Vigilance and fright- and flight behaviour in subpopulations of Svalbard reindeer *Rangifer tarandus platyrhynchus* in Nordenskiöld Land, Svalbard

Vaktsomhet og frykt- og fluktåtferd i subpopulasjonar av svalbardrein *Rangifer tarandus platyrhynchus* på Nordenskiöld Land, Svalbard

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PREFACE

This Master thesis, written at the Department of Ecology and Natural Resource Management at the Norwegian University of Life Sciences, is the final 60 credits of my Master of Science degree in Natural Resource Management. The thesis is part of a larger research programme conducted by The University of Oslo. The field work was funded by The Research Council of Norway, Norwegian Polar Institute and Framkomiteens Polarfond.

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ABSTRACT

Svalbard reindeer *Rangifer tarandus platyrhynchus* survival is based upon minimal energy output and optimal grazing during summer, to withstand a marginal Arctic climate. Svalbard reindeer is by nature relaxed upon encounters with humans, due to the absence of coevolution with predators and humans. Increasing human activity in Svalbard could potentially cause more disturbances for the reindeer. The object of this study was to measure Svalbard reindeer vigilance level, and fright- and flight response towards an approaching human on foot during summer, in a study area with high human activity and no hunting; Adventdalen, compared to areas with a relatively low level of human activity and different degree of hunting and scientific activity; Colesdalen, Reindalen and Sassendalen.

Vigilance level was not different between the study areas, hence there was no difference in vigilance level related to different hunting pressure, human activity and live capturing of reindeer for scientific purposes. Females without calves displayed a higher vigilance level than females with calves and males. Flight initiation distance and distance moved upon disturbance by an approaching human on foot was longer in areas with hunting and scientific activity compared to the area with most human activity and no hunting.

The results were compared with a similar study in Edgeøya in Svalbard, where human activity is very low and no hunting occurs. I found a significant longer flight initiation distance and distance moved in Edgeøya compared to Adventdalen, while there was no difference between Edgeøya and the areas with hunting. Vigilance level was significantly higher in Edgeøya compared to all areas in Nordenskiöld Land grouped together, which might indicate a predator response towards polar bear *Ursus maritimus*.

My results indicate increased energy output and decreased grazing time upon disturbance by humans in areas with hunting. However, there seem to be no difference in energy output between areas with hunting and areas with no hunting and very little human activity. The habituation effect of frequent encounters with humans and the absence of hunting in Adventdalen thus seem to extent the aversion effect of hunting in the other areas.

I conclude that hunting might have led to increased energy output upon disturbance by humans, and that disturbance of Svalbard reindeer should be avoided. However, the short flight initiation distance indicates that this is probably not a problem as long as reindeer are not being approached directly. The present level of human activity in the study areas is therefore most likely not a threat to the Svalbard reindeer and their delicate energy balance.

SAMANDRAG

Svalbardreinen *Rangifer tarandus platyrhynchus* er avhengig av å minimere energibruk og optimalisere beiteaktivitet gjennom sommaren, for å overleve i eit hardt arktisk klima. Av natur er svalbardreinen relativt tam ved møte med menneske, grunna den manglande koevolusjonen med predatorar og menneske. Auka menneskeleg aktivitet på Svalbard kan føre til auka forstyrring for svalbardreinen. Føremålet med denne studia var å måle vaktsomhetsnivå, og frykt- og flyktåtferd mot ein person til fots som bevegar seg direkte mot enkeltdyr eller grupper av rein, i eit område med mykje menneskeleg aktivitet og inga jakt; Adventdalen, samanlikna med område med eit relativt lågt nivå av menneskeleg aktivitet og forskjellig grad av jakt og forskingsaktivitet; Colesdalen, Reindalen og Sassendalen.

Det var ikkje forskjell i vaktsomhetsnivå mellom områda, og derfor ingen forskjell i vaktsomhetsnivå relatert til forskjellig grad av jakt, menneskeleg aktivitet og fanging og merking av rein i forskingssamanheng. Simler utan kalv hadde høgare vaktsomhetsnivå enn simler med kalv og bukkar. Avstanden mellom dyra og observatøren når dyra flykta, og avstand flykta, var lengre i områda med jakt og forskingsaktivitet enn i området med mest menneskeleg aktivitet og inga jakt.

Resultata vart samanlikna med ei lik studie frå Edgeøya på Svalbard, der det er inga jakt og svært lite menneskeleg aktivitet. Eg fann signifikant lengre fluktavstand og avstand flykta på Edgeøya samanlikna med Adventdalen, medan det ikkje var forskjell mellom Edgeøya og områda med jakt. Vaktsomhetsnivået var høgare på Edgeøya enn gjennomsnittet av alle områda på Nordenskiöld Land, noko som kan tyde på ein predatorrespons mot isbjørn *Ursus maritimus*.

Resultata mine tyder på at svalbardreinen kan ha høgare energibruk og redusert tid til beiting ved forstyrring frå menneske i områda der han blir utsett for jakt. Samtidig ser det ikkje ut til å vere forskjell mellom områda med jakt og område med inga jakt og svært lite menneskeleg aktivitet. Hyppige møte med menneske og fråveret av jakt i Adventdalen ser ut til å ha større habitueringseffekt enn den auke i fryktåferd jakt kan ha ført til.

Eg konkluderer med at jakt kan ha ført til auka energibruk ved møte med menneske, og at forstyrring av svalbardreinen bør unngås. Samtidig tyder den korte fluktavstanden på at dette truleg ikkje er eit problem så lenge ein ikkje går direkte mot reinen. Dagens nivå av menneskeleg aktivitet i områda på Nordenskiöld Land er derfor truleg ikkje ein trussel for svalbardreinen og deira delikate energibalanse.

1. INTRODUCTION

Svalbard reindeer *Rangifer tarandus platyrhynchus* is the northernmost population of Rangifer in the world. The conditions for reindeer survival in Svalbard are special, and differ from other sub-populations of *Rangifer* in many ways. The Svalbard reindeer lives in a predator-free environment, and has not co-existed with any predators since the reindeer immigrated to Svalbard at least 7000 years ago (Vanderknaap 1989). Polar bears *Ursus maritimus* are known to occasionally kill reindeer, but this is very rare (Derocher et al. 2000). The co-evolution between predator and prey has thus not occurred here, as for other sub-species of reindeer. Skin warblers *Oedemagena tarandi* and throat warblers *Cephenomyia trompe*, which are known to potentially influence feeding and lying activity in Rangifer during summer (Hagemoen & Reimers 2002), are not present in Svalbard (Tyler 1987).

The long arctic winter makes Svalbard a hostile environment for reindeer. Snow accumulation and ice conditions during winter greatly influence access to forage, and thus reindeer survival and growth rate (Aanes et al. 2000; Kumpula & Colpaert 2003). Temperatures above zero is common in periods during winter, often leading to ground-icing, which can make winter pastures inaccessible to reindeer (Kohler & Aanes 2004). The winter pastures are in general of low quality (Øritsland 1986), and accumulation of fat reserves during summer is thus crucial to withstand the harsh winter (Reimers et al. 1982; Reimers 1984; Tyler 1986). Main mortality occurs in winter and spring due to starvation (Reimers 1983).

Grazing activity level has a distinct peak during summer (Loe et al. 2007). Kastnes (1979) found that Svalbard reindeer spent in average 96 percent of the day during summer grazing, resting and ruminating, in contrast to 71 percent for wild reindeer *Rangifer tarandus tarandus* at Hardangervidda in southern Norway (cited in Reimers et al. 1982). The importance of summer grazing is evident from a dramatic weight loss during winter. Reimers (1980) showed that female reindeer in Svalbard lost 45 percent of body weight during winter, compared to 5 percent for reindeer in Hardangervidda. The same study showed a higher growth rate for young animals during summer for Svalbard reindeer compared to reindeer at Hardangervidda.

The absence of predators and insect harassment is a crucial point in understanding the existence of reindeer in such a marginal environment. Svalbard reindeer do not have the nomadic behaviour known from other sub-species of Rangifer. On the contrary, Svalbard reindeer are seasonally sedentary (Tyler & Øritsland 1989). They have no extensive migrations within- or between seasons. The absence of predators and insects allow longer grazing time during summer, compared to reindeer in the mountains in southern Norway (Reimers 1980). Apparently, survival of Svalbard reindeer is based upon a delicate balance between maximum energy intake in terms of optimal grazing and minimal energy output. Increasing human activity in Svalbard might cause more disturbances for the reindeer, which can lead to reduced grazing time, increased energy output and lower survival and reproduction.

