INTERACTIONS BETWEEN SYMPATRIC REINDEER (RANGIFER TARANDUS TARANDUS) AND SHEEP (OVIS ARIES) ON **ARCTIC PASTURES**

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PREFACE

This thesis, written at the Department of Ecology and Nature Resource Management at the Norwegian University of Life Sciences, is the final 60 credits of my Master of Science degree in Nature Resource Management.

The fieldwork was conducted in Joahkonjárga summer grazing area and Lokkarfjorden grazing area. I wish to share my gratitude to the reindeer pastoralists and sheep farmers for letting me observe their animals. I would also like to thank my two supervisors, Stein Moe and Jonathan Colman, for their support, good advice, and inspiration throughout the work with this thesis. I'm thankful to numerous people for helping me during the summer in Finnmark: Lokkarfjord Beitelag for lending me their cabin and bringing me supplies; Kåre Rapp for helping me organize the vegetation types; the Mikalsen family in Langfjordbotn and Alta for their great hospitality; the Rapp family at Altafjord Camping for always having a spare room; and Daniel for company. Furthermore, I would like to thank Per Bjørklund, Michael Angeloff and Yngve Rekdal at The Norwegian Forest and Landscape Institute for information on the study area and helping me with maps.

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ABSTRACT

Interspecific interactions among sympatric ungulates are an important issue in management and conservation. Interactions between free-ranging semi-domestic reindeer (*Rangifer tarandus tarandus*) and domestic sheep (*Ovis aries*) were studied during summer 2006. These ungulate species are ruminants with similar body sizes, feeding style and diet. Transect surveys, scans and *ad libitum* sampling were applied to examine the potential for competition between the two species on outlying pasture.

Reindeer showed a more varied habitat use, moved around more in the terrain and were more widely distributed over the entire study area than sheep. The species exhibited, however, a considerable niche overlap in vegetation and altitude use. Both species preferred vegetation types with high quality forage and followed the snow melt into higher elevations over the course of the summer. Altitude use for reindeer and sheep showed only weak or no response, respectively, towards recorded weather variables (sun/rain, wind and cloud cover). The species were recorded to be within 1000 meters of each other in 40 % of the observations. The relative densities of reindeer and sheep within the core area were almost equal. Confrontation between the two species was observed only within 30 meters, and in 20 % of 67 encounters. The confrontations do not necessarily imply competition, as no negative result could be ascertained, but may rather be a general response of getting too close; i.e. intrusion of an individual's space. The number of encounters ending in confrontation increased as the distance decreased from 30 towards zero meters. Reindeer and sheep won the same amount of confrontations, and neither species appeared to be dominant over the other. The lack of aggressive behavior and ability to graze together indicate a high degree of interspecific tolerance.

I conclude that with little interference and a considerable interspecific niche overlap, exploitation competition is likely to occur when food is limited. The result suggests, however, that the quality of pasture and the total number of animals should be considered when making management decisions, rather than separation of reindeer and sheep.

Key words: free-ranging, interaction, competition, habitat selection, interference, niche, outfield pasture.

SAMMENDRAG

Beitedyrs påvirkning av hverandre er et sentralt spørsmål i forvaltning og bevaring av arter. Tamrein (*Rangifer tarandus tarandus*) og sau (*Ovis aries*) på felles utmarksbeite ble studert på Øksfjordhalvøya i Vest-Finnmark sommeren 2006. Disse artene er omtrent like store, og begge er drøvtyggere med lik beiteadferd og diet. Faste transekter, scans og *ad libitum* sampling ble benyttet for å kartlegge potensialet for konkurranse mellom de to artene.

Rein hadde en mer variert og omfattende habitatbruk enn sau, samtidig som de vandret mer, og hadde en større utbredelse i studieområdet. Rein og sau hadde likevel betydelig overlapp i bruk av både vegetasjon og høydelag. Begge artene foretrakk vegetasjonstyper med fôr av høy kvalitet, og trakk oppover i terrenget utover sommeren. Rein viste en svak respons til endinger i været, mens sauen ikke ble påvirket. I 40 % av observasjonene fra linjetakseringene befant artene seg innenfor 1000 meter fra hverandre. De relative tetthetene av rein og sau i kjerneområdet (Indre Lokkarfjorden), var omtrent like for begge artene. Konfrontasjon mellom rein og sau ble bare observert når de var nærmere enn 30 meter, og i 20 % av de 67 møtene. Konfrontasjonene indikerer ikke nødvendigvis konkurranse mellom artene, men kan heller være en generell respons på at enkeltindividenes toleranseavstand brytes. Antallet møter som endte i konfrontasjoner økte når avstanden ble redusert fra 30 meter mot null meter. Rein og sau vant likt antall konfrontasjoner, og ingen av artene var dominante på en aggressiv måte. Mangelen på aggressiv atferd og muligheten for å beite svært tett, indikerer en høy grad av toleranse mellom artene.

Jeg konkluderer at med lite interferens og et betydelig overlapp i nisjene til rein og sau er det sannsynlig at det vil oppstå konkurranse når beitet begrenset. Resultatene fra dette studiet tyder likevel på at i stedet for å fysisk skille rein og sau, bør beitekapasiteten og det totale antallet dyr være i fokus i forvaltningsspørsmål.

Nøkkelord: rein, sau, felles beiteområde, interaksjoner, konkurranse, habitat preferanse, interferens, nisje, utmark.

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1. INTRODUCTION

Interspecific interactions among sympatric ungulates are an important issue in wildlife management and conservation (Putman 1996, Arsenault & Owen-Smith 2002). Questions concerning competition between livestock and wild ungulates are often disputed (Madhusudan 2004, Mishra *et al.* 2004). Generally, competition between species can be indirect through reduction in available resources (exploitation competition) or direct through behavioral interactions (direct interference competition, as opposed to indirect interference competition from for example aversion towards excrement (Colman 2000)) (Schoener 1983, Putman 1996, Colman 2000, Begon *et al.* 2006). Interspecific competition may be especially prevalent in connection with the introduction (Voeten & Prins 1999, Forsyth 2000) and/or reintroduction (Reed 2001, Fischer & Gates 2005) of species into a guild of herbivores.

The last remnants of wild reindeer (*Rangifer tarandus tarandus*) populations in Europe are found in Norway (Clutton-Brock, J. 1999), and 40 % of the country's land area is used by semi-domestic reindeer herded by Sámi reindeer pastoralists (Holand 2003). Management of wild and semi-domestic reindeer, and protection of the wild reindeer has high priority for Norwegian wildlife authorities (DN 1995). Domestic sheep (*Ovis aries*) is the most common sympatric ungulate sharing ranges with reindeer (Skogland 1984, Colman 2000), and 2-2.5 million sheep are released onto outlying pastures every summer (Kausrud *et al.* 2006). There has been an ongoing debate over the last decades concerning the issue of interactions between reindeer and sheep (Gausmel 1989, Mysterud & Mysterud 1999, Colman 2000). There are, however, very divergent opinions among stakeholders regarding the aspects of the interaction and how the two species are affected by one another (Ballari 1986, Ravna 2005). A common claim is that sheep show aggressive behavior towards reindeer and displace them into areas with poor forage (Elgvin 1998). If interference competition between the two species exists, one of the species might loose access to important food resources because of the other. The result may be reduced condition for the loosing species when pasture is limited.

