# 3 Reindeer behavioural ecology and use of pastures in pastoral livelihoods

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## Seasonality, reproductive phenology and social organization

Reindeer, and in turn reindeer husbandry, are adapted to the arctic/sub-arctic environment where seasonal variation typically provides abundant food in summer, but there is a food shortage in winter (Kerby & Post 2013). Reindeer accumulate body reserves (fat and muscle tissue) in summer and use these reserves during winter (Klein 1986). As a rule of thumb, food abundance in summer determines the growth and size of animals, while food abundance in winter determines density and fecundity (Klein 1965).

Seasonality of reproduction commonly depends on seasonality in the environment, while the synchrony of parturition may be linked to the risk of predation (Kerby and Post 2013). Reindeer parturition starts in early May and may continue until early June (Figure 3.1). The herders' decision about when to start migration is based on the reindeer's willingness to move, snow conditions and grazing conditions in the calving area.

Before calving, the pregnant females separate from the rest of the herd and last year's calf is usually pushed away from its mother (Espmark 1971; Kojola 1993). At parturition, the female also keeps away from other females, and usually spends some days alone with her new calf; this is believed to strengthen the bond between mother and young (Espmark 1971). The calf follows the mother, often during the whole of the first year of life and learns how to find forage in winter (Kojola 1993). Reindeer seem to invest more in female calves as they follow the mother until the next parturition, while male calves are pushed away earlier (Kojola 1993).

During the post-calving period, females with their calves (and male reindeer, separately) merge to form large herds to escape insects as the likelihood of being harassed is lower in groups (Downes et al. 1986; Mörschel & Klein 1997; Fauchald et al. 2007). The gregarious behaviour is most evident when only mosquitoes and species of Simulidae are present, while the reindeer-specific parasites warble and nose bot flies seem to make the reindeer form smaller herds or spread out more (Downes et al. 1986; Mörschel & Klein 1997; Skarin et al. 2004). The tundra-dwelling reindeer ecotypes exhibit more gregarious

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behaviour than forest-dwelling ecotypes, which tend to form smaller herds (Helle & Aspi 1984). When the calves are older and stronger, the herders gather the herds for calf marking. This usually takes place from the end of June up to the beginning of August, but in some areas, calf marking takes place in mid-September and some remaining calves are even marked in the following winter.

In late summer, when insect harassment has eased, the herd expands over larger areas. Then in early autumn, the bulls prepare for the rutting season and start to gather harems. The rut starts in late September and usually lasts until mid-October. During the rut males loose bodyweight and afterwards they drop their antlers. Bull slaughter usually takes place just before the rut.

Migration to winter pasture takes place in autumn. Before migration, the herds are gathered for slaughter and separation of the remaining herd into winter grazing groups. The reindeer either move to the winter pastures on foot (by herding or by letting them move freely) or on trucks depending on connectivity between the summer and winter pastures. In southern and central parts of the herding area in Finland, most reindeer are kept in enclosures for supplementary winter feeding (Chapter 12).

Females keep their antlers throughout the winter and defend feeding craters for themselves and their calves (Espmark 1964). Large adult females with big antlers have the most dominant position in the herd. The social interactions

