3 Rangifer Diet and Nutritional Needs

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This chapter discusses the importance of nutrition and adaptation to the seasonally changing availability and quality of reindeer and caribou diets, and the subsequent importance this may have for Rangifer health and performance. The topic includes the seasonal diet and nutrient intake, the function of the gastrointestinal tract, nutritional needs, deficiencies and starvation and the effect of nutrition on growth, reproduction and survival, with implications for population dynamics and management.

3.1 SEASONAL HABITAT CHOICE, DIET AND NUTRIENT INTAKE

In order to support nutritional needs for survival and reproduction, reindeer and caribou use a set of foraging strategies at different scales. Migrations between seasonal ranges are typical for most Rangifer herds, wild as well as semi-domesticated. These migrations are several hundred km for many populations of tundra and barren-ground Rangifer subspecies. Forest/woodland and high arctic Rangifer types, as well as some of the tundra-type herds, are more sedentary, although they also perform relocations and select habitat in relation to season.

Migrations from winter to summer ranges can be made along a south–north gradient, from lower to higher altitudes or from inland to coastal areas. This makes it possible for reindeer and caribou to follow snow-melt and the succession of spring green-up and to find areas in winter where the snow is not too deep or dense. Winter ranges are often situated either on open lichen heaths or in forests with a high abundance of terricoulous lichens (Bergerud et al. 2008). Habitats with access to winter-green graminoids and forbs may offer additional forage of high nutritive value (Warenberg 1982).
Summer ranges on open tundra (Figure 3.1) generally consist of a mosaic of vegetation types with large variation in plant composition (Gaare and Skogland 1975). Short-term movements between vegetation types and foraging sites make it possible for the animals to select for high available biomass and high nutritional quality of forage plants.

*Rangifer* ranges are similar over the northern hemisphere with respect to plant composition. Even if species are not altogether the same, genera are usually similar within vegetation types. A large variety of plant species have been identified as being eaten by *Rangifer* through analyses of rumen content, faeces, samples collected from esophageal fistulas or direct observations of grazing animals (Bergerud 1972, Bjune 2000, Russell et al. 1993, Scotter 1967). Research by Skjenneberg et al. (1975) revealed that semi-domesticated reindeer in Norway consumed most plant species that were available (in this case close to 100 species), although lichens, at least when scarce, were clearly selected and mosses were avoided.

Lichens typically dominate the *Rangifer* diet in winter, but there are large variations between different *Rangifer* populations, and lichens are also eaten during the snow-free period if available (Bergerud 1972, Finstad and Kielland 2011, Gaare and Skogland 1975) (Figure 3.2, Table 3.1). In contrast to mainland *Rangifer* subspecies, the high arctic types (Peary caribou and Svalbard reindeer) often have little access to lichens in their habitats and thus few or no lichens in their diets (Bjune 2000, Larter and Nagy 2004). Instead forbs, deciduous shrubs and graminoids typical for these habitats are grazed in varying proportions throughout the year.

Lichens contain carbohydrates with high digestibility for reindeer. In vitro dry matter (DM) digestibility for different *Cladina* species, using inoculum from reindeer adapted to a lichen diet, have been reported to range from about 40% up to 70% (higher for *C. rangiferina* and *arbuscula* than for *C. stellaris*) (Danell et al. 1994, Storeheier et al. 2002, White et al. 1975). The digestibility of *Cetraria islandica* and *nivalis* seems to be similar to that of the most digestible *Cladina* species, while the less favored *Stereocaulon pascale* was shown to be less digestible (Storeheier et al. 2002). The digestibility of arboreal *Bryoria* spp. has been found to be as high as 88% (Danell et al. 1994). Although a good source of energy, most lichens grazed by *Rangifer* are low in protein and macro minerals (calcium, phosphorous, potassium and magnesium) (Ophof et al. 2013). The *Cladonia/Cladina* species contain only around 2% crude protein (on a DM basis), and some arboreal lichens even more (*Bryoria, 5%*). The chemical composition of lichens does not change with season, but
mat-forming lichens (e.g. reindeer lichens) are typically more nutritious in the upper growing part than in the lower part of the lichen thalli (Ophof et al. 2013, Storeheier et al. 2002).

Reindeer and caribou cannot survive the winter on lichens alone, due to the low content of nitrogen and macro minerals. Graminoids and other vascular plants are thus part of the winter forage of most Rangifer herds in winter, adding important nutrients to the diet. In line with this, Helle (1984) observed that, throughout winter, reindeer in northern Finland used not only lichen heaths, but also adjacent feeding sites where they had access to grasses and sedges. For some herds (Russell et al. 1993, Scotter 1967), shrubs dominate the non-lichen part of the diet; however, for many Rangifer populations, graminoids seem to constitute the major fraction of the non-lichen part of the winter diet (Finstad and Kielland 2011, Gaare and Skogland 1975, Thomas et al. 1996).