Studies of response distances (review in Reimers & Colman 2006) and vigilance level (Bøving & Post 1997; Duchesne et al. 2000; Reimers & Svela 2001) have been conducted on several subspecies of *Rangifer*. The object of this study is to examine response distances and vigilance behaviour upon different hunting pressure and different level of other non-lethal human activities. The four areas chosen for this study, Adventdalen, Colesdalen, Reindalen and Sassendalen in Nordenskiöld Land, Svalbard, are different in form of hunting pressure, scientific activity and human activity in general, and offer a good opportunity to investigate differences in reindeer behaviour upon different human interference.

It is expected that reindeer/caribou display less vigilant behaviour in areas where they are not threatened by predators (Bøving & Post 1997). I predict that vigilance rate is lower then what is found for other subspecies of *Rangifer* where predators are present or have been present until recently. Reimers & Svela (2001) predicts only a long-term effect of hunting on vigilance behaviour in *Rangifer*. It is thus unlikely that reindeer in the areas with hunting display more vigilance bouts than reindeer in the area with no hunting but where reindeer often encounter humans. In two of the study areas, reindeer have been captured and collard by scientists each year since 1995. The capturing of reindeer is a potentially unpleasant experience for the reindeer, but following the same reasoning as with hunting; increased number of vigilance bouts is not expected.

In a study of Svalbard reindeer in 1994, Colman et al. (2001) found a slightly longer distance moved in areas with hunting compared to areas without hunting. In this study, 12 years later, I expect this connection to be stronger, as hunting has occurred in a longer period and more animals have experienced hunting. The negative experience related to capturing of reindeer could also lead to increased response distances. I predict no evolutionary changes due to hunting after such a short period.

My results will be compared with results from a similar study of Svalbard reindeer in Edgeøya, another island of the Svalbard archipelago, where no hunting occur and human activity is very low, and where polar bears are common.

2. STUDY AREAS

Svalbard (63000 km^2), a group of islands with Spitsbergen as the largest, is situated in the western Barents Sea, between 74° and 81° north. Despite the location far north, the climate is relatively mild (mean yearly temperature: -6.7 °Celsius; mean precipitation: 190 mm, Longyearbyen Airport 1975-1990: www.yr.no) due to the North-Atlantic Current. The landscape is mountainous with peaks up to 1700 m above sea level. Large areas are covered by glaziers, and summer pastures for reindeer are restricted to the valleys, the coastal plains and the plateaus. The flora in Svalbard is classified as Mid and High Arctic, and vegetation cover is in most places limited to 100-150 m above sea level (Rønning et al. 1996).

The four study areas are all situated in Nordenskiöld Land in Spitsbergen (39000 km^2). Adventdalen (78°12'N, 15°55'E) (150 km^2), Colesdalen (78°05'N, 15°12'E) (94 km^2), Reindalen (77°58'N, 15°57'E) (361 km^2) and Sassendalen (78°17'N, 17°05'E) (193 km^2) are wide U-valleys surrounded by steep mountains of about 300-800 m above sea level (Figure 1).

Figure 1. Nordenskiöld Land in Spitsbergen with the four study areas Adventdalen, Colesdalen, Reindalen and Sassendalen. Map from www.geopolar.no.

Helicopter surveys conducted by the Governor of Svalbard yearly from 1997 to 2005 imply that the summer subpopulations of Svalbard reindeer count approximately 380 in Colesdalen, 510 in Reindalen and 830 in Sassendalen. The population in Adventdalen was in summer 2006 about 800 animals (Tyler et al. 2008 in press).

2.1 Hunting

Hunting of reindeer has occurred in Svalbard since the 17th century, but the extent is presumed to be low until 1860, when human presence in Svalbard increased due to trapping and mining activities. Between 1865 and 1925 the documented harvest is 20 000 animals, but as much as twice this number might have been killed (references in Tyler 1987). As a result of reports of rapidly decreasing density of Svalbard reindeer, and more or less locally extinct populations in Nordenskiöld Land, hunting of Svalbard reindeer was prohibited in 1925. Since then reindeer density has increased, which led to reopening of limited hunting in parts of Nordenskiöld Land in 1983. Hunting intensity has been low, with a yearly take of between 117 and 231 reindeer (Figure 2).

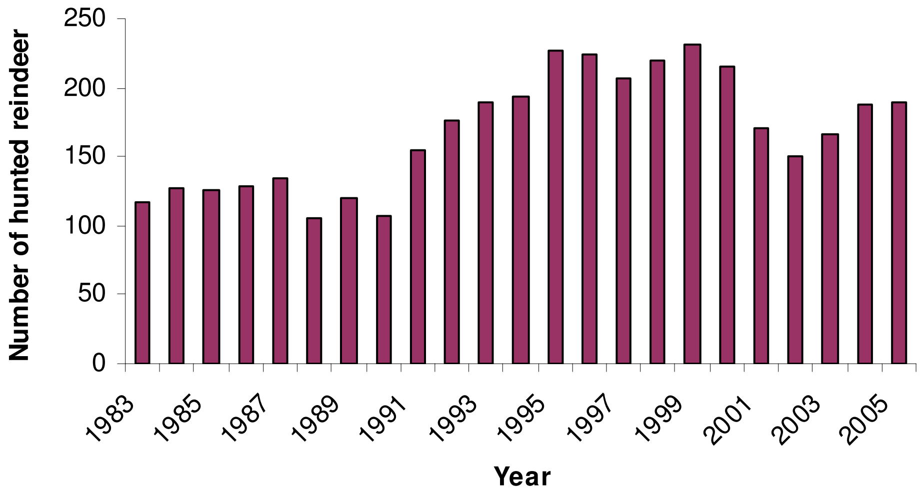

Figure 2. Number of hunted reindeer in Nordenskiöld Land since hunting was allowed in 1983. Hunting statistics from the Governor of Svalbard.

2.2 Tourism

Tourism is the single largest human activity in the Arctic, and fast growing (Snyder et al. 2007). In Svalbard tourism is one of the leading industries, together with coal mining and scientific research. Longyearbyen (2000 inhabitants) is the starting point for most of the tourist activity in Svalbard, and the activity is thus largest in Adventdalen. Numbers of registered guest days in hotels and guest houses in Longyearbyen increased from 30 000 in 1994, to almost 78 000 in 2004 (Sysselmannen 2006). Today there are several tourist companies offering a variety of activities. Short foot trips in the surrounding of Longyearbyen and Adventdalen with tributary valleys are important tourist activities during summer (Norris 1998; Sysselmannen 2006).

2.3 Scientific activity

In a long term research program in two of the study areas, Colesdalen and Reindalen, reindeer have been captured and collared from snowmobile each year since 1995 (Audun Stien, pers. comm.). The reindeer are captured in a net between two approaching snowmobiles. This activity has taken place in March/April each year, and lasted for between 10 days and three weeks (in average 12 days). The last 8-9 years only females already collared have been captured, including their calves which also have been collared. The scientific activity in the two areas is presumed to be similar (Audun Stien, pers. comm.).

Neither locals nor non-resident visitors are instructed to notify the Governor of Svalbard when travelling in the study areas. Therefore there exists no recent statistics of activity level in the specific areas. Colman et al. (2001) used data of tourist activity from Kaltenborn (1991) to classify the areas according to human activity. Since no recent statistics of tourist activity in my study areas exist, it is difficult to track any change in activity since the study of Kaltenborn (1991). I believe the human activity in the study areas are more or less proportional to the situation in 1989, when the study in Kaltenborn (1991) was conducted, and use the measurement of number of people/km^2 from this study. These numbers are probably not similar to the situation today, but the proportions should be the same. This is due to the fact that there is no change in infrastructure in the areas; Adventdalen is still by far the easiest accessible area and the tourist companies offer no arranged activities in the other areas during summertime. Any summer activity in Colesdalen, Reindalen and Sassendalen has to include transport from Longyearbyen either by boat or by hiking. Since there is no network of tourist cabins in the areas, I presume hiking activity to be relatively low, with most activity in the areas closest to Longyearbyen. Colman et al. (2001) used data of human activity and hunting to provide knowledge of the study areas. I use the same factors, with an addition of scientific activity which has been initiated after the previous study (Table 1).

