Reindeer avoidance of pasture contaminated with sheep and reindeer faeces

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Abstract: Contamination by excrements will increase in areas with high animal densities, such as snow free patches with accessible forage in winter and holding paddocks. Avoidance of faeces dropped by other grazers may result in interference competition by reducing optimal forage intake, or offer protection from the transfer of parasites or disease. We conducted two enclosure experiments investigating reindeer (Rangifer tarandus) reactions towards faeces. The first experiment tested whether reindeer avoid pasture contaminated with faeces from reindeer or sheep (Ovis aries). Both high (0.5 kg/m^2) and low (0.05 kg/m^2) concentrations of faeces reduced reindeer grazing compared to no faeces. Reindeer grazed significantly less in areas with high concentration of faeces compared to areas with low concentrations, with equally strong avoidance regardless of faeces source. The second experiment analysed the defecation pattern (random or not) of reindeer in a 50 m x 40 m enclosure to investigate how this pattern might change following the introduction of female sheep or additional female reindeer. Both reindeer and sheep defecated in a non-random pattern that was related to their preferred bedding sites. When sheep visited reindeer, the species' faeces distributions were positively correlated, indicating that reindeer and sheep had an overlap in area utilization, at least while bedding. When additional reindeer were introduced and then removed, the combined resident and visiting reindeers' faeces distributions were negatively correlated with the resident reindeers' faeces distribution following the removal of the visiting reindeer. This suggested that resident reindeer avoided the visiting reindeers' faeces. Resident reindeer also produced fewer total droppings when visited by new reindeer, while the number of droppings did not change when visited by sheep. Thus, resident reindeer were more adversely affected by the introduction of new reindeer even after their removal than by the introduction of sheep. In conclusion, the amount and distribution of excrements will play an important role in reindeer grazing and area use in pastures maintaining high densities of reindeer or reindeer and sheep.

Key words: competition, faeces distribution, grazing, spatial overlap, sympatric ruminants, parasite aversion.

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Introduction

Norway currently manages the remaining Fennoscandian populations of wild tundra reindeer (Rangifer tarandus tarandus) in the mountains of South-Norway. In addition to wild reindeer, reindeer herdsmen (almost exclusively Sami) maintain approximately 183 000 semi-domestic reindeer in the northeastern part of South-Norway and in North-Norway. Domestic sheep are prevalent with wild and semi-domestic reindeer on alpine summer range, exceeding densities of 30 sheep per km^2 in some areas, e.g. in Setesdal-Ryfylke in southwestern Norway (Colman, 2000). To a large extent, reindeer and sheep overlap in plant resource utilization (Skogland, 1984; Ballari, 1986; Colman et al., 1998; Mysterud, 2000). Thus, direct competition between reindeer and sheep would be expected when resources are limited.

Limited information exists on competition between sympatric ruminants like reindeer and sheep (Ballari, 1986; Warren & Mysterud, 1986; Colman, 2000). An indirect form of interference or competition may occur if the species avoid feeding in locations that contain excrements from the other species (Putman, 1996). Data from a stall-fed experiment (Moe et al., 1999) showed that reindeer avoid eating when faeces from either species were mixed in their rations. Questions remain whether reindeer or sheep avert from otherwise preferred pasture locations because of the presence of faeces from the other species.

The amount of excrement and its distribution may be important factors influencing avoidance behaviour, but little is known about the defecating patterns for reindeer on pasture. Reindeer often use small areas of pasture due to spatially limited resources, for example in winter when cratering for forage through snow. Semi-domestic reindeer may also be held in pre-slaughter pens or holding paddocks before or after transportation. In such areas, high animal densities relative to foraging area will increase contamination by excrements.