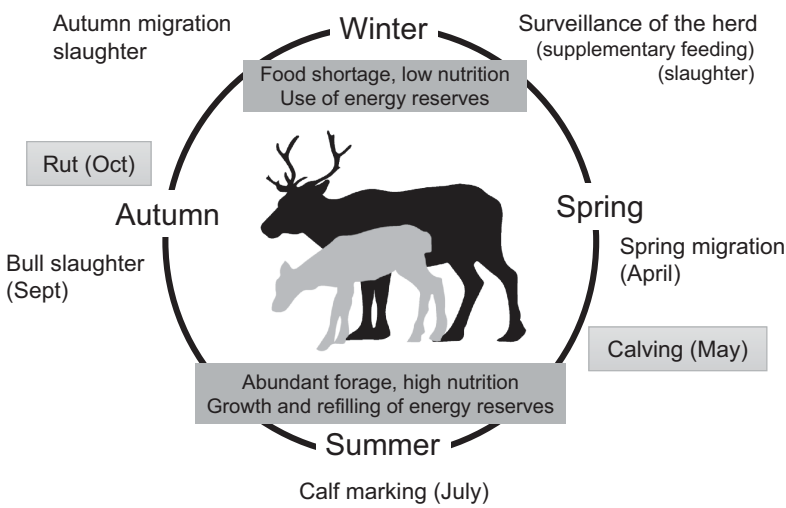


*Figure 3.1* The annual cycle of reindeer husbandry reflects the animals' life history, behaviour and spatial utilization of the land and the herders' main operations as practised in most parts of Fennoscandia, with the exception that bull slaughter is not practised in Finland, but is in many herds in Sweden and Norway. Main annual slaughter of calves takes place in connection with autumn migration from mid-October onwards.

in a reindeer herd help winter foraging resources to be allocated primarily to the reproductive females (Kojola 1993; Holand et al. 2012). Antagonistic behaviour among group members is common and dominant animals may, e.g., steal newly dug craters from subordinate animals, and notably from antlerless males. These fine-scale mechanisms may have implications for resource selection at the population level (Torney et al. 2018) and force low-ranked animals (such as reindeer bulls) to forage in less profitable habitats (Holand et al. 2012). Reproductive females are usually those that lead the movements of the herd (Thomson 1975). They also often act as look-outs and defenders and seem to guard the security of the herd. Herders often equip certain adult females with a bell, and nowadays a GPS-collar, as a way to track down the herd.

## Habitat selection, foraging behaviour and use of seasonal pastures

Reindeer are intermediate ruminants and generalist feeders moving through the landscape utilizing the most nutritious and digestible forage plants in summer (Hofmann 1989; Trudell & White 1981; Iversen et al. 2014), while in winter lichens and evergreen plants dominate the diet and snow controls where the reindeer can graze (Åhman & White 2018). Reindeer selection of habitat is best understood as a series of behavioural decisions at both large and fine temporal and spatial scales, from selecting seasonal areas to choosing the most nutritious part of a plant (Senft et al. 1987; Mayor et al. 2009; Skarin & Åhman 2014). The reindeer's behavioural response and the herder's actions towards the environment vary with reproductive cycle, season, herd density and availability of land. Reindeer herders often refer to the importance of high-quality pastures free from disturbance, where the reindeer can find 'grazing peace' (Inga 2007). Herders' decisions are integrated with the reindeer behaviour and may be hard to separate. In general, herders have the most impact on the large-scale migrations and selection of regional areas, while shorter movements within designated seasonal pastures and fine-scale selection of grazing patches are a choice made by the reindeer. There is usually more intense herding in winter compared to the snow-free season. In summer, most reindeer herds are freely ranging within the borders of the reindeer herding districts.

### *Calving and early summer*

Reindeer show site fidelity to their calving ground, especially parturient females (Schaefer et al. 2000; Garfelt-Paulsen et al. 2021). Within the calving area, females seek out snow-free patches either in the mountain tundra or, if in the forest, close to open areas to give birth to and nurse the calf (Skogland 1984; Skarin et al. 2008, 2015). Males also seek out snow-free mountains or areas, but well separated from the females. When the new green vegetation starts to emerge, reindeer change from a lichen-rich diet to feed on vascular plants. Newly emerging parts of graminoids (e.g. *Anthoxanthum odoratum, Carex*

*bigelowii, Deschampsia flexuosa, Eriophorum angustifolium, E. vaginatum, Nardus stricta*) and dwarf shrubs (*Vaccinium myrtillus*) are important (Warenberg 1982; Skogland 1984) as they are high in nitrogen (protein) and low in fibre, thus being easily digestible (Klein 1990; Åhman & White 2018). Digestibility of the diet has a major impact on energy intake, and thus on reindeer weight gain (White 1983). As soon as they start to emerge, forbs like *Comarum palustre*, *Gnaphalium supinum*, and *Potentilla erecta* start to be eaten, and sprouts and leaves of woody taxa, such as willow and dwarf birch (e.g., *Salix lanata* and *Betula nana*), are also preferred (Warenberg 1982; Skogland 1984).