Table 1. Ranking of human activity, scientific activity and hunting pressure in Adventdalen, Colesdalen, Reindalen and Sassendalen in 2006.

	Adventdalen	**Colesdalen**	**Reindalen**	**Sassendalen**
Total number of people/km^2[a]	>300	70-140	20-70	<20
Distance to closest settlement by foot/boat[b]	0/0 km	30/28 km	39/- km	45/40 km
Number of cabins[c]	>200	12	4	3
Human activity	**High**	**Medium**	**Med-Low**	**Low**
Seasons reindeer captured during scientific work since 1994[d]	0	12	12	0
Scientific activity	**None**	**High**	**High**	**None**
Hunting seasons since 1983[e]	0	21	23	23
Min./max. number of animals hunted since 1983[e]	0/0	17/54	10/49	33/95
Min./max. percent of population estimate hunted since 1997[e]	0/0	4.6/8.1	4.1/8.5	5.1/11.1
Average number of animals hunted per year since 1990[e]	0	31	26	64
Hunting rank order	**None**	**Low**	**Low**	**Medium**

a = Kaltenborn 1991

b = Colman et al. 2001

c = The Governor of Svalbard and the mining company Store Norske, unpublished data

d = Audun Stien pers. comm.

e = The Governor of Svalbard, unpublished data

3. METHODS

Data of vigilance and disturbance were collected by 3 persons during three weeks in July and August 2006 in Adventdalen, Colesdalen, Reindalen and Sassendalen in Nordenskiöld Land, Svalbard. When spotting an animal or group of animals, we video recorded the animal(s) for later measurement of vigilance. Following video recording we disturbed the animal(s) and recorded their response distances. All animal experimentation reported in this paper complies with the current laws regulating the treatment of animals in Norway, and were approved by the Norwegian Animal Research Authority (NARA).

3.1 Vigilance

We spotted single animals and groups of grazing reindeer in the area by binoculars and video recorded (up to 26 X zoom) grazing animals from a hidden position 80 – 800 meters away, depending on the landscape. Grazing was defined as the act of ingesting forage with the muzzle down (Bøving & Post 1997). Observation time was about 10 minutes, but was halted if the reindeer lied down or moved out of sight. A vigilance bout was defined as the act of interrupting feeding to lift the head above the shoulders and observe the surroundings for ≤10 s before returning to feeding (Bøving & Post 1997).

We noted the following parameters while filming:

1. **Group size** [animals were defined as in a group if the distance between them were <50 m].
2. **Group structure** [males, females and yearlings, mixed (all ages and both sexes) or females with calves].
3. **Sex and age of each animal** [female with calf, female without calf (>1 year old), male (>1 year old) or calf].
4. **Wind speed** [The Beaufort Wind Scale: calm, < 1 m • sec^{-1}; light/gentle breeze, 1.6-5.4 m • sec^{-1}; moderate/fresh breeze, 5.5-10.7 m • sec^{-1} or gale, 10.8-17.1 m • sec^{-1}].
5. **Weather** [sunny/partly sunny, cloudy, rain/snow or foggy].

We also noted if the reindeer spotted the observer during filming. In some cases we did not notice that the reindeer spotted us, but this was discovered under analysis of the video tape. The video tapes were played back on a 27" plasma TV-monitor and individual grazing reindeer followed throughout the observation period. Whenever the animal lifted its head above shoulder height for ≤ 10 s this action was identified as a vigilance bout. Slow walking between vegetation hot spots with head down was included in total grazing time. Slow walking with head up was excluded from total grazing time. In some instances the grazing animal disappeared and reappeared within minutes. In these few cases the observation time continued after subtraction of the time out of sight.

3.2 Disturbance

A single person on foot dressed in dark hiking outfit disturbed reindeer by directly approaching them. The observer measured response distances between the reindeer and the observer and the resultant displacement distance by the reindeer after taking flight by use of laser mononoculars Leica Rangemaster 1200 Scan; 1-m accuracy at 1000 - 1200 m.

Before a disturbance we recorded the following parameters:

1. **Group size** [all animals influenced by the disturbance was defined as in a group].
2. **Group structure** [mixed (all ages and both sexes), males, females and yearlings or females and calves].
3. **Activity of the animal/group prior to provocation** [lying, grazing, moving/grazing, lying/grazing or standing].
4. **Wind speed** [The Beaufort Wind Scale: calm, < 1 m • sec^{-1}; light/gentle breeze, 1.6-5.4 m • sec^{-1}; moderate/fresh breeze, 5.5-10.7 m • sec^{-1} or gale, 10.8-17.1 m • sec^{-1}].
5. **Weather** [sunny/partly sunny, cloudy, rain (snow) or foggy].
6. **Terrain in the surrounding area** [level or rugged].
7. **Disturbance in relation to terrain** [downhill, level or uphill].
8. **Wind direction relative to the observer while disturbing** [into the wind (including crossways to the wind) or tail wind].

Once a single animal or a group was spotted, the observer measured the distance to the group (encounter distance). The observer used a `direct approach method` that had an `interrupted pattern`: advancing directly towards the estimated centre of the group at a constant speed (≈ 4 km x h^{-1}) with ≤6 s stops to measure the 3 additional response distances (sight-, alert- and flight initiation distance) defined below. The observer continued to approach the group on all occasions until he reached the position where the reindeer were located at the start of the disturbance. All measurements were made from the position of the directly approaching observer to the closest animal in the group (Colman et al. 2001).

I used wildlife response distance terminology and methodology recommended by Taylor & Knight (2003) modified for my study as follows:

1. **Encounter distance**: the distance between the observer and the closest animal in a group of reindeer before the start of the disturbance.
2. **Sight distance**: the distance between the observer and the closest animal in a group of reindeer when the animal discovered the observer.
3. **Alert distance**: the distance when the reindeer group exhibited an increased alert response by grouping together or individuals urinating with one hind leg extended outward at an exaggerated angle, while staring at the directly approaching observer.
4. **Flight initiation distance**: the distance from the directly approaching observer to the group when the reindeer initially took flight.
5. **Distance moved**: the shortest straight-line distance from where the reindeer took flight in response to the directly approaching observer to where the reindeer resumed grazing or bedded down.
6. **Assessment time**: the time elapsed from sight to flight initiation (estimated from the measured distances and assuming a constant speed of 4 km x h^{-1}).

4. STATISTICAL METHODS

4.1 Vigilance

Data of vigilance bouts per 10 minutes was square root transformed prior to statistical analyses to get residuals with constant variance and minimize deviations from the normal distribution. The initial model included six variables: area; group size; group structure; sex and age of each reindeer filmed; weather and wind speed. Based on Best Subset Regression, a model with five predictors was selected, excluding weather. The data was analysed using a General Linear Model. All possible pair wise comparisons of the predictors with the lowest p-values were conducted by the Tukey method. Untransformed data of vigilance bouts per 10 min in all areas in Nordenskiöld Land grouped together was tested against data from Edgeøya by the Mann-Whitney U-Test. All analyses were done in Minitab 15.

4.2 Disturbance

The response distances (encounter distance, sight distance, flight initiation distance and distance moved) were transformed into their natural logarithms prior to statistical analyses to get residuals with constant variance and minimize deviations from the normal distribution. Assessment time ≥ 1 s was square root transformed and analysed with a linear model including sight distance as a covariate in the analyses. In accordance with Blumstein et al. (2003) I included ln encounter as covariate in the ln sight, ln flight initiation and ln escape response models to control for the effect of this variable. Alert distance was not analysed, due to few samples ($n = 33$) with this response distance. Encounter distance did not change in the four areas, and thus did not imbalance the comparison. I also included interaction between group size and group structure, terrain and disturbance direction relative to wind, and between disturbance direction relative to wind and disturbance direction relative to terrain.

I used automatic selection procedure and the Akaike information criterion; AIC (Burnham & Anderson 1998) for selecting the most parsimonious model. I examined parameter estimates and P-values for the best model, and conducted multiple comparisons with the S-Plus "multicomp" function (Tukey's honestly significant difference) with the default mca for all pair wise differences of adjusted means (Crawley 2002). Multiple comparisons of difference in sight distance, flight initiation distance and distance moved between my study areas and data from Edgeøya were also analysed. All analysis were done in S-Plus 6.2 (Venables & Ripley 2002).