Reindeer and sheep are indeed potential competitors. Both are ruminants with approximately the same body size (Mysterud & Mysterud 1999). Studies have shown a considerable overlap in diet between the two species (Skogland 1984, Bergmann 1997, Mysterud 2000). Skogland (1984) and Bergman (1997) reported 60 % and 85 % diet overlap, respectively. Reindeer and sheep also utilize similar habitat types (Ballari 1986, Melby & Orvik 1986, Gausmel 1989). The high similarity in diet and habitat use between the species indicates competitive interaction when shared food resources are limited (de Boer & Prins 1990, Putman 1996), although the relationship between resource overlap and interspecific

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competition is not clear (Abrams 1980, Lawlor 1980). Studies on area use show little temporal overlap between reindeer and sheep (Ballari 1986, Melby & Orvik 1986). Segregation of the species, despite similar resource use, may among other explanations indicate interference competition with behavioral dominance or displacement by one species towards the other (Clutton-Brock, T. H. *et al.* 1987, Colman 2000). Research on direct interactions between free-ranging reindeer and sheep are rare, with the exception of Colman (2000). Increased knowledge may improve the management of the species and the ecological systems they are part of, and be useful in the communication between different stakeholders.

This study focused on direct encounters between reindeer and sheep and the behavioral responses of the species towards each other. Habitat selection of the animals was also documented. Knowledge of how habitat selection affects distribution of large herbivores across the landscape is a necessary prerequisite for examining competition (Cooke 1997), and information on overlap in resource use is central for the understanding of interspecific competition (Case & Gilpin 1974, Abrams 1980).

This thesis focused on the potential for competition between reindeer and sheep. Based on whether competition existed, I made the following predictions (i) the two species utilize the same vegetation types and altitudes, and thus, would exhibit niche overlap; (ii) the species respond equally to weather conditions concerning their vegetation and altitude use; (iii) one or both of the species would exhibit a change in behavior during direct encounters between them and finally; (iv) the number of encounters with confrontation would increase with decreasing distance between the species.

2. METHODS

2.1 Study site

The study was conducted from 3. June to 5. August 2006 on the Øksfjord peninsula (272 km²) in the Joahkonjárga summer grazing area in West Finnmark, northern Norway (70°10'N, $22^{\circ}30'E$) (Figure 2). Data collection was restricted to the mid-western half of the peninsula, with a core area in Indre Lokkarfjorden (Figure 1). The study area comprised of approximately 35 km², and is dominated by high mountains, where valley bottoms rich in vegetation are enclosed by steep mountainsides. The mountain peaks make up plateaus with weathering materials. Elevations range from sea level to 830 meters.



Figure 1. The core area in Indre Lokkarfjorden, a) Johannadalen and b) Lokkarfjorddalen, summer 2006.

2.1.1 Climate

The study area is found in a subarctic climate (Kottek *et al.* 2006) and has 24 hours of daylight between 16. May and 26. July (*met.no*). The area belongs to the slightly oceanic vegetation section (Fremstad 1998), with a mean precipitation of 810 mm per year (*eklima.met.no*) and precipitation 240 days a year (Moen *et al.* 1999). The total rainfall during the study was more than 200 % of the expected 110 mm. It rained nearly every day (Figure 3), with an average daily rainfall of 4.5 mm. The mean temperature over the same period was 9.5° C (Figure 4), which was 0.6° C below what was expected from an average year (*eklima.met.no*). The growing-season is 133 days near sea level, i.e. number of 24 hours with a mean temperature over 5° C (Moen *et al.* 1999). During the study, there was no ice left on the larger lakes and snow remained only at higher altitudes and mainly in patches on the plateaus at summer solstice 21. June.





Figure 3. Precipitation in the period 3. June - 5. August 2006. The horizontal drawn line shows the daily mean rainfall during the study. Data from Hasvik airport (*eklima.met.no*).



Figure 4. Mean, minimum and maximum 24-hours' temperature in the period 3. June - 5. August 2006. The horizontal drawn line shows the mean temperature during the study. Data from Hasvik airport (*eklima.met.no*).

2.1.2 Vegetation

The study area is divided between the northern boreal and alpine vegetation zones, at lower and higher altitudes, respectively (Moen *et al.* 1999). Gabbros and amphibolites (*www.ngu.no*) which contain vital plant nutrients and weather fairly easy (Heim & Landvik 2003) make the soil fertile and with 24 hours of daylight plants constantly assimilate. The

vegetation in the area is therefore rich in species and very productive (Lyftingsmo 1965). Coastal mountain birch (*Betula pubenscens* sp.) forest grow up to 300 meters altitude (Bråthen & Oksanen 2001).

The vegetation was mapped during July after the major snowmelt. Based on a survey in the area at the beginning of the study period and Fremstad (1998), the vegetation was divided into 12 different vegetation types including impediment (Table 1). Dominant and characteristic plant species within each vegetation type were identified (Mossberg *et al.* 1995). However, there are local variations within the same vegetation types, the borders between them are often vague and mosaics of different types are common. Snow was set as an additional "vegetation type". Vegetation was mapped in 10 % of the study area to give an idea of the availability of each vegetation type. This was done by usage of a 100 m x 100 m grid added to a map scaled 1:50 000. Squares to be mapped were randomly drawn and placed within the grid.

Seashore-ebb was available only half the time due to the high tide twice during the 24 hours, so only half of the available seashore-ebb area at low tide was included in the overall availability of the vegetation types. This was based on the 12-rule of tidal water (Nissen-Lie 2000), where the full low tide is approximately six hours before and after each high tide. The challenge of a highly decreasing amount of snow during the study period was solved by usage of the availability of snow in the middle of July, and snow was therefore excluded as a vegetation type in the core area. Almost 20 % of the study area was unavailable or inaccessible (i.e. for instance water bodies, steep mountain sides and unstable fields of gravel) and was excluded from the available area applied in the analyses.