From a previous pen experiment with reindeer (Moe et al., 1999), we expected reindeer to reduce feeding time on pasture contaminated with reindeer and sheep dung. Although never specifically tested, data from Moe et al. (1999) indicate that reindeer are more avers towards sheep faeces than to reindeer faeces. Studies of within species systems also show that avoidance increases with increased level of contamination (Hutchings et al., 1998). Thus, we tested the following hypothesis:

1) Reindeer spend less time feeding in areas contaminated with faeces from either reindeer or sheep.
2) Reindeer avoidance of areas contaminated with sheep faeces is stronger than towards areas contaminated by reindeer faeces.
3) Reindeer avoidance of areas increases with the faecal concentration regardless of the faecal source.
4) Reindeer defecate in a random pattern that reflects their grazing pattern and not their use of bedding sites.
5) Introducing sheep into an enclosure with reindeer increases interspecies avoidance due to faeces avoidance between species. This reduces areas of faeces overlap both during the co-inhabitation and after the removal of the sheep.
6) Introduction of naive reindeer into an enclosure with resident reindeer will result in co-use of areas by both groups of reindeer. This would suggest a mixing of faeces, measured by comparing faeces overlap following the removal of the visiting reindeer.

Methods

Site description

The study was conducted in an open farm landscape in the Bognelv river valley, about 5 km from Langfjordbotn, Finnmark county, North-Norway (22°19'E, 69°59'N). The experimental area was a level 2 ha field at sea level. It has not been ploughed or sowed during the last 25 years and consist of a homogenous mixture of native and planted grasses. The experiment's location in an open agricultural area, combined with a short distance from the ocean and a cold-water river system, provided an almost constant wind over the experimental area (registered during the experimental period (Eidesen, 2002)). This probably reduced harassment on animals by parasitic flies compared to inland areas.

Experimental design

Experiment 1

This experiment was designed to test reindeer avoidance of sheep and reindeer faeces (predictions 1, 2 and 3). Three 10 m x 10 m enclosures were set up on a level field where no animals had previously grazed, and thus, was free of excrements. Vegetation in the 3 enclosures consisted of a homogenous mixture of earlier planted grasses cut to 15 cm in height two days prior to releasing animals onto the pastures. A height of 15 cm was chosen to facilitate and maintain green growth, provide an average height similar to natural grass pastures, and allow the excrements to be evenly distributed within each treatment square. Each enclosure was divided into 25 squares of 4 m^2. The size of the enclosures and squares was chosen to represent the approximate size of a free ranging reindeer's feeding radius and specific grazing patches while grazing intensely for approximately 30 minutes (Colman, 2000). The inside corners of each 4 m^2 square were measured to the nearest 1 cm and marked with a small white circle of paint on the grass clearly visible to the observer, who sat in a 5 m high observation tower placed 5 m away from the enclosures. The outside corners of the 4 m^2 squares were marked with white paint or a white ribbon on the fence surrounding the enclosure. Four treatments and a control, with 5 replicates in a randomised design were used in each of the 3 enclosures (Table 1). The treatments were high (0.5 kg/m^2) and low (0.05 kg/m^2) concentrations of reindeer (RH, RL, respectively) and sheep (SH, SL, respectively) faeces. The dry matter content in the faeces used was about 50%. This provided a dry matter concentration of 250 g and 25 g per m^2 for high and low faeces concentrations, respectively. If 35% of 80 kg faeces were distributed on 5% of 1 hectare, this would give 56 g

Table 1. The treatment and animal densities used during the 3 periods for the faeces distribution experiment, northern Norway, June 1999.

Period	Date	Enclosures 1	2	3
1	10. - 16. June 1999	3 reindeer	3 reindeer	3 reindeer
2	17. - 23. June 1999	3 reindeer + 3 reindeer	3 reindeer + 3 sheep	3 reindeer + 3 sheep
3	24. - 30. June 1999	3 reindeer	3 reindeer	3 reindeer

dry matter per m² and about 112 g wet weight per m² from one sheep or reindeer (as was supported by the results of experiment 2). Considering that sheep tend to aggregate in camp areas to bed at night (Hilder, 1966; Colman, 2000), and reindeer are occasionally restricted to limited pasture area, the level of faecal contamination in some areas is likely to greatly exceed the highest concentration of 250 g dry matter of faeces per m² used in this experiment.