5. RESULTS

5.1 Vigilance

We video recorded 249 reindeer in the four valleys in Nordenskiöld Land; Adventdalen (n = 60), Colesdalen (n = 78), Reindalen (n = 64) and Sassendalen (n = 47) during three weeks in July and August 2006. Of these, 15 discovered us during filming, and were thus excluded from statistical analysis. Mean group size was 2.4 animals, ranging from 1 to 11. Observation periods ranged from 37 to 1267 s, with an average of 537 s.

The best model based on Best Subset Regression is shown in Table 2. There was a significant difference in vigilance rate between individuals of different sex and age irrespectively of group structure (Table 2 and Figure 3). Females without calves had higher vigilance rate than females with calves and males, irrespective of group structure (Table 3).

Table 2. General Linear Model based on Best Subset Regression of sqrt vigilance bouts per 10 min in Nordenskiöld Land July/August 2006. 3.85 percent of the variance is explained by the model (R^2-adj).

Source	DF	Seq SS	Adj SS	Adj MS	F	P
Area	3	1.1614	0.2757	0.0919	0.14	0.933
Group size	5	0.7313	0.7976	0.1595	0.25	0.939
Group structure	3	1.9925	4.0897	1.3632	2.15	0.095
Age-Sex classes	3	11.7689	12.0251	4.0084	6.31	0.000
Wind speed	2	0.4336	0.4336	0.2168	0.34	0.711
Error	217	137.7692	137.7692	0.6349		
Total	233	153.8568				
S = 0.796794		R^2 = 10.46%		R^2(adj) = 3.85%		

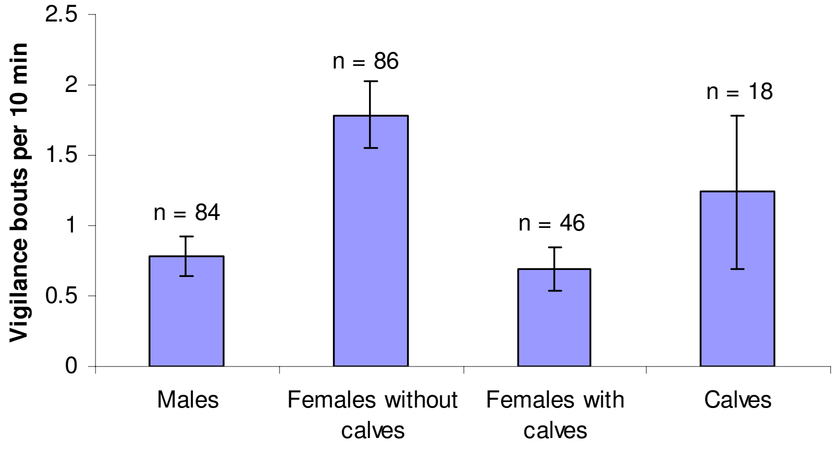

Figure 3. Untransformed data of vigilance bouts per 10 minutes ± SE for reindeer in all study areas in Nordenskiöld Land July/August 2006. The observations where the reindeer had spotted us are excluded. Number of observations above bars.

Table 3. Estimates and test statistics for multiple comparisons of contrasts in the analysis of sqrt vigilance bouts per 10 min in Nordenskiöld Land July/August 2006, based on results in Table 2. CIs are 95 % simultaneous confidence intervals for specified linear combinations by the Tukey method. Intervals excluding 0 are flagged by *.

Variable	Estimate	Lower CI	Upper CI	
Sqrt vigilance bouts per 10 min model:				
Comparison of contrasts				
Age-sex classes				
females without calve vs. females with calves	0.4896	0.1169	0.8623	*
calves vs. females with calves	0.1654	-0.4019	0.7326	
males vs. females with calves	0.0515	-0.3227	0.4258	
calves vs. females without calves	-0.3242	-0.8531	0.2046	
males vs. females without calves	-0.4381	-0.7511	-0.1251	*
males vs. calves	-0.1138	-0.6438	0.4161	

Reindeer in Edgeøya displayed the most vigilance bouts per 10 min compared to the other areas (Figure 4), and significantly more than all areas in Nordenskiöld Land grouped together ($U = 44226.5$, $n_1 = 234$, $n_2 = 181$, $p = 0.0001$).

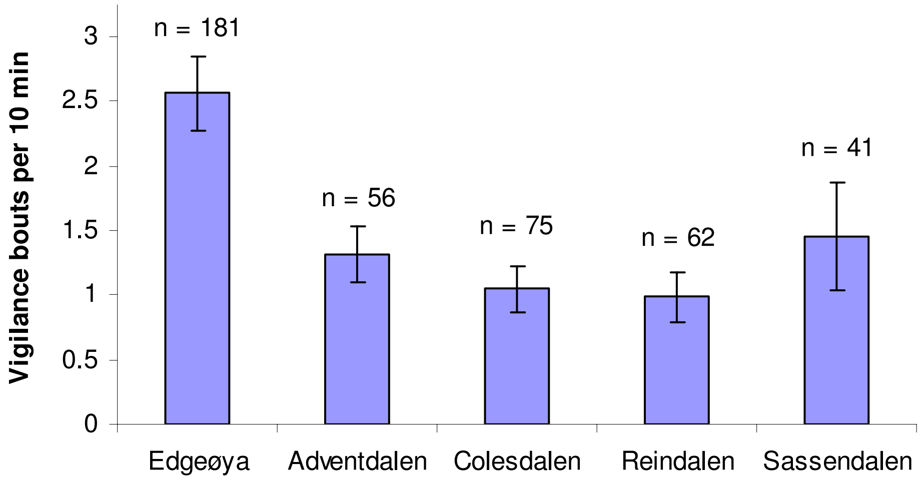

Figure 4. Untransformed data of vigilance bouts per 10 min ± SE in the study areas in Nordenskiöld Land and Edgeøya July/August 2006. The observations where the reindeer had spotted us are excluded. Number of observations above bars.

5.2 Disturbance

We disturbed a total of 61 groups or single reindeer in Adventdalen, Colesdalen, Reindalen and Sassendalen in Nordenskiöld Land, Svalbard, during three weeks in July and August 2006 (Figure 5).

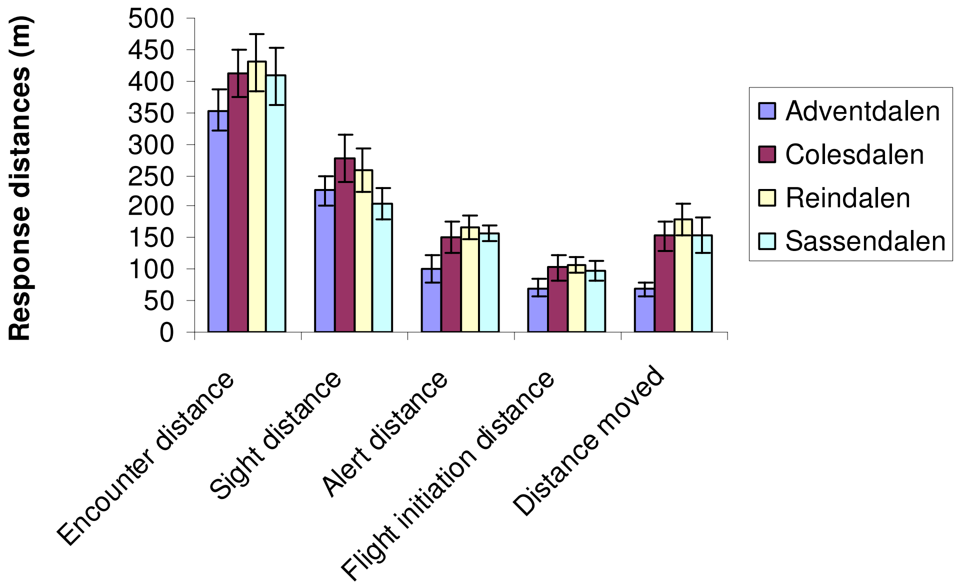

Figure 5. Untransformed response distances (m) ± SE in Adventdalen (n = 17), Colesdalen (n = 13), Reindalen (n = 16) and Sassendalen (n = 15) in Svalbard July/August 2006.

The most parsimonious models selected based on the AIC criterion is shown in Table 4. There was no difference in group size between the four different areas (One-way ANOVA; df = 57, n = 61, F = 0.56, P = 0.646). Flight initiation distance was slightly longer with increasing group size (t = 1.9054, p = 0.0633), while group size had no effect on the other response distances. Groups including females and calves had longer flight initiation distance than mixed groups and males (Table 5). Females and yearlings had shorter distance moved than mixed groups (t = -2.5298, p = 0.0146), while there was no difference in distance moved among the other group structures. Moving/grazing animals had shorter flight initiation distance than lying (t = -2.2628, p = 0.0286) and grazing animals (Table 5).

