The influence of natural and anthropogenic factors on *Rangifer* movements and habitat use

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1. INTRODUCTION

Rangifer tarandus (reindeer and caribou) is a circumpolar species inhabiting the Arctic and sub-arctic regions of Eurasia and North America. It is a key species in the northern hemisphere and has for centuries been a vital resource for many communities and indigenous peoples in the Arctic.

In Fennoscandia most reindeer are semi-domesticated, while smaller herds of wild reindeer exist in mountainous areas in southern Norway and forested areas in eastern Finland. Reindeer herding forms a basis for the Sámi cultural heritage and is an essential economic income to many people within the Sámi society in Fennoscandia. In accordance with international agreements, there is a management goal in Norway and Sweden to ensure the livelihood of the Sámi people, including a sustainable reindeer husbandry, alongside with conservation of landscapes and biodiversity (Nilsson-Dahlström 2003).

Although reindeer are domesticated they are freely ranged within the borders of the herding districts, and their behaviour and habitat selection are comparable to wild reindeer and caribou. *Rangifer* have developed in areas with high spatial and temporal heterogeneity in resource availability. Throughout the year the animals follow the seasonal changes in forage quantity and quality, and depend on access to large heterogeneous land areas to meet their energetic demands (Klein 1970). A constantly increasing infrastructure development has largely changed the terms for the reindeer and the reindeer husbandry in Fennoscandia. Further challenges are caused by the recent 20-30 years of growing predator populations, with a consequent need for management to find compromises between the conflicting interests of carnivore conservation and a sustainable reindeer husbandry.

The main predators of semi-domesticated reindeer in Fennoscandia are the large carnivores: lynx (*Lynx lynx*), wolverine (*Gulo gulo*), brown bear (*Ursus arctos*), wolves (*Canis lupus*) and golden eagle (*Aquila chrysaetos*). Direct losses of reindeer to predation can be substantial (Danell 2011, Hobbs et al. 2012). However, the total effect of predation on herd productivity is still subject to debate. Also, we lack knowledge about behavioural interactions with predators and antipredator strategies in semi-domesticated reindeer.

Anthropogenic activity and infrastructure development is threatening *Rangifer* in large parts of its range. Human development can cause habitat loss by direct cover of areas, indirectly from avoidance effects or by making movements barriers. This can lead to important transport corridors being cut off, and loss of feeding grounds and critical habitats such as calving areas. Changes in foraging conditions do not only have immediate effects on the animal but also affect future performance and its progeny during several years (Gaillard et al. 2000).

The aim of the present review is to give an overview of the existing knowledge of *Rangifer* foraging and antipredator behaviour, and impact of human disturbance on *Rangifer* habitat use. As a theoretical framework I briefly summarize the main theories of foraging and antipredator behaviour in ecology. Finally I discuss the current and future challenges and knowledge gaps related to management of reindeer herding areas in Fennoscandia.

Gathering of reindeer in Gällivare reindeer herding community, Sweden.
Foto: Therese Ramberg Sivertsen

2. FORAGING ECOLOGY

2.1 Hierarchical habitat selection and optimal foraging

Understanding how organisms exploit their environment is central in ecology. Why do animals choose to eat a specific plant, spend time in a certain habitat type or move along a given path? What are the decision-making mechanisms and which factors influence the behavioural decisions?

Generally, in heterogeneous environments, animals should select the resources and areas that give the highest probability to survive and reproduce (i.e. fitness) given the circumstances. Habitat selection studies thus begin with describing the habitats and ends with estimating the consequences of the animals choices of habitat on individual fitness (Rettie and Messier 2000). Johnson (1980) distinguishes between usage and selection of resources, the first being defined as the component of a resource utilized during a fixed time period while the latter is the actual process of which the animal choose the component. If components are used disproportionally to their availability the usage is said to be selective.

The environmental factors influencing the behavioural responses of animals may operate at various spatial and temporal scales. Habitat selection can be considered as a hierarchical process where forage decisions are being made at a range of spatial scales from micro-patches to regional systems (Fig. 1) (Johnson 1980, Senft et al. 1987). Defining the scale of investigation is therefore an essential part of studying habitat selection (Wiens 1973). Four orders of hierarchical spatial scales was identified by Johnson (1980), based on the idea that a selection process is of higher order than another if it is conditional upon the latter (Johnson 1980). Later, Senft et al. (1987) introduced an ecological hierarchy for large herbivore foraging (Fig 1, Table 1).