Fresh reindeer faeces (mixture of 1 to 13 days old) were obtained from adjacent pastures one day prior to the onset of the experiment. Sheep faeces were collected from a sheep farm 12 hours before the experiment began, and were a mixture of 1 to14 days old. Both reindeer and sheep faeces were wet in tepid water 12 hours before the onset of the experiment to provide an equal amount of moisture (i.e. "simulated freshness") to all the faeces. Faeces were then spread as evenly as possible by hand wearing rubber gloves. To facilitate feeding during the experiment, the animals were offered water but not fed for 12 hours prior to the onset of the experiment. Six female reindeer yearlings were used in the experiment. One animal at a time was released into an experimental enclosure for 30-min each. Using 3 enclosures and 6 animals required that only 2 consecutive experimental trials were used per enclosure (3 repetitions in "pasture" with a repeated measure by 2 reindeer in each paddock). This provided the dual advantage of minimising contamination and overgrazing by the first animals.

All 6 reindeer were habituated towards humans and thus, our presence did not appear to influence their behaviour during the experimental trials. The reindeers' feeding time and position within the enclosure was recorded using focal observations (Altmann, 1974). Using a stopwatch with up to 1000 "lap-times", the animals' activities and positions were recorded to the nearest second and included; feeding, standing, walking, and running (the animals never laid down during trials). Feeding was only considered an act of ingesting forage with the animals' muzzle down and actively biting vegetation (grass), and did not include the activity in which the animals were searching the immediate feeding site for food. The acts of biting or searching were clearly visible (and biting was audible) by the observer at all times. The position of the reindeer within the enclosure (within which of the 25 4 m² squares the reindeer was located) was recorded together with every change in activity. Duration of all trials was 30 minutes. For each reindeer, we then tabulated the total amount of feeding combined for each treatment and the control. Differences in the combined time reindeer grazed within treatments were tested using Kruskal-Wallis ANOVA on ranks followed by Student - Newman - Keuls pair-wise multiple comparison procedure (Glantz, 1992).

Experiment 2

Here, we originally used a set up of 6 enclosures each 50 m x 40 m arranged sequentially. The enclosures were homogeneous, i.e. similar with regard to size, shape and vegetation. The fences between the enclosures were covered with fabric to inhibit visual contact among the animals. All corners in each individual enclosure were covered with the same fabric to provide animals with shelter and shade. Two water buckets with running water were placed opposite each other in the middle of the 50 m side in each enclosure to provide the animals with drinking water. All enclosures were cleared of dung at the start of the experiment.

This was part of a larger experiment to study reindeers' within and between group synchronicity and their behaviour response towards sheep (Colman, 2000; Eidesen, 2002). The experiment was divided into three time periods (10-16 June 1999, 17-23 June 1999 and 24-30 June 1999) (Table 1). Three reindeer yearlings (resident reindeer) were released in each of the enclosures at the beginning of period 1. At the beginning of period 2, three sheep were released in 2 enclosures, and three new reindeer were released into 2 other enclosures (visiting reindeer and sheep, respectively). The two control enclosures did not receive visitors. At the end of period 2, the visiting animals were removed from the enclosures and the resident reindeer remained for period 3.