Females and calves had shorter assessment time than mixed groups (t = -2.6580, p = 0.0108) and males (Table 5). The assessment time was shorter when the observer walked towards the reindeer in tail wind vs. into the wind or crossways to the wind (t = -2.6761, p = 0.0104). Assessment time was longer in rugged than in flat terrain (t = 2.9596, p = 0.0049), and positively correlated to sight distance (t = 11.5389, p = <0.0001).

Reindeer in Adventdalen had shorter flight initiation distance and distance moved than reindeer in Colesdalen (flight initiation distance: t = 2.4333, p = 0.0191), and shorter distance moved than reindeer in Reindalen and Sassendalen (Table 5). Assessment time was shorter in Sassendalen than in Adventdalen (t = -2.0803, p = 0.0432), while there was no difference between the other areas (all P-values >0.15).

Table 4. The most parsimonious models (selected based on the AIC criterion) for sight distance, flight initiation distance, distance moved and assessment time in four areas (Adventdalen, Colesdalen, Reindalen and Sassendalen) in Nordenskiöld Land, Svalbard during July and August 2006. Starting model for automatic stepwise AIC selection: Response distance = Area (4) + Group size+ Group structure (4) + Activity (4) + Wind speed (3) + Weather (3)+Terrain (2) + Provterrain (3) + Provwind (2) + Group size x Group structure + Provwind x Terrain + Provwind x Provterrain. Maximum number of parameter levels in parenthesis. Ln encounter was included as covariate in the sight, flight initiation and distance moved response models while ln sight was included as covariate in the sqrt assessment time model.

Variable	Df	Sum of Sq	Mean Sq	F Value	Pr(F)
ln sight distance					
ln encounter	1	8.7096	8.7095	43.4720	<0.0001
Wind speed	2	1.3511	0.6756	3.3719	0.0417
Terrain	1	0.5443	0.5443	2.7168	0.1051
Residuals	54	10.8188	0.2003		
ln flight initiation distance					
Area	3	6.3724	2.1241	6.2030	0.0013
Group size	1	1.2433	1.2432	3.6306	0.0633
Group structure	3	5.2348	1.7449	5.0957	0.0041
Activity	4	4.3357	1.0839	3.1654	0.0227
Wind speed	2	6.0079	3.0040	8.7724	0.0006
Weather	2	2.5275	1.2637	3.6905	0.0330
Terrain	1	1.3485	1.3485	3.9381	0.0535
Residuals	44	15.0670	0.3424		
ln distance moved air					
Area	3	14.2701	4.7567	16.8913	0.0000
Group structure	3	1.8499	0.6166	2.1897	0.1008
Wind speed	2	4.9117	2.4559	8.7209	0.0006
Weather	2	9.5930	4.7965	17.0327	0.0000
Residuals	50	14.0803	0.2816		
sqrt assessment time					
Ln sight	1	635.8517	635.8517	133.1461	0.0000
Area	3	49.0122	16.3374	3.4210	0.0250
Group structure	3	79.9961	26.6654	5.5837	0.0024
Terrain	1	41.8305	41.8305	8.7592	0.0049
Provwind	1	34.2002	34.2002	7.1615	0.0104
Residuals	45	214.9017	4.7756		

Table 5. Selected parameter estimates and test statistics for multiple comparisons of contrasts in Appendix 1. CIs are 95 % simultaneous confidence intervals for specified linear combinations by the Tukey method or the Sidak method for interaction testing (Crawley 2002). Intervals excluding 0 are flagged by *. See Appendix 2 for details.

Variable	Estimate	SE	Lower CI	Upper CI	
In sight model: Comparison of contrasts					
Wind speed					
calm vs. light/gentle breeze	-0.8390	0.3310	-1.6400	-0.0405	*
In flight initiation model: Comparison of contrasts					
Area					
Adventdalen vs. Reindalen	-1.0100	0.2580	-1.7200	-0.3010	*
Adventdalen vs. Sassendalen	-0.9860	0.2600	-1.7000	-0.2710	*
Group structure					
mixed vs. females and calves	-1.2500	0.3510	-2.2100	-0.2880	*
males vs. females and calves	-0.8820	0.2570	-1.5900	-0.1760	*
Activity					
grazing vs. moving/grazing	1.1500	0.3620	0.0863	2.2100	*
Wind speed					
light/gentle breeze vs. moderate/fresh breeze	-1.6200	0.3950	-2.5800	-0.6640	*
Weather					
cloudy vs. foggy	1.7100	0.6480	0.1390	3.2800	*
In distance moved air: Comparison of contrasts					
Area					
Adventdalen vs. Colesdalen	-1.6100	0.2460	-2.2800	-0.9370	*
Adventdalen vs. Reindalen	-1.1600	0.2190	-1.7600	-0.5590	*
Adventdalen vs. Sassendalen	-1.0400	0.2080	-1.6100	-0.4720	*
Wind speed					
light/gentle breeze vs. moderate/fresh breeze	-1.1400	0.3210	-1.9100	-0.3640	*
Weather					
sunny/partly sunny vs. cloudy	-1.1200	0.1930	-1.5800	-0.6500	*
sqrt assessment time: Comparison of contrasts					
Group structure					
males vs. females and calves	3.6200	0.9220	1.0900	6.1500	*

There was no difference in sight distance, alert distance and distance moved between Edgeøya and any of my study areas according to multiple comparisons of contrasts by the Sidak method (not shown in table). Anyhow, when testing the area-factor with Adventdalen as intercept, I found a significant shorter distance moved in Adventdalen than in Edgeøya ($t = 2.5984$, $p = 0.0107$). Flight initiation distance was also shorter in Adventdalen than in Edgeøya, according to the multiple comparisons of contrast [Estimate = -0.5630; SE = 0.185; 95% CI = (-1.090, -0.0341)], while there was no difference between Edgeøya and the other areas.

6. DISCUSSION

There has been expressed concern of the lack of knowledge about the effects of an increasing human activity on the fauna, in Svalbard in general, and the areas closest to Longyearbyen in particular (Vistad 2008). Reindeer in the three areas where hunting occur did display longer flight initiation distance and distance moved than in the area without hunting, which is in accordance with my prediction. Colman et al. (2001) also found longer flight initiation distance and distance moved in the areas with hunting compared to Adventdalen, with an exception of flight initiation distance in Colesdalen. Semi-domesticated reindeer (originated from domesticated reindeer) in southern Norway show shorter response distances than wild reindeer (Eftestøl 1998). Semi-domesticated reindeer subjected to heavy hunting and little human activity other than hunting, also show longer fright distance, flight initiation distance and distance moved than semi-domesticated reindeer in an area with no hunting but with high human activity (Dervo & Muniz 1994). Domestication and frequent encounters with humans thus seem to reduce response distances.

Although I found the longest flight initiation distance and distance moved in the areas with hunting, Colman et al. (2001) found the longest fright distance, flight initiation distance and distance moved in Reinsdyrflya, an area north in Spitsbergen where no hunting occurs and human activity is very low. Flight initiation distance and distance moved in Edgeøya were longer than in Adventdalen, but similar to the areas with hunting. The lack of increased response distances in areas with hunting compared to areas with no hunting and low human activity is in contrast to the many studies of different species showing longer response distances related to hunting pressure (cited in Reimers & Colman 2006). The impact on reindeer behaviour from hunting depends on the hunting procedure, in which degree the hunt is experienced by surviving reindeer in the group (Reimers & Colman 2006). Svalbard reindeer lives in small groups all year with an average size of 2-4 animals (Tyler 1987). The low group size and the absence of co-evolution with predators might be an explanation to why response distances in Svalbard reindeer in areas with hunting do not exceed response distances in areas without hunting and with low human activity. Although polar bears are generally regarded as no significant predator on reindeer (Derocher et al. 2000), it should be mentioned that Edgeøya has a high density of polar bears during summer, greatly exceeding the density in Nordenskiöld Land (Wiig 2000). It is not unlikely that the presence of polar bears leads to longer response distances.