Reindeer are far more sensitive to virtually all sources of anthropogenic disturbance during the calving period than during any other season. This is true for both semi-domesticated and wild reindeer, and it is most likely connected to the fear of predation and the importance of a calm environment for the female and calf (Vistnes & Nellemann 2008; Panzacchi et al. 2013; Skarin & Åhman 2014). Breeding females tend to seek out areas where they can see approaching danger, e.g., predators (Pinard et al. 2012; Sivertsen et al. 2016; Skarin et al. 2018). 'Green-wave surfing' describes how animals are expected to follow waves of resources and select habitats with an optimal balance of forage quality and quantity (Merkle et al. 2016). It has, however, been found that a high abundance of predators (brown bear) may hinder reindeer's optimal use of these resource waves (Rivrud et al. 2018). As the calf grows, the females gradually increase their movements and select ranges in relation to insect harassment and plant phenology (Skarin et al. 2010; Rivrud et al. 2018).

### *Mid and late summer*

Harassment from mosquitoes, blackflies, horseflies and the reindeer-specific parasites, warble and nose bot flies (*Hypoderma tarandi* and *Cephenemiya trompe*), play an important role in habitat selection during summer. In tundra and mountainous regions reindeer typically prefer summits and ridges, and ideally snow patches, to escape the insects (Downes et al. 1986; Hagemoen & Reimers 2002; Skarin et al. 2008, 2010). There is a trade-off between nutritious rich river valleys and wind-exposed summits and ridges (Skarin et al. 2008, 2010). Forest-dwelling reindeer seek out sandy patches, dirt roads, river banks and other open land such as mires and clear cuts (Helle & Aspi 1984). Escaping insects reduces the time available for foraging (Colman et al. 2003), and years with high insect activity have been related to lower slaughter weights in the autumn (Weladji et al. 2003). The negative effects may, however, be reduced in regions with high forage quantity and short distances to insect-free habitats (Skarin et al. 2020). During insect harassment, reindeer may exhibit higher tolerance towards anthropogenic disturbance (Pollard et al. 1996; Skarin et al. 2004): it seems more important to avoid biting insects and warble flies than to avoid other disturbances.

Towards the end of the summer, mushrooms become an important part of the reindeer diet, constituting up to 25 per cent (Boertje 1984; Launchbaugh

& Urness 1993). Northern Sámi herders use the expression *vistit* to explain that 'the reindeer goes after mushrooms' or 'something it likes' (Inga 2007). Herders commonly refer to reindeer spreading out and report that it is hard to gather and herd reindeer during the mushroom season.

### *Autumn and winter*

In autumn, mires are important, because in them reindeer are able to forage green shoots and roots from graminoids and various *Carex* species (Skjenneberg & Slagsvold 1968; Storeheier 2003). As annual plants wither, the role of evergreen perennial plants and lichens increases. Herders usually report that reindeer start eating lichens and dwarf shrubs a while before the snow arrives.

Reindeer have a unique adaptation in being able to digest lichens. Depending on their availability, lichens may comprise up to 70 per cent of the diet of reindeer, although they cannot survive on this alone because of their low nitrogen and macro-mineral content (Storeheier et al. 2003; Åhman & White 2018). The most common terrestrial species eaten by reindeer are the *Cladina* species, although *Cetraria nivalis* have similar digestibility and may also be consumed (Storeheier et al. 2002). Protein sources consist of the green parts of graminoids and some evergreen shrubs (e.g., *Vaccinium myrtillus* and *Empetrum nigrum*) (Boertje 1984; Storeheier et al. 2003; Åhman & White 2018). Mosses may be found in the diet although they are less preferred (White 1983). In forested areas, arboreal lichens (*Alectoria* and *Bryoria*) may constitute an important food source in late winter and when dense snow or ice crust limits the access to ground vegetation.

