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Reindeer and caribou (Rangifer tarandus) response towards human activities

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Abstract: We address the question of how human activities and infrastructure influence reindeer/caribou's (Rangifer tarandus) behaviour and habitat use and review studies based on current methodologies. Anthropogenic activities have a direct affect on Rangifer behaviour through the senses hearing, sight and smell, and all of these are important tools for behavioural risk assessment. Short term indirect responses, such as habituation, sensitisation, avoidance, and displacement, develop through neutral, positive or negative associations towards stimulus in terms of Rangifer's ability to experience, learn, and remember. Long term behavioural responses develop through interaction with predators and, for reindeer, also domestication. A survey of the literature dealing with behavioural studies reveals that although Rangifer in most cases retreat from anthropogenic activities, comfort distances (i.e. distances beyond which animal behaviour or activity are not influenced) are relatively short. In most cases, energetic implications appear moderate and small compared to other natural, biotic influences such as disturbance (and death) caused by insect and/or predator harassment. Unless obstructing access, physical constructions of various kinds apparently have limited effects on Rangifer behaviour or habitat use. On the other hand, constructions that do obstruct or limit access and recreational or other motorized and non-motorized activities appear to have stronger impacts on avoidance and redistribution of Rangifer. Behavioural effects that might decrease survival and reproduction include retreat from favourable habitat near disturbance sources and reduction of time spent feeding with resulting energy depletion over time. Rangifer habitat use, habitat avoidance, and feeding preferences are governed by a complexity of natural interacting factors. Domestication, habituation and sensitisation are essential in shaping Rangifer's adaptability, and should be included in future studies on reindeer and caribou responses towards various anthropogenic activities. Although cumulative effects from human activities are likely, it remains difficult to separate these from natural variations in Rangifer habitat use and demography. Habitat avoidance towards various human infrastructures and activities is reported, but most studies reporting relatively far (4-25 km) avoidance distances relied on measurements of range properties and animal distribution recorded on 1-2 days annually in winter to induce a potential response from the animals and lack important environmental variables and/or alternative hypothesises. This methodology should be improved in order to enable identification of correlation versus causation. Studies relying on animal behaviour measurements can more correctly identify and test responses to various stimuli while also controlling for degree of domestication and other various environmental variables, but only in a limited time and spatial scale. Furthermore, such studies may not necessarily capture potential population consequences from disturbances. Thus, there are important weaknesses in the two leading methodologies (measuring animal behaviour and indirectly mapping regional/population movements and habitat use through measurements of range properties). To best study Rangifer's responses towards anthropogenic infrastructure and activities, we propose that the two methodologies be combined and supplied with modern GPS/telemetry.

Key words: avoidance, behaviour, displacement, environmental variables habituation, infrastructure, sensitisation.

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Introduction

Sustainable development requires an understanding of the effects of the various anthropogenic activities on wildlife populations and habitats. During the past 30 years, many studies have investigated reindeer/caribou responses to human activities. This work has been periodically reviewed and synthesised (Klein, 1971; Shank, 1979; Reimers, 1984; Shideler, 1986; Shideler et al., 1986; Cronin et al., 1998b; Cronin et al., 1998c; Wolfe et al., 2000; Reimers, 2001a; UNEP, 2001; Vistnes et al., 2004b). Not all of these reviews are readily available, nor do they all concur.

Reindeer and caribou belong to the same species (Rangifer tarandus), but different subspecies. (The species is denoted with genus name in this article). Although the basic behavioural repertoire in the various subspecies appears fundamentally uniform (Thomson, 1980), many differences in recorded behaviour relate to degree of domestication and to variable factors in the physical and biological environment, herd size and structure, and past experience. Wild reindeer in Norway, presently (winter 2005-06) numbering some 25 000 animals, are found in 23 more or less separated areas in the mountainous southern part of the country (Fig. 1). All herds are hunted. We identify three types of Norwegian wild reindeer on basis of their genetics and origin (Flagstad & Røed, 2003; Andersen & Hustad, 2004): (1) the original wild reindeer with minor influence from previous (last century) domestic reindeer herding activities (Snøhetta, Rondane and Sølnkletten), (2) wild reindeer with influx of animals from past domestic reindeer herding in the areas (Nordfjella, Hardangervidda, Setesdal-Ryfylke) and (3) feral reindeer with a domesticated origin (reindeer released or escaped from past reindeer husbandry units (Forolhogna, Ottadalen North, Ottadalen South, Norefjell-Reinsjøfjell and several smaller areas. In this article, we also use examples of reindeer/caribou from other parts of the Rangifer distribution area and, in some cases, examples including other ungulate species.

Two general methodical approaches in the study of Rangifer and anthropogenic disturbances involve: (1) Observations of animal behavioural and/or physiological response of individuals or groups of animals to disturbances, and (2) Regional or population-level observations of animals, or indices of range use or their demography that may suggest avoidance of some areas and increased use of remaining areas. We present and compare results from application of the two methodologies on various anthropogenic activities, discuss the frequently very different biological results that the two methods produce, and address strengths and weaknesses in these two leading methodologies. We first present a general discussion of key behaviour

and/or physiological characteristics for *Rangifer* in relation to *Rangifer*-human interactions. We then introduce the two methodologies and proceed with addressing examples for each, highlighting their strengths and weaknesses, before concluding with suggestions for future studies.

General characteristics relevant in *Rangifer*-human interactions

Hearing, vision and smell

Human activities affect *Rangifer* through the senses hearing, sight and smell. In their natural habitat, *Rangifer* experience and must cope with general background noise as a result of wind and precipitation, and more infrequent events like summing noise from harassing insects, thunder, rock fall and avalanches. Human activities contribute with noise from predictable fixed installations like power lines, generators, windmills and unpredictable and moving objects like persons on foot, cars, snowmobiles, aircrafts, helicopters, etc.

The hearing capacity of reindeer ranges from 70 Hz to 38 kHz at a sound pressure of 60 dB (Flydal *et al.*, 2001). The animals have good sound perception in the hearing range from 500 Hz to 32 kHz, with the lowest hearing threshold of 3 dB at 8 kHz. This implies that with the exception of very low frequency sounds, all anthropogenic noise from engines, generators, vehicular traffic, aircrafts, transmission lines, weapon firing and vocalization are readily perceived by reindeer.