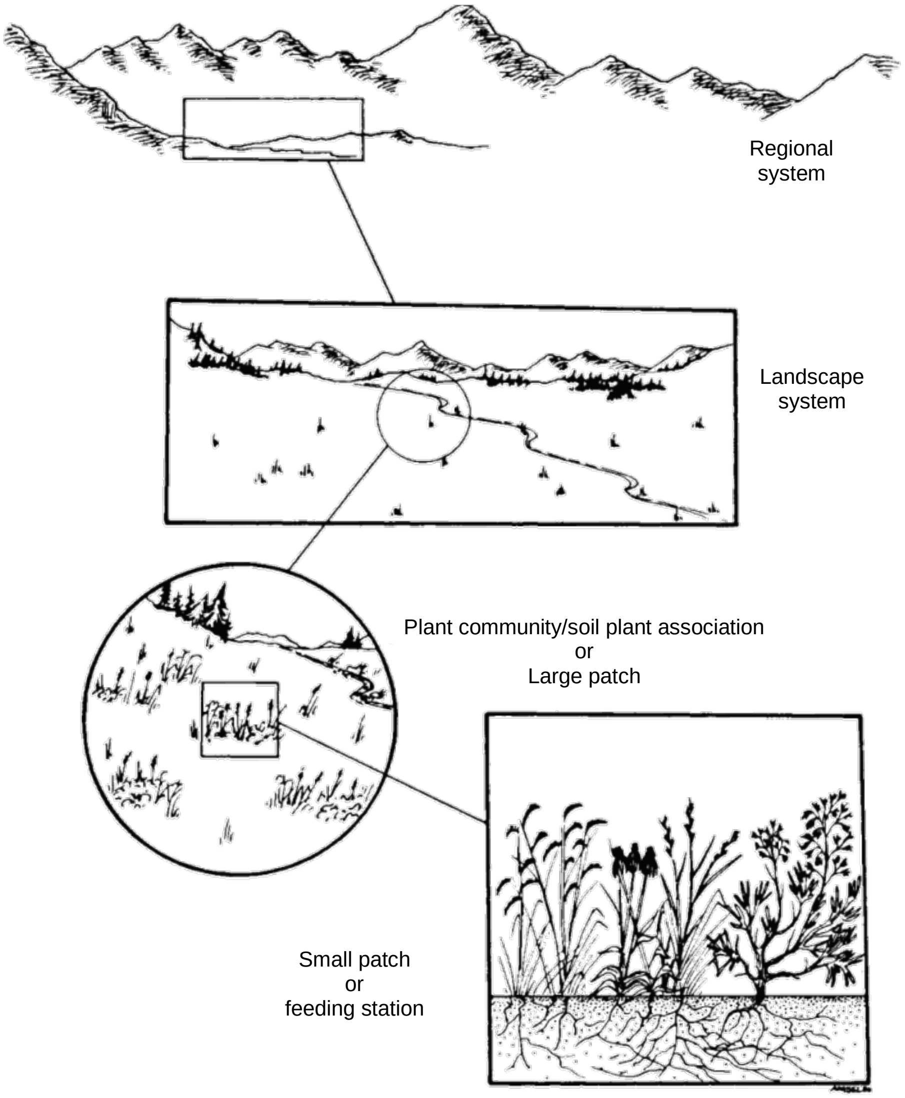

Fig 1. An example of an ecological hierarchy for large herbivores. The different scales are defined by functional parameters rather than physical structures (Senft et al. 1987).

Ecological hierarchical scales			
Johnson (1980)	**Senft et al. (1987)**	**Units of selection within scale**	**Description**
First-order		Region	Species physical and geographical range
Second-order	Region	Landscape	Home range behaviour, migration, nomadism
Third-order	Landscape	Communities/ large patches	Feeding area selection
Fourth-order	Community	Plants or micropatches	Diet selection

Table 1. An overview of hierarchical ecological scales of selection identified by Johnson (1980) and, more specifically for large herbivore foraging, by Senft et al. (1987)

Optimal foraging theory states that animals should forage in a way that maximizes the intake rate of nutrients and energy (MacArthur and Pianka 1966). At the community scale an animal must decide what plants and plant parts to eat and how to move between micro-patches in the plant community to obtain maximal diet quality and adequate quantity. The marginal value theorem states that an animal will remain in a given food patch until nutrient/energy intake rate falls beneath a given level. When to leave a patch will depend on a) the rate of nutrient and energy intake in the given patch, b) the expected intake in other patches and c) the cost of moving to a new patch (Charnov 1976). In general, a positive correlation is expected between the relative preference for food items/communities/habitat types and the food biomass and nutritive quality. This relationship can in turn be modified by other environmental factors such as predation risk, access to water, topography and microclimate. Maximization of nutrient intake may be most important at the smallest scale while other, non-food related, resources may be increasingly important at the landscape and regional scales (Senft et al. 1987).

