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Effects of winter-feeding on reindeer's future ability to utilize natural pastures

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Abstract

Winter feeding of reindeer (*Rangifer tarandus tarandus*) has become an increasingly common management action in reindeer husbandry in Sweden, Finland, and Norway when natural grazing resources are unavailable due to the loss of grazing grounds, disturbances, and icing events. In the short term, feeding increases survival and reproduction, but the long-term effects on reindeer's ability to utilize natural pastures have not been investigated. Herders have raised concerns that fed reindeer, especially calves, do not utilize natural pastures as efficiently as other reindeer. In this thesis, I investigated the short- and long-term effects of winter feeding on reindeer with focus on habitat selection and future foraging behaviour. Interviews were conducted to collect experience-based knowledge on the effects of feeding among reindeer herders. An experimental study was conducted to test how winter feeding of calves during their first winter affects future habitat selection, foraging behaviour, and body weight. I found that there are several unintended effects of feeding that may compromise reindeer's ability to use the natural pastures efficiently. In the interviews, the effects identified by herders were related to physical traits or behaviour; the reported effects varied between herders, as did the perception of whether an effect was positive or negative. In the experimental study, I found that reindeer calves which were fed in enclosures during their first winter of life were less likely to select areas with higher lichen abundance when on natural pasture compared to reindeer that had spent their first winter on natural pasture. Although, the control animals were also provided feed on pasture to some extent their first winter. Understanding the long-term impacts of winter feeding on reindeer and their ability to utilize natural pastures and adapt to changes in the environment may be crucial when evaluating the effects of different external forces on reindeer husbandry. Knowledge of the short- and long-term effects of feeding on reindeer is important for herders when evaluating if, when and how to feed their reindeer.

Keywords: *Rangifer*, winter feeding, habitat selection, foraging behaviour

Effekter av vinterutfodring på renens framtida förmåga att utnyttja naturliga betesmarker

Sammanfattning

Inom renskötseln i Sverige, Finland och Norge har vinterutfodring ökat på grund av konkurrerande markanvändning och klimatförändringar. De kortsiktiga effekterna av utfodring är ökad överlevnad och reproduktion. De långsiktiga effekterna av utfodring är inte undersökta, men det finns indikationer på att unga djur som blivit utfodrade inte klarar sig lika bra på naturbete när de blir äldre. Om djuren blir sämre på att utnyttja naturbetet riskerar extensiva betessystem att förlora sin uthållighet. I denna studie har vi använt kvalitativa och kvantitativa metoder för att undersökta de kort- och långsiktiga effekterna av vinterutfodring med fokus på renens val av betesområde och betesbeteende. I en intervjustudie undersöktes erfarenheterna och effekterna av utfodring bland renskötare. I ett utfodringsförsök undersöktes hur utfodring av kalvar under deras första levnadsvinter påverkar deras framtida val av betesmarker, betesbeteende och vikt. Resultaten från denna studie visar att en oförutsedd effekt av vinterutfodring är att det riskerar att minska renarnas framtida förmåga att nyttja de naturliga betesresurserna. I intervjustudien lyftes effekter relaterade till renens fysiska egenskaper och beteende. Erfarenheterna och de observerade effekterna skiljde sig mellan renägare, liksom även uppfattningen gällande om effekterna var positiva eller negativa för renen. Resultaten från utfodringsförsöket visade att renar utfodrade i hägn under sin första levnadsvinter var sämre på att välja lavrika betesmarker när de var på fritt bete följande vinter jämfört med renar som varit på naturbete under första levnadsvintern. Denna effekt observerades även under renarnas tredje levnadsvinter, två år efter utfodring i hägn. Kunskap om både kort- och långsiktiga effekter av utfodring på renar och deras förmåga att nyttja naturbete är viktig för renägare när de överväger om, när och hur de ska utfodra sina renar, och för att kommunicera effekterna av olika förändringar och störningar.

Keywords: *Rangifer*, vinterutfodring, betesval, betesbeteende

Dedication

To Charlie

Contents

List of publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I. Heidi Rautiainen, Minna Turunen, Birgitta Åhman, Tim Horstkotte & Anna Skarin. Reindeer herders' experience-based knowledge on the effects of winter feeding on reindeer (manuscript)

II. Heidi Rautiainen, Moudud Alam, Paul G Blackwell & Anna Skarin (2022). Identification of reindeer fine-scale foraging behaviour using tri-axial accelerometer data. Movement Ecology, 10(1), pp. 1-12

III. Heidi Rautiainen, Paul G Blackwell, Moudud Alam, Birgitta Åhman & Anna Skarin Long-term effects of winter feeding on reindeer habitat selection and fine-scale foraging behaviour (manuscript)

Paper II is reproduced with the permission of the publishers.

The contribution of Heidi Rautiainen to the papers included in this thesis was as follows:

I. Designed the study together with AS, BÅ and MT. Performed interviews in Sweden, and together with MT, in Finland. Performed the analysis. Wrote the manuscript with support from the co-authors.

II. Designed the study together with AS, MA and PB. Collected all the field data and performed the analysis with support from PB and MA. Wrote the manuscript with support from the co-authors.

III. Designed the study together with AS and BÅ. Performed all field work and data collection and treatment. Performed the main part of the statistical analysis with support from AS, PB and MA. Wrote the manuscript with support from the co-authors.

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1. Introduction

In pastoral systems, herders rely on animals' ability to utilize natural pastures to meet nutritional requirements. These systems are based on the availability of natural forage and the accessibility to season-specific pastures together with the animal’s ability to utilize the available forage. One of the most viable pastoral systems in the world is reindeer husbandry, practised across the Eurasian continent (Holand *et al.* 2022a). In reindeer husbandry, winter feeding of reindeer (*Rangifer tarandus tarandus*) has become an increasingly common management action by herders in Sweden, Finland and Norway when natural grazing resources are unavailable due to loss of grazing grounds, disturbances, and icing events (Åhman *et al.* 2022). Feeding increases survival and reproduction in the short term, but the long-term effects are unclear. There is a fear that frequent use of winter feeding may affect reindeer's future ability to utilize natural pastures. Herders have, for example, raised concerns that fed reindeer, especially those fed as calves, one year old and younger, seem not to utilize the natural forage as effectively as reindeer that have not been fed (Persson 2018; Horstkotte *et al.* 2020). If the reindeer's ability to make use of natural pastures is impaired this may threaten the sustainability of the pastoral reindeer husbandry system. However, a description and quantification of the unintended effects of winter feeding is still lacking. Understanding the long-term impacts of management actions like feeding is necessary when evaluating the effects of different external forces on reindeer husbandry. Knowledge of both the short- and long-term effects of feeding on reindeer is important for herders when evaluating if, when and how to feed their reindeer.

1.1 Reindeer husbandry in northern Europe

Rangifer (reindeer and caribou) are native to arctic and subarctic regions around the world, making them adapted to the harsh environment in these regions. Since the Pleistocene (2.6 million to 11 700 years ago), *Rangifer*'s adaptive responses to seasonal and climatic fluctuations in their environment have enabled them to not only survive but to utilize otherwise unavailable foraging resources and provide meat and other valuable products for humans (Eriksen 1996; Flagstad & Roed 2003; Sommer *et al.* 2014; Costamagno *et al.* 2016; Hufthammer *et al.* 2018). The genus *Rangifer* contains only one species, *Rangifer tarandus*, but there are at least eight acknowledged subspecies, although other subspecies have been suggested or recognized (Roed 2005; Harding 2022). *Rangifer tarandus tarandus* is the subspecies that is domesticated and herded within reindeer husbandry systems (Holand *et al.* 2022a). In northern Europe (Finland, Sweden, Norway, and the Kola peninsula: Figure 1), reindeer husbandry is an essential part of the traditional Sami livelihood and a central part of the Indigenous Sámi culture (Holand *et al.* 2022b).

In Sweden, all reindeer are domesticated and herded within Sámi reindeer husbandry. The reindeer husbandry area in Sweden consists of three types of reindeer herding districts: forest, mountain, and concession herding districts (Figure 1; "herding communities" in papers II and III). In forest and concession herding districts, reindeer remain in forests all year, and move between seasonal pastures within their year-around pastures (land they are allowed to use all-year around) and winter lands (land they are only allowed to use from 1 October to 30 April). Mountain herding districts have their year-around pastures in the mountains (usually used from April to late autumn), and winter pastures in the forest. In Finland, the reindeer husbandry area is divided into the Sámi home area in the north, a central area specially intended for reindeer husbandry, and a southern ("other") reindeer management area. In Finland, there are no long-ranging seasonal migrations between winter and summer areas as a consequence of environmental conditions and historical developments (Stark *et al.* 2023). In the Sámi home area, reindeer herds are generally larger, and herding is more commonly the main source of livelihood, whereas in the central and southern area, herding is often combined with other livelihoods. In Sweden (as in Norway), reindeer herding is an exclusive right for the Sámi, while in Finland, reindeer herding is practised by both Sámi and non-Sámi. The number of semi-domesticated reindeer is around 240 000 individuals in Sweden and 200 000 in Finland (Paliskuntain yhdistys 2023; Sametinget 2023).

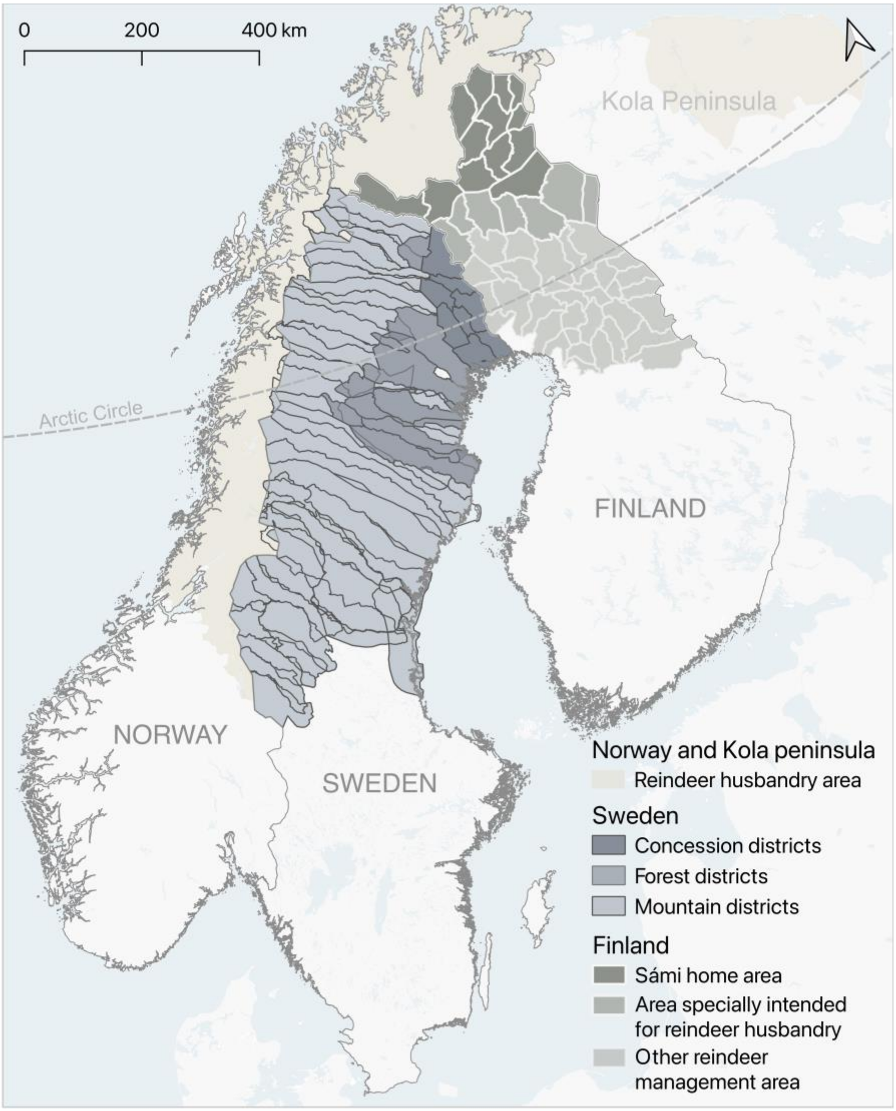


Figure 1. Reindeer husbandry area in Norway, Sweden, Finland, and Kola peninsula, with reindeer herding districts shown for Sweden and Finland. In Sweden, herding districts are divided into concession, forest and mountain herding districts. In Finland, the reindeer husbandry area is divided into the Sámi home area in the north, an area specially indented for reindeer husbandry, and the southern part with non-Sámi reindeer husbandry.

1.2 Habitat selection at different scales

Habitats can be defined as any point in an environmental space used by a species (Aarts *et al.* 2008; Paton & Matthiopoulos 2016). Habitat use is defined as the proportion of time animals spend in a particular habitat (Johnson 1980). Habitat selection is the behavioural process through which an animal chooses a habitat (Johnson 1980) to survive and reproduce (increase fitness). Habitat use is considered selective if habitats are used disproportionally to their availability. In controlled environments, "preference" often refers to the likelihood of a habitat being chosen given that choices are equally available (Johnson 1980). In field studies, however, habitat preference (often used synonymously with selection) refers to the quantification, or statistical description, of habitat selection and the underlying selection process (Beyer *et al.* 2010). Habitat selection may also be estimated at different scales of selection, corresponding to an animal's movement and foraging processes. First-order selection determines the physical or geographical range of a species, while second order determines the home range selection within that range. The selection process within a home range can be further divided into how they utilize the habitat within that home range (third order) and how specific food items are used at specific feeding sites (fourth order; Johnson 1980). In this thesis, habitat selection describes both the statistical evaluations and the underlying selection processes of the reindeer.

Reindeer movement and habitat selection are mainly driven by the search for forage at different scales. At the regional scale, reindeer perform seasonal migrations between summer and winter ranges, and we can for example study their selection of home ranges (second-order selection) within the seasonal range (Skarin & Åhman 2014). At the landscape scale we can study reindeer selection of patches or vegetation communities within the seasonal range, similar to the third-order selection where selection within the home range is evaluated. At the local scale, the reindeer select species and plant parts within the patch or vegetation communities corresponding to studies of the reindeer foraging behaviour (Klein 1990; Mårell *et al.* 2006; Skarin & Åhman 2014). A characteristic of reindeer foraging patterns is the way the animals are in constant movement when grazing, allowing them to carefully select the most nutritious and soluble plant parts from the plant (Warenberg *et al.* 1997). This also characterises their use of the landscape as they are not territorial and do not stay within the same home-range throughout a season as other herbivores may do (Ciuti *et al.* 2003; Borkowski & Pudełko 2007).

1.3 Use of seasonal pastures and foraging behaviour

Reindeer physiology, behaviour and diet are adapted to seasonal variations in availability and the nutrient content of forage in arctic- and subarctic environments to meet the animal's nutritional requirements (Klein 1990; Tyler & Blix 1990). During the vegetative seasons, reindeer maximize nutrient intake in large quantities and with high selection, and they have a high capacity for storing energy and protein as muscle and fat tissue to survive the shortage of forage in winter (Figure 2; Åhman & White 2018). In winter, they show behavioural and metabolic adaptations to save energy (Tyler & Blix 1990) and a unique adaption to utilize lichen as a main energy resource when other forage resources are limited (Palo 1993; Glad *et al.* 2009; Glad *et al.* 2014). Seasonal variations, and reindeer adaption to them, form the basis of reindeer husbandry, and herders adapt their herding strategies (e.g. land use) and practices according to reindeer seasonal movements, and what is important for the reindeer at different times of the year (Skarin *et al.* 2022).