| Table 1. Description and availsMossberg et al. (1995). | ability | (% of study area) of the different vegetation types in the study area (adapted from Fremstad (1998)). Species identified from |
|--------------------------------------------------------------------|---------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Vegetation name and availabilit (Abbreviations in brackets.) | y (%) | Vegetation characteristics |
| Tall-herb woodland (THW) | 0.1 | Tall Betula pubescens, Sorbus aucuparia and Salix caprea. Herbs combined with tall-grasses. Typical species are Anthriscus sylvestris, Bistorta vivipara, Calamagrostis purpurea, Deschampsia cespitosa, Filipendula ulmaria, Geranium sylvaticum, Geum rival, Ranunculus acris, Trollius europaeus and Urtica sp. Ferns, especially Athyrium filix-femina, dominate in patches. |
| Grass-dominated woodland (GDW) | 1.3 | Relatively open woodland. Betula pubescens, few individuals of Juniperus communis, Salix caprea and Sorbus aucuparia. Agrostis capillaris, Deschampsia flexuosa, Festuca ovina and Poa alpigena dominate. Elements of undemanding herbs (Alchemilla ssp., Campanula rotundifolia, Ranunculus acris), ferns (Gymnocarpicum dryopteris, Phegopteris connectilis) and Vaccinium myrtillus. |
| Bilberry woodland (BW | 2.8 | Heaths dominate the herb-layer. Elements of <i>Calamagrostis purpurea</i> , <i>Cornus suecica</i> , <i>Deschampsia cespitosa</i> , <i>D. flexuosa</i> . Includes two "suptypes" (a) Bilberry-crowberry. Large quantity of Empetrum hermaphroditum. Vaccinium uliginosum and V. vitis-idaea are present. (b) Bilberry-small fern. Gymnocarpicum dryopteris, Phegopteris connectilis and V. myrtillus dominate. |
| Grass-dominated scree vegetation and grassland (GDV) | 10.7 | Slopes with loose rock fields and/or gravel. At times disturbed by rock fall and avalanches. Great variation in the level of vegetation cover. Areas previously harvested by people or grazed by livestock are also included. <i>Agrostis capillaris, Anthoxanthum odoratum, Calamagrostis strict, Deschampsia cespitosa, D.flexuosa, Festuca rubra, Nardus stricta, Phleum alpinum, Poa alpina.</i> |
| Heath-dominated scree vegetation (HDV) | 11.4 | Slopes with loose rock fields and/or gravel. At times disturbed by rock fall and avalanches. Great variation in the level of vegetation cover. Heaths are dominant, especially <i>Vaccinium myrtillus</i> . Some patches have a significant part of <i>Deschampsia flexuosa</i> and other grass species in between. Elements of low-herbs. |
| Mire/Bog (M) | 1.5 | In wet areas below 100 meters altitude. Mix between rich and poor areas, most being intermediate. Herbs like <i>Bistorta vivipara</i> , <i>Menyanthes trifolia</i> , <i>Parnassia palustris</i> and <i>Potentilla palustris</i> . Tall sedges like <i>Carex aquatilis</i> and <i>C. rostrata</i> dominate in the wettest areas. Drier areas have a large proportion of <i>Andromeda polifolia</i> , <i>Eriophorum vaginatum</i> and <i>Tofieldia pusilla</i> , and heathery |
| Bilberry-blue heather heath and mountain crowberry heath (H) | 6.5 | Short vegetation, large proportion of bilberry. Heaths dominate, Vaccinium vitis-idaea, Phyllodoce caerulea, Pedicularis lapponica, Deschampsia flexuosa, Betula nana, Luzula spicata, Carex bigelowii, Carex vaginata, Festuca vivipara, Juncus trifidus, Calluna vulgaris. Some places are Empetrum hermaphroditum dominant (70-80 % of the vegetation-cover). |
| Late snow patch vegetation (LSP) | 11.1 | Land with late snowmelt and shortened growing-season. Great variation within the group. Common species in a variety of combinations are <i>Alchemilla alpina</i> , <i>Anthoxanthum odoratum</i> , <i>Carex bigelowii</i> , <i>Cassiope hypnoides</i> , <i>Cryptogramma crispa</i> , <i>Deschampsia flexuosa</i> , <i>Omalotheca supina</i> , <i>Phleum alpinum</i> , <i>Poa alpina</i> , <i>Polystrichum lonchitis</i> , <i>Salix herbacea</i> , |
| Alpine ridge vegetation (ARV) | 3.4 | Vegetation in the mountains. Areas with little snow during winter and which are exposed to wind. Both on base-rich and base-poor rock. Typical species are <i>Diapensia lapponica</i> , <i>Loiseleuria procumbens</i> , <i>Arctostaphylos alpinus</i> , <i>Luzula spicata</i> , <i>Juncus trifidus</i> and <i>Festuca</i> vivipara. On more rich ground are <i>Dryas octopetala</i> , <i>Silene acaulis</i> and <i>Saxifraga</i> |
| Impediment (I) | 49.9 | Little and scattered vegetation on barren and rocky land. Mostly in high alpine areas, but also loose rock fields (screes) with little or no vegetation. Many of the same species as in the other mountain vegetations. <i>Oxyria digyna</i> and <i>Ramunculus glacialis</i> occur frequently. |
| Salt marsh (SM) | 0.1 | Dense, short vegetation in the transition between sea and land. Like a mosaic, often with local dominance of one species. Salt tolerant species, Agrostis stolonifera, Festuca rubra, Leymus arenarius, Euphrasia ssp. In upper areas Campanula rotundifolia, Leontodon sp., Potentilla anserina, Achillea millefolium. |
| Seashore-ebb (S-E) | 0.6 | Sublittoral area, little variation. Flooded by seawater twice every 24-hour. Little and scattered vegetation where species of brown algae dominante. |

METHODS

2.1.3 Present use of the area

Present utilization of the study area has been similar over the last decade, providing summer pasture for variable numbers of free-ranging semi-domestic reindeer and domestic sheep (Figure 5). Reindeer graze on the entire peninsula during summer after arriving from their spring pastures. The first animals, yearlings and females without calves, arrive in late May or beginning of June. This period coincides with the release of sheep into Indre Lokkarfjorden. The reindeer fostering heard, with females and calves, arrives in late June or early July.

In 2006, the first reindeer arrived in the beginning of June while 649 sheep were released on 1. and 2. June. The fostering herd of approximately 4000 reindeer was driven to the peninsula on 25. June, and some of these individuals arrived in the study area on 30. June. From July, approximately 6000 reindeer were present on the peninsula. The reindeer were mostly females and calves. The total herd had < 10 % adult males (reindeer pastoralists, pers. comm. 2006). There were no rams in the study area, only ewes with or without lambs.



Figure 5. The number (n) of reindeer in the spring herd of Joahkonjárga summer grazing area (Reindriftsforvaltningen 2006) and the number of sheep released in Indre Lokkarfjorden (sheep farmers pers. comm. 2006) over the last 20 years.

2.2 Data collection and preparation

2.2.1 Habitat selection

To examine whether reindeer and sheep utilize the same habitat through overlap in use of vegetation and altitude (prediction i), three fixed transects were chosen based on knowledge of migration routes for reindeer and the release areas for sheep. Transects were run through both the lower and the higher elevations, and were located where the terrain was passable

(Figure 2d). Each transect was walked 1-2 times per week and at various time over the 24 hour period, representing 200 hours of survey. Observations were done visually from the ground with the help of binoculars, similar to (Shannon *et al.* 1975, Reed 2001). All animals observed were recorded regardless of distance from a transect. The geographical positions of the animals were marked on a topographic map with scale 1:50 000. Variables recorded at each observation were date, time of the day, species, group size, group composition, vegetation type, presence of the other species within 1000 meters, and activity (feeding, lying, standing, and walking/running) of the animals. External variables (e.g. insects and human activities) that could influence the animals' behavior during the observations were also noted.

The study period was divided in two periods; June and July (including the first week of August). This was done to examine whether vegetation and altitude utilization for both species, and thus niche overlap between the species, changed during the summer. The division between the first and second half of the summer was made between June and July because the snow was gone in most of the study area in the beginning of July, and a change in composition and possibly densities of the reindeer occurred. The first calves were observed 30. June, indicating that individuals from the fostering herds had arrived in the area.

Reindeer were scattered over the entire study area, while sheep were mostly resident in the Indre Lokkarfjorden. Therefore, analyses were based on two scales; 1) the entire study area; i.e. the overall potential for competition on a large (ca 35 km²) geographical scale and considering all available resources and 2) the core area; i.e. the realized/actual effect of a niche overlap at a small (within ca 6.5 km²) geographical scale. Data from the transect surveys were examined without considering the activity of the animals. Observations of the species within 1000 meters of one another were pulled from the transect surveys and used in analyses for the core area. Individuals were considered as single units in the analyses because larger groups often appeared over several vegetation types.

Three measures of habitat use and preference were applied: (a) use, the percentage of all observed individuals recorded in resource state i; (b) preference (P_{ix}); and (c) overall degree of preference, niche breadth (Appendix 1). A measure of niche overlap was applied to examine whether reindeer and sheep utilize the same resources (Appendix 1). However, niche overlap is usually quantitative asymmetric, species x usually affects species y to a different degree than species y affects species x (Hurlbert 1978, Begon *et al.* 2006). A measure of directional overlap was therefore required to supplement the information provided by the niche overlap where direct interaction occurred (Appendix 1).

Data on the distribution of the animals over different altitudes were divided into 50 meters intervals of altitude, and all intervals were assumed to be equal in abundance. This was done to reduce the margin of error due to misjudgements of the exact position of the animals observed.

2.2.2 Effect of weather

To examine how weather affected the vegetation and altitude use by reindeer and sheep (prediction ii), data on weather condition (sun/rain, wind and cloud cover) were recorded together with the other variables during transect surveys and scans. The recorded weather was further supplemented with climatic data on temperature and rainfall from the meteorological weather station at Hasvik airport ($70^{\circ}49^{\circ}N$, $22^{\circ}15^{\circ}E$). The most frequent wind direction in the area during summer is generally northwest (Danneveig 1992), also true for 2006 (*eklima.met.no*), and the climate is influenced by moisture drift from the ocean.