There was no difference in numbers of vigilance bouts per 10 minutes between the areas in Nordenskiöld Land. Hence, reindeer in the areas with hunting and the areas where capturing of reindeer occur, did not display more vigilant behaviour than in the areas without hunting. This is in accordance with my prediction. Some studies have concluded with increased vigilance rate related to human activity (for woodland caribou *Rangifer tarandus caribou*: Duchesne et al. 2000; and mountain gazelle *Gazella gazelle*: Manor & Saltz 2003), while a line of studies of *Rangifer* has indicated that reindeer in areas with low human activity is more vigilant than in areas where reindeer frequently encounter humans (Eftestøl 1998; Reimers et al. 2000; Colman et al. 2001; Reimers & Svela 2001). Svalbard reindeer in Edgeøya seem to be more vigilant than in the populations in Nordenskiöld Land, hence supporting this conclusion. Bøving & Post (1997) found lower vigilance rate for caribou females with calves in West Greenland where large mammalian predators are absent, in contrast to Alaska where predators are present. In accordance with increased flight initiation distance and distance moved, the presence of polar bears could cause a higher vigilance rate in Svalbard reindeer.

In a predator free environment one might expect that Svalbard reindeer keeps vigilance at a minimum. As pointed out by Reimers & Colman (2006), a response to a stimuli that is not essential, is wasted energy. However, the vigilance rate in Svalbard reindeer in the areas in Nordenskiöld Land is similar to what is found for semi-domesticated reindeer in southern Norway, while it is lower than for wild reindeer in southern Norway (Reimers & Svela 2001). The vigilance rate in Edgeøya is also lower than for wild reindeer in southern Norway, while it is higher than for semi-domesticated reindeer in southern Norway (Reimers & Svela 2001). Hence, I failed to verify my prediction that vigilance level in Svalbard reindeer would be lower than in subpopulations of *Rangifer* where predators are present or have been present until recently. Other factors than predation pressure most likely influence the vigilance behaviour in the two areas in southern Norway. While the population of wild reindeer has been subject to hunting "for ever", the population of semi-domesticated reindeer had been hunted for no more than 5 years when the study was carried out. Also, human activity in the area with semi-domesticated reindeer was higher than in the area with wild reindeer. The absence of predators in Nordenskiöld Land, and the previous domestication of the semi-domesticated reindeer in southern Norway might have led to similar vigilance behaviour.

Earlier studies of Rangifer have shown that females with calves have the longest response distances (Colman et al. 2001) and highest vigilance rate (Bøving & Post 1997;

Aastrup 2000; Reimers & Svela 2001). I also found the longest response distances in females with calves, while females without calves had the highest vigilance rate. The low vigilance rate displayed by females with calves might be related to the long grazing time required to compensate for the weight loss during winter, as well as the energy requirement needed to produce milk during the lactation period. Adult male elk *Cervus elaphus* in Rocky Mountains, USA, had lower vigilance rate and fed more than the other age-sex classes (Childress & Lung 2003). Male elk was considered to have the highest requirement to maximise their fat reserves due to the energetic demand of the autumn rut. Hence, the individuals most dependent on maximising grazing time might reduce vigilance to increase grazing time. In a study of activity pattern in Svalbard reindeer, Kastnes (1979) found that females with calves during summer had slightly longer grazing time than females without calves, but no significant difference was found. A higher preference for quality in forage and grazing sites by females with calves might explain the lack of increased grazing time. Currently, I have no data that support this possibility.

My results indicate that initiation of hunting of Svalbard reindeer can have lead to increased energy output and decreased grazing time upon disturbance by humans. However, response distances seem to be similar to areas with very low human activity, as Edgeøya in this case. Habituation to non-lethal human activity in the areas with hunting could be influential, especially since the present hunting has occurred in a relatively short period. However, the constant exposure to humans in Adventdalen far exceeds the human activity level in the other areas in Nordenskiöld Land, and thus any habituation effect.

To verify the impact of disturbance it is necessary to address how survival and reproductive success are affected by behavioural changes due to disturbance (Gill et al. 2001; Vistnes & Nellemann 2008). Future studies should include knowledge of demographic and spatial changes due to human activity. Direct observation of reindeer, for example measuring of response to a direct approaching person and measuring of vigilance bouts, as pointed out by Reimers & Colman (2006), may not ascertain any past experience and acquired behaviour which could have relevance for the animals decisions in any situation. Also, when the sample size is small, this method may not manage to separate the combined effects of correlated variables. The opinion that the individuals with the longest response distances are the most vulnerable could also be challenged. The effect of disturbance might be influenced by other factors, such as the quality and availability of alternative habitats (Gill et al. 2001). When the cost of leaving a feeding site is large, reindeer might stay longer when approached by humans, and hence reduce flight initiation distance.

When discussing the effect of human disturbance, it is worthwhile to mention that the `direct approach method` is a “worst-case scenario”. A `tangential approach`, e.g. when hikers walk tangentially past reindeer on a road or a path, will represent a smaller threat and thus lead to a smaller energy output and reduced lost grazing time compared to the `direct approach method` (Taylor & Knight 2003). The relatively short flight initiation distance in this study indicates that the `comfort distance`, i. e. distance beyond which animal behaviour or activity is not influenced (Colman et al. 2001), is short, and the negative effects of human activity on Svalbard reindeer are low.

My results indicate that Svalbard reindeer in Nordenskiöld Land habituate to human non-lethal activity, and that hunting only gives a small increase in response distances. As there is no difference in vigilance behaviour in areas with and without hunting, the increased alertness and hence energy output upon disturbance by humans will presumably only take place when reindeer are being approached directly by humans. Therefore I suggest any restrictions on human activity should be limited to direct approaching of reindeer. Since this most likely is rare, a simple request to avoid approaching reindeer should be sufficient.

7. REFERENCES

Blumstein, D. T., Anthony, L. L., Harcourt, R. & Ross, G. (2003). Testing a key assumption of wildlife buffer zones: is flight initiation distance a species-specific trait? *Biological Conservation*, 110 (1): 97-100.

Burnham, K. P. & Anderson, D. R. (1998). *Model selection and inference: a practical information-theoretic approach*. New York, Springer. XIX, 353 p.

Bøving, P. S. & Post, E. (1997). Vigilance and foraging behaviour of female caribou in relation to predation risk. *Rangifer*, 17 (2): 55-63.

Childress, M. J. & Lung, M. A. (2003). Predation risk, gender and the group size effect: does elk vigilance depend upon the behaviour of conspecifics? *Animal Behaviour*, 66: 389-398.

Colman, J. E., Jacobsen, B. W. & Reimers, E. (2001). Summer response distances of Svalbard reindeer *Rangifer tarandus platyrhynchus* to provocation by humans on foot. *Wildlife Biology*, 7 (4): 275-283.

Crawley, M. J. (2002). *Statistical computing: an introduction to data analysis using S-Plus*. Chichester, Wiley. IX, 761 p.

Derocher, A. E., Wiig, O. & Bangjord, G. (2000). Predation of Svalbard reindeer by polar bears. *Polar Biology*, 23 (10): 675-678.

Dervo, L. B. & Muniz, A. R. (1994). *Fright behavior in a hunted and an unhunted reindeer (Rangifer tarandus tarandus) population in Southern Norway*, Msc. thesis, University of Oslo. 42 p.

Duchesne, M., Cote, S. D. & Barrette, C. (2000). Responses of woodland caribou to winter ecotourism in the Charlevoix Biosphere Reserve, Canada. *Biological Conservation*, 96 (3): 311-317.

Eftestøl, S. (1998). *Fright behaviour in Norwegian wild reindeer (Rangifer tarandus tarandus) after disturbance by humans on foot or skis*, Msc. thesis, University of Oslo. 38 p.

Gill, J. A., Norris, K. & Sutherland, W. J. (2001). Why behavioural responses may not reflect the population consequences of human disturbance. *Biological Conservation*, 97 (2): 265-268.

Hagemoen, R. I. M. & Reimers, E. (2002). Reindeer summer activity pattern in relation to weather and insect harassment. *Journal of Animal Ecology*, 71 (5): 883-892.

Kaltenborn, B. P. (1991). *Utkast til forvaltningsplan for turisme og friluftsliv på Svalbard*. Lillehammer, NINA. 167 p.

Kastnes, K. (1979). *Svalbard-reinens aktivitetsmønster gjennom året, (Rangifer tarandus platyrhynchus)*, Msc. thesis, University of Oslo.

Kohler, J. & Aanes, R. (2004). Effect of winter snow and ground-icing on a Svalbard reindeer population: Results of a simple snowpack model. *Arctic Antarctic and Alpine Research*, 36 (3): 333-341.