The content of crude protein in most shrubs, graminoids and forbs varies from 4% to about 10% in winter (Heggberget et al. 2002), which is at least two to three times that of most lichens, and the mineral content may be several times higher than in lichens (Ophof et al. 2013). Green shoots of vascular plants and buds of deciduous shrubs are highly digestible and may contain over 20% crude protein (Ophof et al. 2013). Even in small amounts, they may provide a substantial part of necessary protein and minerals, especially in late winter and early spring before snow-melt.

Bryophytes are consumed by Rangifer and in some cases constitute 10–20% of the diet (Boertje 1984), even though they seem to be less palatable and of low nutritional value (Danell et al. 1994). Moss forms a large part of the diet (35–49%) of the Porcupine caribou herd during late spring, prior to green-up and along migration routes that contained few lichens (Russell et al. 1993).

Limitation not only in quality of forage, but also quantity, is a challenge to reindeer and caribou in winter. Snow is a key factor in the winter-feeding patterns of Rangifer. In winter, forage intake is limited by the time it takes to search and dig for food, and there is a trade-off between forage intake and the energy costs associated with searching and cratering. It is crucial for the animal to be able to distinguish sites with enough forage from those with little or no forage. In fact, reindeer can use smell to distinguish good lichen patches from poor patches through soft snow over 90 cm thick (Helle 1984). Accordingly, feeding craters are often made at patches with the highest lichen biomass (Helle 1984, Johnson et al. 2001). Hard snow increases the time needed for cratering, and reindeer and caribou typically choose to crater at locations with the lowest depth and hardness of

**FIGURE 3.2** Reindeer winter forage – lichens, Cladina rangiferina (grey), Cladina stellaris (round/tubby and yellowish white) and some small fractions of Cladina mitis (yellowish white and similar shape as C. rangiferina) (Photo: Birgitta Åhman).
Reindeer and Caribou

snow (Johnson et al. 2001). Arboreal lichens are chosen when deep and hard snow prevents the reindeer from feeding on terrestrial lichens, and are therefore mainly grazed in late winter.

There is a positive relationship between the availability and the intake of lichens (Trudell and White 1981), and snow is thus a key factor for total biomass intake. The availability of forage seems to overrule the nutritional quality of forage in the choice of habitat or feeding sites in winter (Johnson et al. 2001).

The importance of snow for reindeer foraging is demonstrated by traditional classification of winter pastures within reindeer herding, where factors affecting snow properties may be as important as lichen abundance in categorizing a certain land area as good or poor winter pasture (Roturier and Roué 2009).

As snow melts and new green vegetation emerges, vascular plants become increasingly important. Graminoids, deciduous shrubs and forbs will usually dominate the summer diet (Boertje 1984, Finstad and Kielland 2011, Gaare and Skogland 1975), substantially enhancing the nutritional quality of the diet. The early summer diet is characterized by high digestibility and high protein and mineral content. However, the nutritional value of forage varies between plant species, plant parts, climatic conditions and phenological development (Johnstone et al. 2002, Mårell et al. 2006). Peak nitrogen content of between 3 and 4% (corresponding to 19–25% crude protein) has been recorded for several alpine plant species in early growth stages (Mårell et al. 2006). Several of the macro minerals (phosphorus, magnesium and potassium) follow a similar pattern (Mårell et al. 2006, Staaland and Sæbø 1993).

Access to habitats with high plant biomass production and plants of high digestibility makes it possible for reindeer and caribou to increase forage intake considerably in summer compared to winter. For Rangifer, being a ruminant, high digestibility of the diet is crucial to enable the consumption of sufficient biomass of forage. Being able to select the most digestible and protein rich plants and plant parts is therefore crucial if the animals are to obtain enough nutrients for growth (young animals) and for regaining body reserves during the relatively short summer.

In late summer and autumn, reindeer and caribou eagerly eat mushrooms (fruiting bodies of fungi) and often search for habitats where they are available (Boertje 1984, Helle 1981). Mushrooms provide a late summer supply of highly digestible, high protein forage. Caribou and reindeer continue to eat graminoids as well as some woody plants and herbs, but gradually increase the lichen component typical of a winter diet (Boertje 1984, Gaare and Skogland 1975).