Even though Rangifer sight capacity is not examined, we know a good deal from other animals (Jacobs, 1993). There is reason to believe that Rangifer, as for other ungulates, have very good day and night vision. Like other non-primate mammals, Rangifer probably possess a dichromatic vision with maximum sensitivity in the 380-530 nm (nanometer) area (violet to blue) and 530-570 nm area (green to yellow). Hence, they register colours from the part of the wave spectre we perceive as blue/green and yellow. They are probably unable to distinguish between red and green. Accordingly, Rangifer most likely perceive colours, but no particular colour appears to be dominant. For the most part, contrasts and movement betray human presence. Night vision depends on the number of rods in the retina. In Rangifer and many other mammalian species, the middle layer of the eye wall, choroid, contain reflecting elements (tapetum lucidum) that reflect light for another opportunity to be absorbed by the photoreceptors in the retina, thus increasing the light sensitivity of the eye.

With their eyes laterally positioned, for *Rangifer*, like many herbivores, the combined visual fields of

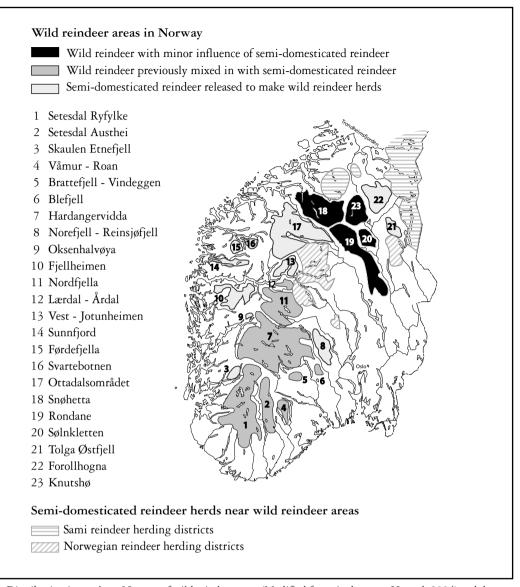


Fig. 1. Distribution in southern Norway of wild reindeer areas (Modified from Andersen & Hustad, 2004) and domesticated reindeer areas (Modified from Reindriftsforvaltningen, 2006).

both eyes cover virtually 360°, both when the head is raised (and the body does not obscure the view) and when grazing (when only the legs obscure the view) (Sjaastad *et al.*, 2003). Therefore, the animals can spot a predator (or human) sneaking up from behind. Their laterally positioned eyes limit the binocular visual field.

Rangifer's sense of smell is not well documented beyond anecdotal knowledge (Lønneberg, 1909; Skjenneberg & Slagsvold, 1968) accumulated by herders, hunters, hikers and scientists. The animal's capacity to capture a scent even under unfavourable wind conditions is well known by wild reindeer hunters.

In those subspecies and/or situations were *Rangifer* perceive humans as a threat, scent represents an immediate flight releaser (Reimers, unpubl. data). Smell alone can trigger flight without input from other senses. However, *Rangifer's* sensuous everyday is certainly more complex than simply reactions according to smell. When scent stimuli are absent, the animals must sort impressions from sight and sound in order to take appropriate behavioural action. Nevertheless, the extent a stimulus leads to a reaction probably depends on earlier experience and proximity to the stimulus. This possibly applies equally to all the senses.

Physiology and disturbances

Following a disturbance, dramatic physiological effects may occur that help an animal to cope with an emergency situation (Cannon, 1929). Gabrielsen & Smith (1995) categorised these effects as passive and active defence. While passive defence reduces activity, heart rate and metabolism and pertain to animals that hide, active defence involve stimulation of the sympatric part of the autonomic nerve system that enables fight or flight. Negative physiological effects from disturbances may be immediate and obvious, such as shock, abortion, or death, or prolonged and less obvious, such as increased weight loss in winter or reduced weight gain during summer. Physiological effects act through the individual to jeopardize condition, reproduction and ultimately survival.

Rangifer and domestication

While the caribou subspecies are wild, the fennoscandian tundra reindeer include domesticated herds (all herds in Finland, Sweden and northern Norway) and a mixture of herds with a mostly wild or a domesticated origin in southern Norway (Fig. 1). All these herds in southern Norway are managed as wild herds and hunted. Several definitions of domestication can be found in the literature, among them Price (1984) defined domestication as "the process by which captive animals adapt to man and the environment he provides". Adaptation is achieved through genetic changes over generations, which involves an evolutionary process, and also through environmental stimulation and experience through an animal's lifetime, which involve ontogenetic processes (Price, 1984). Domestication is the first step of selection and has to be distinguished from taming (Mignon-Grasteau et al., 2005). According to Hemmer (1990) the difference is merely quantitative. With regard to behaviour, it is argued that domestication has mostly resulted in quantitative rather than qualitative changes. Behaviours traits did not appear or disappear, but the threshold of their expression changed (Price, 1999). Therefore, if the opportunity is available, domesticated species can probably in most cases revert to the behaviour observed in their wild counterpart, as the genetic variability is still present in domesticated populations. Consequently, in the following discussions implying reindeer, it is important to know whether the herd in question is domesticated or has a wild or a domesticated origin.

Two key concepts and an energy budget interference Habituation and sensitisation are fundamental processes to be included in discussions of animal behaviour in relation to humans and anthropogenic activities. Upon repeated exposure to stimuli, animals will

behaviourally and physiologically adapt (Peeke & Petrinovich, 1984). Habituation implies that an animal reduces or ceases reacting towards biologically indifferent stimuli without impeding the ability to react to other stimuli (Lorenz, 1965; Ujvári et al., 1998). In contrast to unpredictable stimuli, several forms of human activity generally occur with a more routine presence, and most evidence indicates that ungulates can habituate to this type of activity (Geist, 1971b, a; Espmark & Langvatn, 1985). A basic assumption and evolutionary line of thought proceeds, or ought to proceed with a discussion of animal behaviour in relationship to environmental stimuli: energy spent on indifferent stimuli is wasted energy and nonadaptive. Although the recent arrival of our present day infrastructures and technological activities are not necessarily involved with the evolution of Rangifer genomes, they certainly interact with the base-line behaviour repertoire that has already evolved. An important consideration in this context is the possible behavioural response connected to a genetic change following the domestication process (selection by human) of the reindeer as shown for other livestock species (Boissy et al., 2005; Mignon-Grasteau et al., 2005).

Sensitisation contrasts habituation; the animal amplifies its behavioural and physiological reaction upon repeated or strengthened negative exposure (Peeke & Petrinovich, 1984).