Kumpula, J. & Colpaert, A. (2003). Effects of weather and snow conditions on reproduction and survival of semi-domesticated reindeer (*R-t. tarandus*). *Polar Research*, 22 (2): 225-233.

Loe, L. E., Bonenfant, C., Mysterud, A., Severinsen, T., Øritsland, N. A., Langvatn, R., Stien, A., Irvine, R. J. & Stenseth, N. C. (2007). Activity pattern of arctic reindeer in a predator-free environment: no need to keep a daily rhythm. *Oecologia*, 152 (4): 617-624.

Manor, R. & Saltz, D. (2003). Impact of human nuisance disturbance on vigilance and group size of a social ungulate. *Ecological Applications*, 13 (6): 1830-1834.

Norris, S. (1998). *Ferdsel knyttet til turisme på Svalbard: registreringer utført av Sysselmannen på Svalbard og Info-Svalbard : årsrapport 1997*. Longyearbyen, Sysselmannen på Svalbard. 22 p.

Reimers, E. (1980). Activity pattern; The major determinant for growth and fattening in rangifer? *Reindeer/Caribou Symposium II*, Part B: 466-474.

Reimers, E. (1983). Mortality in Svalbard Reindeer. *Holarctic Ecology*, 6 (2): 141-149.

Reimers, E. (1984). Body composition and population regulation of Svalbard reindeer. *Rangifer*, 4: 16-21.

Reimers, E. & Colman, J. E. (2006). Reindeer and caribou (*Rangifer*) response to human activities - a literature review. *Rangifer*, 26: 55-71.

Reimers, E., Colman, J. E., Dervo, L. B., Eftestol, S., Kind, J. & Munic, A. (2000). Frykt- og fluktavstander hos villrein. *Villreinen*: 76-80.

Reimers, E., Ringberg, T. & Sørumgard, R. (1982). Body-Composition of Svalbard Reindeer. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, 60 (8): 1812-1821.

Reimers, E. & Svela, S. (2001). Vigilance behaviour in wild and semi-domestic reindeer in Norway. *Alces*, 37 (2): 303-313.

Rønning, O. I., Lid, D. T. & Brekke, A. (1996). *Svalbards flora*. Oslo, Norsk polarinstitutt. 182 p.

Snyder, J., Snyder, J. M. & Prokosch, P. (2007). *Tourism in the polar regions: the sustainability challenge*. Nairobi, United Nations Environment Programme. 55 p.

Sysselmannen. (2006). *Turisme og friluftsliv på Svalbard*. Sysselmannens rapportserie, vol. 1/2006. Longyearbyen, Sysselmannen på Svalbard.

Taylor, A. R. & Knight, R. L. (2003). Behavioral responses of wildlife to human activity: terminology and methods. *Wildlife Society Bulletin*, 31 (4): 1263-1271.

Tyler, N. J. C. (1986). The realtionship between the fat content of Svalbard reindeer in autumn and their death from starvation in winter. *Rangifer*, Special edition no. 1: 311-314.

Tyler, N. J. C. (1987). *Natural limitation of the abundance of the High Arctic Svalbard reindeer*, University of Cambridge. XX, 321 p.

Tyler, N. J. C. & Øritsland, N. A. (1989). Why don't Svalbard reindeer migrate. *Holarctic Ecology*, 12 (4): 369-376.

Vanderknaap, W. O. (1989). Past Vegetation and Reindeer on Edgeoya (Spitsbergen) between C-7900 and C-3800 Bp, Studied by Means of Peat Layers and Reindeer Fecal Pellets. *Journal of Biogeography*, 16 (4): 379-394.

Venables, W. N. & Ripley, B. D. (2002). *Modern applied statistics with S*. New York, Springer. XI, 495 p.

Vistad, O. I. (2008). *Miljøeffekter av ferdsel og turisme i Arktis: en litteratur- og forstudie med vekt på Svalbard*. Lillehammer/Trondheim, Norsk institutt for naturforskning. 124 p.

Vistnes, I. & Nellemann, C. (2008). The matter of spatial and temporal scales: a review of reindeer and caribou response to human activity. *Polar Biology*, 31 (4): 399-407.

Wiig, Ø. (2000). *Kunnskapsstatus for isbjørn ved Svalbard og framtidige behov for kartlegging, overvåking og forskning*. Tromsø, Norsk polarinstitutt. 34 p.

Øritsland, N. A. (1986). *Svalbardreinen og dens livsgrunnlag*. Oslo, Universitetsforlaget. 184 p.

Aanes, R., Saether, B. E. & Øritsland, N. A. (2000). Fluctuations of an introduced population of Svalbard reindeer: the effects of density dependence and climatic variation. *Ecography*, 23 (4): 437-443.

Aastrup, P. (2000). Responses of West Greenland caribou to the approach of humans on foot. *Polar Research*, 19 (1): 83-90.

APPENDIX 1

Parameter estimates, 95% confidence limits (CI) and test statistics for the analysis of response distances of wild reindeer disturbed by an intruding person in four areas (Adventdalen, Colesdalen, Reindalen , Sassendalen) in Nordenskiöld Land July/August 2006, based on the best models selected based on the AIC criterion. Ln sight distance: R^2 = 0.4732; ln flight initiation distance: R^2 = 0.5856; ln distance moved: R^2 = 0.6739; sqrt assessment time: R^2 = 0.7935.

Variable	Value	SE	Lower CI	Upper CI	t value	Pr(>|t|)
ln sight distance						
(Intercept)	-0.4237	0.8377	-2.0656	1.2182	-0.5058	0.6150
ln encounter	0.8282	0.1256	0.5820	1.0744	6.5933	<0.0001
Wind speed (light/ gentle breeze vs. calm)	0.8390	0.3313	0.1897	1.4883	2.5322	0.0143
Wind speed (moderate/fresh breeze vs. calm)	0.7016	0.3875	-0.0579	1.4611	1.8105	0.0758
Terrain (rugged vs. flat)	0.2037	0.1236	-0.0386	0.4460	1.6483	0.1051
ln flight initiation distance						
(Intercept)	3.1839	0.5528	2.1004	4.2674	5.7595	0.0000
Colesdalen vs. Adventdalen	0.7077	0.2908	0.1377	1.2777	2.4333	0.0191
Reindalen vs. Adventdalen	1.0110	0.2583	0.5047	1.5173	3.9146	0.0003
Sassendalen vs. Adventdalen	0.9859	0.2601	0.4761	1.4957	3.7897	0.0005
Groupsize	0.0880	0.0462	-0.0026	0.1786	1.9054	0.0633
Group structure (males vs. mixed)	0.3689	0.2823	-0.1844	0.9222	1.3067	0.1981
Group structure (females and yearlings vs. mixed)	0.3612	0.3373	-0.2999	1.0223	1.0708	0.2901
Group structure (females and calves vs. mixed)	1.2512	0.3505	0.5642	1.9382	3.5697	0.0009
Activity (grazing vs. lying)	0.2342	0.2409	-0.2380	0.7064	0.9721	0.3363
Activity (moving/grazing vs. lying)	-0.9151	0.4044	-1.7077	-0.1225	-2.2628	0.0286
Activity (lying/grazing vs. lying)	-0.3378	0.3030	-0.9317	0.2561	-1.1150	0.2709
Activity (standing vs. lying)	-0.3586	0.6975	-1.7257	1.0085	-0.5141	0.6098
Wind speed (light/gentle breeze vs. calm)	-0.4070	0.3744	-1.1408	0.3268	-1.0870	0.2829
Wind speed (moderate/fresh breeze vs. calm)	1.2153	0.5266	0.1832	2.2474	2.3076	0.0258
Weather (cloudy vs. sunny/partly sunny	0.2167	0.2274	-0.2290	0.6624	0.9528	0.3459
Weather (foggy vs. sunny/partly sunny)	-1.4934	0.6599	-2.7868	-0.2000	-2.2630	0.0286
Terrain (rugged vs. flat)	-0.3432	0.1729	-0.6821	-0.0043	-1.9845	0.0535
ln distance moved air						
(Intercept)	3.7907	0.4023	3.0022	4.5792	9.4233	0.0000
Colesdalen vs. Adventdalen	1.6087	0.2457	1.1271	2.0903	6.5473	0.0000