1.3.1 Snow-free season

In early spring, usually in April, reindeer start migrating from lower altitudes in winter ranges to higher altitudes in summer ranges (Kumpula & Colpaert 2007). This makes it possible for them to follow the snowmelt and succession of spring green-up (Mårell *et al.* 2006; Åhman & White 2018). Reindeer select the early green parts of vascular plants (e.g. *Festuca ovina, Eriophorum vaginatum, Deschampsia flexuosa),* the roots and early sprouts of sedges found early in mires (e.g. *Carex*) and buds from deciduous shrubs (e.g. *Betula* and *Vaccinum*) with high digestibility and protein content (Klein 1990; Ophof *et al.* 2013). Female reindeer depend on their body reserves for foetal growth and lactation, and they give birth to their calves in May (Barboza & Parker 2008; Åhman & White 2018), before the vegetative growing season. Reindeer have a 'follower' breeding strategy, and calves follow their mothers from birth. During this time, reindeer are especially sensitive to disturbances (Skarin *et al.* 2022). As the snow melts, vascular plants become increasingly important (Åhman & White 2018), and reindeer move to areas with early vegetation succession e.g. mires, wet areas, and deciduous forests (Warenberg *et al.* 1997). As soon as more vegetation starts emerging, reindeer feed on deciduous shrubs (e.g. *Salix* and *Betula*), grasses and sedges (e.g. *Carex, Poa alpina, Eriophorum angustifolium*) and herbs (e.g. *Alchemilla, Solidago virgaurea, Comarum palustre*) in meadows, mires and grass heaths (Skogland 1980; Warenberg 1982; Skogland 1984).

During the summer and autumn, reindeer need to cover their energy costs for growth and activity and build up their body reserves to survive the food shortage in winter (White *et al.* 2014). By the end of the summer, autumn, and occasionally in early winter, reindeer eat mushrooms when available (Inga 2007), of which *Boletus* are preferred (Kreula *et al.* 1976).

From September, as the digestibility of summer pasture decrease, the reindeer gradually increase their relative intake of lichen in their diet (Finstad & Kielland 2018); plants found in mires (*Carex*) become increasingly important again, as does *Vaccinum* (Warenberg *et al.* 1997). The rutting season starts in mid-end September and lasts until mid-October. This is also the time when complete weaning usually occurs. After weaning, the calf depends on its own utilization of forage to survive the winter (Åhman & White 2018). In their first winter, calves (especially female calves) still follow the mother and may do so until the next parturition (Espmark 1971; Kojola 1993). In late autumn, reindeer start migration from higher altitudes in summer to lower altitudes in winter (Kumpula & Colpaert 2007). This makes it possible for them to find winter pastures with favourable snow conditions (Åhman & White 2018).

1.3.2 Winter

Winter grazing conditions are considered good when lichen abundance is high, and snow conditions are favourable, that is when there is low snow depth and soft snow with almost no freezing events (Ryd & Rassa 2001). In the beginning of winter, when snow depth is still shallow (< 40 cm), lichens are usually of low importance to reindeer (Kumpula 2001; Ryd & Rassa 2001). The reindeer are constantly on the move and do not stay in an area for long, even if lichen abundance is high (Kumpula 2001; Ryd & Rassa 2001). As snow depth increases (< 70 cm), reindeer begin to dig in the snow for lichen (e.g. *Cladonia* and *Cetaria nivalis*) and evergreen vascular plants such as forest wiregrass (*Deschampsia flexuosa*), cottongrass (*Eriophorum*; Klein 1990; Mathiesen *et al.* 2005). They tend to select and stay in areas with a high lichen abundance to dig, graze, and sleep as long as grazing conditions are favourable (Kumpula 2001; Ryd & Rassa 2001). Kumpula (2001) found that selection for high lichen abundance was strongest around February. In some areas, the highest proportion of lichen may be ingested in March (Mathiesen *et al.* 2000). In winter, reindeer's energy and nitrogen (protein) balance are negative (catabolic phase; Pösö 2005). A negative energy balance and the subsequent weight loss in winter is considered a regulated process, and reindeer often lose 10−20% of their body mass (Tyler & Blix 1990; White *et al.* 2014). Meanwhile, energy requirements for activity are high because of the energy costs associated with the search and digging for forage under the snow; these energy costs increase with more difficult grazing conditions e.g. denser and more crusted snow (Fancy & White 1985). When energy expenditure increases for digging, they need to make a trade-off between the energy cost of digging and the benefits of food intake (Fancy & White 1985). This trade-off is an important determinant for the choice of feeding site for the *Rangifer* species (Fancy & White 1985; Kumpula 2001). As snow becomes too hard due to, for example, ice formation or the snow depth becoming too deep, old coniferous forests with arboreal lichens (*Bryoria* and *Alectoria*) become essential for their survival (Kumpula & Colpaert 2003; Rosqvist *et al.* 2022).

OLD BOREAL FORESTS
Arboreal lichens (Bryoria, Alectoria) become essential for survival when ice crust forms and access to ground vegetation is limited in late winter

BOREAL FORESTS
Lichens e.g., Cladonia, Cetraria
Wintergreen shrubs e.g., Vaccinum, Empetrum
Wintergreen grasses and sedges e.g., Festuca ovina, Eriophorum

MIRES, WETLAND AND DECIDUOUS FORESTS
Seeks to places were snow melts yearly and vegetation begin early e.g., water streams and mires

Deciduous shrubs e.g., Betula, Vaccinum
Grasses and sedges e.g., Carex, Festuca ovina, Deschampsia flexuosa

MIRES, BOREAL- AND DECIDUOUS FORESTS
Digestibility of forage decrease
Sedges (in mires), root parts
Mushrooms e.g., Boletus
Ground lichens become more important
Deciduous shrubs and grasses e.g., Calluna, Vaccinum

MEADOWS, CLEARCUTS, DECIDUOUS FORESTS AND GRASS HEATHS
Deciduous shrubs e.g., Salix and Betula
Grasses and sedges e.g., Carex, Poa alpina, Eriophorum angustifolium
Herbs e.g., Alchemilla, Solidago

Figure 2. Illustration of reindeer seasonal habitat and diet. Photos: Minna Turunen (plants), Helén Sundqvist, and Heidi Rautiainen.

1.4 Winter feeding of reindeer in Sweden and Finland

1.4.1 Reasons for feeding

Winter feeding of reindeer has become increasingly common in Norway, Sweden, and Finland for several reasons. In Sweden and Finland, loss of winter pasture due to modern forestry, together with reduced connectivity, has made it more difficult for reindeer to both find good winter pastures and to move between them (Axelsson-Linkowski *et al.* 2020). In Sweden, over 70% of lichen-rich forests have been lost since the 1950s (Sandström *et al.* 2016). Competition for land (e.g. wind- and hydro power, mining, infrastructure, forestry, human activity, and predators) leads to direct and indirect habitat loss due to fragmentation and disturbances, reducing the accessibility of pastures (Kivinen *et al.* 2012; Skarin *et al.* 2018). For example, hydropower development has destroyed migration routes and other developments, and forestry and infrastructure create barriers and fragmentation of the landscape (Kivinen *et al.* 2012; Tyler *et al.* 2021; Horstkotte *et al.* 2022).

Another important reason for winter feeding is the severe winter conditions with icing reducing the accessibility of pasture. In northern latitudes, warming occurs more than three times faster than the global mean leading to varying temperatures and higher winter precipitation levels (Post *et al.* 2019; Walsh *et al.* 2020). Fluctuating temperatures and increased precipitation in winter leads to ice formation which then restricts access to the vegetation on the ground. When icing is followed by considerable amounts of snow (> 70 cm), the pastures become inaccessible, making winter feeding necessary to ensure reindeer survival. These conditions occur more often and earlier in the season, decreasing the availability of lichens. When availability of or accessibility to ground lichens is limited due to ice-crust formation together with a lack of alternative old boreal forest with arboreal lichens, reactive measures such as winter feeding are used as an adaptation strategy (Tyler *et al.* 2007; Brännlund & Axelsson 2011; Turunen *et al.* 2016; Persson 2018).

1.4.2 Previous and present winter-feeding

Winter feeding of reindeer was trigged by a series of particularly severe winters in the late 1960s, resulting in acute starvation and subsequent reindeer losses (Turunen & Vuojala-Magga 2014; Åhman *et al.* 2022). This promoted the use of hay as supplementary feed for reindeer and became the start of the commercial production of grain-based feeds specially intended for reindeer. In the southern parts of the Finnish reindeer herding area, the feeding of reindeer developed in close interaction with agriculture and became common practice in the southern regions in the 1980s (Turunen & Vuojala-Magga 2014). In Sweden and Norway, the use of feeding has increased since at least the late 1980s (Bårdsen *et al.* 2017), when "clean” feed was provided to reindeer before slaughter to reduce radioactive contamination caused by the Chernobyl accident (Åhman 1999).

Winter feeding is increasingly used as a management strategy to prevent starvation when natural forage is unavailable due to ground icing, commonly referred to as “emergency feeding” (Åhman *et al.* 2022). In Sweden and Northern Finland, winter feeding varies across regions and years, depending on the availability of natural pastures and winter conditions (Hukkanen 2012) In some regions, winter feeding has become a regular routine and is carried out over longer time periods. This is most common in the southern reindeer management area in Finland, with some herders feeding pregnant females in enclosures until calves are born in spring (Turunen & Vuojala-Magga 2014). Hence, many reindeer herders in Finland have a long experience of winter feeding.

Winter feeding may be provided on natural pastures or in enclosures. During feeding on natural pastures, reindeer usually obtain a major part of their food through grazing. In Finland, open fences are sometimes used, where the reindeer are provided feed within a fenced area that they can freely exit at any time to dig for natural pasture (Hukkanen 2012). In enclosures, the daily food intake of reindeer mainly depends on the feeds provided to them by the herder.

Throughout the thesis, “feed” is referred to as the food provided to reindeer by the herder, and “food” is used as a general term irrespective of whether it is provided by herders or grazed by the reindeer on natural pasture.

1.4.3 Effects of winter feeding

Winter feeding of reindeer has been shown to increase survival and female reproductive success as measured by foetal growth rate and early calf survival (Rognmo *et al.* 1983; White 1983), increased calf percentage (percentage calves of the total herd), and body mass (Eloranta & Nieminen 1986). Feeding may, on the other hand, increase susceptibility to stress

(Forristal *et al.* 2012), infectious diseases (Tryland 2012; Tryland *et al.* 2019) and metabolic problems (Åhman *et al.* 2018). In addition, there have been concerns among reindeer herders that feeding may lead to unintended effects on behaviour, such as tameness, habitat selection, grazing behaviour and migration patterns (Vuojala-Magga *et al.* 2011; Horstkotte *et al.* 2020). This may, eventually, compromise the reindeer's ability to make use of natural pastures (Turunen & Vuojala-Magga 2014; Persson 2018; Horstkotte *et al.* 2020).

The long-term effects of winter feeding on habitat selection and behaviour have not been investigated in reindeer. Currently, the research is also limited for wildlife and other deer species, and most research related to the behavioural effects of winter feeding of other free-ranging ungulates is related to the effects during feeding. For example, feeding of wild ungulates may lead to altered space-use, habitat selection and migration patterns (Sahlsten *et al.* 2010; Van Beest *et al.* 2010b; Bojarska *et al.* 2020), increased susceptibility to predators (Oja *et al.* 2015), and inter- and intra-specific competition among animals (Grenier *et al.* 1999; Milner *et al.* 2014).

2. Aims

The aim of this thesis was to investigate the short- and long-term effects of winter feeding on reindeer with a focus on habitat selection and foraging behaviour. In paper I, we investigated the experience-based knowledge of the short- and long-term effects of winter feeding on reindeer. To evaluate reindeer foraging behaviour, we developed a method to classify reindeer behaviour from accelerometer data (paper II). To test the effects of winter feeding we conducted an experiment to compare habitat selection, foraging behaviour and body weight of previously fed and non-fed individuals (paper III). Specifically, the following questions were investigated:

1. What is the experience-based knowledge among reindeer herders of the long- and short-term effects of winter feeding on reindeer (with focus on foraging behaviour)?
2. How can reindeer's fine-scale behaviour be classified using tri-axial acceleration sensors?
3. How does ad libitum supply of feed during the calves' first winter affect habitat selection and fine-scale foraging behaviour in their following winter?
4. How does the feeding of reindeer calves during their first winter affect body weight after their second and third winter?

3. Material and methods

3.1 Herders’ experience-based knowledge of the effects of winter feeding on reindeer (paper I)

In paper I, we investigated herders' experience-based knowledge of winter feeding of reindeer. We interviewed nine reindeer herders in Sweden and ten in Finland. Herders were represented by three females and 16 males based on their experience of winter feeding. In total, 23 herders were invited to participate in the interviews. Initially, we contacted herders known from previously, with known experience of winter feeding. We had two criteria for contacting a herder, namely that they had experience of winter feeding, and that they had fed reindeer in enclosures at least once. Winter feeding was defined as the feeding of reindeer intended for breeding, apart from short-term feeding during herding events such as round-ups and migration. In addition, we used a snowball sampling technique to recruit more informants. Snowball sampling refers to sampling in which our initial informants are asked to assist in identifying other potential informants (Naderifar *et al.* 2017). Our aim was to find informants that represented a variation of geographical locations and herding practices. In Sweden, we interviewed herders from two mountain herding districts, six forest herding districts and one concession herding district (Figure 3). In Finland, we interviewed two herders from the Sámi home range in the north, one herder working at a reindeer research station, and seven herders from the southern reindeer herding area.

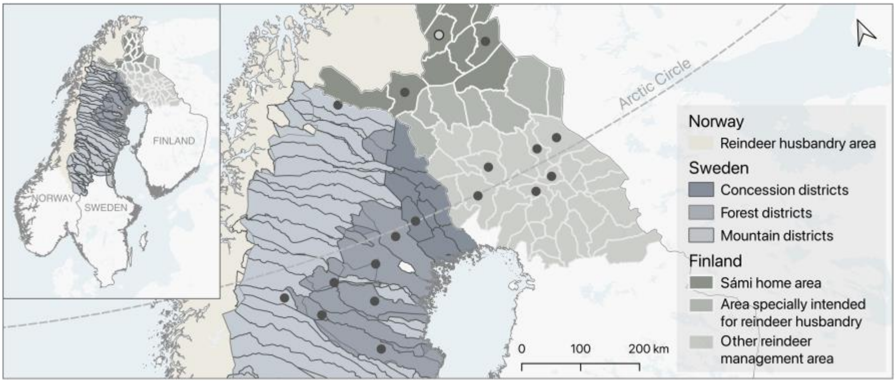


Figure 3. An illustration of the 19 study sites for semi-structured interviews with reindeer herders to investigate the experiences and effects of winter feeding in Sweden and Finland. All interviews were conducted between November 2019 and April 2022. Adapted from Figure 1 in paper I.

3.1.1 Interviews and analyses

Semi-structured, in-depth interviews with individual herders addressed general information about the herding district, winter-feeding practices over time and the short- and long-term effects of feeding. The interviews were conducted face-to-face between November 2019 and April 2022, using open-ended questions. A topic guide was used to ensure that all pre-defined topics were covered (Table 1). Herders were asked to describe their herding district, and experiences of feeding, and to recall yearly variations in the environment and significant events. Open-ended questions were asked until at least ten years of history had been covered. In relation to feeding, herders were asked to describe practices and routines, as well as their observations of how feeding affected the reindeer.

The interviews were audio-recorded and lasted between 24 and 112 minutes (70 minutes on average). Interviews in Sweden were conducted and transcribed in Swedish. Interviews in Finland were conducted and transcribed in Finnish and translated into English before analysis. Individual interviews were coded using NVivo software (QSR Software, NVivo 14) using a thematic analytical approach (Rubin & Rubin 2005; Braun & Clarke 2006).