Environmental factors that affect reindeer response behaviour Insects, specifically warble flies (Hypoderma tarandi), nose bot flies (Cephenemyia trompe) (hereafter referred to as oestrid flies) and species of tabanidae, mosquitoes (Aedes spp., culicidae) and simulidae influence Rangifer behaviour and may amplify or decrease response thresholds in relation to human activities. Even though reindeer are disturbed by human activities, they can increase their tolerance towards humans if insect harassment is severe, as shown for domesticated reindeer (Skarin et al., 2004). When insect activity was moderate to high, more caribou were observed within the Prudhoe Bay oil field than when insect activity was low (Pollard et al., 1996). Oil field gravel pads and roads were used as insect relief habitats (Murphy & Curatolo, 1987; Pollard et al., 1996), as animals frequently occupy and take advantage of the shade of buildings and pipelines (Fancy, 1983) and cabins in wild reindeer areas (Reimers unpubl. data). Water may also offer a relief habitat as observed on Thelon river North-west Territories in 1992 (Reimers, unpubl. data). In a study of caribou and parasitic insect activity during late June and July 1993, Noel et al. (1998) found no differences in distribution of bull dominated, cow/calf dominated or mixed sex groups on gravel pads or tundra in the Prudhoe Bay area. This indicates that maternal caribou did not behave differently than males while exposed to insect harassment

An increased response threshold is also observed in *Rangifer* during the rutting season in October, when fright and flight distances were shorter than during summer (Reimers *et al.*, 2000; 2006). Possibly as a result of intense concentration towards intra-species social interactions, reindeer are generally less concerned with other environmental stimuli of any sort during the rut. On the other hand, a decreased response threshold with increased vigilance and alertness is shown among reindeer herds subjected to intensive hunting (Baskin & Skogland, 2001).

The two methodologies

Method 1: Direct observations

Direct observations attempt to identify behavioral changes in terms of avoidance, fright- and flight behaviour, increased restless behaviour (walking, standing, running) or physiological responses (heart rate, stress hormones). Studies involving direct measurements such as *Rangifer*'s reactions towards disturbances described below have the opportunity to include and test the environmental variables effecting the animals' decisions there and then.

However, they may not manage to ascertain the historical importance of past experience and acquired behaviour or to separate combined effects of correlated variables if the sample size is too small. As human foot traffic illicit the most clear-cut behavioural and physiological response in ungulates, we deal with this aspect initially.

Persons moving on foot or skis

Reindeer responses to persons moving on foot or skis has been measured during three sampling periods of March (winter), July (summer), and September-October (autumn hunting and rutting period) in seven wild reindeer areas in southern Norway (Reimers et al., 2000; Reimers et al., 2003; Reimers et al., 2006) and Reimers (unpubl. data). A single person (the observer) dressed in dark hiking clothing, disturbed reindeer during daylight hours by directly approaching them. The observer used Leica Geovid 7x42 BDA laserbinoculars (1 m accuracy at 1000 m) to measure response distances between the reindeer and the observer and the resultant displacement distance by the reindeer after taking flight. These studies show that reindeer with a domesticated origin (domesticated reindeer released to become wild reindeer herds: North Ottadalen, Forolhogna and Norefjell-Reinsjøfjell) have shorter response distances towards humans

on foot or skis than wild reindeer in Rondane, Hardangervidda and Setesdal-Ryfylke (Dervo & Muniz, 1994; Kind, 1996; Eftestøl, 1998; Reimers et al., 2000) and (Reimers et al., unpubl. data) (Fig. 1). The most important factor influencing response distances was, in addition to area (each area represents an independent population), herd size. Likely reflecting safety in numbers (Hunter & Skinner, 1998), large herds allowed the observer to approach closer than small herds (Reimers et al., 2006). An explanation for longer response distances among reindeer with wild origin compared to reindeer with a domesticated origin might be an interplay between long term affects of hunting among the former and previous domestication schemes among the latter. This is in accordance with the general assumption that hunting shapes fright behaviour in ungulates toward humans. In an evolutionary and historic perspective, this is certainly true. However, negative effects of animal behaviour towards humans caused by present day hunting may apply in some areas and for some species (Behrend & Lubeck, 1968; Dorrance et al., 1975; Schultz & Bailey, 1978; Klein, 1980; Mclaren & Green, 1985; Jeppesen, 1987; de Boer et al., 2004), but not others (Hodges et al., 2000). For example, Grau & Grau (1980) and Kufeld et al. (1988) reported no increase in dispersal or home range abandonment by whitetailed deer (Odocoileus virginianus) or mule deer (Odocoileus hemionus), respectively, as a consequence of hunting pressure. Similarly, Colman et al. (2001) found no correlation between response distances and the intensity of hunting on Svalbard reindeer. The lack of learning effects may relate to the absence of herd formation in this reindeer subspecies.

Hunting's influence on the animals' behaviour towards humans depends on the actual hunting procedures, i.e., how much "the hunt" is experienced by individuals in the population that survive the hunt i.e. learning or sensitisation. Or, possibly equally important, hunting may also lead to directional selection for more vigilant animals that in turn results in longer response distances.

The level of anthropogenic activities appears to be an additional important explanatory factor for different response intensities by reindeer towards humans. The more people the reindeer are exposed to, the less shy the reindeer become (Reimers *et al.*, 2000; Colman *et al.*, 2001; Skarin *et al.*, 2004; Reimers *et al.*, 2006; Skarin, 2006). This indicates a possible habituation process, and therefore, it will be increasingly important to test for habituation as development and tourism in alpine areas increases and is forecasted to continue increasing in the decades to come.

Cassirer et al. (1992) report a similar pattern with longer response distances in elk (Cervus canadensis) in

areas with little vs. areas with high level of cross country skiing in Yellowstone National Park. Work by Johnson (1986) (cited in Phillips & Alldredge (2000)) and Kuck et al.(1985) on elk, Hicks & Elder (1979) on bighorn sheep (Ovis canadensis), Linnell & Andersen (1995) on roe deer (Capreolus capreolus) and Borkowski (2001) on sika deer (Cervus nippon) indicate little or no effect of hiking or logging activities on habitat use, activity or reproductive success in these species.