2.3 Foraging ecology of Rangifer

Resource selection in *Rangifer* reflects the seasonality of the arctic and subarctic regions, with large variations in food availability and often low forage biomass, but where the annual phenological succession of vegetation tends to be highly predictable, thus allowing for strong habitat selection by the species (Klein 1970, Skogland 1984b). To make use of the spatial and temporal changes in forage availability and quality throughout the year *Rangifer* needs access to large areas with heterogeneous landscapes and terrain (Klein 1970, White and Trudell 1980, Mårell and Edenius 2006). In general the diet composition of *Rangifer* depends on the nutrient contents, digestibility, amount of secondary compounds and relative availability of potential food (White and Trudell 1980, Skogland 1984b).

At the regional scale most *Rangifer* populations perform seasonal migrations between summer and winter ranges. The animals arrive at the calving grounds with the initiation of plant growth in spring. At this time of year habitat selection is relatively narrow, but as the snow melts and plant growth increases the animals can select among several habitats types (Skogland 1984b). For *Rangifer* populations living in mountainous and open areas, the calving grounds are often located at higher elevations and in rugged terrain (Bergerud et al. 1984, Bergerud and Page 1987, Barten et al. 2001, Gustine et al. 2006), while forest-dwelling populations commonly use wetland habitats (Brown et al. 1986, Cumming et al. 1994, James et al. 2004). These areas often provide spatial separation from predators and alternate prey (Bergerud et al. 1984, Bergerud et al. 1990, James et al. 2004, Latham et al. 2011). In rugged terrain the topography promote snow ablation with a continuous and prolonged emergence of high nutrient vegetation, as well as serving as escape terrain from predators (Bergerud et al. 1984, Nellemann and Cameron 1996).

In summer most *Rangifer* populations prefer to feed in elevated areas (White et al. 1981, Skarin et al. 2008). However, some forest-dwelling herds of woodland caribou typically remain in the forest-wetland habitats used for calving (Brown et al. 1986). During this period the animals are almost constantly moving, actively selecting different forage plant communities or species (White et al. 1981). As the snow gradually disappears, environmental factors such as light and soil conditions become increasingly important for plant productivity, while the importance of ruggedness may decrease (Mårell and Edenius 2006). Throughout the season *Rangifer* continue to favour plants in an early growth phase that generally have a high nutritive value. During the leafing and flowering stages alpine and arctic plants commonly have high levels of total non-structural carbohydrates and nitrogen and only small amounts of indigestible cell wall elements (see Skogland 1984b). Insect harassment, by oestrid flies in particular, also strongly influences animal movements during summer (Helle and Tarvainen 1984, Hagemoen and Reimers 2002). To get insect relief the animals are often forced to less productive habitats, such as snow patches, wet marshes or wind-exposed sites at higher elevations (Hagemoen and Reimers 2002, Skarin et al. 2010). During intense insect harassment objects that normally deflect reindeer movements loose their role as effective barriers and the shortest route to insect relief sites is often chosen (White et al. 1981).

In winter *Rangifer* generally prefer to feed on lichens (Bergerud 1972, Skogland 1984b, Danell et al. 1994, Kojola et al. 1995), and to a lesser degree on dwarf shrubs, mosses, sedges and grasses. The intake of dwarf shrubs and vascular plants; however, increases with lower abundance of lichens (Skogland 1984b, Kojola et al. 1995). Terrestrial lichens are obtained by digging craters in the snow (White et al. 1981). The distribution and movements of *Rangifer* in winter are highly correlated with the effects of snow structure and snow depth on locomotion and access to food resources (White et al. 1981, Nellemann 1996, Heithaus et al. 2008).

Forest-dwelling reindeer in Scandinavia commonly prefer to feed at hills and highlands in fall and early winter, and then move down to lower elevations as snow starts to accumulate (Kumpula and Colpaert 2007, Heithaus et al. 2008). Within the winter grounds the reindeer adjust to variations in lichen quality and accessibility that are constantly changing with the interaction of snow cover, temperature, forest structure and ground characteristics (Heithaus et al. 2008). However, commercial forestry and other types of human activity in reindeer herding areas have made restrictions on reindeer movements, negatively affecting the availability of winter forage (Kumpula and Colpaert 2007, Heithaus et al. 2008).