The enclosures were separated into squares by extending string between the fences and the number of pellet groups (defined below) was counted in each square. Due to time limitations in regards to the

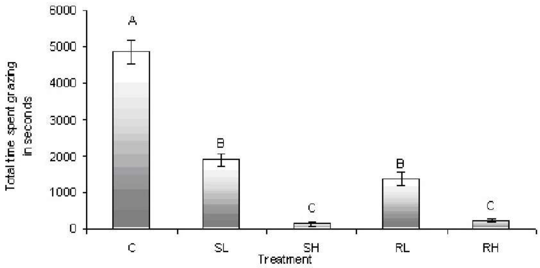

Fig. 1. Reindeer (n=6) grazing time (±SD) on areas contaminated with different concentrations of sheep and reindeer faeces. C-control, SL-low concentration of sheep faeces, SH-high concentration of sheep faeces, RL-low concentration of reindeer faeces, RH-high concentration of reindeer faeces. Columns with the same capital letter are not significantly different (ANOVA on ranks followed by Student-Newman-Keuls multiple comparison method, P<0.05).

behaviour experiment, we were unable to count faeces in all 6 enclosures. Enclosure 1 and 3 were separated into 48 squares, each 42 m^2. Because the fence poles were placed closer together in enclosure 2 than in enclosure 1 and 3, enclosure 2 was separated into 56 squares, each 36 m^2. Square size was defined out of practical purposes and on the basis of balancing the largest possible size of squares within the enclosure and an adequate number squares for a successful statistical analysis for faeces distribution. We controlled for unequal square size by analysing averages, i.e. relative values. We also assumed that there were enough squares in both cases (48 squares or 56 squares) and that they were similar enough in size (each 42 m^2 or 36 m^2, respectively) to properly represent the true faeces distribution in each enclosure.

After each of the 3 periods, we counted and recorded the location of sheep and reindeer faeces in the three enclosures. Faeces were recorded as the number of pellet groups in a square. One pellet group indicated one animal's defecation. The pellet groups were either soft deposits of faeces or a group of hard, often scattered, pellets, both easily identified as a single, independent pellet group. No faeces were removed in any of the enclosures during the experimental periods and this led to a high accumulation of faeces during the experiment. The average number of defecations per reindeer or sheep per day was calculated as the total number of pellet groups deposited in each enclosure at all periods added up and divided by the number of animal grazing days.

With this experiment, we first aimed to investigate the defecation pattern (random or not, and average number of defecation's per animal per day) for reindeer in an enclosure situation (prediction 4). We used a χ^2- test for agreement with a Poisson series (Elliott, 1977) to test whether reindeer pellet groups were randomly distributed inside the enclosures. When the variance is larger than the mean, aggregation occurs. If the variance was equal to the mean, the distribution was random. If the variance was less than the mean, distribution was regular. If the defecation pattern were to be random (and not related to bedding sites), we could then assume that reindeers' defecation pattern reflects their grazing pattern. If this were to be true, we could then test whether reindeer avoided grazing where there were faeces from either species using the same correlation analyses described below. We assumed that this part of experiment 2 was not compromised by the lack of recordings in all 6 enclosures.

We also explored how the defecation pattern changed for resident reindeer following the introduction of 3 adult female sheep or additional 3 adult female reindeer into the enclosures by testing for a positive or negative correlation (overlap) between the animals' faeces distributions (prediction 5 and 6). In connection with this, we also tested whether the resident reindeers' faeces distribution was correlated after the removal of the 3 visiting animals in order to test for an eventual avoidance of faeces from either species as a result of their visit. We used a Spearman rank order correlation to compare distribution of sheep and reindeer faeces, spatial changes in distribution of faeces between the different periods, and changes in distribution of faeces with increasing and then decreasing animal density following the introduction and then removal of additional animals (avoidance towards faeces from either species). The lack of recordings in all 6 enclosures meant that we were unable to include the original replications for each treatment. All statistical analyses were performed using the program Sigmastat (Jandel Scientific, 1994).