Because availability of the vegetation types was dependent on altitude, only the association between altitude use and weather parameters was analyzed.

2.2.3 Direct interactions

Direct interactions between reindeer and sheep were recorded with instantaneous scan sampling (Altmann 1974) at 15 minutes intervals to examine prediction (iii) and (iv). The scan sampling was carried out when reindeer were present in the core area together with sheep, and occurred mostly in Lokkarfjorddalen and Johannadalen. In addition to the scan sampling, *ad libitum* sampling (Altmann 1974) was carried out, as in previous behavioral studies (Colman 2000, Côté 2000). The same variables were documented as for the transect surveys. However, during each confrontation, the following behaviors were recorded in both species: looking up, standing, grouping together, walking away, running away, and ignoring. The geographical position was recorded as information for the observed groups' position in the terrain (flat/slope), average distance and altitude level compared to the closest individual(s) of the other species. Binoculars and a telescope were used during the observations. Laser binoculars were used to measure the distance between the species.

Observations of the species within 1000 m of one another were also extracted from the transect surveys and added to the scans and *ad libitum* samples, resulting in a total 413 and 375 observations of reindeer and sheep, respectively. Groups were considered as single observation units and observations of inactive animals (i.e. groups lying) were excluded from the analyses to strengthen the statistical independence.

To compare the behavioral responses of reindeer and sheep during each encounter, the reaction of each species towards the other was assigned as neutral if no confrontation occurred. If a confrontation occurred, a winner and looser species was assigned. The looser was defined as the species which was displaced or most interrupted during the confrontation, while the winner was the species that appeared to be dominant or not interrupted. An interruption was defined as a change in behavior to an alert or stressed state for at least two minutes. Possible outcomes of an encounter were therefore: both species were neutral, either reindeer or sheep won, or both species lost. Group size was not considered in the analyses as they were relatively similar for both species (reindeer; mean = 11, range = 1-50, SD = 13.1, sheep; mean = 8, range = 2-36, SD = 9.24), and did not appear to influence the outcome of any of the recorded encounters.

2.3 Statistical analyses

The chi-square goodness-of-fit test (Byers *et al.* 1984, Siegel & Castellan 1988) was applied to compare the use and availability of the vegetation types and altitude. A contingency table analysis with the chi square homogeneity test (Fowler *et al.* 1998) was used to examine whether the utilization of the vegetation and altitudes changed within one species between June and July. The same procedure was applied to test for similarities in preferences of vegetation and altitude.

Spearman's rank correlation (Fowler *et al.* 1998) was applied to test for association between the weather parameters and altitude use.

Binary logistic regression (Agresti 2002) with responses confrontation/no confrontation, was applied to test for the differences in interference with decreasing distance between the species (prediction iv). Distance was set to be continuous. The percentage interference and the ratio of reindeer (R) winning to sheep (S) winning was calculated. A Fisher exact test (Siegel & Castellan 1988) was used to test whether a difference existed in the number of wins between the species.

Statistical analyses were done using Minitab[®]15 Statistical Software (Minitab Inc.) and StatsDirect 2,6,2 (StatsDirect Ltd) at 5 % significance level.

3. RESULTS

Reindeer and sheep were observed on 153 and 199 occasions, respectively, during the transect surveys. The number of sheep within the study area was relatively stable throughout the summer, while the number of reindeer varied considerably (Appendix 2). The number of reindeer in the core area peaked at about 300 individuals in the beginning of July. Plotted for the entire summer combined, reindeer were more uniformly scattered throughout the study area, while the sheep remained aggregated in the core area (Figure 6).



Figure 6. The number of times a species was observed at approximately the same geographical position (i.e. in the same 100 m x 100 m square) when all data were combined, illustrating the distribution of reindeer and sheep within the study area on the Øksfjord peninsula during summer 2006.

3.1 Habitat selection

For all data pooled over the entire study area, the 12 vegetation types and snow were generally not used in proportion to their availability by either reindeer or sheep (Table 2a).

Table 2. a) Vegetation used (% represented by each vegetation type) by reindeer and sheep in June, July and for the summer 2006 combined, compared with vegetation availability in the entire study area on the Øksfjord peninsula. χ^2 tests were used to compare use and availability. Vegetation types with < 1 % availability (THW, SM, S-E and snow) where pooled together in one category. Each χ^2 test has therefore d.f. = 9.) b) Preferences (P_{ix}) for the 12 vegetation types and snow.

| Vegetation type ^t and availability (%) | | | July | | Summer 2006 | | |
|---------------------------------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|---------------------------------------------------------|--------------------------------------------------------|--------------------------------------------------------|--------------------------------------------------------|--|
| | | Sheep (n = 684) | Reindeer $(n = 1223)$ | Sheep (n = 1353) | Reindeer $(n = 1752)$ | Sheep (n = 2037) | |
| | | | | | | | |
| 0.1 | 0.00 | 0.88 | 0.00 | 0.00 | 0.00 | 0.29 | |
| 1.3 | 3.59 | 6.58 | 5.07 | 3.18 | 4.62 | 4.32 | |
| 2.8 | 1.51 | 3.80 | 0.57 | 0.89 | 0.86 | 1.87 | |
| 10.7 | 37.81 | 74.12 | 13.82 | 64.75 | 21.06 | 67.89 | |
| 11.4 | 29.87 | 6.29 | 21.01 | 9.31 | 23.69 | 8.30 | |
| 1.5 | 6.24 | 1.75 | 0.98 | 0.74 | 2.57 | 1.08 | |
| Н 6.5 0.19 | | 2.48 | 9.65 | 4.51 | 6.79 3.83 | | |
| 11.1 | 10.59 | 0.00 | 26.08 | 4.95 | 21.40 | 3.29 | |
| 3.4 | 3.97 | 0.29 | 2.70 | 0.00 | 3.08 | 0.10 | |
| 49.9 | 0.00 | 0.00 | 1.96 | 0.00 | 1.37 | 0.00 | |
| 0.1 | 0.00 | 1.75 | 1.88 | 3.84 | 1.31 | 3.14 | |
| 0.6 | 5.86 | 2.05 | 3.76 | 7.83 | 4.39 | 5.89 | |
| 0.6 | 0.38 | 0.00 | 12.51 | 0.00 | 8.85 | 0.00 | |
| | $\chi^2 = 1011.32$ | $\chi^2 = 3241.40$ | $\chi^2 = 3570.73$ | $\chi^2 = 5549.41$ | $\chi^2 = 3746.64$ | $\chi^2 = 8530.17$ | |
| | P < 0.001 | P < 0.001 | P < 0.001 | P < 0.001 | P < 0.001 | P < 0.001 | |
| | | | | | | | |
| | 0.00 | 8.80 | 0.00 | 0.00 | 0.00 | 2.90 | |
| | 2.76 | 5.06 | 3.90 | 2.45 | 3.55 | 3.32 | |
| | 0.54 | 1.36 | 0.20 | 0.32 | 0.31 | 0.67 | |
| | 3.53 | 6.93 | 1.29 | 6.05 | 1.96 | 6.34 | |
| | 2.62 | 0.55 | 1.84 | 0.82 | 2.08 | 0.73 | |
| М | | 1.17 | 0.65 | 0.49 | 1.71 | 0.72 | |
| Н | | 0.38 | 1.48 | 0.69 | 1.04 | 0.59 | |
| | 0.95 | 0.00 | 2.35 | 0.45 | 1.93 | 0.30 | |
| | 1.17 | 0.09 | 0.79 | 0.00 | 0.91 | 0.03 | |
| | 0.00 | 0.00 | 0.04 | 0.00 | 0.03 | 0.00 | |
| | 0.00^{*} | 17.50 | 18.80 | 38.40 | 13.10 | 31.40 | |
| | 9.77 | 3.42 | 6.26 | 13.05 | 7.32 | 9.82 | |
| | 0.63 | 0.00 | 20.85 | 0.00 | 14.75 | 0.00 | |
| | $\begin{array}{c} \text{(\%)} \\ \hline 0.1 \\ 1.3 \\ 2.8 \\ 10.7 \\ 11.4 \\ 1.5 \\ 6.5 \\ 11.1 \\ 3.4 \\ 49.9 \\ 0.1 \\ 0.6 \\ 0.6 \\ \end{array}$ | $\begin{array}{r c} & \begin{tabular}{ c c c c } \hline June & \\ \hline Reindeer \\ (n=529) & \\ \hline 0.1 & 0.00 \\ 1.3 & 3.59 \\ 2.8 & 1.51 \\ 10.7 & 37.81 \\ 11.4 & 29.87 \\ 1.5 & 6.24 \\ 6.5 & 0.19 \\ 11.1 & 10.59 \\ 3.4 & 3.97 \\ 49.9 & 0.00 \\ 0.1 & 0.00 \\ 0.6 & 5.86 \\ 0.6 & 0.38 \\ \chi^2 = 1011.32 \\ P < 0.001 & \\ \hline 0.00 \\ 2.76 \\ 0.54 \\ 3.53 \\ 2.62 \\ 4.16 \\ 0.03 \\ 0.95 \\ 1.17 \\ 0.00 \\ 0.00^* \\ 9.77 \\ 0.63 & \\ \end{array}$ | $\begin{array}{r c c c c c c c c c c c c c c c c c c c$ | $\begin{array}{c c c c c c c c c c c c c c c c c c c $ | $\begin{array}{c c c c c c c c c c c c c c c c c c c $ | $\begin{array}{c c c c c c c c c c c c c c c c c c c $ | |