Table 1. Topic guide used in semi-structured interviews with reindeer herders in Sweden and Finland to investigate the experience-based knowledge of winter feeding of reindeer

Topic	Subtopics
Herding district	General description of the herding district including environment, predators, disturbances etc.
Experience of feeding	
Winter feeding	Reasons (that may vary between years and circumstances)
Routines	Enclosures/facilities, feeding practices, animals, period, amounts and type of feed
Effects, short- and long-term	Effects on the reindeer that may include behaviour or different physical traits, and how these depended on routines (above) and circumstances

3.2 Feeding experiment (paper II and III)

To test the effects of feeding on reindeer's future behaviour, we conducted a feeding experiment and investigated the effects of winter feeding on reindeer habitat selection and foraging behaviour (paper III). The animals in the feeding experiment were also used to develop a method to classify reindeer behaviour from accelerometer data (paper II, see section 3.3).

3.2.1 Study areas

The experiment was performed in two Sámi reindeer herding districts in northern Sweden – Sirges (N66°41′, E19°37′, centre point of the herding district) and Ståkke (N66°6′, E18°47′) – between 21 November 2019 and 7 April 2022. Herding districts are divided into several reindeer herding groups (*siidas*) commonly formed by family units. The experiment was conducted in one siida group in each district. In Sirges, feeding on natural pasture has been provided on a regular basis for about ten years, whereas in Ståkke feeding on natural pasture had been offered about five times to various extents over the past ten years before our experiment.

3.2.2 Experimental design

In the beginning of the winter season 2019/2020 (hereafter named winter 2020), reindeer calves born in May 2019 were randomly selected from the main reindeer herd and divided into a feeding group (Sirges n = 43, Ståkke A n = 42), and a control group (Sirges: n = 50 and Ståkke A: n = 50; Figure

4). The feeding groups were fed in enclosures and the control groups were kept on natural pastures together with their main reindeer herd. In April 2020, the feeding groups were released to the natural pasture and allowed to merge with the main herd. Due to particularly severe winter grazing conditions in the winter of 2020, both control groups were fed on pasture from January to April (Figure 4, see paper III for details). We repeated the experiment in Ståkke the following winter, on reindeer calves born in May 2020 (Ståkke B feeding group n = 45, Ståkke B control group n = 55). Severe winter grazing conditions also followed in the winters of 2021 and 2022.

In 2021, feeding with pellets on pasture was provided to the reindeer in Sirges from 16 January to 21 March, and in Ståkke from 10 March to 2 April. In Ståkke in the winter 2022, feeding with silage on pasture was provided from 28 February to 30 March. When all reindeer were on natural pasture, after each treatment period, 15 reindeer in each of the six feeding and control groups were fitted with GPS and accelerometer devices to follow their movement and behaviour. The groups in Sirges were followed for one winter until 28 March 2021. The groups in Ståkke A and B were followed until 7 April 2022 (i.e. one and two winters, respectively). All reindeer within the six groups (N = 285) were individually marked with ear tags throughout the study period.

Measurements of body weight and pregnancy examination

We measured body weight on all animals (N = 285) two times each winter (Figure 4). To account for weight gain caused by gestation, abdominal palpation (Paul 2014) was performed by two observers for pregnancy detection on 28 March 2021 (Sirges) and 10 April 2021 (Ståkke A), and 7 April 2022 (Ståkke A and B).

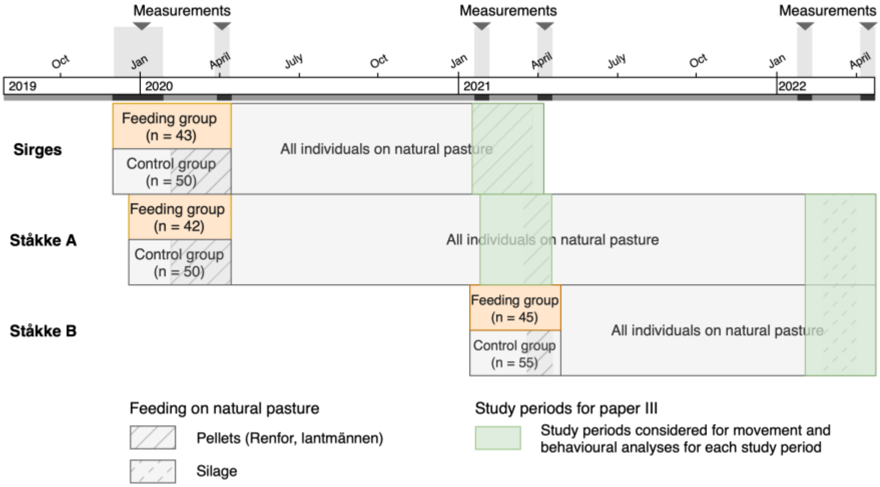


Figure 4. Experimental design and study periods considered for the analyses of locational (movement) and behavioural data in paper III. Body weight was measured two times each winter (measurements).

3.3 Behavioural classification using accelerometer data (paper II)

In paper II, we developed a method to classify reindeer foraging behaviour from accelerometer data. The process of gathering behavioural data from accelerometers involved main steps: 1) the acquisition of accelerometers and video recordings of behaviour, 2) pre-processing of acceleration data and feature extraction, 3) model training and validation, and 4) model selection and behavioural classification (Figure 5). The best performing model was then selected for classification of activities from free-ranging individuals in paper III.

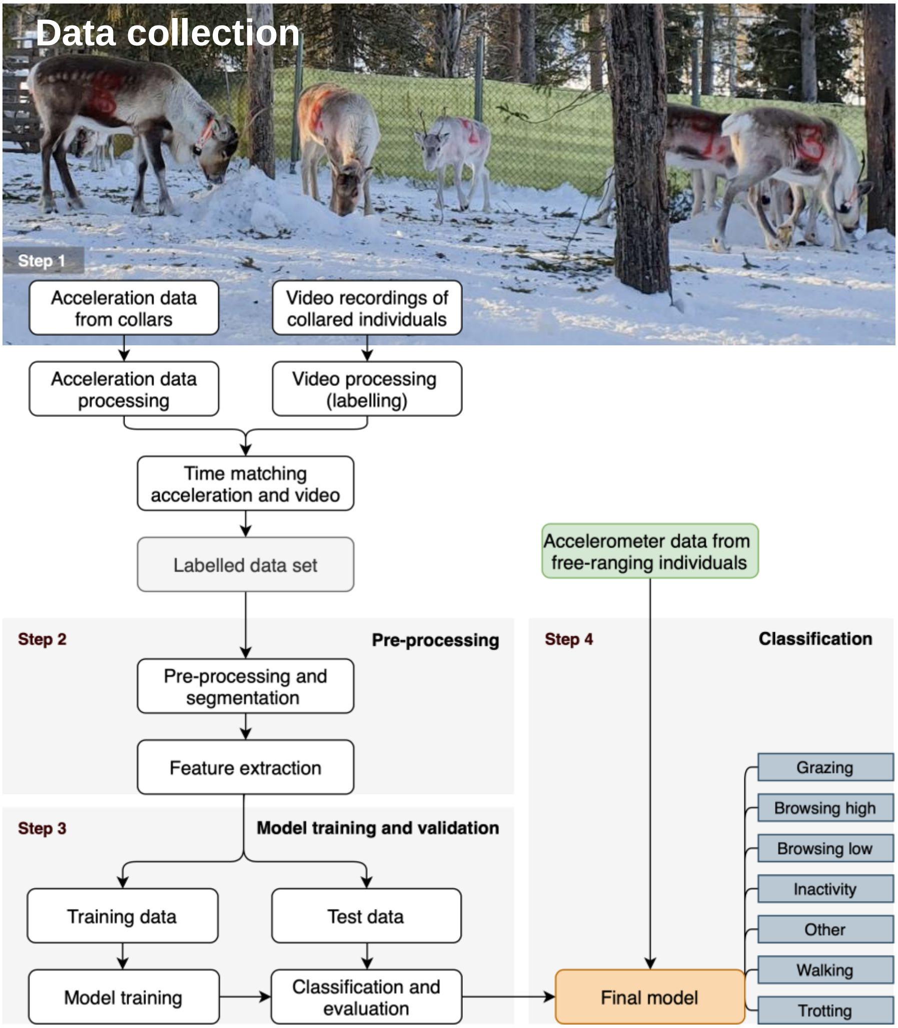


Figure 5. Behavioural classification workflow to predict seven behavioural classes for reindeer in paper II: 1) grazing from the ground, 2) browsing from trees, 3) browsing from shrubs, 4) inactivity, 5) other behaviours, 6) walking, and 7) running.

3.3.1 Step 1: Data collection

Animals, accelerometer attachment and video recordings

Acceleration loggers (Axy-4: Technosmart) were attached to the ventral side of the neck on a total of 19 fenced semi-domesticated female reindeer in

Ståkke and Sirges in winter 2020. In Sirges, ten reindeer (nine month old) were video recorded for four days and in Ståkke, nine reindeer (two two-year-olds and seven nine-month-olds) were video recorded for six days. The two-year-old reindeer were not part of the rest of the experiment. To encourage the browsing behaviour needed for model training, small trees with arboreal lichens were placed in the enclosures. Video and acceleration data was collected simultaneously, and the videos were manually time-synchronized with accelerometers.

Behavioural observations

Video recordings were labelled (annotated) using BORIS (Version 7.9.8) with behaviours based on a pre-defined ethogram to continuously define what the reindeer were doing. In total, 39 hours of video recordings were annotated into the behavioural categories. This gave us time series for all labelled behaviours, which were then matched with the corresponding time series of acceleration from the accelerometers (Figure 6). This data set is referred to as the labelled data set.

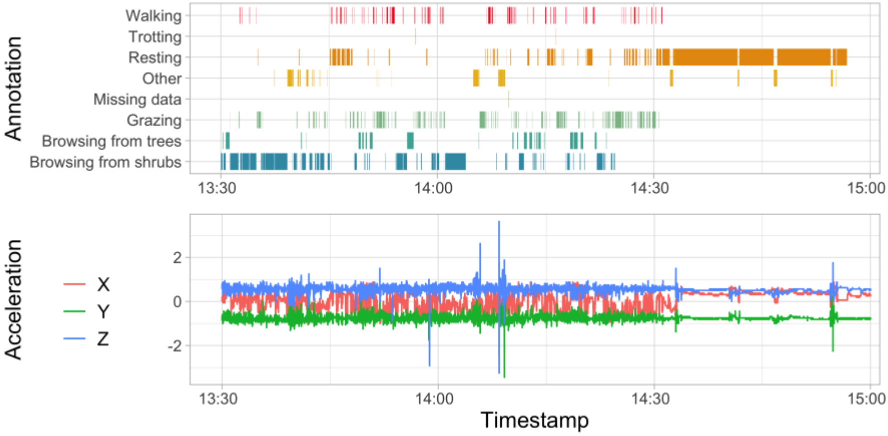


Figure 6. Illustration of time matching of behaviours from video recordings and acceleration data to create a labelled data set in paper II.

3.3.2 Step 2: Data processing

The processing of accelerometer data included pre-processing, segmentation, and feature extraction. Acceleration data (X, Y and Z) was smoothed using a running mean of five seconds to remove most of the gravitational (static) component of acceleration from the acceleration caused by motion (dynamic acceleration). The accelerometer data was then segmented into 2, 3, and 5 second windows. From each segment of data, summary statistics (e.g. mean, standard deviation, interquartile range) to find characteristics in the data set, hereafter referred to as features (Figure 7).

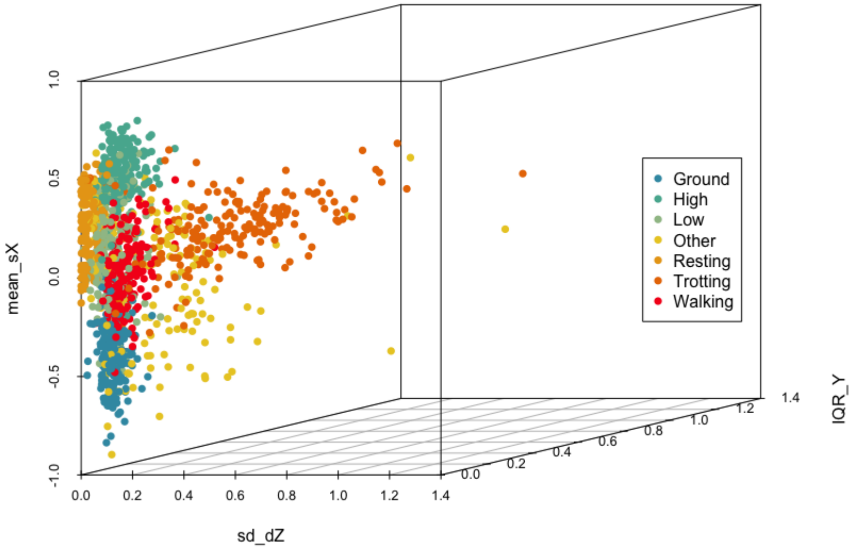


Figure 7. Data distribution using three statistical features 1) mean static acceleration of X-axis (mean_sX), 2) standard deviations of dynamic acceleration of the Z-axis (sd_dZ) and 3) interquartile range of Y-axis (IQR_Y) when using two second windows for segmentation (paper II).

3.3.3 Step 3 and 4: Model training, validation, and selection

The features and corresponding labelled behaviours were used to learn classification models to distinguish between labelled behaviours (from video recordings) given the characteristics in the accelerometer data. The supervised classification models used were Support vector machines, Random forests, and hidden Markov models (for description see paper II).

For model training and validation, we used leave-one-subject-out cross-validation (Figure 8). This was to account for variability among individuals used in training and ensure that one individual never occurred in training and validation data sets at the same time for each iteration. In this way, data from one individual was always left out in each fold and was utilized as a test set. We selected the model based on the highest behaviour-specific sensitivity, precision and accuracy, and overall accuracy across behaviours, and the best model was then used for paper III.

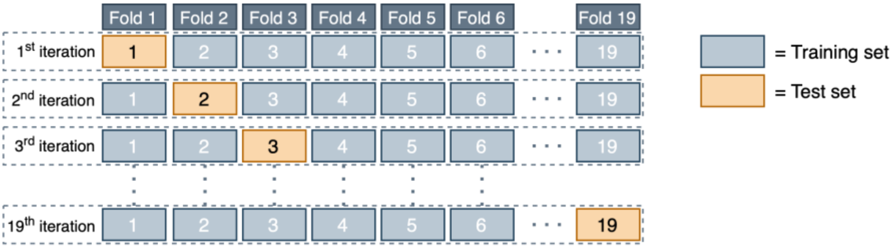


Figure 8. Leave-one-subject-out cross validation used for model training and validation to predict reindeer behaviour from acceleration data (paper II).

3.4 Habitat selection and foraging behaviour (paper III)

We used habitat selection functions (Aarts *et al.* 2013) based on GPS data (locational data) and habitat characteristics (habitat variables) to compare relative habitat selection strength between reindeer in the feeding and control groups (3.2.2 Experimental design, Figure 4). Furthermore, we used the behavioural data from the accelerometers to compare fine-scale foraging behaviour between the groups using multinomial logistic regression.

3.4.1 Movement and behavioural data

When all reindeer were on natural pasture 15 reindeer in each group (feeding and control) were fitted with collars equipped with GPS and accelerometers. In our analyses, we used a total of 19,586 GPS locations (Sirges n = 7428, Ståkke A n = 8973 and Ståkke B n = 2936) at a four-hour fix rate (for details on data and study periods see paper III).

Hidden Markov models were used to classify reindeer fine-scale behaviour from accelerometers into seven behavioural classes: grazing, browsing from shrubs, browsing from trees, walking, trotting, inactivity, and other behaviours using the method developed in paper II. Grazing is based on the head angle and thus includes digging and searching for food on the ground.

