populations does not correspond with the variation in body size dimorphism (French deer are less dimorphic but segregate more than Norwegian red deer), suggests that above the 20% dimorphism threshold needed (Illius & Gordon 1987) other factors determine how often males and females are found in the same groups.

Our set of five hypotheses is not exhaustive. We have not considered the 'social factors hypothesis' stating that individuals will group with the same sex and age due to similar social needs and constraints (Bon 1991; Bon *et al.* 2001). The social factors hypothesis received some support in a recent experimental study of captive sheep, but the authors acknowledged that additional factors are needed to explain sexual segregation in nature (Pérez-Barbería, Robertson & Gordon 2005). However, we would not be able to disentangle Bon's social factors hypothesis from the activity budget hypothesis in our study as both hypotheses predict much larger social than spatial segregation. For that we would need detailed behavioural observations of focal animals of known age. A sexual difference in activity budget may derive both from social factors and deviating nutritional needs and may rather be regarded as an outcome rather than the fundamental cause for social segregation (Bowyer 2004; Mooring & Rominger 2004). However, as the majority of time outside the rutting season is spent foraging and ruminating, we argue that the nutritional-based activity budget hypothesis is more likely than the social factors hypothesis.

#### ON THE SPATIAL COMPONENT OF SEXUAL SEGREGATION

The level of spatial segregation is meaningless to compare between studies unless spatial scale is taken into consideration (Bowyer, Kie & Van Ballenberghe 1996; Bowyer 2004). We provide an improved methodology for how to separate social and spatial segregation at different scales. According to the activity budget hypothesis, the sexes will separate only in time (male groups inhabit a patch one moment – female groups the next, as they do not differ in affinity to a site). Most real data sets will encounter problems when it comes to separating temporal and spatial segregation on a small scale (See Materials and methods). We suggest that spatial segregation at small scale must be analysed relative to

what would be expected from random. When doing this we found that a large proportion of small-scale spatial segregation (but not all) was indeed an artefact expected from random shuffling of groups in space (Fig. 1b) and that the randomized spatial segregation coefficient did not drop to zero before the spatial scale was close to 1 km<sup>2</sup>. This scale reflects where spatial segregation is independent from social segregation. Moreover, the scale dependency in spatial segregation (Bowyer *et al.* 1996) in our study is entirely caused by data depletion at small scale (subtracting the observed from the simulated line removes the negative relationship between segregation and scale). Therefore care must be exercised when investigating sexual segregation to take into account the spatial scale that the data are analysed over.

#### NO EVIDENCE THAT INDIRECT COMPETITION IS TAKING PLACE

Social segregation was not affected by density, except during calving when the sexes were less segregated at high than low density. There was a slight decrease in spatial segregation with increasing density during calving, early- and mid-summer (Fig. 2). In late summer, however, the spatial segregation was marginally higher at high than low density (Fig. 2). Such a pattern is expected from the indirect competition hypothesis, if males leave common pastures because the quantities of palatable plants are reduced from mid- to late summer as a consequence of high grazing pressure (when density is high). Despite this, males and females grazed in more similar vegetation communities at high than at low density all summer, which weakens the indirect competition hypothesis as a likely mechanism for segregation in Svalbard reindeer. This is in accordance with numerous other studies (moose *Alces alces* L. Miquelle *et al.* 1992; kudu *Tragelaphus streptoceros* Pallas: du Toit 1995; mountain goat *Oreamnos americanus* Blainville: Bleich *et al.* 1997; red deer: Conradt, Clutton-Brock & Thomson 1999; Conradt *et al.* 2001; white-tailed deer *Odocoileus virginianus* Zimmermann: Kie & Bowyer 1999). In mule deer *Odocoileus hemionus* Rafinesque, males foraging together with females increase cropping rate as density increases (a pattern not found in pure male groups), indicating a foraging cost for males staying in mixed groups at high density (Weckerly *et al.* 2004). Still, this did not result in a significant density-dependent increase in sexual segregation (Weckerly *et al.* 2004).

A density-dependent decrease in body weights could lead to more similar body size in males and females, as males would reduce body size to a higher extent than females (Leberg & Smith 1993; Leblanc, Festa-Bianchet & Jorgenson 2001). However, given the large body size dimorphism in Svalbard reindeer (females are 33% smaller than males) and the fact that they are primarily limited by climate (Aanes, Sæther & Øritsland 2000; Albon *et al.* 2002), it is unlikely that size dimorphism in

high-density years declines to an extent that would affect optimal activity pattern or diet preference in Svalbard reindeer. No effect of density on segregation is therefore consistent with both the activity budget hypothesis and the nutritional needs hypothesis.

Spatial segregation was generally lower at high than low density in most periods (Fig. 2). The short summer is a period of intense grazing. The time devoted to foraging is 55–60% during spring and 65–70% during summer (Kastnes 1979). Site selection is in most periods linked to optimizing nutritional intake in both sexes, at least at fine scales (Senft *et al.* 1987). The fact that spatial segregation between sexes occurs implies that they have different selection criteria for one or more currencies that vary in space, which in our case was not fully captured through vegetation communities, such as slope and aspect. Good patches for males and good patches for females may be differently distributed and large-scale site selection may be linked to the encountering frequency of good patches. However, sex-specific shifts in range use due to density could not be detected from kernel estimates (Fig. S1a, electronic appendix).

