Testing five hypotheses of sexual segregation in an arctic ungulate

LEIF EGIL LOE*, R. JUSTIN IRVINE†, CHRISTOPHE BONENFANT*, 
AUDUN STIEN‡, ROLF LANGVATN§, STEVE D. ALBON†,
ATLE MYSTERUD* and NILS CHR. STENSETH*

*Centre of Ecological and Evolutionary Synthesis (CEES), Department of Biology, University of Oslo, PO Box 1066 Blindern, N-0316 Oslo, Norway; †The Macaulay Institute, Craigiebuckler, Aberdeen AB15 8QH, UK; ‡Department of Biology, University of Tromsø, N-9037 Tromsø, Norway; and §The University Centre in Svalbard (UNIS), N-9170 Longyearbyen, Norway

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.

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
is that intake is limited by the incisor arcade breadth scales as Weight

when grass swards are grazed to short levels at high density, whereas intake is about isometric (Weight

When the scaling coefficient of intake is lower than requirements (Weight

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). Conradt (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-Barberia & Gordon 1998; Mysterud 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 (Conradt 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 km² area, including Colesdalen, Semmeldalen and parts of Reindalen, with adjacent side valleys.
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 age) 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 Gunnerus. 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, S, SW, E, W, SE, NE), slope (flat <5°, moderate 5–20°, steep >20°) and vegetation community was recorded (see below).
DENSY 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) *Alpocerus* L.–*Eriophorum* L.–heath; (6) *Phanzya* 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 Conradt (1998b). To detect aggregation patterns during the rut we did not use the modifications of the original index (Conradt 1999), which restricts the segregation coefficients between 1 (full segregation) and 0 (random associations between males and females). With the original index (Conradt 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. Conradt 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.

\[ SC_{social} = 1 - \frac{N}{X \cdot Y} \sum_{i}^{l} \frac{x_{i} \cdot y_{i}}{n_{i} - 1} \]  

\[ SC_{habitat} = 1 - \frac{M}{Z \cdot W} \sum_{i}^{l} \frac{z_{i} \cdot w_{i}}{m_{i} - 1} \]  

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 \( Y \)).

\[ SC_{social} = 1 - \frac{M}{Z \cdot W} \sum_{i}^{l} \frac{z_{i} \cdot w_{i}}{m_{i} - 1} \]  

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;
Sexual segregation in Svalbard reindeer

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

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

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 m² (1213 grids) and up to 2 km² meters (85 grids).

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

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 extrabinnomial 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
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. The scale where spatial segregation approaches independency from social segregation (i.e. where simulated values approach zero) was $c.1 \text{ km}^2$ 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.
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 hypothesis (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...
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 $[-0.085 \pm SE 0.089]$ 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 ($SC_{\text{sexual}} = 0.56$ 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 \( (SC_{\text{social}} = 0.75 \) and \( SC_{\text{habitat}} = 0.30 \) during calving; Bonenfant et al. 2004) and Scotland \( (SC_{\text{social}} > 0.90 \) during winter; \( SC_{\text{habitat}} = 0.40 \) during April; Conradt 1999), but higher than for red deer in Norway \( (SC_{\text{social}} = 0.30 \) and \( SC_{\text{habitat}} = 0.15 \) 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-Barberia, 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 sexual 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\(^2\). 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 strepsiceros 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
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).

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 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 who 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.

References


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.