3.4.2 Habitat selection functions

Habitat selection functions refer to the use of logistic regression to model the relationship between use and availability (Keating & Cherry 2004). This estimates the probability that a location will be used depending on the frequency of used (observed) and available (random) locations. Habitat selection can thus be quantified using locational data (observed locations, represented by the value “1”) in relation to habitats that are accessible for an animal i.e. random locations considered available but not selected by an individual (represented by the value “0”). This was to determine whether an animal was using a patch, or habitat, disproportionately more (or less) than what is available. Accordingly, we fit a logistic regression model:

$$\mathrm{logit}(p_i) = \log\left[\frac{p_i}{(1 - p_i)}\right] = \beta_0 + \beta_1 x_{1i} + \ \dots + \beta_k x_{ki} + \varepsilon_i$$

where $i = 1, \dots, n$ is the index of patches, and the probability of use of each patch p_i is modelled as a function of k habitat characteristics variables $x_1, \dots, x_k$, using a logit link function. An example of habitat characteristics is the elevation of the patch. Residuals are denoted with ε_i. The effects of the k habitat characteristics are denoted by the coefficients $\beta_1, \dots, \beta_k$ respectively. For use-availability (or case-control) designs the p_i depends on the ratio of used and available locations, and only odds ratios are interpreted (Hailpern & Visintainer 2003; Keating & Cherry 2004):

$$w(x_i, \beta_k) = \exp\,(\beta_0 + \beta_1 x_{1i} + \ \dots + \beta_k x_{ki})$$

where, again, $x_1, \dots, x_k$ represents the habitat variables and the $\beta_0, \dots, \beta_k$ are the coefficients of habitat choice. This is interpreted as the relative strength of habitat choice, where $\beta_k > 0$ is interpreted as selection, or preference, of a habitat, while $\beta_k < 0$ is interpreted as avoidance of a habitat.

To estimate home range selection (second-order selection) of feeding and control groups, we used generalized linear mixed-effect logistic regression models with habitat variables (Figure 9) at both observed and available locations as independent variables (for details see paper III). The available locations were sampled within the available area for the reindeer at regional scale within the winter range (Figure 10).

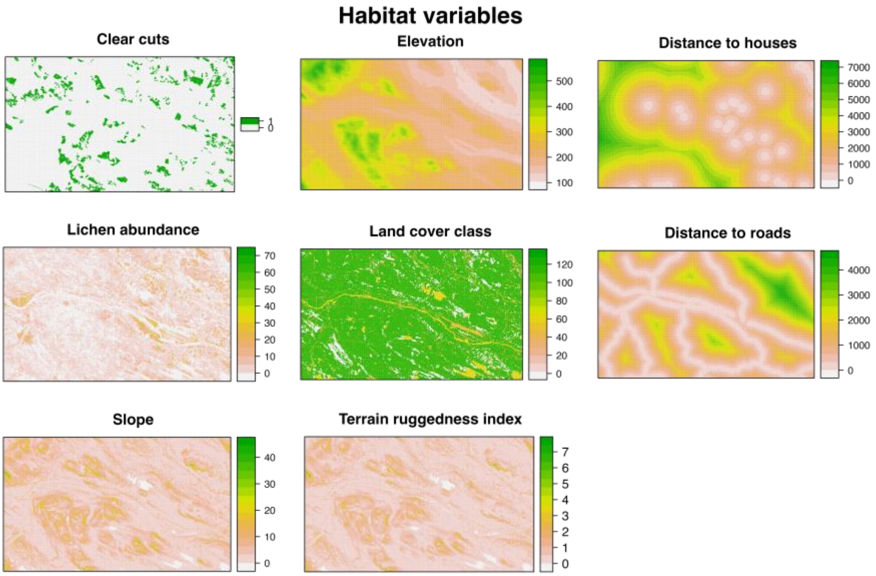
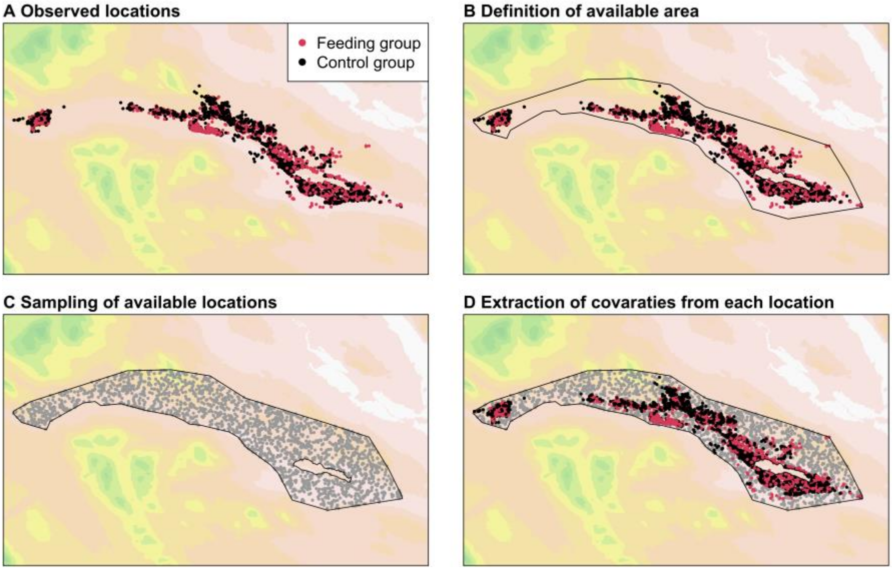


Figure 9. Habitat variables considered in the habitat selection functions and multinomial logistic regression models in paper III (for details, see paper III).


A Observed locations

B Definition of available area

C Sampling of available locations

D Extraction of covaraties from each location

Figure 10. Step-by-step procedure for preparation to estimate habitat selection of home range (second-order selection; paper III). First, the GPS positions (observed locations) of all reindeer in the given area and period were selected (A). The area considered available for all reindeer was defined based on the home range area estimated on the observed locations and herding strategies, barriers, and reindeer range use (B). Within the available area, ten available (random) locations for each observed location were sampled (C). Habitat variables were extracted at both observed and available locations (D). Elevation is used as a background map and available locations are only shown for one individual for illustrative purposes.

To estimate habitat selection within the home range (third-order selection), series of observed locations were considered using step-selection functions (SSF: Fortin *et al.* 2005). In SSF consecutive locations are defined as steps (Figure 11). From these, available locations are drawn and represent locations that are available to the individual at each step. Each step at time *t* was paired with ten available steps with the same starting point fitted with a conditional mixed Poisson model (for details see paper III). Extraction of habitat variables was similar to the procedure in the data preparation for the home range selection dataset. Specifically, we extracted habitat variables at the endpoint of each step and the corresponding available locations (Signer *et al.* 2019).

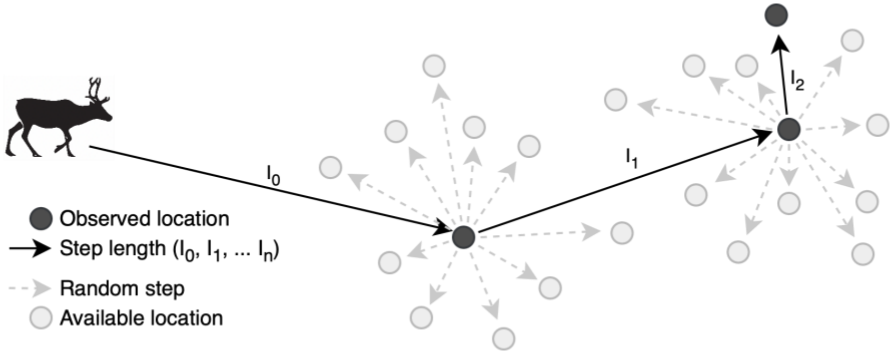


Figure 11. An illustration of observed and available locations used to estimate habitat selection within home range (third-order selection; paper III). In step selection functions, available locations are sampled based on simulated movements from preceding locations and compared with used locations (end points of steps) and randomly selected turn angles based on a uniform distribution between 0 and 2π (360°). Ten available (random) locations for each observed location were used.

To provide an example of relative selection of home range, I predicted the final model over a raster to visualize the selection of home range placement for the feeding and control group in one study area and year. Predicted values (0−1) were binned into ten quantiles and elevation and lichen into seven quantiles (Boyce *et al.* 2002; Morris *et al.* 2016).

3.4.3 Fine-scale behaviour

From the classified behaviours we extracted the behaviour at each GPS-location. We used multinomial logistic regression to investigate how habitat variables affected reindeer fine-scale foraging behaviour between the groups (for details see paper III). The most common behaviour (resting) was set as the reference.

4. Main results

4.1 Reindeer herders’ experience-based knowledge of the effects of winter feeding (paper I)

In paper I, we used in-depth interviews to investigate herders’ observations of the physiological and behavioural effects of winter feeding on reindeer and discuss the indirect and direct risks in the short- and long-term. All the interviewed herders had experience of feeding reindeer, at least occasionally, during the last decade. The identified effects of feeding on reindeer were mostly related to physical traits or behaviour (Figure 12). We classified effects as “short-term” when they were observed during feeding and in the following summer, and “long-term” when they were observed from the following autumn onwards, or as an effect of several years of feeding. Effects on physical traits included survival, weight, body condition (including muscle and fat reserves, and to some extent physical strength), reproduction, transmittable diseases, and gastrointestinal problems. In terms of behavioural effects, we could identify five main themes: tameness, habituation, foraging behaviour, migration, and maternal care. The reported effects varied between herders, as did the perception of whether an effect was positive or negative. Below, I present some of the main results, focusing on the reported effects related to foraging behaviour and body condition.

In the short-term, the positive effects included, for example, improved weight and body condition during feeding and in the following summer. Another short-term effect was that the reindeer became used to humans, which was considered positive by some herders, and negative by other herders. It was, for example, considered positive when the intention was to use feeding regularly, as this made it easier to introduce feeding, but it was considered negative in some cases when feeding was not used on a regular basis. When feeding females in enclosures during calving their new-born calves learn to eat supplementary feed straightaway. This was considered positive by some herders, as it became easier to introduce the calves to feeding the next winter. On the other hand, some herders considered it negative that the calves learn to favour feed instead of natural pasture. Other negative short-term effects included how reindeer became lazy and waited for feeding and left good grazing grounds to eat only feed rather than try to dig for available natural pasture.

In the long term, some herders observed improved body condition the following winter, while others observed reduced body condition if the reindeer were not fed again, especially if winter grazing conditions became difficult. When discussing foraging behaviour, it was raised that fed reindeer may leave the herd in search of previous or current feeding places, if they had been fed the previous winter. This was considered negative. When feeding calves in enclosures, some herders believed that calves missed the opportunity to learn from their mothers how to find natural forage in the following winter. However, it was also raised that previously fed reindeer were easier to introduce to feeding in following years, which was considered beneficial when winter feeding was needed.

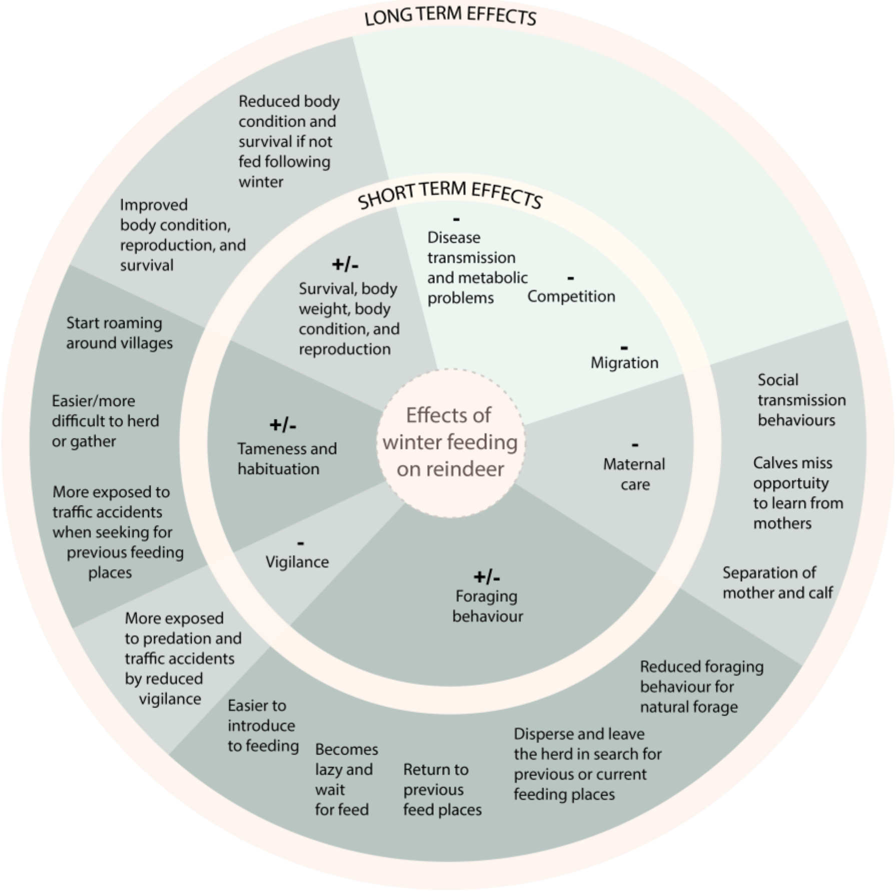


Figure 12. Short- and long-term effects of winter feeding on reindeer reported by herders in Sweden and Finland (paper I). Specific examples are only included for long-term effects. “Short term” is defined as effects observed during feeding and in the following summer, and “long-term” effects are those observed in the following autumn or onwards, or as an effect of several years of feeding. Effects clearly considered as positive are indicated with (+) and effects considered as negative are indicated with (-). If both positive and negative effects are observed this is indicated with (+/-).