Vehicular traffic

Even though many species exist in ecological niches in close proximity to humans, larger animals perceive humans as a threat to be avoided or kept at a distance. Much of this behaviour is most likely a consequence of co-evolution between humans as predators and their various prev species (Hamilton, 1971; Hunter & Skinner, 1998) and hence has a genetic base. Modern humans disguised in mechanical devices expressing a variety of technological stimuli are recent events in the natural environment, and animals may have not vet developed defence strategies to cope with such "threats". Conventional wisdom relating to this is that mammals and birds allow a much closer approach when approached by motorized vehicles than when approached by persons on foot. Unless such vehicles are used in contexts that are imagined as threats, many of these stimuli will probably remain without biological relevance.

Off road vehicles (ORVs) relevant for Rangifer include 3-, 4-, 8-weelers, motorbikes and snowmobiles. Three studies investigated the fright- and flight behaviour of three subspecies of Rangifer provoked by snowmobiles moving 20 km/hour towards the animals. The Svalbard reindeer (Tyler, 1991) and the caribou in Newfoundland (Mahoney et al., 2001) are accustomed to snowmobiles, as they are the main source of transportation and communication during winter, and thus, appear habituated (the animals responded with very short fright and flight distances upon disturbance). Wild reindeer in Setesdal-Ryfylke (Fig. 1) (Reimers et al., 2003) are less tolerant towards the machines and response distances are consequently longer in this area. This may be a result of strict regulations on recreational use of snowmobiles on mainland Norway, resulting in limited experience towards snowmobiles by reindeer in Setesdal-Ryfylke. However, distance moved after a disturbance in this area was shorter when exposed to snowmobiles than when disturbed by skiers (Reimers et al., 2003), indicating a more relaxed fright behaviour towards the former.

Based upon a number of studies on other ungulate species ORVs, primarily snowmobiles, e.g. (Bollinger et al., 1973; Dorrance et al., 1975; Richens & Lavigne, 1978; Schultz & Bailey, 1978; Eckstein et al., 1979; MacArthur et al., 1982; Moen et al., 1982; Mclaren & Green, 1985; Freddy et al., 1986; Yarmoloy et al., 1988; Colescott & Gillingham, 1998), it seems justified to conclude:

- Ungulates habituate to ORVs driving along fixed, and for the animals', predictive trails.
- Ungulates pursued or chased by or hunted from ORVs change their behaviour and habitat use in response to the disturbance.

Roads and railways

As pointed out by Wolfe *et al.* (2000) in their review, the physical appearance of roads (and railroads) may influence *Rangifer* reaction due to road elevation or snow banks. However, traffic appears to be the ultimate factor influencing *Rangifer* movement.

A classical situation frequently referred to (Skogland & Mølmen, 1980; Nellemann et al., 2000; Wolfe et al., 2000) is the barrier effect of the highway (European road E6) and a parallel railroad crossing over the Dovre plateau, splitting the alpine area in the three wild reindeer areas Snøhetta, Knutshø and Rondane North (Fig. 1). The over 1000 reindeer pitfalls dating back to 1800 and earlier centuries confirm reindeer migration over this transportation corridor between summer pastures in West (Snøhetta) and winter pastures in the east (Rondane, Knutshø and Sølnkletten) (Andersen & Hustad, 2004). Due to over-harvest, there were few wild reindeer present in southern Norway during the first half of 1900 (Reimers, 1981) and, although it may have occurred, we have no information on animal migration during these years. After WW II and during the 1950s, the reindeer population increase in Snøhetta resulted in overgrazing of the winter pastures there (Gaare, 1968) and lead to annual migrations of herds over the transportation corridors to the winter pastures in Knutshø in early winter and return to Snøhetta before calving in May (Krafft, 1981). During 1960-65, the population was culled from some 20 000 animals to its present level of 2000 to 3500 animals (Reimers, 1968; Jordhøy, 2001). In spite of the population decrease, the migration pattern was maintained at least until 1980 (Krafft, 1981). From 1968 to 1978, migration activity was monitored every year and the number of animals migrating over the road and railroad varied between 225 and 727 animals annually (Krafft, 1981). We have no detailed information on reindeer migration across the transportation corridors after 1980 besides that animals continued to cross until 1984 (E. Gaare, pers. comm.). It appears that once established (in this case as a result of overgrazing), a migration pattern continues in spite of population decrease and traffic increase. After some time it gradually ceases as a result of lichen pasture improvement and possibly more important, the loss of animals maintaining the migration tradition.

In Denali National Park, the number of visitors visiting the park, mostly in buses and cars, increased from 42 000 in 1972 to 350 000 in 1999. According to Burson et al. (2000) and Yost & Wright (2001), the increased traffic has not affected numbers, distribution or behaviour of caribou, grizzly bears (Ursus arctos), mountain sheep (Ovis dalli dalli) and possibly also moose (Alces alces) along the 130 km park road. Flight response from vehicles occurred, but in less than 1.3% of total observations for each species (Burson et al., 2000). Although these reports indicate habituation to the park road and the traffic, one must bear in mind that animals are protected in the park and people normally do not go out of the busses/cars. Furthermore, they apparently only surveyed the proximate zones of the road, generally within 1-2 km to the road, and may thus have included mostly animals tolerant to disturbances, or perhaps used an overestimation of males that generally are more tolerant than females. Nevertheless, the animals that were recorded had become habituated.

Habituation to the presence of highways was also observed for caribou at crossing points near Kootenay Pass, British Columbia (Johnson & Todd, 1981).

Aircrafts and helicopters

High altitude (900-3000 m) aircraft had no behavioural effect on domesticated reindeer (Espmark, 1972), and probably do not affect ungulates in general. For caribou exposed to overflights with jet fighters (A10, F15, F16) 33 m or lower above ground, at distances between 375-1647 m and speed at 470-807 km/hour resulting in a sound pressure of 94-106 dB recorded on the animals, Maier et al. (1998) found little response behaviour in winter, moderate in the insect season and strongest right after calving. They concluded that the caribou response was mild, but that the aircraft activity resulted in a change of activity cycles and daily movements. As the experimental animals were darted from helicopters for tagging and instrumentation, sensitisation to engine noise may have been a confounding factor.