Results

Experiment 1

Each reindeer was allowed 30 minutes in the experimental enclosure and as expected, spent most of that time, from 63.9% to 97.2%, grazing. Reindeer spent significantly less time grazing in both the high- and the low-contaminated squares compared to the control for both reindeer and sheep faeces treatments (ANOVA on ranks, P<0.05; Fig. 1). This would suggest faecal contamination of a site reduces its preference as a site for foraging. Reindeer spent significantly less time grazing in high-contaminated

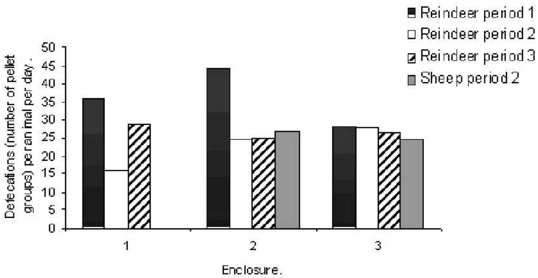

Fig. 2. Mean number of defecations (recorded as pellet groups) per animal per 24 hour in 0,5 ha enclosures 1, 2 and 3 during June 1999 (period 1: 10-16, period 2: 16-23 and period 3: 23-30).

squares with sheep or reindeer faeces compared with low-contaminated squares regardless of faecal source (ANOVA on ranks, $P<0.05$; Fig. 1), lending support to prediction 3. However, no significant difference ($P>0.05$) was found between source of faeces and its influence on avoidance of a contaminated area (ANOVA on ranks, $P>0.05$; Fig. 1). Thus, reindeer apparently do not avoid areas contaminated with sheep faeces moreso than similar areas contaminated with reindeer faeces.

Experiment 2

The mean number of defecation's per 24 hour for reindeer and sheep (among all three periods) was 27.3 (±7.26 SD) and 25.8 (±1.10 SD), respectively. When 3 visiting reindeer were introduced, the mean number of defecation's per reindeer per day for the resident reindeer dropped from 35.5 in period 1 to 16.1 defecations in period 2. This may reflect a reduction in grazing among individuals that in turn likely reflects increased inter-specific competition within the group. This was further supported when the mean number of defecation's per reindeer per day for the resident reindeer rose again to 28.9 in period 3, following the removal of the visiting reindeer (Fig. 2). Compared with visiting sheep, the mean number of defections per reindeer per day did not change during or after the sheep were introduced in either group 2 or 3 (Fig. 2).

Spatial distribution of reindeer pellet groups was not uniform across the area; 35% were distributed on 16% of the area (χ^2-test for agreement with a Poisson series, $P<0.01$). For sheep, the spatial distribution of pellet groups indicated 35% of the faecal output was found on 19% of the area (χ^2-test for agreement with a Poisson series, $P<0.01$). Both species usually defecated within one minute after rising from a lying bout. In light of this, and also contradicting prediction 4, we could not relate the reindeers' faeces distribution to their grazing pattern and thus, no further assumptions towards this relationship could be made.

Concentrations of sheep and reindeer faeces were positively correlated ($r=0.32$, $P=0.001$, $n=104$) following the period sheep and reindeer had been together (recorded at the end of period 2 in enclosure 2 and 3). This indicated that reindeer and sheep did not segregate themselves, at least while bedding. When the sheep were removed, no significant correlations ($r=-0.14$, $P>0.05$, $n=104$) were found between the resident reindeers' faeces at the end of period 3 and all the sheep and reindeer faeces combined from period 2. Faeces avoided by the resident reindeer towards the visiting reindeer most likely occurred, reflected in a negative correlation ($r=-0.33$, $P=0.02$, $n=48$) between the faeces distribution for the resident reindeer in period 3 and the combined faeces for resident and visiting reindeer in period 2. Furthermore, a positive correlation ($r=0.43$, $P=0.003$, $n=48$) was found when comparing the resident reindeers' faeces distribution after period 3 with their distribution after period 1, indicating a return for the resident reindeer to a "normal" pre-additional-reindeer-visit pattern when the visiting reindeer were removed.

Together with the results from the number of defecations per reindeer per day, the inter- and intraspecies faeces correlation analyses demonstrate that the introduction of additional reindeer resulted in a considerably stronger negative effect on the resident reindeer than the introduction of sheep.