NOTE: ^{*}This value is probably an underestimate due to few observations since no reindeer were observed in SM during the transect surveys, while they were present in SM during scans.

^tTHW, tall herb woodland; GDW, grass-dominated woodland; BW, bilberry woodland; GDV, grass-dominated scree vegetation and grassland; HDV, heath-dominated scree vegetation; M, mire/bog; H, bilberry-blue heather heath and mountain crowberry heath; LSP, late snow patch vegetation; ARV, alpine ridge vegetation; I, impediment; SM, salt marsh; S-E, seashore-ebb.

Preferences (Table 2b) for grass-dominated vegetations were high by both species throughout summer. Sheep almost exclusively utilized these vegetation types, while reindeer also preferred the heath-dominated loose rock field (scree) vegetation. Salt marsh and seashoreebb were heavily utilized during the study period by both species. In June, mires were preferred by both species, although to a much higher extent by reindeer. Snow was preferred by reindeer in July, but no sheep were observed on snow. Sheep utilized the tall-herb woodland and bilberry woodland in June, while late snow patch vegetation and bilberry-blue heather heath and mountain crowberry heath were preferred by reindeer in July.

Vegetation use in the core area (Figure 7) was similar to that for the entire study area (Table 2). Preference for vegetation types in the entire study area compared for June and July varied significantly for both reindeer ($\chi^2 = 335.89$, d.f. = 11, P < 0.001) and sheep ($\chi^2 = 125.83$ d.f. = 9, P < 0.001). Preference for vegetation types in the core area also changed considerably for both reindeer ($\chi^2 = 116.92$, d.f. = 7, P < 0.001) and sheep ($\chi^2 = 76.06$, d.f. = 6, P < 0.001) between June and July.



Figure 7. Availability (% of the core area) and use (% of the total observed individuals) of the vegetation types by reindeer and sheep. June, July and the entire summer 2006 combined. Core area, Indre Lokkarfjorden. R, reindeer; S, sheep and Sum., summer.

NOTE: GDW, grass-dominated woodland; GDV, grass-dominated scree vegetation and grassland; HDV, heath-dominated scree vegetation; M, mire/bog; H, bilberry-blue heather heath and mountain crowberry heath; LSP, late snow patch vegetation; SM, salt marsh; S-E, seashore-ebb. The category "Others" include: THW, tall herb woodland; BW, bilberry woodland; ARV, alpine ridge vegetation and I, impediment.

The altitude intervals for the entire study area were used unequally by both reindeer and sheep. Altitude intervals were also used differently when comparing June, July and the entire summer combined (Figure 8a). Close to 60 % of the sheep were found below 50 m altitude throughout summer, while reindeer were more evenly distributed between 0-600 m.a.s.l. in general throughout summer (Figure 8a). However, the preference for different altitudes varied considerably for both reindeer ($\chi^2 = 204.97$, d.f. = 10, P < 0.001) and sheep ($\chi^2 = 143.70$, d.f. = 10, P < 0.001) between June and July. There was a tendency for both species to use higher altitudes in July than June (Figure 8a, Appendix 3). The majority of the animals in the core area were observed below 200 m; approximately 78 % of the sheep in both months together with 94 % and 58 % of the reindeer in June and July, respectively (Figure 8b), and for the summer combined, 89 % and 75 % for reindeer and sheep, respectively (Figure 8b). However, the preference for different altitudes in the core area varied for both reindeer ($\chi^2 = 39.38$, d.f. = 6, P < 0.001) and sheep ($\chi^2 = 31.83$, d.f. = 7, P < 0.001) between June and July.



Figure 8. Proportions (%) of reindeer and sheep observed at the different altitudes (m.a.s.l.) in June, July and entire summer 2006 combined on the Øksfjord peninsula. Both reindeer and sheep were unevenly distributed over altitudes. **a**) Entire study area. Reindeer ($\chi^2 = 203.26$, $\chi^2 = 844.33$ and $\chi^2 = 749.48$, d.f. = 10, P < 0.001) and sheep ($\chi^2 = 2159.50$, $\chi^2 = 4322.39$ and $\chi^2 = 6394.96$, d.f. = 10, P < 0.001) **b**) Core area. Reindeer ($\chi^2 = 451.51$, $\chi^2 = 571.10$ and $\chi^2 = 976.10$, d.f. = 10, P < 0.001) and sheep ($\chi^2 = 1172.65$, $\chi^2 = 1665.87$ and $\chi^2 = 2799.56$, d.f. = 10, P < 0.001). R, reindeer; S, sheep and Sum., summer.

A high degree of niche overlap in vegetation use was recorded for reindeer and sheep, both for the entire study area, but especially in the core area because of the prevalence of sheep here (Table 3). Within the core area, the niche breadth for reindeer was almost twice the size of that for sheep in June, while the species had similar niche breadths in July (Table 3). The niche overlap in altitude (Table 3) was greatest in June, with 71 % of the reindeer and 70 % of the sheep observed below 100 meters (Figure 8b). In July, 46 % of reindeer were observed above 100 meters (Figure 8b), and the niche overlap in altitude for reindeer and sheep was reduced (Table 3). However, and despite the significant niche overlap in both vegetation and altitude use, preferences differed significantly between the species. This was true for the entire study area and in the core area (χ^2 -tests, all p-values < 0.001).

| | | Veget | ation | Altitude | | | | |
|------------|-------------------------------|-------|-------------------------------|-------------------------------|-------|-------------------------------|--|--|
| Period | Niche breadth, B ^a | | Niche overlap, L ^b | Niche breadth, B ^c | | Niche overlap, L ^d | | |
| | Reindeer Sheep | | _ | Reindeer | Sheep | _ | | |
| Study area | | | | | | | | |
| June | 0.31 | 0.16 | 3.27 | 0.72 | 0.24 | 1.49 | | |
| July | 0.21 | 0.14 | 2.80 | 0.59 | 0.23 | 1.14 | | |
| Sum. 2006 | 0.29 0.15 | | 2.79 | 0.70 | 0.24 | 1.22 | | |
| Core area | | | | | | | | |
| June | 0.41 | 0.24 | 1.62 | 0.32 | 0.19 | 3.12 | | |
| July | 0.37 | 0.36 | 1.95 | 0.43 | 0.24 | 2.58 | | |
| Sum. 2006 | 0.47 | 0.33 | 1.71 | 0.37 | 0.22 | 2.77 | | |

Table 3. Niche breadth for reindeer and sheep, and the niche overlap between the species in the different periods and the entire summer 2006 combined. Calculations are done for both vegetation and altitude, and for the entire study area and in the core area.