Harrington & Veitch (1991) found no change in activity or migration pattern during winter in Labrador caribou subject to low flying (30 m) F16 aircrafts. The animals reacted with excitation when the aircraft passed, but resumed normal activity shortly after. These results are in agreement with experimental data on domesticated reindeer in an enclosure (Berntsen, 1996). An F 16 was flown over the animals (7 adult females; 2 of them equipped with heart rate trans-

mitters) at altitudes varying between 61 and 610 m and airspeed at 796 km/hour. The animals showed a transitory brief increase in heart rate and no visible change in behaviour. Likewise, Lawler et al. (2005) report short-term impacts of military overflights on caribou in the Fortymile Caribou Herd during calving. Observations of domesticated reindeer in Halkavarre aircraft bombing field in northern Norway (Reimers, 2001a) support behavioural data reported by Berntsen (1996) and Lawler et al. (2005). During two days in august 2001, small herds of domesticated reindeer were observed and video recorded 1.8-3 km from a military training target area. During 0948 to 1045 am August 14, reindeer were flown over 37 times by either one or two (in pair) low flying (down to 60 m altitude) F16s dropping bombs (227 kg TNT), firing 20 mm machineguns and CRB-7 air to ground [missiles (Reimers, 2001a). The reindeer response included rising when lying (bombs), gathering or transient faster movement (machine gun firing or fast climbing aircrafts after bomb dropping or weapon firing) or in most cases, no visible behavioural response.

Correspondingly, Krausman et al. (2004) were unable to relate military activities (e.g., overflight noise, noise from ordnance delivery, ground-based human activity) to the population decline of Sonoran pronghorn (Antilocapra americana sonoriensis). Clearly, as indicated by the authors, additional work needs to be done, but military activity as measured in their study was not a limiting factor.

Contrary to these reports, Harrington & Veitch (1992) found that woodland caribou exposed to low flying aircrafts under or right after the calving season suffered higher calf mortality than in an adjacent control herd. The mean daily number of overflights varied between 0.8 and 1.0 and the sample sizes were small, 17 animals (9, 4 and 4 pregnant females darted from helicopter and tagged for later identification in 1987, 1988 and 1989, respectively, of which 7 (4, 1 and 2 the respective years) had calves in October. As the experimental herd (Red Wine Mountain) inhabited an area with a high predation pressure contrary to the control herd (Mearley Mountain), it is difficult to distinguish between aircraft harassment and predation. Sensitisation relating to previous helicopter experience and negative consequences of darting pregnant females may add to the list of confounding factors that challenge the authors' conclusion. Controlled experiments with the effects of simulated aircraft noise on desert mule deer and mountain sheep (Weisenberger et al., 1996) showed that heart rate increased but returned to normal within 60-180 s. Corresponding results are reported by Krausman et al. (1998) measuring response in mountain sheep to F16 aircrafts passing over the animals at 125 m above ground. However, Krausman et al. (1998) in conformity with Murphy et al. (1994) and Maier et al. (1998) found that females with young lambs or calves were less tolerant during lambing/calving.

Helicopters

A few studies/observations of domesticated reindeer show a high degree of tolerance towards low altitude helicopter overflights, both in terms of heart rate and behavioural response (Berntsen, 1996; Reimers, 2001a). Miller & Gunn (1979) and Gunn & Miller (1980) reviewed a number of factors influencing Peary caribou response to helicopter overflights and report a variety of responses. It is difficult to summarize their extensive work besides that they were unable to record pathological consequences, splitting up of herds or splitting up of mothers and calves. According to the authors, the caribou calmed down rapidly after an over-flight, and a passing altitude of 200-400 m caused no measurable stress. No study to date has addressed wild reindeer response to helicopters.

Fixed wing aircrafts

Valkenberg & Davis (1985) compared two caribou herds in Alaska: the Western Arctic Herd, which at that time was rarely over flown by aircrafts, and the Delta Herd that was exposed to regular air traffic in altitudes below 150 m. While the Western Arctic Herd revealed a flight pattern from running (25%), walking (55%) and none/little reaction (15%), the Delta Herd response pattern included walking (30%) and none/little response (70%). The results indicate that repeated overflights even at low altitudes result in habituation. Corresponding results are reported by Krausman et al. (1986) for desert mule deer. Aircraft approaches that were more direct (as determined by the aircraft's elevation and horizontal distance) were more likely to elicit fleeing or to disrupt resting in mountain sheep (Frid, 2003).

Reindeer behaviour within enclosures with power lines and windmills

In an experimental setup in North Ottadalen Flydal (2002) and Flydal & Reimers (2002) tested whether two parallel 132 and 300 kV power lines had any effect on area use, activity changes and restless behaviour like running, walking and standing for enclosed domesticated reindeer. Eight different groups with three female yearling reindeer were continuously observed in four enclosures (each 50 m x 400 m), two experimental enclosures under the parallel power lines and two controls. The reindeer showed no systematic differences in the measured behaviour

patterns or habitat use between the four enclosures that could indicate fright or stress as a consequence of the power lines.

In the only Scandinavian windmill study on Vikna, Flydal et al. (2004) tested whether a wind turbine and its rotor movement had any effect on area use, activity changes, vigilance bouts and restless behaviour like running, walking and standing for enclosed domesticated reindeer during autumn in 1999 and 2000. Five different groups of reindeer in a 450 m long, 8 hectare, enclosure close to a wind turbine were manipulated by turning the wind turbine rotor on and off, and compared with reindeer in a control enclosure without wind turbine exposure. The reindeer showed no systematic differences in the measured behaviour patterns between the two enclosures that could indicate fright or stress as a consequence of the wind turbine or rotor movement. In fact, the favorite bedding site was located close (100 m) to the wind turbine.

Based on the present day experience by reindeer herdsmen in Sweden and Finland towards existing windmill parks, Eftestøl *et al.* (2004) found no negative effect in terms of disturbances towards the animals. It is important to note that the existing windmill parks have fewer windmills and much less infrastructure (roads, power lines, generator houses, etc.) than the many larger parks in the planning. In the future, it will be necessary to study this new development and how *Rangifer* will react in the short and long term.

It is noteworthy that Flydal (2002) (for power lines) and Flydal *et al.* (2004) (for windmill parks) were large scale, replicated experiments. In neither experiment did the reindeer in the experimental enclosures show different behaviour, habitat use or movement patterns from the animals in the control enclosures. Although as difficult as it may be to transfer such data to free ranging individuals, they justify some skepticism to the notion of the fragility of reindeer to human infrastructure.

Method 1: Conclusion

A survey of the literature reveals that although *Rangifer* in most cases respond to anthropogenic activities, behavioural and physiological responses generally appear to be brief and moderate. Comfort distances (i.e. distances beyond which animal behaviour or activity are not influenced) are relatively short. *Rangifer* with a wild origin appear to have longer response distances than reindeer with a domesticated origin. However, in most cases, energetic implications appear moderate and small compared to other natural, biotic influences such as disturbance (and death) caused by insect and/or predator harassment (Mörschel & Klein,

1997; Colman, 2001; Hagemoen & Reimers, 2002; Nybakk et al., 2002; Wittmer, 2005).