Also in arctic and alpine regions do *Rangifer* migrate to feeding grounds with thinner and softer snow cover during winter (Nellemann et al. 2001). Within the winter ranges rugged terrain usually provide more favourable snow conditions for feeding (White et al. 1981, Nellemann 1996). In rugged terrain, narrow exposed ridges with high microtopographic diversity are preferred, here the snow is typically blown away, favouring locomotion, while smaller patches of snow persist and protect the lichens underneath in less exposed parts (Nellemann 1996).

Although poor in protein and macrominerals, lichens are rich in structural carbohydrates that are easily digestible for the reindeer rumen flora and an essential source of energy in the cold season (Klein 1990, Danell et al. 1994). *Rangifer*, like other ruminants, can cope with the low protein intake due to a high ability to decrease nitrogen excretion and recycle it to the rumen (Wales et al. 1975) . The energy to drive this process is mainly derived from the carbohydrates in the lichens (Giesecke 1970, White and Gau 1972). Feeding on lichens, compared to vascular plants, may in fact be a benefit in cold weather and when energy intake is low. Eventual surplus of nitrogen would have to be excreted with urine, thus increasing water requirements, which is satisfied by eating snow, resulting in a thermal energy cost for the animal (Soppela et al. 1992).

3. PREDATION

3.1 Antipredator behaviour and optimal foraging

Animals are generally expected to modify their habitat use and movement patterns to their perception of risk, often balancing conflicting demands of foraging and safety (Sih 1980, Lima 1998, Brown 1999). Thus, in addition to having a direct lethal effect on their prey, predators may also have nonlethal impact through behavioural responses to predation risk, resulting in costs related to feeding, activity levels and reproduction (Sih 1980, Lima and Dill 1990, Brown et al. 1999). In some cases nonlethal effects of predators may be even more important than direct mortality on prey populations (Brown et al. 1999).

With predators present animals may adjust foraging behaviour in order to increase safety, either by changing to lower quality, but safer habitats (Sih 1980), increase their levels of vigilance (Lima 1998, Brown 1999, Frid and Dill 2002) or decrease activity (Lawler 1989). Thus, predator presence can cause reduced feeding time and lower diet quality, which may result in lower body mass or reduced fat content of females, lower survival rates of both adults and calves during stress periods and lower birth mass of calves in spring. All this may have implications for population dynamics (Laundré et al. 2001).

3.2 Spatial variation in predation risk

In a heterogeneous landscape certain areas and habitat features may be coupled to higher risk of predator encounters, and to be detected and captured, while other areas may function as prey refugees (Kauffman et al. 2007, Laundré et al. 2010). Indeed, prey-predator systems are assumed to persist over the longer term due to variability in predation risk in space and time (Ellner et al. 2001). The spatial variation in predation risk can occur at a number of scales from entire landscapes to habitat types, terrain characteristics and escape impediments (Laundré et al. 2010). Kunkel and Pletcher (2000) showed that moose were more likely to be killed by wolves at lower elevations, and at open sites farther from forest cover. In contrast, Bergman et al. (2006) found that elk were more vulnerable to wolf predation closer to edges of burned forest and rivers, probably because switches in landscape structure in this system reduced escape efficiency.

Predation risk can be decomposed into the probability of a prey encountering a predator and the conditional probability of being killed given an encounter (Lima and Dill 1990, Hebblewhite et al. 2005, Atwood et al. 2009). The probability of encountering a predator is in many cases related to predator distribution and abundance (Hebblewhite et al. 2005, Heithaus et al. 2008). The chance of being killed given an encounter will, however, be context dependent, varying with predator hunting mode, prey escape tactics and terrain and habitat features (Hebblewhite et al. 2005, Heithaus et al. 2008). A key question is thus how prey adjust their behaviour to the spatial variation in predation risk and further, how prey weight encounter risk against their conditional probability of death (Heithaus et al. 2008).

The concept “landscape of fear” represents the variation in predation risk experienced by prey across a heterogenic landscape and puts predation risk and behavioural responses on a quantifiable spatial scale (Fig.2) (Laundré et al. 2010).