Discussion

Reindeer avoided pastures contaminated with dung compared to uncontaminated areas of the pasture (control). This supports the theory that reindeer avoid foraging in areas contaminated with faeces. Furthermore, as faeces concentration increased, a stronger avoidance was recorded. This would indicate that faecal density does affect use of areas in which reindeer forage. However, we found no significant ($P>0.5$) difference in pasture use depending on its source of faecal contamination, i.e. from reindeer or sheep. Van der Wahl et al. (2000) found that Svalbard reindeer avoided pastures having a high density of reindeer dung. Other intraspecific experiments have shown sheep reject pasture contaminated with sheep faecal material, with a stronger avoidance associated with increasing faecal concentrations (Hutchings et al., 1998).

Besides Moe et al.'s (1999) stall-fed study, studies of indirect interference competition in the form of faeces avoidance between sympatric herbivores are lacking. Although some have shown otherwise (White & Hall, 1998; Clutton-Brock et al., 1987), selective grazing by large herbivores to avoid faecal contaminated areas on pastures is well documented (Marten & Donker, 1964; Hafez, 1975; Forbes & Hodgson, 1985; Hutchings et al., 1998; 1999). Such grazing distribution patterns may affect pasture utilisation (Arnold, 1962). On the other hand, the deposition of faeces may create patches of grass with a relatively high level of nutrients and energy (Haynes & Williams, 1993). These relatively nutrient rich patches can attract herbivores for grazing. However, they may also represent a risk of parasitic infection to herbivores as a result of the migration of helminth parasite larvae from the faeces to the sward (Sykes, 1978). Van der Wahl et al. (2000) hypothesised that Svalbard reindeer (R. t. platyrhynchus) minimised their risk of gastro-intestinal nematode infection by avoiding patches having a high faecal density. Helminth parasites have been shown to affect the growth rate, fecundity and probability of mortality of their hosts (Anderson, 1978; Gulland, 1992). In the light of this, there should be a strong selective force on the host to minimise the detrimental consequences of parasitism through faecal avoidance (Hutchings et al., 1998; 1999). Reindeer and sheep share many abomasal nematodes (Bye, 1987) that those reduce growth in sheep (Sykes, 1978) and may potentially also reduce growth in reindeer. Thus, reindeer growth rates on summer ranges may be improved if they avoid foraging on areas contaminated with reindeer or sheep faeces if other forage is not limited. In West Greenland, Clausen et al. (1980) found a severe drop in cow/calf ratios from 70 to 24 calves per female from June to August. They showed that the death of most calves was a result of severe E. coli infections presumably transmitted through faeces consumed while grazing in intensively contaminated (faeces concentrations of 4500 kg/ha) Poa pratensis grassland areas (Clausen et al., 1980). Our study suggests that reindeer have evolved a strong inter and intraspecific faeces avoidance behaviour and this may drastically improve their fitness to contracting parasite and/or E. coli infections.

Sheep faeces distribution in our second experiment showed that sheep tend to defecate more in certain areas than others, as was expected. King (1993) and Hilder (1966) found that a third of the faecal output was in less than 5% of the paddock area for merino sheep in Australia. White & Hall (1998) on the other hand, found in their study of lambs that a third of the faecal output was concentrated in 15.7% of the paddock area. That amount is similar to our study, where 35% of sheep faecal output was on 19% of the area, and 35% of reindeer faecal output was on 16% of the area, i.e. reindeer pellet groups were non-randomly distributed in the enclosures. This was a new finding for reindeer. At least in an enclosure situation, reindeer defecation patterns were strongly related to preferred bedding sites, as it was for sheep. Wild reindeer do not usually have preferred bedding sites that they return to in any consecutive manner. However, sheep and semi-domestic reindeer often return to bedding sites within their home range or pre-arranged grazing areas, both while free ranging and especially when held in paddocks. We suggest that reindeer and sheep would defecate in a similar pattern as we recorded regardless of whether they were free ranging or not, i.e. mostly within one minute of standing up following a laying bout and consequently, close to a bedding site. Thus, at least for semi-domestic reindeer, care should be taken to include enough area in a paddock to allow for grazing and bedding sites as two separate areas.