In winter, the availability of lichens and other ground vegetation is highly dependent on snow conditions (Helle 1984; Inga 2007; Roturier & Roué 2009). In the Sámi languages, there are numerous words for snow and snow conditions related to reindeer grazing (Ryd & Rassa 2001). Good grazing conditions depend on stable temperature and precipitation resulting in soft snow that is easy to dig in throughout the winter. In addition, under the canopy of old trees in mature forests, the snow usually stays softer and thinner (Chapter 4; Inga 2007; Horstkotte et al. 2014). Repeated fluctuations above and below freezing point and extreme snow depth are known to cause problems for reindeer grazing. Herders have different strategies to help the reindeer find food under such circumstances. Reindeer may be split into smaller units with frequent movements according to local variations in grazing conditions or allowed to spread out and seek patches with suitable grazing conditions for themselves. Another possibility is supplementary feeding (see Chapter 12).

## Evolving use of pastures

The past wild reindeer populations in Fennoscandia lived in various vegetation and landscapes types using different areas depending on the biogeography and availability of forage. Early reindeer pastoralism (see Chapters 1 and

2) developed with varying degrees of nomadism, longer seasonal migrations between vegetation zones (mountain vs forest areas) in some areas and shorter migrations, primarily between different habitat types within the same vegetation zone (lichen-rich forest vs mires), in others. Use of land has always been adjusted to the reindeer's needs and adapted to the landscape.

Early reindeer herding was not restricted by national borders. In Sweden and Norway, migration typically took place along large river valleys, with winter pasture towards the eastern Baltic coast and summer pasture towards the Atlantic coast in the west. Reindeer further north in Finnmark Norway and east in Finland and Russia migrated from winter ranges in forests in Russia and Finland to summer ranges along the northern Atlantic coast in Norway and Finland. Over time, reindeer herding has however been forced to adapt to the gradual closing of national borders (Chapter 1), leading to sub-optimal utilization of pastures in many areas (Tyler et al. 2021). There were forced relocations of reindeer and Sámi reindeer herders within Sweden (Cramér & Ryd 2012), summer pastures were transformed to winter pastures in Norway (Tveraa et al. 2007) and in a large part of Finland reindeer herding changed to having all seasonal pasture within boreal forest.

## Present organization and pasture use

The present use of pastures by reindeer and reindeer husbandry in Norway, Sweden and Finland thus has different ecological and historical backgrounds. Today, three main forms of reindeer herding strategy can be distinguished: (1) seasonal migrations between mountain or Atlantic coast summer pastures to winter pastures in taiga or tundra (Sweden and Norway), (2) seasonal migration between summer pasture on inland mountains and winter pasture by the Atlantic coast (Norway) and (3) year-round grazing in the taiga or mountain area (Sweden and Finland) (Chapter 1). In all countries, reindeer husbandry is divided into reindeer herding districts, the size of the districts and number of reindeer within each district vary considerably, depending on the landscape, historic borders and administrative decisions (Chapter 9).

### *Norway*

The reindeer husbandry is divided into 84 summer reindeer herding districts and, within some districts, herds are further divided into smaller units. The herds in Finnmark (47) move between Atlantic coastal summer pastures and winter pastures in the interior with continental climate and generally shallow snow and good access to forage (Figure 3.2). In Troms, some herds stay year-round on islands, while others make short migrations between summer pastures along the coast and winter pastures further inland. The winter pastures in this region are under the strong influence of the oceanic climate and are frequently inaccessible due to deep and/or crusted snow. In Nordland and Nord-Trøndelag, reindeer use summer pastures in the inland mountains, often close