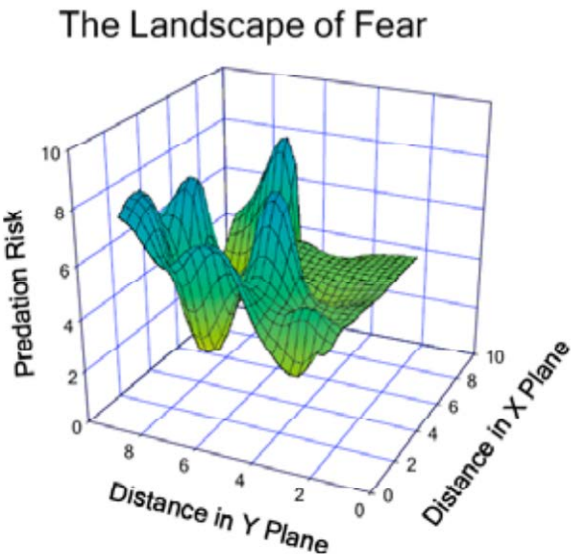

Fig 2. Example of a landscape of fear where the x and y axis are the physical coordinates of an area, and the z-axis is the level of predation risk experienced by the prey (Laundré et al. 2010)

A number of studies confirm that animals adjust their behaviour to the distribution of predation risk across the landscape, often at the expense of nutritional requirements. Hernández and Laundré (2005) documented a shift in elk habitat use from riskier open meadows to forest edges and reduced diet quality in areas with wolves compared to areas without wolves. Similarly Creel et al. (2005) found that elk moved into protective wooded areas when wolves were present.

Few studies have assessed the simultaneous impact of resource distribution and predation risk on habitat use. Willems and Hill (2009) estimated the probabilistic measures of range use of vervet monkeys by combining effects of habitat characteristics and perceived risk of predation. They found that predator avoidance and resource availability accounted for >60% of total variation in space use intensity, and that the effect of avoidance can exceed those of forage resource distribution.

3.3 Antipredator behaviour in *Rangifer*

Rangifer usually space away from predators and alternate prey to avoid predator encounters when selecting calving grounds (Bergerud et al. 1984, Bergerud and Page 1987, James et al. 2004) and winter ranges (Cumming et al. 1994, Mosnier et al. 2003). Avoidance of areas preferred by alternate prey of wolves and bears, such as moose, simultaneously reduce the risk of encountering predators (James et al. 2004). Within the seasonal ranges terrain features that minimize encounter risk and promote predator detection and escape probabilities are often selected (Bergerud and Page 1987).

Calving grounds

Some *Rangifer* populations in North America separate spatially from predation risk by migrating several hundred kilometres northwards to calve in areas above the tree line, thereby avoiding the high densities of predators that are present further south (Bergerud and Page 1987). At the calving grounds the animals gather in larger groups, which reduces the probability for calves to be detected by predators and is a suitable tactic in areas with low predator densities (Bergerud and Page 1987). More sedentary *Rangifer* populations may space away from predators and alternate prey with shorter migratory movements to calving grounds on islands and along shore lines (Bergerud 1985, Bergerud and Page 1987), in elevated areas (Bergerud et al. 1984, Bergerud and Page 1987) or in forest wetland habitat (Brown et al. 1986). Within the calving areas the females usually space out to increase searching time, and thus reduce encounter rate, of predators (Bergerud and Page 1987).

Calving grounds of *Rangifer* populations in open or mountainous habitats are mostly located in rugged, heterogeneous terrain at higher elevations (Bergerud et al. 1984, Bergerud and Page 1987, Barten et al. 2001, Gustine et al. 2006). In these areas parturient females decrease the probability of encounters with predators by being spaced away from the travel corridors of wolves and bears along the valley bottoms and by spreading out in the landscape (Bergerud and Page 1987, Seip 1992). High elevations also promote predator detection and rugged terrain make it easier to escape from predators (Bergerud et al. 1984). Further, in heterogeneous terrain snow melts in smaller patches regardless of spring phenology, providing a cryptic background for calves and females (Bergerud and Page 1987).

Forest-dwelling herds of woodland caribou calve within forest wetland habitat, less preferred by predators and alternate prey (Brown et al. 1986, Bergerud and Page 1987, James et al. 2004, Latham et al. 2011). In Alberta spatial separation from the preferred habitats of black bears, wolves and alternate prey species (moose) was evident for calving ground habitat selection of woodland caribou (James et al. 2004, Latham et al. 2011). Caribou had a strong selection against well-drained habitats preferred by wolves and moose (James et al. 2004) and against upland mixed woods generally preferred by black bears, although some bears moved into caribou calving areas (Latham et al. 2011).