NOTE: ^aHulbert's (1978) general measure of niche breadth. ^bHulbert's (1978) index. ^cLevin's (1968) measure of niche breadth. ^dLloyd's (1967) index of interspecific patchiness.

Proportions of reindeer observed within 1000 meters of sheep during the summer were 39.89 %, 39.90 % and 39.89 % for June, July and the entire summer combined, respectively. Proportions of sheep observed within 1000 meters of reindeer were 39.77 %, 38.43 % and 38.88 % for June, July and the entire summer combined, respectively. The relative density between the species in the core area was measured through directional overlap. The number of sheep encountered by a reindeer on average in each vegetation type was four in June, ten in July and 14 for summer combined. The number of reindeer encountered by a sheep was three in June, eight in July and 11 for the entire summer combined. "Mean crowding" (Appendix 1) on reindeer by sheep in each altitude interval was 77 in June, 130 in July and 200 for the

summer combined. "Mean crowding" on sheep by reindeer was 60 in June, 101 in July and 162 for the summer combined.

3.2 Effect of weather

Reindeers' altitude use was more sensitive to weather conditions than sheeps'. Reindeer tended to utilize the higher altitudes on warm, calm and clear days, although this trend (Table 4) was very weak (Fowler *et al.* 1998). There was no association between differences in weather and altitude use by sheep (Table 4).

Table 4. Association between weather parameters and altitude use by reindeer and sheep for the entire study area, Øksfjord peninsula, summer 2006. Number of observations (n) and Spearman's rank correlation coefficient (r_s).

| | Rein (n = | deer 153) | Sheep (n = 199) | | | |
|-------------|----------------|--------------|--------------------|---------|--|--|
| | r _s | P-value | r _s | P-value | | |
| Temperature | 0.2815 | < 0.001 | - 0.0332 | 0.641 | | |
| Rain | - 0.0507 | 0.533 | - 0.0553 | 0.438 | | |
| Wind | - 0.2082 | < 0.01 | - 0.1256 | 0.077 | | |
| Cloud cover | - 0.3465 | < 0.001 | - 0.0626 | 0.379 | | |

3.3 Direct interactions

Reindeer and sheep were closer than 30 meters and 100 meters for 18 % and 46 % of the observations, respectively (Table 5).

Table 5. The number (n) and proportions (%) of recorded sightings of free-ranging reindeer and sheep at intervals within 1000 meters of each other. Based on transect surveys, scans and *ad libitum* sampling during summer 2006, Indre Lokkarfjorden.

| Distance (m) | (n) | (%) |
|--------------|-----|--------|
| 0 - 30 | 67 | 18.48 |
| 0 - 50 | 119 | 32.78 |
| 0 - 100 | 168 | 46.28 |
| 0 - 200 | 193 | 53.17 |
| 0 - 500 | 257 | 70.80 |
| 0 - 1000 | 363 | 100.00 |

Confrontations between reindeer and sheep were only observed when the species were within 30 meters of each other. However, 80 % (54 out of 67) encounters within 30 meters resulted in neutral behavior reactions by both species (Figure 9). Reindeer won six and lost seven confrontations, while sheep won five and lost eight confrontations. There was no difference between the number of confrontations won by reindeer and sheep (P > 0.99, Fisher exact test).



Figure 9. Free-ranging, sympatric semi-domesticated reindeer and domestic sheep on summer pasture. Indre Lokkarfjorden, summer 2006.

The proportions of encounters with confrontation increased as the distance between the species decreased from 30 meters towards zero meters (reindeer, $G^2 = 5.34$, d.f. = 1, P = 0.02 and sheep, $G^2 = 5.09$, d.f. = 1, P = 0.02).

4. DISCUSSION

4.1 Habitat selection

Reindeer were scattered throughout the study area, while sheep were aggregated in the core area. Reindeer were also more evenly distributed over different vegetation types and altitudes, and had a larger niche breadth than sheep. However, the two species had a considerable niche overlap in vegetation and altitude use. My result supports Skogland's (1984) study from Hardangervidda. He found that, although reindeer and sheep used the same vegetation types, reindeer had a more varied area and vegetation use.

Grazing ruminants appear to have an excellent memory of the location of preferred food (Lynch *et al.* 1992), and both reindeer and sheep can exhibit predictable distribution patterns from year to year (Skogland 1984, Garmo & Skurdal 1998). Free-ranging sheep usually spend the summer within restricted ranges (Skogland 1984, Ballari 1986, Garmo & Skurdal 1998), while reindeer are more meandering feeders (Gaare & Skogland 1975) that tend to have a strong response to a spatially heterogeneous resource distribution (Märell & Edenius 2006). Ballari (1986) found no indication of the stationary behavior of sheep being affected by the temporary influence of wandering reindeer in his study area. Skogland (1983) examined reindeer at three locations with different densities of sheep and found no difference in reindeers' utilization of the vegetation types. Accordingly, my observed distribution of reindeer and sheep within the entire study area could have been representative for either species regardless of the presence of the other. Area use for these two species may result mainly from social learning and the transfer of information regarding available resources through generations (Launchbaugh & Howery 2005), and less by interspecific interactions.

Reindeer and sheep have limited rumen capacity, and both have a bite off and nibbling feeding technique (Gaare & Skogland 1975, Arnold & Dudzinski 1978, Punsvik *et al.* 2006). Thus, both species are selective feeders (Skogland 1990, Garmo & Skurdal 1998), and niche overlap was expected. However, it is believed that reindeer should be more selective than sheep (Hofmann 1989), and Skogland (1984) found that vegetation used by sheep during summer was less predictable in relation to phenological changes than that of reindeer. This indicates that sheep can spend more time in one limited area, consuming lower quality forage, while reindeer wander more and actively choose food of high quality while feeding (Bevanger & Jordhøy 2004).

I found the high degree of niche overlap observed to be caused by both species preferring the grass-dominated vegetation types together with other more scarce vegetation types (i.e. salt marsh and seashore-ebb), while avoiding the large areas of impediment. For the same reason, the niche breadths for both species were relatively small, compared with observations in earlier studies of the species (e.g. Ballari 1986). Preferences for plants high in nutrients (protein and minerals) determine the selectivity for both reindeer and sheep (Wielgolaski 1975, Arnold & Dudzinski 1978, Bevanger & Jordhøy 2004, Punsvik *et al.* 2006). Preference of the grass-dominated vegetation types was probably due to the high productivity and quality of forage (Bjørklund *et al.* 2007). Salt marsh and seashore-ebb were likely important resources for minerals for both species (Garmo & Skurdal 1998, Holand 2003). Mineral content of food was for instance an important determinant of the spatial distribution of the ungulates within the Serengeti national park (McNaughton 1988). Minerals in general are often limited for grazers, and access to minerals partially determines the sheeps' range of movement in my study area (Bjørklund *et al.* 2007).

I observed a tendency in both species, and especially in reindeer, of dispersing into higher altitudes as summer progressed. This concurs with earlier observations of both reindeer and sheep following the successive snow melt and grazing on new emerging plant growth high in nutrient quantity (Skogland 1974, Skogland 1984, Nedkvitne & Garmo 1985, Melby & Orvik 1986, Gausmel 1989). Migration movements along resource gradients are well known from temperate zones as well as from the tropics (McNaughton 1990, Albon & Langvatn 1992).