Reindalen vs. Adventdalen	1.1581	0.2191	0.7287	1.5875	5.2850	0.0000
Sassendalen vs. Adventdalen	1.0417	0.2085	0.6330	1.4504	4.9964	0.0000
Group structure (males vs. mixed)	-0.2758	0.2099	-0.6872	0.1356	-1.3139	0.1949
Group structure (females and yearlings vs. mixed)	-0.7211	0.2850	-1.2797	-0.1625	-2.5298	0.0146
Group structure (females and calves vs. mixed)	-0.1957	0.2662	-0.7175	0.3261	-0.7350	0.4657
Wind speed (light/gentle breeze vs. calm)	-0.7731	0.3214	-1.4030	-0.1432	-2.4052	0.0199
Wind speed (moderate/fresh breeze vs. calm)	0.3653	0.4404	-0.4979	1.2285	0.8293	0.4109
Weather (cloudy vs. synny/partly sunny)	1.1175	0.1934	0.7384	1.4966	5.7795	0.0000
Weather (foggy vs. sunny/partly sunny)	0.1337	0.5751	-0.9935	1.2609	0.2325	0.8171
Sqrt assessment time						
(Intercept)	-28.9495	3.5545	-35.9163	-21.9827	-8.1445	0.0000
In sight	7.5206	0.6518	6.2431	8.7981	11.5389	0.0000
Colesdalen vs. Adventdalen	0.8183	1.0087	-1.1588	2.7954	0.8113	0.4215
Reindalen vs. Adventdalen	-1.3011	0.8931	-3.0516	0.4494	-1.4568	0.1521
Sassendalen vs. Adventdalen	-1.7620	0.8470	-3.4221	-0.1019	-2.0803	0.0432
Group structure (males vs. mixed)	0.7365	0.8645	-0.9579	2.4309	0.8519	0.3988
Group structure (females and yearlings vs. mixed)	-1.1923	1.3028	-3.7458	1.3612	-0.9152	0.3650
Group structure (females and calves vs. mixed)	-2.8853	1.0855	-5.0129	-0.7577	-2.6580	0.0108
Terrain (rugged vs. flat)	1.9977	0.6750	0.6747	3.3207	2.9596	0.0049
Provwind (tail wind vs. into the wind/crossways to the wind)	-2.1331	0.7971	-3.6954	-0.5708	-2.6761	0.0104

APPENDIX 2

Parameter estimates and test statistics for multiple comparisons of contrasts in Appendix 1. CIs are 95 % simultaneous confidence intervals for specified linear combinations by the Tukey method or the Sidak method for interaction testing(Crawley 2002). Intervals excluding 0 are flagged by *.

Variable	Estimate	SE	Lower CI	Upper CI	
In sight model: Comparison of contrasts					
Wind speed					
calm vs. light/gentle breeze	-0.8390	0.3310	-1.6400	-0.0405	*
calm vs. moderate/fresh breeze	-0.7020	0.3880	-1.6400	0.2320	
light/gentle breeze vs. moderate/fresh breeze	0.1370	0.2110	-0.3710	0.6460	
In flight initiation model: Comparison of contrasts					
Area					
Adventdalen vs. Colesdalen	-0.7080	0.2910	-1.5100	0.0915	
Adventdalen vs. Reindalen	-1.0100	0.2580	-1.7200	-0.3010	*
Adventdalen vs. Sassendalen	-0.9860	0.2600	-1.7000	-0.2710	*
Colesdalen vs. Reindalen	-0.3030	0.2960	-1.1200	0.5090	
Colesdalen vs. Sassendalen	-0.2780	0.2800	-1.0500	0.4920	
Reindalen vs. Sassendalen	0.0251	0.2310	-0.6090	0.6590	
Group structure					
mixed vs. males	-0.3690	0.2820	-1.1400	0.4070	
mixed vs. females and yearlings	-0.3610	0.3370	-1.2900	0.5660	
mixed vs. females and calves	-1.2500	0.3510	-2.2100	-0.2880	*
males vs. females and yearlings	0.0077	0.2860	-0.7780	0.7930	
males vs. females and calves	-0.8820	0.2570	-1.5900	-0.1760	*
females and yearlings vs. females and calves	-0.8900	0.3560	-1.8700	0.0877	
Activity					
lying vs. grazing	-0.2340	0.2410	-0.9420	0.4740	
lying vs. moving/grazing	0.9150	0.4040	-0.2730	2.1000	
lying vs. lying/grazing	0.3380	0.3030	-0.5520	1.2300	
lying vs. standing	0.3590	0.6970	-1.6900	2.4100	
grazing vs. moving/grazing	1.1500	0.3620	0.0863	2.2100	*
grazing vs. lying/grazing	0.5720	0.2470	-0.1540	1.3000	
grazing vs. standing	0.5930	0.6620	-1.3500	2.5400	
moving/grazing vs. lying/grazing	-0.5770	0.3780	-1.6900	0.5320	
moving/grazing vs. standing	-0.5570	0.7320	-2.7100	1.5900	
lying/grazing vs. standing	0.0207	0.6800	-1.9800	2.0200	
Wind speed					
calm vs. light/gentle breeze	0.4070	0.3740	-0.5010	1.3200	
calm vs. moderate/fresh breeze	-1.2200	0.5270	-2.4900	0.0621	
light/gentle breeze vs. moderate/fresh breeze	-1.6200	0.3950	-2.5800	-0.6640	*
Weather					
sunny/partly sunny vs. cloudy	-0.2170	0.2270	-0.7680	0.3350	
sunny/partly sunny vs. foggy	1.4900	0.6600	-0.1070	3.0900	

cloudy vs. foggy	1.7100	0.6480	0.1390	3.2800	*
ln distance moved air: Comparison of contrasts					
Area					
Adventdalen vs. Colesdalen	-1.6100	0.2460	-2.2800	-0.9370	*
Adventdalen vs. Reindalen	-1.1600	0.2190	-1.7600	-0.5590	*
Adventdalen vs. Sassendalen	-1.0400	0.2080	-1.6100	-0.4720	*
Colesdalen vs. Reindalen	0.4510	0.2460	-0.2200	1.1200	
Colesdalen vs. Sassendalen	0.5670	0.2270	-0.0521	1.1900	
Reindalen vs. Sassendalen	0.1160	0.2050	-0.4450	0.6780	
Group structure					
mixed vs. males	0.2760	0.2100	-0.2980	0.8500	
mixed vs. females and yearlings	0.7210	0.2850	-0.0581	1.5000	
mixed vs. females and calves	0.1960	0.2660	-0.5320	0.9230	
males vs. females and yearlings	0.4450	0.2530	-0.2470	1.1400	
males vs. females and calves	-0.0801	0.2100	-0.6540	0.4940	
females and yearlings vs. females and calves	-0.5250	0.3000	-1.3400	0.2940	
Wind speed					
calm vs. light/gentle breeze	0.7730	0.3210	-0.0033	1.5500	
calm vs. moderate/fresh breeze	-0.3650	0.4400	-1.4300	0.6990	
light/gentle breeze vs. moderate/fresh breeze	-1.1400	0.3210	-1.9100	-0.3640	*
Weather					
sunny/partly sunny vs. cloudy	-1.1200	0.1930	-1.5800	-0.6500	*
sunny/partly sunny vs. foggy	-0.1340	0.5750	-1.5200	1.2600	
cloudy vs. foggy	0.9840	0.5730	-0.4000	2.3700	
sqrt assessment time: Comparison of contrasts					
Area					
Adventdalen vs. Colesdalen	-0.8180	1.0100	-3.5900	1.9500	
Adventdalen vs. Reindalen	1.3000	0.8930	-1.1500	3.7500	
Adventdalen vs. Sassendalen	1.7600	0.8470	-0.5630	4.0900	
Colesdalen vs. Reindalen	2.1200	0.9830	-0.5790	4.8200	
Colesdalen vs. Sassendalen	2.5800	0.9490	-0.0235	5.1800	
Reindalen vs. Sassendalen	0.4610	0.8910	-1.9900	2.9100	
Group structure					
mixed vs. males	-0.7360	0.8640	-3.1100	1.6400	
mixed vs. females and yearlings	1.1900	1.3000	-2.3800	4.7700	
mixed vs. females and calves	2.8900	1.0900	-0.0947	5.8700	
males vs. females and yearlings	1.9300	1.1100	-1.1200	4.9800	
males vs. females and calves	3.6200	0.9220	1.0900	6.1500	*
females and yearlings vs. females and calves	1.6900	1.3200	-1.9400	5.3300	