Predation risk may also drive fine-scale selection of calving sites within the calving grounds. Shrub cover can obscure the visibility of the calves, making it harder for predators to detect them (Bowyer et al. 1998)**,** at the same time offering important spring forage for parturient females (Créte et al. 1990). Gustine et al. (2006) found that caribou calf survival was higher at calving sites with dense shrub cover. In contrast, Briand et al. (2009) did not document any effects of vegetation cover on female caribou habitat selection in summer. This could have been because the study covered the whole snow free period, not only the calving season. However, Pinard et al. (2012) similarly documented that caribou with calves selected sites with less vegetation cover, apparently choosing probability of predator detection over concealment. Further, also at this finer scale of selection *Rangifer* may avoid habitat preferred by alternate prey species as an antipredator strategy (James et al. 2004, Briand et al. 2009). For instance, woodland caribou showed preference for calving sites with less available forage to moose (Briand et al. 2009). Additionally, *Rangifer* may choose calving sites at elevated locations for a better overview, and adjust the choice of slope directions according to the prevailing winds, to prevent the scent from reaching the predators (Bergerud et al. 1984, Gustine et al. 2006).

Trade-offs between foraging and predation risk have been documented for *Rangifer*, and may be particularly pronounced for parturient females due to increased nutritional demands during lactation and the higher vulnerability of calves to predation (Skogland 1984a, Bowyer 1991). Selection of elevated areas for calving grounds may be at the expense of nutritional requirements (Bergerud et al. 1984). Low land areas are commonly associated with higher vegetation biomass (Barten et al. 2001, Gustine et al. 2006). In comparison the food are usually less nutritious and less abundant at high elevations (Bergerud et al. 1984, Bergerud and Page 1987, Barten et al. 2001). In North-America this trade-off have been apparent for caribou, where males and females without calves fed at lower elevations than parturient females, getting access to more forage, but with higher risk of predation (Bergerud et al. 1984, Barten et al. 2001). Also for semi-domesticated reindeer this is a well-known pattern (Birgitta Åhman 2012, pers. comm.). Further, females with calves have been observed to move to lower elevations some weeks after parturition, when their calves were more mobile and less vulnerable to predation (Bergerud et al. 1984, Barten et al. 2001). However, rugged terrain at high elevations typically provide good micro-climate conditions for vegetation, enhancing forage quality (Nellemann and Cameron 1996, Gustine et al. 2006). Thus, parturient females may be able to increase the intake of quality forage in rugged terrain by feeding in a highly selective manner and thus offset the cost of staying at higher elevations with lower forage biomass. Indeed, Barten et al. (2001) could not document any differences in diet composition in parturient females at higher elevations compared to non-parturient females feeding at lower elevations, despite the lower forage biomass available for the parturient females.

Winter refugees

Also on winter ranges *Rangifer* may space away to reduce predation risk (Cumming et al. 1994). Woodland caribou in Ontario selected wintering habitats in sparsely stocked forested areas with abundant cover of ground lichens, while avoiding other adequate habitats of mixed woods and arboreal lichens. This distribution was negatively correlated with the distribution of wolves and moose in the area (Cumming et al. 1994). In Quebec, an increased preference in woodland caribou for habitats at higher elevations in winter coincided with increased densities of coyotes. This effect was likely due to reduced predation risk at elevated plateaus, where predators were easily detected (Mosnier et al. 2003). Similarly Seip (1992) documented that woodland caribou in British Colombia selected subalpine forests at high elevations, spatially separated from wolves and moose that resided in valley bottom forest and shrub lands. On a smaller spatial scale, Briand et al. (2009) found that caribou during winter fed at sites abundant in lichen, while simultaneously avoiding sites that are more attractive to moose.

4. HUMAN DISTURBANCE

4.1 Habitat loss and habitat fragmentation

Increases in human activities and infrastructure development including roads, power lines, logging, tourist resorts, agriculture, mining, wind power and hydropower dams have in recent time considerably reduced and changed the habitat of *Rangifer* across the arctic and subarctic regions (Bradshaw et al. 1997, Klein 2000, Wolfe et al. 2000, Mahoney and Schaefer 2002, Weladji and Forbes 2002). Human encroachment can cause losses of grazing land and other key habitats such as calving grounds both directly, and indirectly from avoidance effects and blocking of migration routes. Further, human disturbance can affect *Rangifer* activity patterns, causing decreased feeding time and/or increased energy expenditure, and may alter inter-specific interactions.