Method 2: Indirect observations/pasture registrations Indirect observations attempt to identify animal distribution and area use, most often by measuring range properties, such as lichen cover and/or height, and then test these measurements amongst zones along linear distances from infrastructure. During winter and in alpine habitats, reindeer graze on wind swept ridges with limited snow accumulation that favour lichen growth and availability, especially the species Cetraria nivalis and Cladonia stellaris, the favourite winter food of reindeer (Gaare, 1968; Gaare & Skogland, 1975; 1980).(Gaare, 1968; Gaare and Skogland, 1975, 1980) Studies involving infrastructure often attempt to test habitat avoidance by measuring height and/or cover of specifically lichens, with the main assumption that lichen height and cover reflects reindeer grazing pressure. This demands in-depth knowledge on natural environmental variables influencing movement patterns or range use by Rangifer, as well as the plant communities and their ecological interactions, dynamics and succession, in order to conclude correctly that sparse lichen resources solely reflects heavy grazing and abundant resources indicate the absence of grazing (and reindeer). Strength in this methodology is the potential for document accumulated population effects over relatively longer time periods (many years and decades), contrary to direct observation studies that frequently reflect short term events.

Cabins and tourist resorts

Cabins and tourist resorts are potential sources of disruption, primarily due to associated traffic. In a study of effects of outdoor recreational areas on range use by domesticated reindeer, Helle & Sarkela (1993) recorded reindeer and pellet groups in three zones: 0-5 km (1), 5-10 km (2) and 10-15 km (3) adjacent to a holiday resort in Saariselkä, Finland. Reindeer densities increased in the birch and pine forests in parallel with a decreasing trend in outdoor activities moving away from the resort. The area of heaviest recreational use during summer was also used more by male reindeer than females. Pellet group density in the birch and pine forest compartments increased significantly from zone 1 to zone 3, both in summer and winter. In contrast, the alpine hilltop zones, making up 11% of the total area, showed no statistically significant difference in pellet-group density in either summer or winter. The authors suggested, that reindeer respond to disturbance by shifting to an open habitat where they have superior control over their environment. However, it may also mean that hilltops are preferred feeding sites during winter due

to thinner snow cover or during summer due to early snowmelt and high production or more wind and less insect harassment, and thus, negate the alleged disturbing effects.

Nellemann et al. (2000) measured impacts of tourist resorts and cabins on wild reindeer in Rondane (southern Norway, Fig. 1). They obtained data on distribution of reindeer from snowmobile population surveys made by the local authority during 1 or 2 days in February-March in the period 1991 to 1996 and compared these with measurements they made on snow and vegetation characteristics. Maternal reindeer avoided a 10 km zone around the resort. Cows and calves increased in density from 0.6 ± 0.6 (standard deviation (?)) reindeer km² at 5 to 10 km from the resort to 7.6 ± 2.2 reindeer km² at 15 to 25 km from the resort. Bulls and yearlings were more tolerant, constituting nearly 92% of all observed animals 5 to 10 km from the resort. Nearly all animals avoided the zone within 5 km of the resort. The research group arrived at corresponding results in Nordfjella (Nellemann et al., 2001; Vistnes et al., 2001) and Setesdal-Ryfylke (Nellemann et al., 2003) wild reindeer areas (Fig. 1) and reported that areas within 4 km (Setesdal-Ryfylke) and 5 km (Nordfjella) from resorts or from roads and power lines in combination were avoided in all study years (> 10 years). In Repparfjord (northern Norway), inhabited by domesticated reindeer, Vistnes & Nellemann (2001) reported that mean reindeer density within preferred habitat during calving in May was 22% of the density in the area >4 km from a county road and cabins located along a river in a valley bottom (1.47 vs. 6.68 reindeer/km², respectively). Areas < 4 km from anthropogenic structures were avoided despite low levels of human traffic and a high proportion of preferred habitat. The infrastructure cause for the avoidance behaviour in this herd of domesticated reindeer suggested by the authors invites some comments. Recreational use of cabins and the reindeer habitat was, according to the authors, virtually zero during May, which is the same period reindeer arrive in the area for calving. Reindeer herdsmen (the only users of snowmobiles in the area in May) use the machines to deflect the reindeer from migrating towards and congregate along a permanent reindeer fence built to separate the reindeer herd from neighboring herds. The reindeer continued to press east towards the fence in spite of daily snowmobile herding. Why are the reindeer more tolerant to this fence and associated snowmobile driving than from power lines, a distant and forest covered road and cabins with little or no traffic? Alternative explanations for the migrational drive towards open and higher country are the reindeer' avoidance of forested areas with

unfavorable snow conditions and higher predation risk during the calving season in May (Barten *et al.*, 2001; Skarin *et al.*, in press).

The wild reindeer avoidance figures from Nordfjella (Nellemann et al., 2001; Vistnes et al., 2001) and from Rondane (Nellemann et al., 2000) in southern Norway were contrived from aerial counts or ground surveys from snowmobiles carried out mostly during one or two days in winter (February-April). Decreasing lichen height with increasing distance from the respective tourist resort (or other infrastructure involved) was taken as an indirect measure of increasing grazing pressure by reindeer at increasing distance from the infrastructures. The avoidance distances reported where there was "reduced use" stretched over vast areas with variable topography and altitude, microclimate, range properties (such as plant communities, soil and geological elements) and more. Thus, indirect measurement of reindeers' area use may reflect entirely different aspects of pasture characteristics that in turn were likely influenced by additional factors besides grazing pressure. For example, the tourist resorts involved in these studies are located in the periphery of the mountain-areas at lower altitudes along or below the timberline zone. These habitats are generally avoided by reindeer in winter and during calving due to deep and soft snow and possibly predation risks in addition to avoidance of human activities.

Roads and road traffic

While roads alone are likely not perceived as a threat to *Rangifer*, road traffic frequently is (Reimers, 1986; Cronin *et al.*, 1998a; Trombulak & Frissell, 2000).

Wild reindeer migration between the southern and northern regions of the Hardangervidda area in southern Norway are not well quantified, but have probably decreased in frequency in winter after the highway Rv7 was opened year-around in 1984. This is supported by a study of GPS collared female reindeer, where only 2 of 23 attempts (reindeer approach the road) to cross Rv7 during 2002-2005 have been successful (Bevanger *et al.* 2005; Strand *et al.*, 2006).