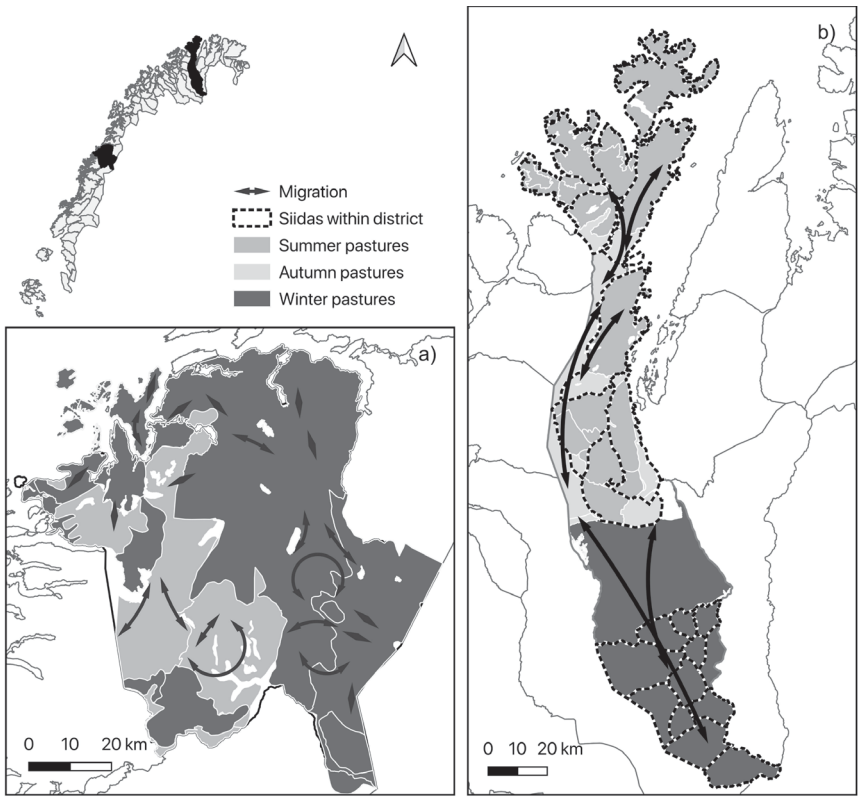


*Figure 3.2* Use of and migration routes between summer, autumn and winter pastures in (a) Saltfjellet reindeer herding district in Nordland and (b) Kárašjoga oarjjabealli reindeer herding district in Finnmark.

to the Swedish border, and winter pastures along the Atlantic coast or in the lowlands where precipitation more often falls as rain and the snow is shallower. In Sør-Trøndelag and Hedmark, most reindeer move into continental winter pastures in the Femunden area with generally shallow snow and good access to food. Five reindeer herding districts are operated by non-Sámi people on Concession areas in the mountain range at the southern fringe of the reindeer herding area, adjacent to the wild reindeer herds.

### *Sweden*

In Sweden, the 51 reindeer herding districts are divided into year-round land (used primarily in the snow-free period) and winter pastures where reindeer are only allowed to stay from 1 October to 30 April. There are 33 mountain herding districts. These are mostly long and narrow and use summer pastures

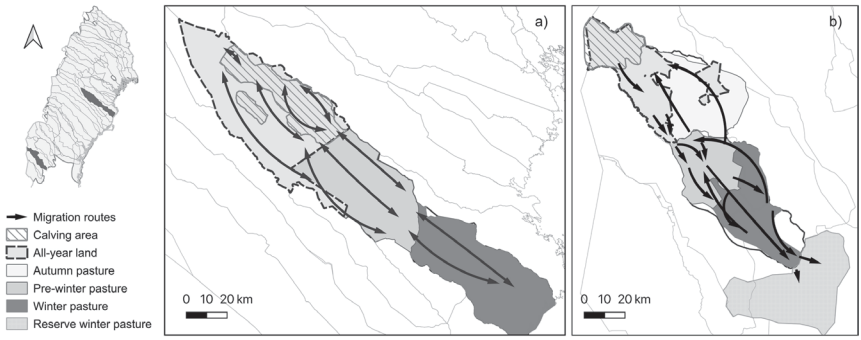


*Figure 3.3* Use of and migration between calving area, summer, autumn and winter pastures in (a) Malå forest reindeer herding district in Västerbotten County and (b) Mittådalen mountain reindeer herding district in Jämtland County, Sweden. In April, migration is usually undertaken on foot to the calving and summer (year-round land) pastures solely in the forest or the mountain region, respectively.

in the mountains in the west and winter pastures in the boreal forest in the east towards the Baltic coast (Figure 3.3). There are ten forest herding districts, one in Västerbotten County and nine in Norrbotten County, that use pasture in the boreal forest areas all year. Winter pastures in Sweden are generally influenced by a cold continental climate with proper snow winters; however, pastures close to the Baltic coast may be influenced by a more maritime climate. Migrations between seasonal pastures are undertaken on foot or by truck, depending on the connectivity between the pastures. Eight Concession herding districts rotate the reindeer in the forest region between the Kalix River in the west and the Torne River (Finnish border) in the east.