The similar utilization of available resources indicates a potential for exploitation competition between reindeer and sheep. It is, however, only where species graze the same pasture that a niche overlap has an actual effect (Putman 1996). I found that reindeer and sheep were sympatric in the core area in 40 % of the observations. Species grazing sympatric on pasture may be indicate facilitation (Bell 1971), cooperative behavior (Bartos et al. 2002, Stensland et al. 2003) or simply due to lack of competition (Prins et al. 2006). The first and second explanations likely do not apply to Indre Lokkarfjorden. No systematic pattern in the sequence of grazing among the species was observed, indicating little facilitation (de Boer & Prins 1990). Large predators were also absent in the area, thus aggregation of the species was likely not in response to increased predator detection and protection (cooperative behavior). My result supports the third explanation. It is uncertain whether food resources during my study were limited or not. The pasture in Indre Lokkarfjorden is of very good quality, but the full potential for grazing is probably utilized (Bjørklund et al. 2007). Despite large niche overlap and similar preferences by the two species, the difference in preferences was statistical significant. This suggest complementary foraging to some extent (Torstenson et al. 2006).

4.2 Effect of weather

Weather conditions in Indre Lokkarfjorden had a weak effect on reindeer and no effect on sheep. Ballari (1986) and Melby & Orvik (1986) found a positive correlation between altitude use and temperature for both species on Reinøya and in Trollheimen. Melby & Orvik (1986) also found a positive correlation between rainfall and altitude use. However, rain appears to have little effect on general behavior unless it is particularly heavy (Arnold & Dudzinski 1978). My results do not contradict these two studies, although I found only weak or no trends, and this study thus support Colman (2000) who observed that compared to reindeer, sheep behavior patterns were less affected by variable climate. It has been shown that during summer, climatic variables such as wind, rain, cloud cover, and temperature are strongly correlated with insect activity (Anderson et al. 1994, Anderson & Nilssen 1996, Mörschel 1999), but have little or no direct effect on reindeer activity; i.e. the insects affect the reindeer and the weather affects the insects (Skogland 1984, Hagemoen & Reimers 2002). Summer 2006 was cold and extremely wet in my study area (eklima.met.no). This probably hindered harassment by nose bot flies (Cephenemyia trompe) and warble flies (Hypoderma tarandi), and limited the need for refuges (e.g. snow patches). The insect activity during the summer was generally low, but black flies (Simuliidae spp.) and horseflies (Tabanidae spp.) were seen on the warmer, sunny days in July. I observed reindeer on snow patches only during a few warm days, with 94 % of the observations from two days. However, the reindeer were not stressed, as they commonly are during insect harassment (Skogland 1984, Colman 2000, Hagemoen & Reimers 2002). Anderson & Nilssen (1998) suggested that reindeer used snow patches to assist thermoregulation. With maximum temperatures below 20°C, it was unlikely that heat stress occurred for either species during my study (Arnold & Dudzinski 1978, Hagemoen & Reimers 2002). The range of variation in the weather variables might also have been too narrow during the summer of 2006 to allow any patterns in potential effects of weather to be manifested.

4.3 Direct interaction

Confrontation between reindeer and sheep was observed, but only when the species were closer than 30 meters. This, however, does not necessarily imply competition. Most of the encounters were neutral (80%), and the species approached each other to within a meter without any recognizable confrontation. Thus, sheep and reindeer were only a vague source of disturbance for each other from a behavioral point of view. My result support previous observations of no interspecific exclusion in ruminants through aggressive behavior (Bartos *et*

al. 2002, Prins *et al.* 2006). Reed (2001) found that mountain goats (*Oreamnos americanus*) were dominant over sympatric mountain sheep (*Ovis canadensis canadensis*). Sheep yielded space or other resources in 39 out of 107 encounters between the species, while eight encounters resulted in reaction by mountain goats from the presence of sheep. Reed (2001) suggested that because mountain goats exhibit relatively high intraspecific aggressiveness (Fournier & Festa-Bianchet 1995, Côté 2000), they will be aggressive in interspecific interactions with other similar sized ungulates, hence dominance may be expected. Importantly, however, Reed (2001) does not clarify the composition of the groups observed; males tend in general to be more aggressive than females (Lynch *et al.* 1992). The number of wins during encounters was similar in reindeer and sheep, indicating that neither was dominant. Although I observed interference between the species, neither of the species exhibited aggression towards the other. This could be expected, because intraspecific aggressiveness in ewes (Lynch *et al.* 1992) and in reindeer females in fostering herds (Skogland 1984) is relatively rare.

Group size could be an important factor during encounters. Colman (2000) observed that reindeer were not dominant in an aggressive manner, but suggested that reindeers' much larger average group size caused sheep, with relatively few individuals in a group, to retreat from reindeer approaching in groups of up to hundreds of individuals more often than visa versa. The group sizes of sheep and reindeer in Indre Lokkarfjorden were similar, and might have contributed to the low degree of interference between the two species.

It can be questioned whether the large number of neutral interactions represented tolerance or an absence of intrusion between the species. Half of the 14 encounters within five meters and two thirds of the 28 encounters within ten meters were neutral. This, together with the lack of aggressive behavior, indicates a relatively high degree of interspecific tolerance. Importantly, however, interference competition is unlikely to evolve unless there is exploitation competition (Case & Gilpin 1974). But, even if resources were limited, individuals might have been better off with tolerance of others, i.e. costs of aggression could be higher than the benefits (Drickamer *et al.* 2002). With exploitation competition, food depletion takes place by the first individual, irrespective of species identity, that encounters a resource item (de Boer & Prins 1990). Studies have shown that sympatric grazing result in an increase in intensity of feeding (Arnold & Dudzinski 1978), indicating that each individual tries to get its share.

Because of the similar relative densities of reindeer and sheep in the Indre Lokkarfjorden, it was logical that the species had a similar amount of encounters with each other. In Skogland's (1984) study from Hardangervidda, there were almost eight times more reindeer than sheep per km². He found that sheep were within 700 meters of reindeer in 16 % of the reindeer observations, while reindeer were within 700 meters of sheep for 41 % of the sheep observations. In Colman's (2000) study in Setesdal-Ryfylke, there were 15 times more sheep than reindeer per km². In his case, sheep were within 1000 meters on 84 % of the reindeer observations. These three studies show that the percent of encounters for one species with another is relative to the density for each of the two species.

I found that the number of encounters ending in confrontation increased as distance decreased from 30 meters towards zero meters. These confrontations were likely not due to interspecific competition, although a similar pattern was found within the range from 0-200 meters in wild reindeer and sheep (Colman 2000). However, with six out of 13 confrontations within five meters, I suggest that this may be a general response of getting too close and affecting an individual's own space. The individual space (i.e. the distance at which individuals will tolerate each other) is believed to be 2-3 body lengths in ungulates (Arnold & Dudzinski 1978). This was supported by (Colman 2000), who found that reindeer not being harassed by insects and sheep had exactly the same average distance, approximately two body lengths, between individuals in a group. Sheep prefer to associate with sheep of the same breed and develop a group identity, so when other sheep are introduced, even if they are of the same sex and age, it may take several weeks for the groups to become integrated (Arnold & Dudzinski 1978). This is due to a higher tolerance of familiar individuals than unfamiliar ones. Assuming that the same holds for reindeer, it follows that with a large majority of encounters between reindeer and sheep resulting in neutral interaction (this study and Colman 2000), an increase in total number of encounters may result in a habituation effect and interference might actually decrease.