According to Cameron *et al.* (1992), Nellemann & Cameron (1996) and Nellemann & Cameron (1998), calving or lactating caribou belonging to the Central Arctic Herd (CAH) avoided areas up to 4-10 km from roads and constructions associated with the Prudhoe Bay oil field, resulting in heavier grazing pressure outside these areas. These findings have invoked predictions towards negative effects of human caused displacement of caribou into habitats with sub-optimal foraging conditions. Cameron & Ver Hoef (1996) and Cameron (1997) suggested that decreased calf production by the CAH herd in the late 1980s and early 1990s was related to decline in body condi-

tion of females exposed to oil development. According to Murphy & Lawhead (2000), this interpretation of data remains unsubstantiated. Recent studies in the Prudhoe Bay oil field area (e.g. Ballard et al., 2000; Cronin et al., 2000; Murphy & Lawhead, 2000) show the CAH herd increased from 5000 to 27 000 animals since the oilfield was developed in the 1970s (Cameron et al., 2002) and 32 000 animals in 2002 (Alaska Dept. of Fish and Game, unpubl. report). Clearly, this population growth does not rule out effects from roads and other installations. Based on parturition status determined from fixed-wing aircraft (Cameron et al., 1993). Cameron (1997) reported a lower overall fecundity of CAH caribou west of the Sagavanirktok River (area of intensive and extensive petroleum development) compared to a disturbance free control area east of the river during 1988-94. Habitat loss and disruption of movements were suspected to have contributed to a reduced plane of summer nutrition, declined body condition and hence, more breeding pauses. East-west differences in population density and habitat quality were not controlled for and may, as pointed out by the author, be implicated. With the opening of the Badami petroleum development east of the river in 1996, the undisturbed status of the control area was compromised (Cameron et al., 2002). According to The National Research Council (2003, Table 8-1), radio collared females showed a continued significant lower parturition rate west compared to east of the river the following years (1998-2001) in spite of development east of the river, with no area difference in calf survival in either 1988-1994 or 1998-2001. These results call for more detailed analyses of actual population dynamic consequences from such installations in interaction with relevant biotic factors like range, predators and insect harassment.

In an attempt to limit caribou road crossings and reduce collisions, Brown *et al.* (2000) added repellent compounds to the salt (NaCl) and sand mixture along roads (that attracted the animals in the first place) to discourage licking of salt by the caribou on roads in Alberta, Canada. This illustrates that avoidance behaviour ceases or is reduced when something positive is available, for example, either as road salt or saltlicks spread out in sheep (*Ovis aries*) pastures or moose habitats or in wild reindeer areas (Reimers unpubl. data).

Power lines

Avoidance from roads and power lines in combination has been reported in Norway in areas with wild reindeer (Nordfjella, Snøhetta and North Ottadalen) (Nellemann *et al.*, 2001; Vistnes *et al.*, 2004a) and domesticated reindeer (Repparfjord) (Vistnes & Nellemann, 2001). From one day aerial winter popu-

lation surveys in February to April during the period 1986 to 1998, (Nellemann et al., 2001) found that areas in Nordfiella within 2.5 km from power lines were used less than available by reindeer in 6 of 8 sampling years, and areas beyond this zone were used more than expected. Furthermore, areas within 5 km from power lines and roads in combination were avoided all years. In correspondence with this, (Nellemann et al., 2001) reported lichen biomass (dry weight) 19 times lower in background areas compared to areas < 2.5 km from power lines in Nordfjella. In North Ottadalen, lichen biomass was 5.3 times higher in areas east of two power lines in combination with a winter closed road compared to the west side (Vistnes et al., 2004a). The roads and the power lines in both Nordfjella and North Ottadalen (Reimers, 2001b) are located in the periphery and at lower altitudes in the areas and invite alternative hypotheses for wild reindeer avoidance.

In Repparfjord (Vistnes & Nellemann, 2001) found that mean domesticated reindeer density by the power line corridor without traffic was 27% of the density > 4 km from the power line for comparable habitat. Correspondingly, almost 74% of all available forage was located within the avoided 0 - 4 km from the power line. The authors conclude that reindeer avoid technical structures such as power lines, even with low or extremely low levels of associated human traffic.

Reimers et al. (2007) studied the barrier and aversion effect of a 66 kV power line transecting the range of wild reindeer in North Ottadalen, using aerial surveys of reindeer distribution (direct measurement of reindeer use) and lichen measurements (indirect measurement of reindeer use) at varying distances from both sides of the power line. The aerial surveys and ground observations showed that reindeer crossed underneath and grazed under and on both sides of the power line regularly during the last 31 years. This was confirmed by the lichen measurements, indicating a higher use of lichen pastures along ridges close to and under the power line compared to those at increasing distances and up to 3 km from the power line. The results support the finding by Reimers (2001b), Flydal (2002) and Flydal & Reimers (2002), but contrast with studies referred above indicating strong barrier and aversion effects of similar (and larger) power lines for Rangifer migration and grazing behaviour in alpine terrain (Vistnes & Nellemann, 2001; Vistnes et al., 2004a).

Seismic lines, forestry and associated roads

Forestry has fragmented winter pastures of a herd of 350 woodland caribou in Alberta, Canada (Smith *et al.*, 2000). Monitoring radio-collared caribou, they found the size of home range to be unchanged, but

animals moved away from active cutting areas and kept a longer distance to these areas than to older cutting fields. In a similar study of radio-collard woodland caribou in Newfoundland, Chubbs *et al.* (1992) found that 4 males and 10 females maintained similar mean distances from clear cuts, 3 males and 10 females were farther away and 2 females were closer. Sex and age ratios indicated that significantly fewer females and calves were present near clear cuts than elsewhere in the study area.

Based on an interactive cumulative effects model that could be used to assess both natural and anthropogenic factors influencing survival of woodland caribou, Weclaw & Hudson (2004) suggest that the most detrimental factor on caribou population dynamics is the functional loss of habitat due to avoidance of good quality habitat in proximity of industrial infrastructures. Likewise, McLoughlin et al. (2003) suspected and Dyer et al. (2001) found that the current distribution, intensity, amount, and type of human activity in and near woodland caribou ranges likely compromise the integrity of caribou habitat. By extrapolating avoidance distances to the entire study area, Dyer et al. (2001) calculated that 22-48% of their study area would receive reduced use by caribou. Avoidance effects were highest during late winter and calving and lowest during summer.