#### THE SEASONAL PATTERN AND EFFECT OF REPRODUCTIVE STATUS

Social and spatial segregation peaked during early summer and not during calving. Females with calf are more segregated from males than females without calf during the first two summer periods, but not during calving. Energy expenditure in females is highest during the early stage of lactation (Loudon 1985). During this period reproducing females may differ maximally from barren females (and males, Clutton-Brock, Albon & Guinness 1989) with respect to nutritional needs and requirement for free water (for milk production) and rumen and intestine physiology (Barboza & Bowyer 2000), but also in time devoted to grazing. The peak in sexual segregation in early summer comes at a time where spatial variation in biomass and quality is high and lactation demands are greatest. The peak in early summer is expected from the nutritional needs hypothesis as it states that males, females with calf and females without calf, will have largely different forage selection currencies during this time period (Clutton-Brock *et al.* 1987; Main, Weckerly & Bleich 1996; Barboza & Bowyer 2000; Bowyer 2004).

Svalbard reindeer calves are vulnerable to predation by arctic foxes just after birth (see Linnell *et al.* 1995 for a general review). Consequently, if predator avoidance was driving sexual segregation it should peak during the calving period (Bleich *et al.* 1997; Kie & Bowyer 1999). During calving (in June), the study area is a mosaic of snow-covered and snow-free ground. Both females giving birth and foraging reindeer most likely prefer snow-free to snow-covered ground. The limitation of snow-free space may explain why spatial and social segregation is comparatively low during the calving season.

A peak in social segregation during early summer is compatible with both the nutritional needs hypothesis and the activity budget hypothesis (if the sexes differ maximally in activity budgets during this time period), but not with the predation risk hypothesis. However, the peak in spatial segregation during early summer supports only the nutritional needs hypothesis. Svalbard reindeer have lived without significant predators for at least 5000 years, Arctic foxes occasionally take calves (Tyler 1987), but no vegetation type provides high enough shelters to visually hide from foxes. Support for the predation-risk hypothesis despite a lack of predators has been found in red deer (Bonenfant *et al.* 2004), but this population had been free from predators for a much shorter time period (*c.* 100 years). In sum, these factors may explain why the predation risk hypothesis is less likely in Svalbard reindeer than in most other ungulate populations.

#### PARTIAL SUPPORT FOR THE WEATHER SENSITIVITY HYPOTHESIS

Sexual segregation in winter and the pre-rut season tended to be higher and group size tended to be lower in windy than in calm weather. Higher absolute heat loss relative to intake rate may lead to higher weather sensitivity in large (males) than small (females) ungulates and adverse weather may be an especially potent force for causing segregation in arctic zones (Conradt *et al.* 2000). If this argument is true, male ungulates (which are more sensitive to adverse weather than females) may have to choose between good foraging sites and sheltered sites in windy weather if the best foraging sites do not also provide the best shelter. Although we found that the parameter estimate goes in the direction that males seek shelter to a higher degree than females (as expected from the weather sensitivity hypothesis; Conradt *et al.* 2000), the effect of sex on shelter-seeking was far from significant. Wind may affect social segregation in the seasons with rough weather, but that is not enough to explain the substantial degree of spatial segregation observed.

As there is weak habitat segregation and weak effect of wind, a large part of the spatial segregation remains unexplained. One possibility is that our vegetation types only to a limited extent catch relevant nutritional differences in space. Differences in biomass and quality of forage plants may be more variable within than between vegetation communities, i.e. in some areas all vegetation communities contain forage plants of high quantity and/or quality while in other areas all vegetation types contain less palatable food. Such a spatial correlation will most likely be caused by local (even microscale) variation in climate and the duration of snow cover. The fact that males and females select differently with respect to aspect and slope supports this suggestion as snow cover drives plant phenology and hence, plant quality and quantity (Albon & Langvatn 1992; Van der Wal *et al.* 2000b; Mysterud *et al.* 2001).

## Conclusions

We have tested a set of predictions that are capable of separating five processes that may lead to sexual segregation (Table 1). We conclude that there was partial support for the activity budget hypothesis, the nutritional needs hypothesis and the weather sensitivity hypothesis, but no single hypothesis is in line with all patterns of social, spatial and habitat segregation observed in Svalbard reindeer (Table 1). Hence, as earlier reported for red deer *Cervus elaphus* L. (Bonenfant *et al.* 2004), multiple causes of sexual segregation in sexually dimorphic ruminants may be the general rule rather than the exception.

## Acknowledgements

We are grateful to all the field assistants that have taken part in the data collection over the years and to the Research Council of Norway for support to LEL, CB, AM (YFF project) and RL (Terrøk and Arktisk Lys). NERC has also generously funded the project. Thanks to Jon Yearsley and to two anonymous referees for valuable comments on an earlier version of the manuscript.

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Received 1 July 2005; accepted 7 December 2005

### Supplementary material

The following supplementary material is available as part of the online article (full text) from <http://www.blackwell-synergy.com>

**Fig. S1.** Spatial distribution of pure female, pure male and mixed groups at high and low density during early and mid summer, and of groups with calves and all other groups at high and low density during the calving period (2–19 June).

**Fig. S2.** The effect of density on selection of five vegetation types in male and female reindeer in summer.

**Fig. S3.** Social segregation from males in female Svalbard reindeer with and without calves, and between females with and females without calves.

**Fig. S4.** Presence of male and female Svalbard reindeer at different aspects during the summer season (early to late summer).

**Fig. S5.** The effect of wind on social segregation and group size throughout the year in Svalbard reindeer.