4.2 Classification of reindeer fine-scale behaviour (paper II)

In paper II, we found that common behaviours, such as grazing (accuracy ≥ 88%) and inactivity (accuracy ≥ 90%), were easily identified by all three models (Figure 13). The models did not discriminate browsing-high and

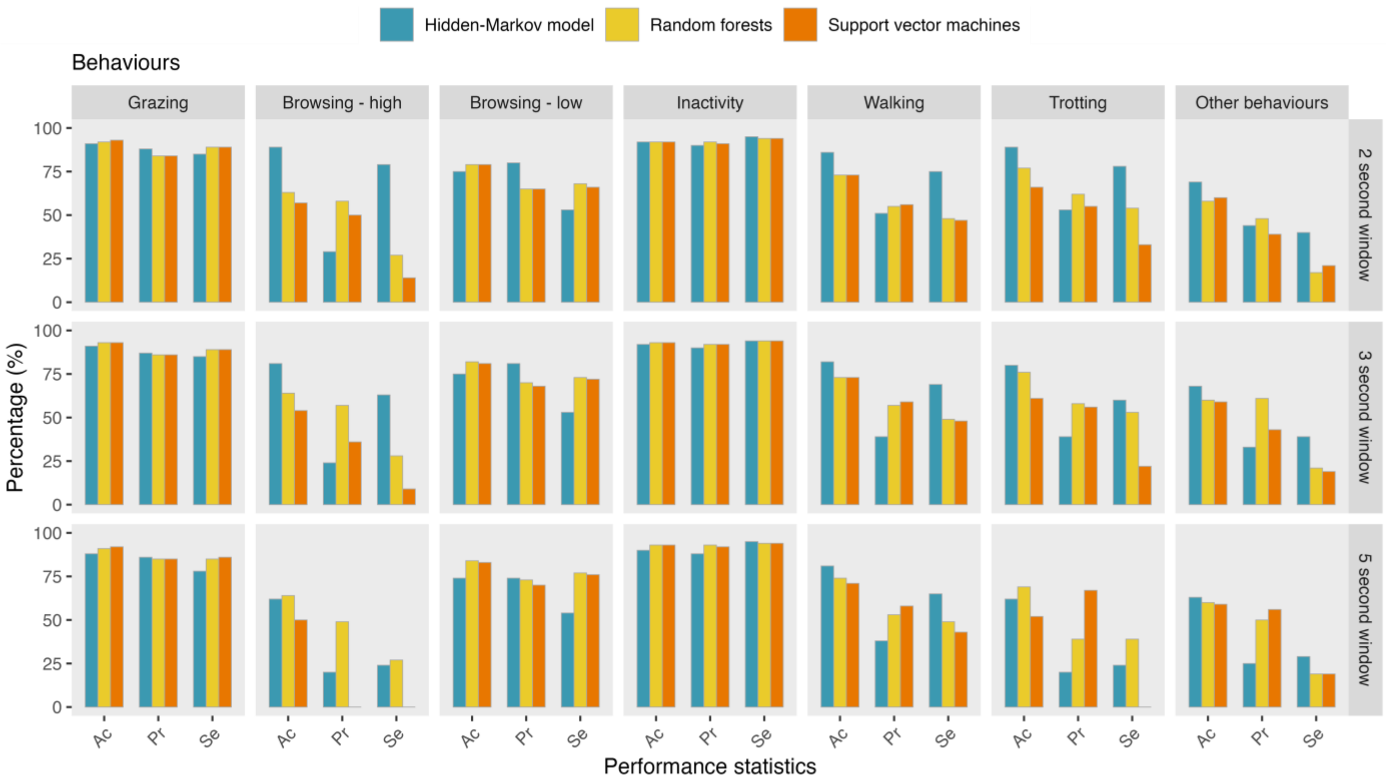


Figure 13. Performance statistics (%) of hidden Markov models (HMM), Support vector machines (SVM), and Random forests (RF), and using time-domain features in 2, 3 and 5 second windows (paper II). Behaviour-specific metrics are given as sensitivity (Se), precision (Pr), and accuracy (Ac).

movement to the same extent. For the three models applied, Random forests using 5 second windows had the highest overall performance with an accuracy of 85%. Increasing the window size led to improved performance for both the Random forests and Support vector machines, while the hidden Markov models performed better with smaller window sizes. The best-performing hidden Markov model using 2 second windows was better able to classify undersampled behaviours (i.e. browsing-high and trotting) compared to the best performing Random forests and Support vector machines. Thus, by considering the serial dependence between behaviours, hidden Markov models were able to best predict behaviours based on naturally unbalanced data. This model was selected as our final model and used for the prediction of reindeer fine-scale behaviour on natural winter pasture (Figure 14) for paper III.

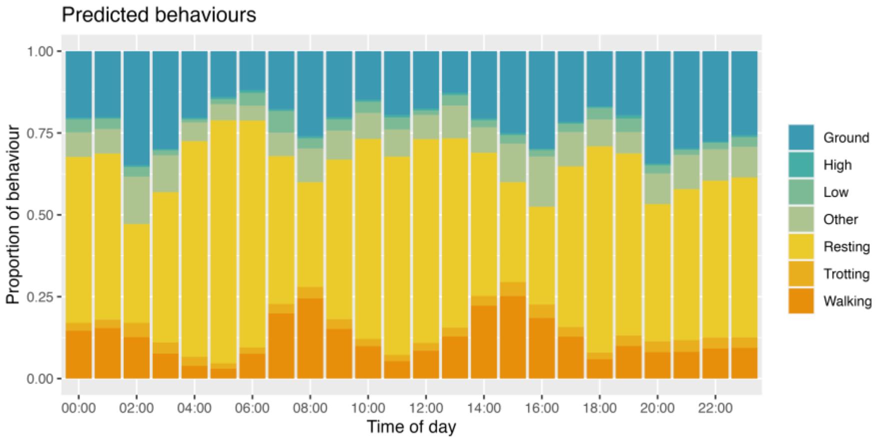


Figure 14. Proportion behaviour of reindeer in winter classified using methods in paper II. Proportion of behaviours per hour for one individual (ID 274) averaged across two days in winter (February). Data from one reindeer calf born in 2019, which was not provided winter feeding, representing one of the control individuals in paper III.

4.3 Long-term effects of winter feeding on reindeer habitat selection and fine-scale foraging behaviour (paper III)

4.3.1 Habitat selection

In paper III, our main results showed that winter feeding of reindeer calves in enclosures during their first winter reduced their selection of lichen on natural winter pastures in consecutive winters. In the selection of home range, all animals in Ståkke and Sirges reindeer herding districts preferred areas with high lichen abundance, but feeding groups were less likely to use areas with higher lichen abundance compared to the control groups in all cases ($P \leq 0.02$, Figure 15). This effect lasted for two years after feeding when the individuals had become adult reindeer. In the selection of lichen within the home range, no differences were found between groups one year after feeding. Two years after feeding, previously fed animals were less likely than control animals to select areas with higher lichen abundance when they selected habitat within the home range.

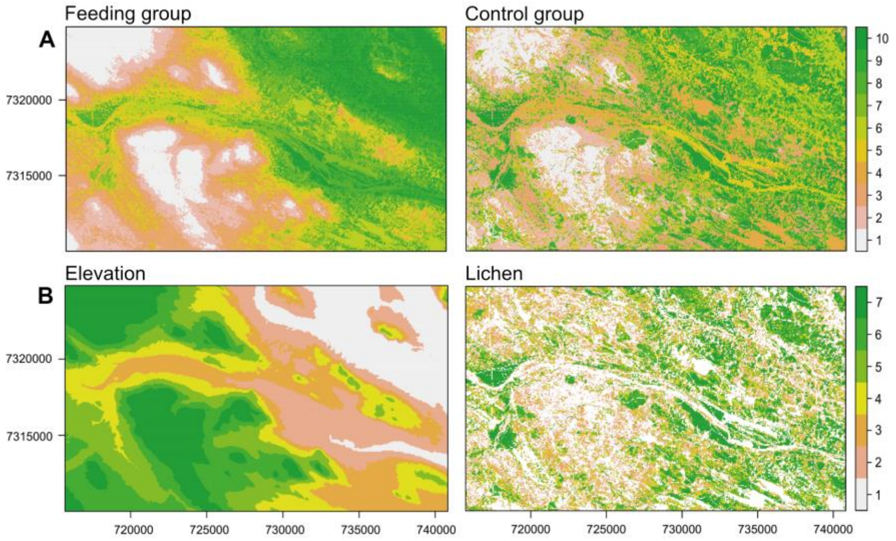


Figure 15. Predicted marginal effects estimated from habitat selection functions of reindeer selection of home range area for feeding and control group in Ståkke A 2021, northern Sweden, in relation to lichen abundance. Predicted values (0–1) are binned into ten quantiles, lower values (< 5) represent avoidance of habitat and higher values (> 5) represent selection (A). The environmental maps of the same area for elevation and lichen, respectively, with values for elevation above sea level and lichen abundance into seven quantiles (B; Figure 4 in paper III).

4.3.2 Fine-scale behaviour

When studying reindeer fine-scale behaviour, predicted from the accelerometers, reindeer in the feeding group in Ståkke B 2022, for example, increased their time grazing as lichen abundance and distance to the feeding places increased. However, differences in fine-scale behaviour between the groups was mainly determined by topographic characteristics and distance from the feeding troughs. The second winter after feeding we found no differences in fine-scale behaviour between the groups.

4.3.3 Body weight

Measurements of weight loss showed that all animals lost on average 6% of their body weight from mid-winter to early spring. In 2021, there was an effect of area ($F_{1;\,105} = 9.1$, $p = 0.003$), and the animals in the feeding groups in Ståkke A had a smaller mean weight loss ($F_{1;\,105} = 4.1$, $p = 0.04$) while there were no differences between groups in Sirges (Figure 16). In 2022, we found an effect of age ($F_{1;\,87} = 6.8$, $p = 0.01$) and an interaction between feeding and control groups and age ($F_{1;\,87} = 4.1$, $p = 0.03$), but no significant effect of pregnancy. One year after feeding, in Ståkke B 2022, mean weight loss was smaller for control reindeer than fed reindeer. Two years after feeding, in Ståkke A 2022, fed reindeer had smaller weight loss than control reindeer.

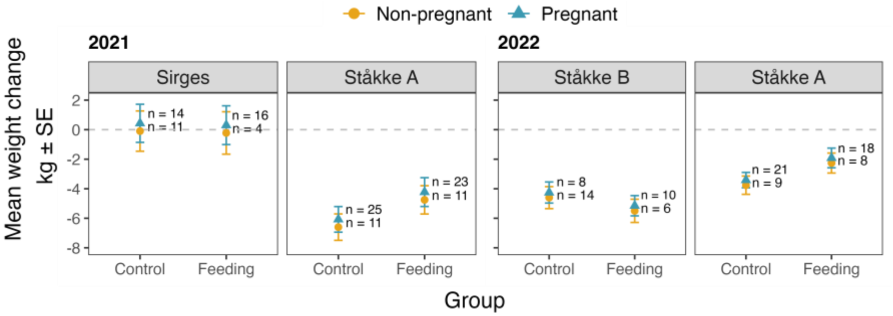


Figure 16. Predicted weight loss (kg ± SE) of pregnant (triangles) and non-pregnant (circles) females in feeding and control groups before and after each study period in Sirges, Ståkke A 2021, Ståkke B 2022, and Ståkke A 2022. Dashed lines represent the intercept for zero weight change (Figure 7 in paper III).

5. General discussion and conclusions

The overall aim of this thesis was to investigate the effects of winter feeding on reindeer with a primary focus on long-term effects and foraging behaviour. Our results indicate that there are unintended negative effects of feeding, and that animals which have been fed previously may have difficulties to efficiently use forage on natural pastures. In paper I of this thesis, we investigate the experience-based knowledge on the effects of winter feeding on reindeer. In paper II, we developed a method to remotely monitor reindeer foraging using accelerometers. In paper III, we investigated the effects of winter feeding on reindeer's future ability to utilize natural pastures, measured by habitat selection, foraging behaviour and body weight. Below, I will discuss the results from these three studies related to reindeer's ability to utilize natural pastures, their foraging success and the methods used to evaluate this quantitively.

5.1 Unintended long-term effects of feeding on reindeer

5.1.1 Ability to utilize natural pastures

Based on the interviews (paper I), we conclude that the observations on reindeer foraging behaviour differ between herders, as does perceptions of whether the observed effects are positive or negative. The majority of the herders had not observed any long-term effects, but many of them fed reindeer on a regular basis (every year), which may have made it difficult to observe grazing behaviour when feed was not provided. At least two herders expressed that it was difficult, or not an option, to stop regular winter feeding once it had been started. Some herders reported that regularly fed reindeer (on pasture or in enclosure) become lazy, and, having the option, may leave good grazing grounds to eat only feed rather than try to dig for available natural pasture. Our results on reindeer habitat selection (paper III) supported the observations from the herders that previously fed individuals may be less efficient in finding high-quality pasture. We found that reindeer that had been fed during their first winter (the feeding groups) were less likely to select home ranges with high lichen abundance compared to control animals. Two years after feeding (Ståkke A 2022) the fed reindeer were also less likely to select habitats with high lichen abundance within the home range compared to control animals. In the interviews, herders referred to that calves fed in enclosures may not learn how to find natural forage, or that they may learn to go for winter feeding instead of natural forage. Thus, winter feeding may potentially act as an evolutionary (or ecological) trap if young animals do not learn essential skills or learn maladaptive behaviours (Schlaepfer *et al.* 2002) which are not useful on natural pastures when feed is not provided. Our examples show that reindeer may select poor-quality habitats, or search for feed provided by herders, even if high-quality habitats are available. If the animals have difficulties finding natural forage the herder might be forced to continue to provide feed, which will gradually lead to increased dependence on feeding. Furthermore, there is a risk that such maladaptive behaviours are transmitted to other individuals and future generations through social learning (Donaldson *et al.* 2012).

The control groups were managed by the herders, together with the rest of the reindeer in their herd, during their first winter. We were therefore unable to prevent feeding on pasture when it became necessary due to the severe winter grazing conditions. In addition, reindeer in all groups were provided some feed on natural pasture when we observed their grazing behaviour during the second and third winter. In spite of access to feed the control animals were more likely to find high-quality pasture compared to the animals from the feeding groups. Thus, the way feed is provided to the reindeer seems to be important for their future foraging behaviour. Some of the interviewed herders also said that they had developed strategies to overcome negative effects on behaviour. For example, three herders experienced less waiting behaviour when using roughages instead of pelleted feed. Two herders advised against feeding in enclosures because of the adverse behavioural effects. Five of the herders had observed less adverse behavioural effects when feeding reindeer on natural pasture, compared to when they were fed in enclosures. By choosing to feed the reindeer on pasture they could avoid that reindeer reduce their grazing or that mother-offspring bonds were deteriorated. Feeding reindeer on pasture may, thus, be a way to avoid or reduce the negative effects of feeding on reindeer foraging behaviour.

5.1.2 Body weight

In the interviews, some herders reported that feeding improved body weight or body condition in the following winter, while others reported that feeding resulted in lower body weights in the following winter. There were also some herders that had not observed any long-lasting effects of feeding on body condition. Similarly, our experimental results on the effects of feeding showed that the effects on body weight development the winter following feeding varied (paper III). One of the feeding groups (Ståkke A 2021) lost less weight over winter than the control group. This effect was, however, not found in the group fed the second year or in the other herding district (Sirges). The positive effect found in Ståkke may reflect that the previously fed animals were easier to introduce to feed again, resulting in higher energy intake compared to controls. This corresponds to herders' view that previously fed reindeer are easier to feed again (paper I).

It is well documented that winter feeding of reindeer generally has positive effects on body weight. Feeding adult females has secondary effects as it improves calves body weight at birth and in the following autumn, and thus, improves herd productivity (Rognmo *et al.* 1983; Eloranta & Nieminen 1986; Rönnegård *et al.* 2002). This may also have beneficial effects on future herd productivity, at least when feeding is provided on a regular basis, although it may compromise the reindeer's ability to find natural pasture when winter grazing conditions become difficult.

5.1.3 Risk of negative selection (paper I and III)

From a broader perspective, reindeer evolutionary adaptations such as habitat selection, foraging behaviour, and physiological adaptations are all consequences of natural selection favouring individuals that possess the ability to adapt to different environmental conditions (phenotypic plasticity). This includes behavioural plasticity acquired through learning, for example, when choosing the best habitat (Schlaepfer *et al.* 2002). Several of the interviewed herders raised concerns for a loss of natural selection pressure among the reindeer, and that feeding of reindeer may lead to loss of important genes needed to survive on natural pastures. The results from paper III, showing that fed reindeer are less likely to select lichen rich areas, confirm that reindeer grazing behaviour may be affected in a negative way, while their body weight seem less affected. Thus, regular feeding of reindeer every winter may lead to a biased selection of individuals that prefer feeding in front of natural pasture, while reducing the selection pressure on important traits needed for winter survival on natural pasture (Schmidt & Hoi 2002; Rodriguez-Hidalgo *et al.* 2010). A long-term effect of regular feeding may therefore be selection of animals with a tolerance for anthropogenic conditions (feeding) and animals acquiring new adaptions, such as searching for feed provided by herders rather than selection for animals possessing the skills to find natural forage (Shydlovskyy & Kuzyo 2016), another form of evolutionary trap. This is beneficial if feeding continues to be used on a regular basis, and to buffer density and climate effects, but risks reducing natural selection pressure and the phenotypic plasticity needed for animals to survive under natural conditions by buffering against environmental variation. This can create a transition to a system that is difficult to escape from (Landauer *et al.* 2021; Moen *et al.* 2022).