5. CONCLUSION AND MANAGEMENT IMPLICATIONS

Reindeer and sheep had a considerable niche overlap in vegetation and altitude use; supporting prediction (i). Reindeer tended to utilize the higher altitudes on warm, calm and clear days, while no such pattern was observed in sheep; only partly supporting prediction (ii). Prediction (iii) was not supported. Reindeer and sheep grazed in close proximity (within a meter) without any aggression towards each other. Confrontations were only observed when the species were closer than 30 meters, and in 20 % of the encounters. The number of encounters with confrontation increased as the species came closer; supporting prediction (iv). Importantly, however, with a relatively high degree of tolerance, an increase in number of encounters will most likely induce a habituation effect. With a considerable niche overlap between reindeer and sheep, and no interspecific exclusion through aggression (direct interference competition), one can expect exploitation competition when food resources are limited. Therefore, instead of separating reindeer and sheep, management decisions should be based on the total number of animals present compared to pasture quality and quantity.

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Measures

Measures for habitat preference, niche breadth, niche overlap and directional overlap applied to examine whether reindeer and sheep utilize the same habitat through overlap in use of vegetation and altitude.

Vegetation

1.
$$P_{ix} = \frac{U_{ix}}{a_i}$$
 The habitat preference index (P_{ix} for species *x* and vegetation type *i*) was adapted from Hunter and Franklin *et al.*. The index varies from $P_{ix} = 0$ (total avoidance), through $P_{ix} = 1.0$ (no preference) to higher values for increasing degrees of preference.

2.
$$B' = \frac{X^2}{A\sum_i (x_i^2/a_i)}$$

Hulbert's general measure of niche breadth, allows for variation in vegetation abundances
$$(a_i)$$
 of the vegetation types. The measure assumes values ranging from a_{min}/A to 1.0, where a_{min} represents the abundance of the least abundant vegetation type.

3. $L = \frac{A}{XY} \sum_{i} \frac{x_i y_i}{a_i}$ Hulbert's index. Measure for the overlap in distribution of the species over the vegetation types. The index varies from L = 0 (no resource state is shared by the two species, indicates that the two species are completely dissimilar), through L = 1.0 (both species utilize each resource state in proportion to its abundance, complete overlap), to L > 1.0 if each species utilizes certain resource states more intensively than others and the preferences of the two species coincide (Lawlor 1980).

4.
$$Z_{x(y)} = \sum_{i} \frac{x_i y_i}{Xa_i}$$
 Rathcke's (1976) coocurrence coefficient for directional overlap, allows for variation in vegetation abundances (a_i) . The measure equals the density of species y encountered, on the average, by an individual of species x. The reciprocal measure $Z_{y(x)}$ is calculated in an analogous way.

<u>Altitude</u> (All altitude intervals were assumed to be equal in abundance.)

| 5. | B = | $\frac{1}{n\sum_{i}p_{xi}{}^{2}}$ | Levins' (1968) measure of niche breadth. The measure can take values ranging from 1/n (when only a single vegetation type is used) to 1.0 (when each vegetation type is utilized in proportion to its abundance) |
|----|-----|-----------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| | | | its abundance). |

6.
$$L = n \sum_{i} (p_{xi} p_{yi})$$
 Lloyd's (1967) index of "interspecific patchiness" for niche overlap. The index may take the same values as in equation 3.

7.
$$Z_{x(y)} = \sum_{i} \frac{x_i y_i}{X}$$
 Lloyd's (1967) "mean crowding on species 1 by species 2" measure for directional overlap. The measure equals the density of species y encountered, on the average, by an individual of species x.

Variables referred to in the measures

A = the total study area

- Y = the total number of individuals of species *y* observed
- n = total number of resource states

$$a_i$$
 = (the proportion of the study) area covered by vegetation type *i*

 x_i = number of individuals of species x observed in resource i

 y_i = number of individuals of species y observed in resource type *i*

 $p_{xi} = x_i/X$, proportion of individuals of species x that are found in resource i

 $p_{yi} = y_i/Y$, proportion of individuals of species y that are found in interval i

 U_{ix} = the proportion of individuals of species *x* observed in resource *i*

X = the total number of individuals of species *x* observed

Result from the transect surveys

Outline of the number (n) of reindeer and sheep recorded by mapping the positions of the animals within the study area – summer 2006, Øksfjord peninsula. Numbers in brackets () indicate observations where the species were within 1000 meters of one another, these are included in the total. Three different transects were used (Figure 2d). *Transect was not completed due to bad weather. **Transect from the previous day was completed.

| | | | Reindeer | | | Sheep | | | | | |
|---------------|-----------------|----------|------------------|------|---------------------------------|-------|------------------|------|------|----------------|--|
| Date | Start (time) | Transect | Observations (n) | | Observations Animals (n) (n) | | Observations (n) | | An | Animals (n) | |
| June | | | | | | | | | | | |
| <u>10.</u> | 12:30 | 1 | 1 | | 5 | | 0 | | 0 | | |
| 12. | 10:35 | 2 | 11 | (8) | 91 | (77) | 4 | (4) | 64 | (64) | |
| 14. | 10:15 | 3 | 1 | | 7 | | 10 | ~ / | 100 | × / | |
| 17. | 10:05 | 2 | 10 | (9) | 112 | (109) | 7 | (5) | 114 | (75) | |
| 19. | 11:10 | 1 | 6 | (2) | 116 | (9) | 0 | | 0 | | |
| 20. | 17:05 | 1 | 9 | | 109 | | 2 | | 30 | | |
| 22. | 11:55 | 3 | 6 | (3) | 30 | (8) | 12 | (11) | 97 | (94) | |
| 25. | 23:50 | 2 | 2 | | 31 | | 7 | | 46 | | |
| 28. | 15:45 | 3* | 0 | | 0 | | 11 | | 102 | | |
| 29. | 16:40 | 2 | 3 | (1) | 28 | (8) | 9 | (1) | 131 | (39) | |
| <u>July</u> | | | | | | | | | | | |
| 2. | 19:00 | 3 | 11 | (2) | 112 | (11) | 8 | (5) | 122 | (113) | |
| 4. | 11:00 | 1 | 18 | (7) | 367 | (109) | 3 | (3) | 28 | (28) | |
| 6. | 11:40 | 2 | 17 | (16) | 226 | (214) | 12 | (12) | 101 | (101) | |
| 8. | 11:05 | 3* | 4 | (1) | 78 | (1) | 9 | | 136 | | |
| 9. | 14:10 | 3** | 0 | | 0 | | 0 | | 0 | | |
| 10. | 11:00 | 2 | 4 | (1) | 78 | (2) | 10 | (8) | 139 | (111) | |
| 12. | 11:30 | 1 | 0 | | 0 | | 1 | | 10 | | |
| 13. | 11:00 | 1 | 1 | | 9 | | 3 | | 17 | | |
| 15. | 10:30 | 3 | 3 | | 39 | | 13 | | 113 | | |
| 17. | 12:30 | 2 | 1 | | 5 | | 13 | | 143 | | |
| 19. | 13:15 | 1 | 3 | | 35 | | 3 | | 14 | | |
| 22. | 12:45 | 2 | 0 | | 0 | | 15 | | 132 | | |
| 25. | 21:20 | 1 | 1 | | 24 | | 1 | | 6 | | |
| 27. | 11:20 | 3 | 5 | (3) | 30 | (26) | 9 | (2) | 95 | (6) | |
| 28. | 14:45 | 2 | 2 | (1) | 2 | (1) | 8 | (2) | 116 | (9) | |
| 29. | 12:15 | 1 | 2 | | 2 | | 0 | | 0 | | |
| 30. | 16:05 | 1 | 2 | | 2 | | 0 | | 0 | | |
| <u>August</u> | | | | | | | | | | | |
| 1. | 11:40 | 3 | 11 | (2) | 116 | (57) | 9 | (6) | 56 | (42) | |
| 3. | 10:05 | 2 | 12 | (7) | 84 | (65) | 18 | (15) | 122 | (107) | |
| 5. | 11:30 | 1 | 7 | (1) | 14 | (2) | 2 | (2) | 3 | (3) | |
| Total | | | 153 | (64) | 1752 | (699) | 199 | (76) | 2037 | (792) | |