4.2 The risk-disturbance hypothesis

The risk-disturbance hypothesis predicts that animals will relate to non-lethal human disturbance in the same way as they do to the risk of predation, thus resulting in the associated costs of anti-predator behaviour (Frid and Dill 2002). Prey animals have imperfect information of the predator’s whereabouts and their assessment of predation risk is based on cues in the environment. In general, prey animals are expected to maximize fitness by overestimating the risk of predation (Frid and Dill 2002). Predation risk is related to an interaction of factors affecting encounter, attack and capture probabilities, including structure of the environment, social factors, distribution and abundance of predators and predator behaviour. As the prey respond to changes in these factors rather than the actual predation rate, one should expect animal responses to non-lethal human disturbance to follow the same decision rules as to predation risk (Frid and Dill 2002).

4.2 Impact from human development on *Rangifer*

The methodologies applied to assess the impact of anthropogenic activity on *Rangifer* behaviour and performance can be divided into two main categories, depending on scale: i) Local scale effects (0-2 km, short-term) of the physiological and/or behavioural responses of groups or individual animals to disturbance and ii) Regional scale studies (larger scale: beyond 2 km, long-term), using GPS, faecal pellet group counts or measurements of vegetation cover and biomass to determine changes in habitat use at the population level (Reimers and Colman 2006, Vistnes and Nellemann 2008).

Local scale effects

Effects of human disturbance on *Rangifer* behaviour at a finer scale have been measured through documentation of fright- and flight reactions, restless behaviour or physiological responses (Reimers and Colman 2006).

Flydal et al (2009) made experiments testing the effects of power lines on reindeer behaviour. Behaviour of reindeer inside enclosures (50 x 400 m) with power lines was compared to that of reindeer inside enclosures without power lines. The authors concluded that in these settings power lines were a minor disturbing effect. A similar experiment was performed by comparing reindeer behaviour between enclosures with and without a windmill (Flydal et al. 2004). No systematic changes in behaviour that could indicate stress or fright due to windmill exposure were documented.

Populations subject to hunting may become more sensitive to human approaches and hence display more pronounced fright responses than non-hunted populations. Reimers et al. (2009) found that the distance at which wild reindeer started to flee when approached by a human increased after initiation of hunting. However, overall changes in behaviour after initiation of hunting where relatively light. Generally, flight response of ungulates seems to be most pronounced when approached by humans on foot, while vehicles and humans on horseback appear less disturbing (Reimers and Colman 2006, Stankowich 2008).

Regional scale effects

While local effect studies only document immediate responses in animal groups or individuals to disturbance, regional scale studies carried out over longer time period focus on general changes in movement patterns and habitat use at the population level.

In addition to direct removal of land, infrastructure may cause habitat loss through avoidance and barrier effects. Numerous studies have reported negative impacts of human infrastructure on *Rangifer* space use at the regional scale (Johnson et al. 2005, Vistnes and Nellemann 2008, Vors and Boyce 2009, Nellemann et al. 2010, Polfus et al. 2011)

In the absence of alternative habitat, avoidance behaviour usually causes a decrease in preferred habitat available. Increased *Rangifer* densities in habitat farther away from the disturbance, lead to high grazing pressure and “overuse” of the ranges. Nellemann et al. (2001) showed that densities of wild reindeer were almost 95 % lower in areas within 5 km from power lines associated with roads and ski trails, compared to areas farther away. Also, very low plant biomasses and changed composition of lichens indicated overgrazing in the areas with higher *Rangifer* densities. Likewise, in Alaska a marked decline in calving caribou abundance was observed in areas closer than 4 km from oil field infrastructure, and increased densities in areas with lower quality forage farther away (Nellemann and Cameron 1996). In Canada, woodland caribou avoided areas up to 9 km from towns, roads and cabins (Polfus et al. 2011). Large scale avoidance of human activity and infrastructure have also been documented for semi-domesticated reindeer in Norway (Vistnes and Nellemann 2001) and Finland (Anttonen et al. 2011).

Human development can act as complete or partial barriers hindering *Rangifer* movements within their range and preventing the animals from reaching important calving areas or feeding grounds (Nellemann et al. 2003, Vistnes et al. 2004). For example, although physically possible to cross, linear infrastructures such as roads and power lines can work as partial barriers for reindeer movements if they are perceived as dangerous habitat (Nellemann et al. 2001, Vistnes et al. 2004).

Under certain conditions linear infrastructure may facilitate movements of large predators such as wolves and bears and potentially increase the access of predators into *Rangifer* habitat (James and Stuart-Smith 2000). James and Stuart-Smith (2000) found that wolves killed more caribou close to linear corridors compared to the rest of the caribou range and that caribou at the same time avoided areas closer to the corridors.

5. DISCUSSION

The reindeer herding areas in Fennoscandia are facing a constant pressure from human activity and infrastructure development. At the same time populations of large carnivores are increasing, causing an additional challenge to reindeer husbandry.