5.1.4 Degradation of important winter pasture (paper I)

One herder raised a concern around the possible deterioration of grazing grounds when feeding on pasture. This has also been raised by herders previously (Horstkotte *et al.* 2020) and increased local grazing pressure have been observed when feeding other deer species (van Beest *et al.* 2010a; Peterson & Messmer 2011). It has been shown that left-over feed, especially when using silage or hay, may change vegetation composition and reduce lichen abundance (Turunen *et al.* 2013). Thus, negative effects of increasing grazing pressure due to loss of pasture (Axelsson-Linkowski *et al.* 2020), may be further aggravated by winter feeding on pasture.

5.1.5 Reduced social cohesion and loss of tradition (paper I)

It was raised in the interviews that when reindeer are managed at feeding places and not mixed with other herds, collaboration and communication between reindeer herders disappear. Another aspect raised was that, although feeding may be economically profitable, it cannot be considered as traditional reindeer herding. Concerns were raised that systems relying on feeding may outcompete the more traditional, extensive nature-based herding system. However, it was also raised that, although not traditional herding, many herders feel they have no other option than to feed.

5.2 Methods for tracking and evaluating animal behaviour (paper II and III)

Estimations of habitat selection of *Rangifer* (reindeer and caribou) are often based on locational GPS data with no information on the underlying behavioural context. Different habitats may, however, serve to fulfil different life-history goals, and habitat selection of reindeer may therefore vary depending on behavioural priorities, such as foraging, giving birth to offspring or avoiding predators (Kumpula 2001; Sivertsen *et al.* 2016). Direct observational methods have been used in *Rangifer* (Falldorf 2013; Smith *et al.* 2023), but these are labour intensive, especially when monitoring free-ranging animals in remote areas. There may also be a risk of disturbance and bias due to the presence of humans (Brown *et al.* 2013). There has, however, not been any available validated methods to remotely classify reindeer behaviour to achieve continuous fine-scale behavioural data over longer periods of time (weeks or months).

In our studies of reindeer grazing behaviour, we used a combination of GPS (for habitat selection and movement pattern) and accelerometers (for fine-scale grazing behaviour). Being able to classify reindeer behaviour using accelerometers provides a useful tool to remotely monitor reindeer behaviour in areas where direct observations are difficult or impossible. Remote monitoring also allows us to continuously monitor reindeer behaviour over long time periods. This may help to explain the reason an individual selects a certain habitat, beyond just describing what habitats they have selected. For example, we found that feeding groups in Ståkke (A and B), one year after feeding were more likely to select home ranges with coniferous forest, where lichen abundance is usually higher, compared to the control group, which instead preferred deciduous forests and open lands. However, our analysis of behaviour showed that the fed group also spent more time wandering around in coniferous forests and less time grazing than the control group. With behavioural data it is possible to make inferences on how habitats are used. In this case, even though animals from the control group spend less time in coniferous forest, they seem to be more efficient at finding and utilizing the available pasture.

Previous studies have used a variety of approaches to deal with behavioural specific habitat selection models. In this thesis, a single behaviour over a ten second window at each four-hour GPS position was used, and the probability of reindeer behaviour at different habitat variables was estimated, but a longer proportion of time may also be used. Other studies have used separate step selection functions for different behaviours (Suraci *et al.* 2019; Karelus *et al.* 2020; Picardi *et al.* 2021), or integrated hidden Markov model-step selection function to allow behaviours to depend on habitat selection (Klappstein *et al.* 2022). To investigate habitat selection and behaviour of coyotes (*Canis latrans*), Ellington *et al.* (2020) used hidden Markov models to predict movement behavioural states based on step length and turning angles. In this thesis (paper II and III), a finer classification of behaviour is used providing a robust method to compare the groups using locational data at four-hour fixes. However, further development of methods, especially when using higher resolution locational data would provide a method allowing the consideration of the serial dependency of both behaviour and movement, and hence, a more detailed understanding of how reindeer use the habitats and why. By excluding behaviour in other contexts, where the aim is to make predictions rather than comparing groups, there may be a risk of incorrect inferences. For example, not including behaviour may lead to underestimation of the strength of selection (or avoidance) if only one behaviour is associated with a specific habitat type (Roever *et al.* 2013).

In summary, by considering behavioural data we can better understand the underlying process of habitat selection and predict how animals might respond to management changes such as feeding on natural grazing areas. There is an obvious potential to simultaneously utilize and analyse behaviour classified from accelerometers and GPS location data to improve the recognition of reindeer utilization of pastures, leading to better understanding of the extent and reasons habitats are used.

5.3 General considerations and limitations

Our results on the long-term effects of feeding show obvious variations. This is not surprising since the way reindeer react on feeding may be affected by several factors, such as the timing, regularity, type of feed, and feeding routines, as well as life history of reindeer, and the distribution, availability, and accessibility of winter pastures. I acknowledge that all prerequisites and experiences of feeding that exist within the reindeer herding district are not covered by this work. This is partly because of a limited number of herders (n = 19) representing a limited geographical range. More interviews, also covering Norway, would contribute to more insights on the effects of winter feeding of reindeer and the different strategies used by herders to avoid undesired effects.

6. Practical implications and future perspectives

Knowledge of the short- and long-term effects of feeding on reindeer can be useful for herders when evaluating if, when and how to feed their reindeer. Both the interviews and the experiments indicate that there is a risk that young reindeer being fed in enclosures during their first winter may reduce their ability to utilize natural pastures. The result of my work also shows that it might be better to plan for feeding on pasture compared to in enclosures, as reindeer foraging behaviour seems less affected when the animals have access to natural pasture. There is, however, reason to consider possible negative effects on the vegetation structure when feeding on pasture.

Reindeer herders are sometimes provided financial support for feeding from the industry to compensate for loss or fragmentation of grazing grounds due to industrial development. There is a risk that such compensations result in irreversible effects on the reindeer's ability to utilize natural pastures, thereby undermining future nature-based reindeer husbandry, even if land, for example, is restored after an encroachment. A major difference between Finland and Sweden is that in parts of Finland reindeer do not depend on natural winter pasture anymore; it seems difficult to return from this system. In other parts of Finland (as in most of Sweden), feeding is more restricted to winters with severe grazing conditions. Thus, in large parts of the reindeer husbandry area there is still a possibility to prevent a transition to a system that is difficult to escape from. Although winter feeding can be used to buffer loss of land and climate change, it may risk the sustainability of the current extensive herding systems. Furthermore, if pastures are not used, previous studies have raised the risk of losing grazing rights over land (Landauer *et al.* 2021; Moen *et al.* 2022).

One important follow-up to the experimental part of this thesis would be to compare grazing behaviour and fitness after feeding on pasture with that of reindeer kept on natural pasture the whole winter, without any access to feed. This would show whether it is the access to natural pasture that is the key for future foraging success or if it is the feeding itself that affects the reindeer's ability to manage only on natural pasture. However, observations from herders indicate that the foraging success of reindeer depends on a combination of the extent of feeding and access to natural pasture. Further interviews in herding districts with different prerequisites and feeding practices, together with long-term experimental studies, would contribute to a better understanding of the persistency and underlying reasons for the observed effects, and provide suggestions for how they may be avoided. By monitoring habitat selection and the fine-scale behaviour of reindeer that are left to rely solely on natural pastures after having been regularly fed for several years it would be possible to evaluate the reversibility of behavioural changes caused by feeding. Results from this thesis highlights the relevance of further investigations of the underlying reasons for altered habitat selection and grazing behaviour. It would be of particular interest to investigate the importance of mother-offspring bond and social learning on reindeer grazing behaviour.

In conclusion, the main challenges experienced by reindeer husbandry today are loss of land and climate change that forces herders to use feeding as a recurrent management action. Feeding is an efficient short-term strategy to buffer environmental variability but may risk the reindeer's future ability to sustain on natural forage. To retain appropriate foraging behaviour and adaptability to environmental variation, winter feeding of reindeer needs to be used with care and awareness of unintended long-term risks. This may be especially important for reindeer's ability to cope with the ongoing climate change and increased land use from other competing land uses.

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Populärvetenskaplig sammanfattning

Inom renskötseln i Sverige, Finland och Norge har vinterutfodring ökat på grund av konkurrerande markanvändning och klimatförändringar. De kortsiktiga effekterna av utfodring är ökad överlevnad, vikt och reproduktion. De långsiktiga effekterna av utfodring har inte undersökts tidigare, men det finns indikationer på att renar som blivit utfodrade när de är unga inte klarar sig lika bra på naturbete när de blir äldre. Om djuren blir sämre på att utnyttja naturbetet riskerar extensiva betessystem som renskötseln att förlora sin uthållighet. Målet med vår forskning har varit att förstå hur utfodring påverkar renarnas val av betesmarker, betesbeteende och vikt följande vinter efter utfodring.

I vårt projekt har vi undersökt de kort- och långsiktiga effekterna av vinterutfodring med hjälp av kunskap och erfarenheter från renskötare i Sverige, och även i Finland där utfodring varit praxis sedan 80-talet. Intervjuer genomfördes med totalt 19 renägare som utfodrat sina renar åtminstone vissa år under de senaste tio åren. För att undersöka de långsiktiga effekterna av utfodring genomförde vi även ett utfodringsförsök där syftet var att jämföra val av betesområden, betesbeteende och viktutveckling hos renar som utfodrats, respektive inte utfodrats. Två grupper av honkalvar från olika samebyar blev utfodrade i hägn under sin första levnadsvinter (vintern 2020). Lika många honkalvar valdes ut som kontrolldjur och fick gå kvar på bete med övriga renar. På grund av svåra vinterbetesförhållanden vintern 2020, blev de frigående renarna i kontrollgrupperna stödutfodrade på bete under en del av vintern. För att få en kontrollgrupp som enbart betat naturligt bete upprepades försöket i en av samebyarna vintern 2021. Även vintern 2021 blev vinterbetesförhållandena besvärliga och renarna stödutfodrades med ensilage under en månad. Kontrollgrupperna har alltså inte enbart betat naturligt bete. Försöksgrupperna gav därför främst svar på om det är någon skillnad i betesbeteende på renarna som utfodrats i hage eller fritt på bete i skogen.

Resultaten från studien visar att vinterutfodring riskerar att minska renarnas förmåga att utnyttja de naturliga betesresurserna. I intervjuerna med renägarna lyftes effekter relaterade till renens fysiska egenskaper och beteende. Erfarenheterna och de observerade effekterna skiljde sig mellan renägare, och det gjorde även uppfattningarna om huruvida effekterna var positiva eller negativa för renen. Resultaten från utfodringsförsöket visade att renarna som var utfodrade i hägn under sin första levnadsvinter var sämre på att välja lavrika betesmarker när de var på fritt bete följande vinter jämfört med renarna som var på naturbete under sin första levnadsvinter.

Kunskap om både kort- och långsiktiga effekter av utfodring på renar, och renarnas förmåga att nyttja naturbete, är viktig kunskap för renägare när de överväger om, när och hur de ska utfodra sina renar. Likaså, i beslut om markanvändningsfrågor är det viktigt att vara medveten om utfodringens effekter. När exempelvis exploateringar och bruk av mark i renskötselområdet riskerar att minska tillgången på betesmark, och förlorat bete behöver ersättas, bör andra alternativ än utfodring diskuteras, eftersom utfodring riskerar att ytterligare försämra möjligheterna att nyttja den betesmark som finns kvar.

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II

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Movement Ecology

METHODOLOGY **Open Access**

Identification of reindeer fine-scale foraging behaviour using tri-axial accelerometer data

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Abstract

Animal behavioural responses to the environment ultimately affect their survival. Monitoring animal fine-scale behaviour may improve understanding of animal functional response to the environment and provide an important indicator of the welfare of both wild and domesticated species. In this study, we illustrate the application of collar-attached acceleration sensors for investigating reindeer fine-scale behaviour. Using data from 19 reindeer, we tested the supervised machine learning algorithms Random forests, Support vector machines, and hidden Markov models to classify reindeer behaviour into seven classes: grazing, browsing low from shrubs or browsing high from trees, inactivity, walking, trotting, and other behaviours. We implemented leave-one-subject-out cross-validation to assess generalizable results on new individuals. Our main results illustrated that hidden Markov models were able to classify collar-attached accelerometer data into all our pre-defined behaviours of reindeer with reasonable accuracy while Random forests and Support vector machines were biased towards dominant classes. Random forests using 5-s windows had the highest overall accuracy (85%), while hidden Markov models were able to best predict individual behaviours and handle rare behaviours such as trotting and browsing high. We conclude that hidden Markov models provide a useful tool to remotely monitor reindeer and potentially other large herbivore species behaviour. These methods will allow us to quantify fine-scale behavioural processes in relation to environmental events.

Keywords: Activity recognition, Tri-axial accelerometer, Random forests, Support vector machines, Hidden Markov models, *Rangifer tarandus*

Introduction

Monitoring animal behaviour enables a better understanding of animal behavioural ecology in an evolutionary context e.g., inter- and intra-specific interactions such as competition and population dynamics [1]. Investigation of fine-scale animal behaviour can improve the understanding of animals' functional response to the environment [2] and provide an important indicator of animal welfare [3]. Initial responses to stressors related to changes in animal management or environment are often behavioural and can provide the first indications of stress or impaired health of an individual [4, 5]. Tri-axial acceleration sensors have been frequently used to study fine-scale animal behaviours in both wild [6, 7] and domesticated species [8, 9]. As an example, many studies have successfully been able to classify foraging behaviour in a range of species such as harbour seals (*Phoca vitulina*), arctic ground squirrels (*Urocitellus parryii*) and roe deer (*Capreolus capreolus*) [10–12]. However, each sensor type needs validation to confirm and quantify its capacity to accurately classify specific species behaviours.

Reindeer and caribou (*Rangifer tarandus*) is a key species inhabiting the circumpolar north [13]. With the rapid and extreme climate and environmental change going on in the arctic and subarctic regions, there is a need to understand how this affects reindeer behaviour. Reindeer are ruminants of an intermediate, opportunistic

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feeding type [14], mainly feeding on fresh herbal plants and graminoids and to some degree browsing shrubs and trees in summer and adapted to feed mainly on ground and arboreal lichens in winter [15]. Knowledge of reindeer fine-scale grazing could for example reveal reindeer's ability to suppress the increased growth of woody taxa in the arctic [16, 17] and their ability to search for lichens [15]. Domesticated reindeer in free-roaming systems provide an excellent opportunity to validate accelerometers for *Rangifer* taxon aligning specific behaviours to the accelerometer data. Acceleration sensors have previously been used on reindeer and caribou for estimation of activity patterns [18–20], but have not yet been validated for prediction of fine-scale foraging behaviour.

The acceleration (in m/s^2 or G-forces (g)) measured by a sensor in three dimensions (X, Y and Z) [Reviewed by: 21], may be separated into both static and dynamic acceleration [22, 23]. Animal body orientation may be registered using the static acceleration caused by gravitational force acting on the accelerometers [24, 25]. Removing the gravitational component, the dynamic acceleration is revealed. This makes it possible to identify patterns in the acceleration waveform that corresponds to an observed behaviour [26, 27].

Supervised machine learning (ML) algorithms are effective ways to classify features of animal acceleration data into pre-defined behavioural categories [28–32]. To train and validate such algorithms, movement data is collected using acceleration sensors on the animal at the same time as the animal behaviour is recorded through direct observation [33, 34], or with a camera [35]. Animal behaviour is classified into different behavioural categories and then accelerometer data is annotated with the recorded behavioural categories [36, 37]. The raw acceleration annotated with the corresponding behaviour is normally pre-processed (using running means [38, 39] or low- and high pass filters [22, 40]) to reduce noise or to separate static and dynamic acceleration. Then the data is segmented into windows, followed by extraction of characteristics of acceleration data (features), selection of features, and modelling [41]. The features and their corresponding classified behaviours are used to train the models, which learn to distinguish between the classified behaviours given the differences in the acceleration data [41]. Once a model is trained, it can be used on new data (e.g., new individuals) to quantify different behaviours performed by the animal. This enables fine-scale behavioural studies over long time periods under conditions where direct observations are difficult due to constraints such as visibility or geographic scale [20, 21, 42].