### *Finland*

In Finland, the reindeer herding area is divided into 54 reindeer herding districts: the 13 northernmost are Sámi reindeer herding districts and the others are Finnish reindeer herding districts. A mosaic of various coniferous forests and mires dominates the landscape in the southern and central parts of the herding area, while in the north tundra and mountain birch forests are more common. The natural scattering and short distance between winter and summer pastures in Finland have made the seasonal pasture rotation system more sedentary than in Sweden and Norway (Figure 3.4). In the small districts in the south and central parts of the reindeer herding area, reindeer move freely between summer and winter pastures. In the larger districts in the middle and northern parts, there is a distinct migration between seasonal pastures. Several of these districts have also separated the summer and winter pastures by fences, to avoid

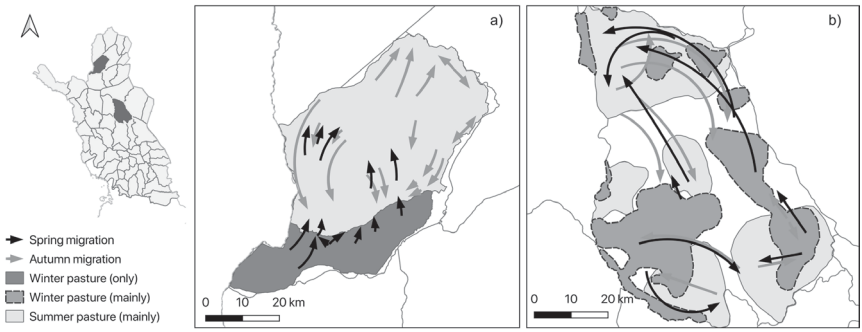


*Figure 3.4* Use of and rotation between summer and winter pasture in (a) Muotkatunturi Sámi Finnish reindeer herding district and (b) Oraniemi Finnish reindeer herding district in the northern and central parts of the reindeer husbandry area in Finland, respectively.

trampling of winter lichen pastures by reindeer in summer. In the north, most Sámi districts have either a clear separation of seasonal pastures by means of fences or they herd the reindeer to the different seasonal pastures.

## Concluding remarks

The fundamental resource for reindeer herding is reindeer access to pastures in all seasons. Over time, the closing of national borders, loss of land to industry and infrastructure and growing disturbance from various human activities have led to loss of suitable land for reindeer grazing (Chapters 4 and 5).

There has been an actual loss of land, resulting in areas that the reindeer cannot use anymore, barriers in the terrain limiting the access to an area and disturbances making reindeer avoid otherwise suitable grazing areas. Although, reindeer as a species seem to exhibit behavioural plasticity in relation to disturbances, they often move away from disturbance (Helle et al. 2012; Skarin & Åhman 2014), indicating the importance of disturbance-free pastures where they can find grazing peace.

The quality of pastures for reindeer is partly favoured by their own grazing, e.g., stimulating the creation of graminoid meadows on summer ranges and favouring biodiversity in general (Bråthen et al. 2007; Sundqvist et al. 2019). Indeed, closing the border between Finland and Norway and thus preventing reindeer in Finland from leaving the winter grounds and migrating to the summer pastures in Norway caused degradation of lichen-rich heaths and turned them into graminoid heaths with dwarf shrubs and mosses, leaving the herds with little lichen pasture on the Finnish side of the border (Kumpula 2006; Tyler et al. 2021). Biodiversity and availability of high-quality pasture for reindeer are also challenged by the increased greening and shrubification of the

tundra caused by climate change (Macias-Fauria et al. 2012). However, recent research suggests that reindeer suppress the growth and regrowth of woody taxa (Bråthen et al. 2017; Skarin et al. 2020), and grazing may thus counteract albedo feedbacks and mitigate climate warming (teBeest et al. 2016; Meredith et al. 2019).

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