Method 2: Conclusion

Rangifer area use in relation to infrastructure based upon radio collared or GPS-collared animals (Dyer et al., 2001, 2002; McLoughlin et al., 2003; Bevanger et al., 2005; Strand et al., 2006) has convincingly demonstrated the effect of infrastructure on animal distribution and the applicability of a precise method.

Combining indirect observations that attempt to identify animal distribution and area use reflected in measurements of range properties on favored winter nutrition in relation to infrastructure has potential. Extensive measurements of range properties (lichens) along with environmental factors that influence pasture independent of grazing, and thus, actually possess the data necessary for unambiguously addressing animal grazing pressure, are necessary in order to confirm the comprehensive responses reported, and in particular for wild and domesticated reindeer in Norway (Nellemann et al., 2000; Nellemann et al., 2001; Vistnes & Nellemann, 2001; Vistnes et al., 2001; Nellemann et al., 2003; Vistnes et al., 2004a). Although the avoidance zone relating to roads and seismic lines may be limited, such as shown for woodland caribou, extrapolating avoidance distances to the entire study area, Dyer et al., (2001, 2002) calculated that a significant part of their study area would receive reduced use by caribou.

General conclusion

In light of the important implications involved when studying the effects of anthropogenic activities on wildlife such as Rangifer, extra robust study designs must be devised for direct and indirect testing to control for the numerous environmental variables influencing behaviour reactions, movement and area use, and especially pasture parameters independent of the animals' involved. Because of the likelihood for uncontrollable variables clouding any certain interpretation of lichen measurements, pasture measurements alone are not sufficient to conclude whether reindeer area use has been influenced by human infrastructure. Thus, more data are needed on important variables influencing both the animals (natural variation in range use over more time than some few days in February to April) and the pasture (e.g. altitude's effect on lichen height) before one can conclude on infrastructure avoidance of Rangifer herds. Direct behavioural observations provide more robust data for testing the animal's reactions towards specific stimuli, but have time, spatial and population scale limitations. Direct visual observations and GPS/ telemetry tracking provide optimal information on regional movement and area use as shown for woodland caribou, but may be misleading when testing for barrier and aversion effects if all potential correlated variables are not controlled for and causality is difficult to confirm (i.e., you can see where an animal is located, but not necessarily know why the animals are there). We propose that future studies combine direct and indirect methodologies in order to combine the successful, robust attributes of both and simultaneously remove their respective weaknesses. In order to provide appropriate knowledge, we must improve our study designs by including replication (additional areas, populations, disturbance sources, and transects), control areas (and for method 2, "control transects" that measure lichen parameters along a similar gradient and at the same distance as the "test transects", but out from random points in the mountain range that do not begin near a disturbance source) and importantly for field studies, include more of the many important environmental variables correlated to the animals' and their pasture's ecology.

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Rein og caribous reaksjon på forskjellige menneskelige aktiviteter og installasjoner

Abstract in Norwegian / Sammendrag: Vi adresserer spørsmålet om hvordan menneskelig aktivitet og infrastruktur påvirker rein/ caribous (Rangifer tarandus) atferd og områdebruk og gjennomgår publiserte arbeider basert på aktuelle metoder. Antropogene aktiviteter har direkte effekt på reinens atferd via hørsel, syn og lukt; alle er viktige for deres risikovurdering. Kortsiktige indirekte reaksjonsmønstre, slik som habituering, sensitivisering, unnvikelse og fortrengning utvikles gjennom nøytrale, positive eller negative opplevelser av stimuli i henhold til erfaring, læring og hukommelse. Utviklingen av permanente atferdsmønstre skjer ved samvirke med predatorer og for reinens del, også ved domestisering. En litteraturoversikt om atferdsstudier viser at selv om Rangifer i de fleste tilfeller unnviker antropogene virksomheter, så er de avstander dyrene velger å ha mellom seg og infrastruktur uten at normalatferden endres, relativt korte. De energimessige implikasjonene er også beskjedne sammenlignet med virkningen av naturlige stressfaktorer så som forstyrrelser (og død) forårsaket av insekter og predatorer. Fysiske installasjoner av ulik art har også begrenset effekt med mindre de fysisk hindrer Rangifers områdebruk. På den annen side vil fysiske installasjoner, som hindrer eller begrenser bruken av områder, og trafikk, både fottrafikk og trafikk med motorkjøretøy, kunne ha sterkere virkning på unnvikelsesatferd og områdebruk. Atferdsmessige effekter som kan redusere overlevelse og reproduksjon omfatter unnvikelse fra beiteområder nær forstyrrelseskilder. For Rangifer er det negative resultatet av dette øket aktivitet, redusert beitetid og nedbygging av energireserver. Rangifers områdebruk, unnvikelsesatferd og næringspreferanser bestemmes ut fra et kompleks av naturlige og gjensidig påvirkende faktorer. Domestisering, habituering og sensitivisering som er sentrale begrep i utformningen av Rangifers tilpasningsevne, bør inkluderes i fremtidige studier av rein og caribous reaksjon på antropogene aktiviteter. Selv om en kumulativ atferdseffekt av menneskelige aktiviteter er mulig, er det vanskelig å skille slike fra naturlige variasjoner som følge av variasjoner i områdebruk og bestandsdynamiske forhold. Habitatunnvikelse som følge av menneskelig påvirkning er rapportert. De fleste studiene som rapporterer relativt lange unnvikelsesavstander (4-25 km) er imidlertid basert på målinger av beiteslitasje og lokalisering av dyr registrert i løpet av 1-2 dager årlig i løpet av vinteren og mangler viktige miljøparametere og/eller alternative hypoteser. Denne metoden bør forbedres for å kunne skille mellom korrelasjon og kausalitet. Målinger av atferd gjør mulig en mer korrekt testing av Rangifers reaksjon på ulike antropogene stimuli samtidig som man kontrollerer for graden av domestisering og forskjellige miljøfaktorer. Atferdsstudiene avgrenses imidlertid i både tid og rom og vil vanligvis ikke fange opp eventuelle bestandsdynamiske konsekvenser av forstyrrelser. Det hefter følgelig svakheter ved begge de to dominerende metodene som i dag anvendes; måling av atferd og bestandsfordeling og indirekte kartlegging av områdebruk ved måling av beiteslitasje. For å oppnå en bedre studiedesign for måling av Rangifers reaksjon på antropogen infrastruktur og tilknyttede aktiviteter foreslår vi at de to metodene kombineres og suppleres med GPS/telemetri teknologi.