Generally, the performance of behaviour classification relies on a fixed placement and orientation of the sensors [43, 44]. This can be achieved using harnesses, halters, or glue-on tags [37, 45–47]. However, often sensors are attached to a collar around the neck of the animal [8, 48], and then it is likely that the sensor will change its position and orientation relative to the animal's body orientation. This may cause significant errors and reduced recognition rate [49]. The variability caused by displacement of the sensors may be accounted for by using robust features derived from the raw sensor output. For example, the net acceleration computed from all three axes (the Euclidean norm of the acceleration vector) is less sensitive to changes in sensor orientation or placement [50, 51]. Alternatively, information about angles around X (roll) and Y (pitch) using a gyroscope or magnetometer can be used to correct the accelerometer sensor displacements using rotation matrices [52, 53]. Such correction has to our knowledge seldom been applied on data collected with collar-attached sensors.

We equipped reindeer with collar-attached accelerometers and registered their behaviour using video cameras to find the best model predicting reindeer foraging behaviour, such as grazing on ground lichens and browsing on shrubs and arboreal lichens in trees. The main objective of our study was to develop and validate a method for classifying foraging behaviour of reindeer using tri-axial acceleration sensors. We evaluated Random forests (RF), Support vector machines (SVM) and hidden Markov models (HMM) to find the best model to classify acceleration data into pre-defined behavioural categories.

Methods

Study area, animals and management

In this study, we simultaneously collected video and acceleration data from in total 19 semi-domesticated female reindeer in Ståkke and Sirges Sami reindeer herding communities in northern Sweden. Initially, ten individuals per herding community were randomly selected from two groups of 40 animals being supplementary fed in a feeding experiment conducted in each community. In Sirges, the ten reindeer (nine-month-old) were kept in a 300 m^2 enclosure from 27 February to 2 March 2020 (Fig. 1). In Ståkke, the ten reindeer (two two-year-old and eight nine-month-old) were kept in a 150 m^2 enclosure from 4 to 9 March 2020; one of the nine-month-old individuals was difficult to capture for collar fitting and was excluded from sensor attachment. In both enclosures, reindeer lichens (*Cladonia rangiferina* and *Cladonia arbuscula)* and commercially available pelleted reindeer feed (Renfor nära ®, Lantmännen, Sweden) were dug down under the snow to encourage natural grazing and digging behaviour. In addition, small trees covered with arboreal lichens (*Bryoria fuscescens*) were placed in the enclosures to encourage browsing behaviour.

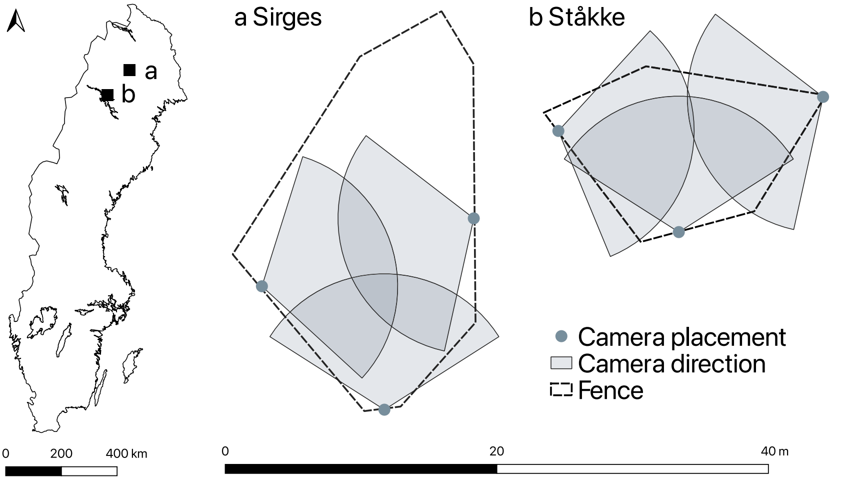

Fig. 1 Enclosures with placement of cameras used for video recordings of ground-truth behaviour of ten and nine reindeer, respectively, fitted with acceleration sensors in (**a**) Sirges reindeer herding community and (**b**) in Ståkke reindeer herding community, both in northern Sweden

Video recordings

Three cameras (Axis Communications, 2025-LE Network Camera) were used and placed to cover the whole enclosure and enable video recordings of the animals from different angles. The reindeer were video recorded from 6 AM until 6 PM. In total, we generated 50 h daytime video (15 frames per second) on each individual.

Accelerometer data

We used a three-axial accelerometer (Axy-4; 9 × 15 × 2 mm; 0.7 g) including a temperature sensor [54] positioned on the ventral-right side of the neck attached to a GPS-collar (Pellego) [55], with a total weight of 330 g. See Additional file 2: Fig. A1, illustrating the attachment and directions of the accelerometer. We choose to configure the accelerometers to a sampling rate of 10 Hz with 8-bit resolution at ± 8 g. Sampling rate of temperature was set to 0.2 Hz. At these settings, the sensor could store four months of data. Sampling rate was chosen according to Nyquist's criterion i.e., that sampling rate should be at least twice the highest frequency component of the signal [56, 57]. Reindeer activities, like other large herbivores, were expected to involve frequencies of 5 Hz [58, 59]. Thus, sampling frequency of a minimum of 10 Hz was required to detect motions. The same computer was used for calibration and time synchronization of the accelerometer internal clock. All accelerometers were shaken in front of all cameras prior to attachment to acquire a reference for time synchronization [60]. Collars were attached to mimic the conditions surveying freely ranging reindeer, when the size of the collar needs to allow for growth of the neck, as these reindeer were still in their growth stage. Acceleration data was retrieved using Axy Manager Version 1.8.3.0 [60].

Behavioural observations

An ethogram was created after consulting the reindeer herders about typical reindeer behaviours and two hours of behavioural observations in the enclosures (Table 1). In total, 39 h of acceleration data from 19 individuals were annotated into 17 behavioural categories. On an average two hours of annotations were performed for each individual from the first day of video recordings. Behaviours were first annotated into the main categories: browsing high, browsing low, grazing, digging, lying, standing, moving, agonistic behaviour, scratching head against tree, other and missing data. If a behaviour did not fit the listed behaviours or if an animal expressed more than one of the listed behaviours at the same time, we annotate it as "other". The latter occurred on a few occasions when one reindeer was digging and grazing at the same time. Total number of recorded behaviours for each individual are presented in Additional file 1: Table A2. Video recordings were annotated using BORIS Version 7.9.8 [61]. Reindeer have a polycyclic activity pattern with all typical behaviours occurring in bursts both day and night [62, 63] throughout the year [64]. Thus, we

Table 1 Main behavioural categories of 19 video recorded reindeer attached with tri-axial accelerometers used for model training and corresponding subgroups (behavioural categories) included within each main behaviour

Behaviour	General description	Subgroup	Description
Grazing	Lower the head to the ground and foraging from the ground. Mouth close to the ground		From ground while standing still or taking one or two steps without moving head position or while walking slowly and foraging from the ground. Mouth positioned close to the ground
Browsing high	Moving lips towards a branch in a tree or a high shrub		Standing on all four legs, stretching the neck upwards, head level above shoulder height (minimum 45º head angle) or standing on the hind legs, stretching the neck upwards
Browsing low	Moving lips towards a low branch in a tree or a low shrub		Standing on all four legs, moving the head forward or downwards without mouth touching the ground
Inactivity (lying)	Belly or side on the ground with folded or extended legs and head in different positions	Resting	Folded legs with head raised from the ground facing forward or with the neck bent on the side
		Sleeping	Head close to ground (on ground or against body) in the same position
		Ruminating	Lying with legs folded and belly on the ground, head raised from the ground facing forward or with the neck bent on the side while chewing
		Grooming[a]	Lying with legs folded and belly on the ground, head moving against legs or body
Inactivity (standing)	Standing on all four legs without moving forward without chewing		
Walking	Moving forward by alternately moving the legs from one point to another		Lifting all four legs in a symmetric movement and moving forward, with mouth up from the ground (not grazing)
Trotting	Moving forward by alternately moving the legs from one point to another		Simultaneous movement of hoof paired two by two diagonally (trotting) or three-beat gait faster than the average trot (running)
Digging [a]	Standing and repetitively scratching on ground with one front leg at least two times in a row		
Agonistic behaviour [a]	Pushing away an individual or being pushed away by another individual		
Scratching head against tree [a]	Repeated head movement against branches on trees without having contact with the lips on branch		
Missing data [a]	Animal out of sight		
Other [a]	Undefined		

[a] Behaviours classified as "other".

expect to cover the most common behaviours occurring in night-time from the daytime recordings.

Behaviours used in model training

Closely related behaviours with high similarity in acceleration waveforms were merged before model training i.e., grazing behaviour included grazing, grazing from a hole, and grazing while walking, and inactivity included sleeping, ruminating, standing, and resting. Running was merged with trotting due to low occurrence. To quantify reindeer foraging behaviour, a total of seven remaining behavioural categories were used for model training: grazing, browsing low, browsing high, inactivity, walking, trotting, and other behaviours. Behaviours such as walking in rough terrain were not observed in the video recordings and were therefore not included in the training and validation.

Analyses of accelerometer data

Raw acceleration data (X, Y and Z) were first smoothed using a running mean of five seconds removing most of the static acceleration (gravitational component of acceleration) from the dynamic acceleration [e.g., 12, 23, 27]. The GPS device (175 g) acted as a counterweight to avoid unwanted collar rotations around the neck. However, this happened to some extent, and when reindeer are free-ranging the accelerometers will also be prone to unwanted rotations. From the estimated static acceleration, the angles around X (roll) and Y (pitch) were calculated [65; Table 2] to estimate accelerometer orientation. To validate our estimated angles, our filtering method and equations for pitch and roll were compared with true angles derived from a dataset collected with IMU sensors (accelerometer and gyroscope; Byström, unpublished data). To adjust for the position of the accelerometer when a collar had rotated, a rotation matrix around the X-axis was calculated to transform the sensor's measurements into fixed measures based on the estimated angle (α) around the X-axis (Table 2). The ℓ^2-norm of raw accelerometer axes was calculated to assess an orientation-independent index of acceleration magnitude [49, 66].

Acceleration data were then segmented into 2-, 3-, and 5-s windows using fixed-size non-overlapping sliding windows [67]. As a result, behaviours occurring during short timespans (< 2 s) were dropped from the data after segmentation. See Additional file 1: Table A3–A5, for final number of windows for each behaviour and individual when using 2-, 3-, and 5-s windows, respectively. Summary statistics were calculated from each segment of data resulting in 50 features. To avoid overfitting and computational load, we removed highly correlated

Table 2 Processing (A) performed on raw acceleration data after applying a sliding window of five seconds prior to segmentation and summary statistics (features) calculated (B) for each window (two-, three-, and five-second windows) after segmentation

A	Data processing	Term	Equation	Description
	Static acceleration	sX, sY, sZ	$sX_i = \frac{1}{51}\sum_{i-25}^{i+25} X_i$	Gravitational component of acceleration (9.81 m/s^2 = 1 g) caused by gravitational force acting on the accelerometers [16, 17, 35]
	Dynamic acceleration	dX, dY, dZ	$dX_i = \lvert X_i - sX_i \rvert$	Dynamic acceleration measures acceleration caused by animal movements where the gravitational component is removed [e.g., 12, 23, 27]
	Roll (φ)	roll	$\mathrm{atan2}(sY, sZ)$	Rotation around the X-axis (roll) given in Euler angles ranging between ± π radian (equivalent to ± 180º) using 2-argument arctangent function, implemented as atan2 in R
	Pitch (θ)	pitch	$-\mathrm{atan}\left(\frac{sX}{\sqrt{sY^2+sZ^2}}\right)$	Rotation around the Y-axis (pitch) given in Euler angles ranging between ± π/2 rad (equivalent to ± 90º) using arctangent function, implemented as atan in R
	ℓ^2-norm of raw accelerometer axes	Norm	$\sqrt{X^2 + Y^2 + Z^2}$	Orientation-independent measure of acceleration magnitude [42, 62]
	Rotation matrix	$R_x(\varphi)$	$\begin{bmatrix} 1 & 0 & 0 \\ 0 & \cos\varphi & -\sin\varphi \\ 0 & \sin\varphi & \cos\varphi \end{bmatrix}$	Rotation matrix around X-axis to adjust for rotations around the neck

B	Summary statistics	Term	Description
	Mean	mean	Mean value for each axis in each window
	Minimum	min	Minimum value for each axis in each window
	Maximum	max	Maximum value for each axis in each window
	Median	m	Median for each axis in each window
	Interquartile range	IQR	Third quantile (Q3) subtracted by the first quantile (Q1) for each axis in each window
	Standard deviation	sd	Standard deviation for each axis in each window

features and used 12 features for model training and validation: m_roll, IQR_roll, mean_sX, sd_sX, mean_dX, max_dX, m_Y, IQR_Y, min_sY, max_sY, sd_dZ and mean_dZ, with m_roll being the combination of median (m, Table 2B) and Roll (roll, Table 2A) and so forth. To further decrease predictor variables to avoid overfitting, we selected the most influential variables for classification using forward feature selection for each window size implemented with the "CAST"-package [68]. Distribution of annotated data using three features (mean_sX, IQR_Y, and sd_dZ) and 2 s windows are shown in Additional file 2: Fig. A2. All data processing and analyses were performed using R version 4.0.3 [69] and RStudio version 1.3.1093 [70]. In this study, time-domain metrics were considered.

Random forests

Random forests (RF) is a classification method that combines an ensemble of classification trees [71, 72]. Each classification tree defines decision rules to partition the dataset into subsamples with similar properties. A RF randomly selects observations and features to build multiple classification trees from a dataset. The predictions of each individual tree are averaged to give an overall classification decision [71]. Thus, the RF corrects for overfitting. In addition, RF is robust with respect to noise [71]. We initially constructed 500 trees using the "randomForest"-package [73], and used the "caret"-package [74] to tune the number of variables chosen at each iteration.

Support vector machines

Support vector machines (SVM) is a supervised machine learning algorithm which finds optimal separating hyperplanes (decision boundaries) that separate the data points into the different classes. We implemented multiclass SVM using the "caret"-package [74] and radial kernel function using the "kernlab"-package [75]. Tuning was performed using the "caret"-package [74] to find the optimal regularization parameter C and kernels smoothing parameter gamma.

Hidden Markov models

An hidden Markov model (HMM) is a stochastic time-series model involving an observable state-dependent process and an underlying, unobservable state process. The goal is to learn about the hidden states (in our case behaviours) by observing the state-dependent process [acceleration metrics; 26]. The hidden states are assumed to follow a first-order Markov chain, and the probability distribution of an observation at time t is assumed to depend only on the state at time t, independently of all other observations and states [76, 77]. Thus, HMM takes into account the serial dependence between observed behaviours, unlike RF and SVM.

To fit an HMM, we need to specify the number of states and the form of the observation distributions. In our case, the number of states is the number of pre-specified behaviours, and we used state-dependent multivariate normal distributions for the observations. The transition probability matrix of the Markov chain and the parameters of the observation distributions can then be estimated by maximum likelihood, using the Forward Algorithm to evaluate the likelihood efficiently. Given a fitted HMM, the Viterbi algorithm can be used to reconstruct the most likely states (behaviours) corresponding to the observations. See for example Leos-Barajas et al. [26].