Information concerning dunging behaviour of free ranging animals is limited, and it is unclear to what extent the behaviour patterns observed in an enclosure are merely an effect of confinement, as suggested by Odberg & Francis-Smith (1976) and Edwards & Hollis (1982). However, our results are consistent with Putman (1996), who discussed that animals generally deposit more excreta on areas where they congregate, or at specific latrine sites within a home range or territory. Grazing behaviour of 20 lambs was investigated after sheep faeces were removed from randomly chosen areas, and the removal of faeces had no effect on grazing behaviour (White & Hall, 1998). The only correlation between faecal abundance and behaviour was that night lying tended to be on areas where faecal abundance was high (White & Hall, 1998).

When introducing sheep to reindeer inhabited enclosures we found that the locations of reindeer and sheep faeces were positively correlated. In period 2 when six reindeers were together, the average number of defecations per reindeer per 24 hours dropped from 35.5 in period 1 to 16.1 in period 2, indicating less food intake. Importantly, the average number of defecations per reindeer per day rose to 28.9 when the animal density was halved again. In the enclosures where sheep were introduced to reindeer, reindeer defecations remained constant and similar to pre- and post-treatment levels. Thus, resident reindeer appeared more negatively affected by the introduction of new reindeer than by introduction of sheep, lending support to the claim that interspecific competition is stronger than intraspecific competition (Caughley & Sinclair, 1994). These results were supported by the behaviour data recorded for the same experiment (Eidesen, 2002). For example, the behaviour study showed that reindeer in the reindeer groups were considerably more aggressive towards each other than the animals in the reindeer-sheep and control groups.

In a pasture situation, we predicted reindeer to avoid contaminated areas only as long as food unaffected by faeces is available. The reindeer in the first experiment were hungry at the onset of the experiment and grazed intensively, in addition to being limited by the size of the enclosure. We would expect less hungry, free ranging reindeer to show more avoidance towards faeces than hungry and enclosed reindeer, similar to what was found for sheep (Hutchings et al., 1998). We also suggest that in a high density, high-contaminated situation, reindeer grazing, and ultimately their condition, will be less than optimal regardless of resource availability because of their avoidance of faeces.

Reindeer and sheep utilize similar preferred vegetation (Skogland, 1984; Colman et al., 1998), and we have shown that reindeer may also avoid areas with an accumulation of sheep and especially reindeer faeces. As a consequence, reindeer may be loosing access to important range if animal densities are high and preferred vegetation is limited. This effect may be strengthened if bedding sites are located in or near preferred areas within a pasture, as they often are (Colman et al., 1998; Colman, 2000). Thus, avoidance of faeces dropped by other grazers most likely results in interference competition by reducing optimal forage intake. However, the same avoidance should provide protection from the transfer of parasites or disease, and thus, also act on improving the animal's overall survival and fitness (Van der Wahl et al., 2000).

The lack of replication in the second experiment undermined the value of its results. However, the behaviour data from this experiment (Eidesen, 2002), using all 6 enclosures, lends strong support to the results presented here. Another concern is whether enclosure size in either study allowed for the animals to express their full range of behaviours studied. Wild and semi-domesticated reindeer alike are occasionally restricted to limited pasture where high densities will lead to limited movement and increased contamination by excrements. We also extrapolated information on the feeding and movement behaviour of free ranging reindeer (Colman, 2000) when designing the size of our paddocks. Thus, in terms of measuring reindeers' reaction towards faeces while feeding and other "dunging" behaviour, we maintain that the size of our enclosures were adequate.

In conclusion, the amount and distribution of excrements from either species may play an important role in reindeer grazing and area use, especially in pastures maintaining high densities of reindeer or reindeer and sheep. In light of this, management decisions towards pasture size and animal density should include calculating separate areas for bedding sites where faeces concentrations are high and grazing utilization is low.

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