Since *Rangifer* depend on access to large heterogeneous land areas, and movement corridors to connect habitats used for feeding, resting and reproduction, they are particularly vulnerable to landscape alterations. For example cutting off a transport corridor can have serious consequences in a *Rangifer* population if this prevents access to important calving grounds or winter ranges.

The likelihood of finding impacts of human activity on *Rangifer* habitat use has been shown to be strongly dependent on the spatial and temporal scales of the study (Vistnes and Nellemann 2008). Generally, most short term responses of *Rangifer* to disturbance appears to be rather brief and moderate, with relatively small energetic implications (Reimers and Colman 2006). In contrast, numerous studies have during the last decades documented regional scale avoidance by reindeer to human activity and infrastructure (Vistnes and Nellemann 2008). However, there are still uncertainties concerning the effects of human development in reindeer herding areas. One remaining challenge is to document the impact of wind power on semi-domesticated reindeer (Helldin et al. 2012). The wind power industry is increasing extensively in northern Fennoscandia. Planned wind parks do in some areas exceed several hundred wind mills, with associated infrastructures of roads and power lines and human activity. Although a few studies have assessed local scale effects on reindeer, regional scale studies will be necessary to predict effects of wind power on *Rangifer* populations. Furthermore, since several different disturbance sources now often appear within close distances, there is a need to gain more knowledge of the simultaneous impact from different sources of disturbance.

Populations of large carnivores in Fennoscandia were heavily hunted and reached very low numbers during the 1800s until the mid 1900s, when they were gradually protected. In the last decades the populations have increased substantially. In Sweden the government accommodates compensations to the reindeer herders for the financial burdens caused by carnivores. However, these payments are based on crude estimates of losses of reindeer to predation, and the reliability of this system has never been assessed (Hobbs et al. 2012). Danell (2011) calculated the loss to predation of semi-domesticated reindeer in Sweden to be 25-30 % of the total winter herd. Recent findings in Sweden estimate declines in the annual harvest of reindeer by approximately hundred animals for each lynx family group or wolverine reproduction present within a reindeer herding area (Hobbs et al. 2012). Further, an on-going study in Northern Sweden has found high brown bear predation rates on calves during the first weeks after birth (Karlsson et al. 2012). Nevertheless, questions remain about the overall effects of predation on reindeer herd productivity, including total predation rates, variation in predator-caused mortality among different sex and age-classes in the herd, the degree of compensatory mortality, and further, how predation rates vary with other factors, such as landscape, climate, predator densities, predator individual traits, prey densities and prey group composition (Tveraa et al. 2003, Hobbs et al. 2012). Furthermore, insight into the behavioural interactions between reindeer and their predators will give a more complete picture of reindeer-predator dynamics. One question is to what degree anti-predator strategies exist among semi-domesticated reindeer after generations of domestication and a long period with an almost complete absence of large carnivores. Generally *Rangifer* rely on escape tactics and avoiding predator encounters to minimize predation risk (Bergerud and Page 1987). Bergerud (1985) hypothesized that *Rangifer* cannot survive in co-existence with predators unless there are habitat features that provide escape of young with calves. For conservation of *Rangifer* populations it is therefore important to preserve calving refugees, winter refugees and travel corridors between (Cumming et al. 1994), but in order to do this one need to understand the behavioural nature of reindeer-predator interactions.

Further, it would be of interest to estimate the costs of antipredator behaviour in terms of lower energy and nutrient intake and increased energy expenditure. Generally, by quantifying the spatial distribution of predation risk and the costs associated with antipredator behaviour we can make more precise predictions about the effects of predator-prey relationships on prey and predator population dynamics, and how this in turn affects other parts of the ecosystem (Laundré et al. 2010). Such knowledge will also help to understand how modifications of the landscape may alter predator –prey interactions (Kunkel and Pletscher 2000). Moreover, understanding which factors are influencing the risk of predation and how the presence of predators shape movements in *Rangifer* will aid in making more correct predictions of how human development affect predation rates, reindeer movements and resource selection.

Although much work have been done on *Rangifer* habitat use and effects of natural and anthropogenic factors, there is still a need to better understand the cumulative impact of several types of infrastructure in combination with natural factors. Moreover, in order to maintain a sustainable reindeer husbandry and balance the different interests within nature management, it is crucial to understand how landscape and habitat mediates *Rangifer*-predator interactions, and how *Rangifer* habitat use and movement corridors between resource patches are influenced by human activity and infrastructure development in combination with predators, other natural environmental factors and landscape features.

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