Training and validation

To account for variability among individuals used in the training and to make generic predictions on new (unseen) individuals, we used leave-one-subject-out cross-validation for model evaluation. This ensured that an individual never occurred in the training and validation dataset at the same time for each iteration of k. Thus, data from one individual was always left out in each fold and was utilized as a test set. This was repeated until data from all individuals were classified. To retain the naturally unbalanced behaviours across individuals, the dataset was not balanced across individuals, and we used an unequal number of behavioural classes from each individual. Confusion matrices $[n_{ij}]$ were used to summarize model performances where i, j denotes the number of observations belonging to ground-truth behaviour i that were predicted by the model to be behaviour j (see calculations in Additional file 1: Table A1). We computed behaviour-specific sensitivity, precision and accuracy and overall accuracy across behaviours. Cross-validation was implemented using the "CAST"-package [68] for RF and SVM.

Results

Model development and evaluation

Random forests was tuned for the optimal number of variables chosen at each iteration (2 s windows: mtry = 2, 3 s windows: mtry = 3, and 5 s windows: mtry = 4) and the number of trees was set to 50 (ntrees = 50, Additional file 2: Fig. A3). Future feature selection using RF to find the most important variables out of twelve resulted in eight predictor variables used for 2 s windows (mean_sX, sd_dZ, IQR_Y, IQR_roll, max_dX, min_sY, sd_sX and m_Y), nine predictor variables used 3 s windows (mean_sX, sd_dZ, IQR_Y, IQR_roll, max_dX, min_sY, sd_sX, mean_dX and m_Y), and seven predictor variables used for 5 s windows (mean_sX, sd_dZ, IQR_Y, IQR_roll, max_dX, sd_sX and min_sY). This subset of variables was later used for SVM and HMM. For RF, overall accuracy was 100% (Kappa = 1) in the training datasets for all sliding windows (2 s, 3 s and 5 s). Model overfitting was checked for RF by reducing number of trees, and the result did not differ (qualitatively) with number of trees as small as 50. Regions of tuning parameter gamma (γ) and optimal regularization parameter C (default values for C were 0.25, 0.5, 1, 2, 4) passed from training were used for SVM (2 s windows: $\gamma = 0.225$, C = 1, 3 s windows: $\gamma = 0.217$, C = 1, and 5 s windows: $\gamma = 0.308$, C = 0.5). Further tuning of hyperparameters for SVM provided better overall accuracy but increased bias towards dominant classes and were not able to classify undersampled behaviours. Similarly, bias towards dominant classes increased with increased window size (Table 3). In the training dataset for SVM, overall accuracy and Kappa was 86% and 79% for 2 s windows, 89% and 83% for 3 s windows and 88% and 81% for 5 s windows, respectively. Training set accuracy and Kappa for HMM was 82% and 73% for 2 s windows, 82% and 73% for 3 s windows and 80% and 68% for 5 s windows, respectively.

Model performance

Grazing (accuracy ≥ 88%) and inactivity (accuracy ≥ 90%) were easily identified by all three models. However, for browsing low, the models did not discriminate the behaviours to the same extent (Table 3). Most confusion was found between browsing low and browsing high for all models. For the three models applied, the highest overall accuracy (85%) was found for RF using 5 s windows (Table 3). Increasing window size (from 2 to 5 s window segmentation) improved overall accuracy of RF and SVM whereas overall accuracy of HMM increased with smaller window size. The best performing HMM (using 2 s windows) had better performance across all individual behaviours and was able to classify browsing high (Table 3). Similarly, HMM had better performance of trotting compared to the best performing RF and SVM (Table 3). Confusion matrices and F1-scores are provided in Additional file 1 (RF: Table A6, SVM: Table A7, HMM: Table A8, F1-scores: Table A9).

Discussion

We illustrate application of collar-attached acceleration sensors to quantify reindeer fine-scale behaviour. Using data from 19 reindeer, we tested the supervised machine learning algorithms RF, SVM, and HMM to find the best model classifying reindeer behaviour. Overall, HMM performed best in predicting individual and rare behaviours, while RF and SVM were biased towards dominant classes and less able to handle rare behaviours such as trotting and browsing high.

Predicting grazing, accuracy varied between 88% (HMM) and 93% (RF and SVM). Our results were similar to Alvarenga et al. [78] and Barwick et al. [79] classifying five sheep behaviours using halter and collar-attached accelerometers, respectively. Other studies have reported prediction accuracy and sensitivity for feeding behaviours from 77% to 96% and 75% to 100%, respectively [29, 80–82]. In these studies, sheep and cow behaviour were classified and the predictive performance tended to increase with a lower number of behavioural classes included in

Table 3 Performance statistics (%) of Random forests (RF), Support vector machines (SVM) and Hidden-Markov models (HMM) using time-domain features in 2-, 3- and 5-s windows (2 s, 3 s and 5 s)

		Grazing			Browsing high			Browsing low			Inactivity			Walking			Trotting			Other				
	Window size	**Se**	**Pr**	**Ac**	**Se**	**Pr**	**Ac**	**Se**	**Pr**	**Ac**	**Se**	**Pr**	**Ac**	**Se**	**Pr**	**Ac**	**Se**	**Pr**	**Ac**	**Se**	**Pr**	**Ac**	**K**	**Overall accuracy**
RF	2 s	**89**	**86**	**93**	25	56	62	68	64	79	**94**	92	92	45	53	72	**57**	**61**	**78**	18	51	59	72	82
	3 s	**89**	**86**	**93**	**28**	**57**	**64**	73	70	82	**94**	92	93	**49**	**57**	73	53	58	76	**21**	**61**	**60**	75	84
	5 s	86	85	92	25	49	62	**77**	**74**	**84**	**94**	**93**	**93**	49	52	**74**	34	34	67	19	50	59	**76**	**85**
SVM	2 s	89	84	93	**14**	**50**	**57**	66	65	79	**94**	91	92	47	56	73	**33**	55	**66**	**21**	39	**60**	72	82
	3 s	**89**	**86**	**93**	9	36	54	72	68	81	**94**	**92**	**93**	**48**	**59**	**73**	22	56	61	19	43	59	74	83
	5 s	86	85	92	0	0	50	**76**	**70**	**83**	**94**	**92**	**93**	43	58	71	0	**67**	52	19	**56**	59	**75**	**84**
HMM	*2 s*	***85***	***88***	***91***	***79***	***29***	***89***	*53*	*80*	*75*	***95***	***90***	***92***	***75***	***51***	***86***	***78***	***53***	***89***	***40***	***44***	***69***	***72***	***82***
	3 s	**85**	**88**	**91**	68	26	83	**54**	**80**	**75**	**95**	90	92	69	39	82	79	40	89	36	40	67	**72**	**82**
	5 s	78	86	88	24	20	62	54	74	74	**95**	88	90	65	38	81	24	20	62	29	25	63	66	78

Behaviour-specific metrics are given as sensitivity (Se), precision (Pr), accuracy (Ac), and overall model performance are presented as overall accuracy and Cohen's kappa (K)

Behaviours other than grazing, browsing high, browsing low, inactivity, walking, and trotting are included as "other" in model training

Highest behaviour-specific metrics for each model are presented in bold and the overall best performing model is highlighted in italic the models [29, 80–82]. Similarly, Turner et al. [83] found a reduction in overall accuracy when more behavioural classes of sheep behaviour were included in the models using RF, SVM and Deep learning techniques. For example, RF performed best using three behavioural classes with an overall accuracy of 83%, whereas overall accuracy dropped to a maximum of 72.4% for a RF model when using nine classes. Support vector machines achieved 77% overall accuracy using three behavioural classes but dropped to 58% when using nine behavioural classes [83]. In our models, seven behavioural classes were used of which feeding was separated into three subgroups (grazing and browsing high or low). Our results also indicated that when behaviour was classified as browsing high, this was generally correct, but that actual browsing high behaviour was often classified as browsing low (see confusion matrices in Additional file 1, Table A6–A8). This most likely depended on the two behaviours only being separated by the change in angle of the head. The accelerometer was attached to the neck, and the change of the neck angle when browsing high or low might not have been large enough to separate the acceleration pattern for the two behaviours. Thus, there was not a clear difference in acceleration between the two behaviours and the sensitivity for browsing high was lower than for other behaviours only reaching 79% (HMM, 2 s windows), 28% (RF, 3 s windows) and 14% (SVM, 2 s windows). In our dataset, browsing high was also a relatively rare behaviour only expressed by a few individuals. More annotations on rare behaviours could further have improved our classification accuracy, at least for those with distinct feature characteristics. For example, by visualizing the distribution using three statistical features (Additional file 2: Fig. A2) for our seven behavioural classes, it seems like browsing high has a distinct cluster. Nevertheless, RF and SVM failed to predict browsing high.

Annotating behavioural data to the accelerometer data is time-consuming, why a common challenge is to produce a dataset with a sufficient number of observations for each behaviour across individuals. Datasets with too few ground-truth observations are prone to overfitting. In addition, without enough individuals, it may not be possible to generate generalizable results on new individuals. To overcome this problem overlapping windows may be used when segmenting the data. The common data are shared across successive time windows, usually with 50% overlap between the two windows [84]. Using 50% overlap compared to no overlap may increase classification performance significantly [85]. Bersch et al. [67] compared classification performance in human activity recognition data using 0%, 25%, 50%, 75%, and 90% overlap and found a higher accuracy with increased overlap compared to no overlap. Riaboff et al. [86] found that the best prediction performance of cow behaviour was achieved when using 90% overlap. However, there is a risk of information leakage resulting in over-optimistic results when data is shared across adjacent windows [87]. With our large dataset (90,052 labelled samples for one-second windows for seven behavioural categories) it was not necessary with overlapping windows for segmentation. Information leakage could therefore be avoided in our model training.

It is important that an animal's movement pattern is observed over an optimal time window to be able to identify different behaviours. Hence, window size may have a significant impact on the prediction results [67]. In our evaluation of window size on model performance, we found that RF and SVM had slightly higher performance accuracies at longer window sizes, while HMM had higher performance at shorter window sizes (Table 3). Hidden Markov models consider the serial dependence between behaviours and will most likely gain more information from using shorter time windows. Thus, optimal window size depends on the model selected to classify behaviour.

We had one collar rotating clearly around the neck of the animal. If collar rotations are not accounted for this may result in significant errors when using collar-attached acceleration sensors [49]. One way of dealing with collar rotations is to use orientation-independent features such as the total magnitude of all axes [49]. There may be a risk of decreased recognition rates due to loss of dimensionality when using orientation-independent features [43], but Kamminga et al. [49] and Barker et al. [50] used orientation-independent features and found that feeding behaviour of goat and cow was predicted with an accuracy of 83% and 86%, respectively. Alternatively, rotation matrices can be used for correcting sensor rotations [52]. To reduce the effect of collar rotations, we transformed the data along the X-axis using rotation matrices enabling better discrimination between the behaviours. Thus, total magnitude of axes were removed to avoid over-fitting. Using more individuals with rotating collars and combining magnetometers and/or gyroscopes to provide the true angles, would provide further insight into the impact of using rotation matrices on model performance. Increasing the number of sensor outputs, however, shortens battery life and capacity of the sensor.

Cross-validation is necessary to evaluate the reliability of a model [88, 89]. In many studies, cross-validation is performed using random K-fold cross-validation [e.g., 29, 35], or leave-one-out cross-validation [90] when data is randomly split across individuals into training and validation data. Using these methods, it is likely that observations from all individuals are present in each fold and the model is both trained and validated on all individuals. Random K-fold cross-validation may be suitable for models that will be used to monitor the same group of individuals again. However, this tends to show over-optimistic results and may not assess a generic performance on new individuals [89]. Other studies have used a single random split of training and validation data [59, 91]. Model performance in these studies with experimental settings when animals are fenced is high (overall accuracy ranging from 95 to 98%), but may not be generalizable and good enough to be used on data from new individuals.

It may be challenging to label behaviours on enough individuals to capture the individual variation in a population, especially in wild and free-ranging species. In our study, we strived for a model that would be applicable when reindeer are free-ranging and able to predict behaviour of new individuals. Therefore, leave-one-ID-out cross-validation was used. In other words, we made sure that each fold of observations from one individual was not present in both training and validation data. Leave-one-ID-out cross-validation may increase the variance of the results and significantly reduce prediction accuracy by 40 percent due to the individual variation [89, 92]. However, it will evaluate the generic performance of the models as it includes data from unseen objects, compared to traditional K-fold cross-validation [89, 93]. To our knowledge, this is rarely implemented for classification models on animal-borne accelerometer sensors but has been used for behaviour classification of e.g., meerkat (*Suricata suricatta*), sheep and cattle [80, 94, 95]. A reason for this could be the time-consuming work of compiling a large enough dataset to perform leave-on-ID-out cross-validation as in Riaboff et al. [96].

Many machine learning algorithms are sensitive to unbalanced classes decreasing overall performance [97–99]. Therefore, stratified cross-validation to handle unbalanced datasets is sometimes used [35, 100] and is recommended by Riaboff et al. [101]. In our data, behaviours were unbalanced because some activities were not equally frequently performed across individuals. However, to retain the naturally unbalanced frequencies, behaviours were not stratified. Hidden Markov models had lower overall performance compared to RF and SVM but were able to better predict rare classes and thus under-sampled behaviours (browsing high and trotting). Compared to Smith et al. [94] implementing leave-one-subject out cross-validation using SVM for activity classification of six cow behaviours, our F-scores were higher (Additional file 1, Table A9). Other techniques during data collection could be considered, such as active learning to deal with naturally unbalanced datasets [102]. It is also possible to use a refined systematic approach during the labelling process to obtain more balanced datasets, by collecting just enough observations for each class to avoid under- and oversampling.

Our methods enabled generation of detailed classification of activity data from collar-attached acceleration sensors. Being able to document reindeer fine-scale foraging patterns have a wide range of applications. For example, in management of reindeer information on how reindeer behaviour is affected by management actions, extreme weather events, human presence, changes in habitat structure and land fragmentation are essential. As an example, supplementary feeding has become more common due to competing land use and climate change [103, 104]. Supplementary feeding might be beneficial in the short term but might risk the reindeer's future ability to search for natural fodder such as ground lichens under the snow, especially under extreme conditions. Warm and wet weather in winter increase icing on the ground and in the snow, restricting access to ground lichens [105]. Such conditions may try reindeer foraging skills searching, finding, and digging for lichens under the snow. In addition, from a climate change perspective with increasing shrubification of the arctic tundra, our method could be vital to quantify reindeer foraging intensity on shrubs and trees and its ability to suppress this vegetative greening [17, 106].

In conclusion, classification of remote fine-scale foraging behaviours from accelerometer data provides means to answer a wide range of questions related to animal behaviour, physiology, and ecology. Our results demonstrate that behaviours can be distinguished by isolated sequences of accelerometer data applying time domain features using a sampling frequency of 10 Hz. Hidden Markov models was able to best predict behaviours based on naturally unbalanced data and thus provide a useful tool to remotely monitor reindeer behaviour and to quantify how foraging behaviour of reindeer is affected by winter feeding.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s40462-022-00339-0.

Additional file 1. Contains supplementary tables including equations for performance statistics, number of recorded behaviours for each individual, confusion matrices, and F1-scores.

Additional file 2. Contains supplementary figures including illustrations of sensor attachment, data distribution using three statistical features, and out-of-bag error of random forests.

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Author contributions
HR and AS conceived and designed the experiments. HR analysed the data with input from MA and PGB. HR wrote the manuscript with input from all authors. AS received grants for the experiment. All authors approved the final version of the manuscript.

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Availability of data and materials
Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.8sf7m0cs7.

Declarations

Ethics approval and consent to participate
All applicable institutional and/or national guidelines for the care and use of animals were followed. The methods used in this study comply with the current laws of Sweden. We obtained ethical permissions from the Umeå Board for Laboratory animals (Dnr A 40–2019 and Dnr 5.2.18–13750/2019).

Consent for publication
Not applicable.

Competing interests
The authors declare that they have no conflict of interest.

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This thesis investigates the short- and long-term effects of winter feeding on reindeer with focus on habitat selection and future foraging behaviour. The results indicate that, as an unintended effect, feeding may have negative effects on reindeer's ability to use the natural pastures.

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