### TABLE 3.1
Seasonal Diet of Reindeer and Caribou, Average and Range (Minimum-Maximum) Values Reported from Different Rangifer Herds

<table>
<thead>
<tr>
<th></th>
<th>Lichen</th>
<th>Shrub&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Graminoid</th>
<th>Forb</th>
<th>Fungi&lt;sup&gt;b&lt;/sup&gt;</th>
<th>Moss</th>
<th>Other</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spring (Apr-May)</td>
<td>62%</td>
<td>8%</td>
<td>12%</td>
<td>1.6%</td>
<td>0%</td>
<td>9%</td>
<td>8%</td>
</tr>
<tr>
<td>(56–69%)</td>
<td>(5–14%)</td>
<td>(10–14%)</td>
<td>(1–2%)</td>
<td>–</td>
<td>(7–10%)</td>
<td>(4–17%)</td>
<td></td>
</tr>
<tr>
<td>Summer (June-Aug)</td>
<td>32%</td>
<td>29%</td>
<td>23%</td>
<td>8%</td>
<td>5%</td>
<td>3%</td>
<td>4%</td>
</tr>
<tr>
<td>(10–62%)</td>
<td>(13–49%)</td>
<td>(10–51%)</td>
<td>(0–41%)</td>
<td>(0–25%)</td>
<td>(0–6%)</td>
<td>(0–12%)</td>
<td></td>
</tr>
<tr>
<td>Autumn (Sep-Oct)</td>
<td>58%</td>
<td>9%</td>
<td>19%</td>
<td>4%</td>
<td>5%</td>
<td>3%</td>
<td>2%</td>
</tr>
<tr>
<td>(34–87%)</td>
<td>(2–21%)</td>
<td>(5–47%)</td>
<td>(0–12%)</td>
<td>(0–12%)</td>
<td>(1–5%)</td>
<td>(0–7%)</td>
<td></td>
</tr>
<tr>
<td>Winter (Dec-Mar)</td>
<td>65%</td>
<td>11%</td>
<td>12%</td>
<td>1.0%</td>
<td>0.3%</td>
<td>6%</td>
<td>4%</td>
</tr>
<tr>
<td>(34–88%)</td>
<td>(5–26%)</td>
<td>(0–28%)</td>
<td>(0–7%)</td>
<td>(0–11%)</td>
<td>(2–13%)</td>
<td>(0–11%)</td>
<td></td>
</tr>
</tbody>
</table>


<sup>a</sup> Woody plants, from which mainly leaves and shoots are eaten.

<sup>b</sup> Fungi content is strongly influenced by annual and seasonal availability.
3.2 THE GASTROINTESTINAL TRACT

Both the anatomy and function of the gastrointestinal tract in reindeer and caribou are adapted to a diet with large variations in structure and nutrient content over the year. The species *Rangifer tarandus* is generally regarded as an intermediate mixed feeder on a scale from grazers to browsers or concentrate selectors (Hofmann 1989). Grazers are represented by, for example, cattle and sheep, which are able to digest high amounts of fibrous grass, while browsers (e.g. moose and roe-deer) are adapted to a diet with high digestibility. As opposed to grazers, concentrate selectors are characterized by a narrow mouth, relatively small rumen and reticulum, small omasum, shorter intestine and a large distal fermentation chamber (caecum). The retention time for digesta is shorter than for grazers, and the microorganisms in the rumen are less capable of digesting cellulose (Mathiesen 1999).

Most studies on the gastrointestinal function on *Rangifer* are made on semi-domesticated Eurasian tundra reindeer (*R. t. tarandus*) or on the high arctic Svalbard reindeer (*R. t. platyrhynchus*). The sub species are generally alike with regard to the gross anatomy of the digestive tract (Mathiesen et al. 2005), although Staaland et al. (1979) point out the shorter intestines and larger caecum – important for mineral absorption – as characteristics of *R. t. platyrhynchus* as compared to *R. t. tarandus*.

Investigations by Mathiesen et al. (2000) show that reindeer have the narrow and pointed muzzle and rather low crowned molariform teeth considered typical for selective feeders. They also have large lips, and prominent first incisor teeth, which help to select for the most digestible and nutritious parts of the vegetation.

A major part of the processing of food in *Rangifer*, as in other ruminants, occurs in the rumen-reticulum (hereafter referred to as rumen) where less digestible carbohydrates, like cellulose and hemicellulose, are degraded by various microorganisms. Rumination, the chewing of regurgitated forage, will break the food into smaller particles and facilitate further processing by microorganisms.

Animals ruminate in bouts following feeding. Daily feeding and ruminating patterns of captive reindeer and caribou differ depending on time of year. Eriksson et al. (1981) and Maier and White (1998) recorded daily feeding and ruminating patterns of captive reindeer during different seasons. Both studies found four to six activity peaks per 24 hours in winter (6 hours daylight) and six to nine peaks in summer (with continuous or near-continuous daylight), representing three more events than in free-ranging reindeer (van Oort et al. 2007) and caribou (Maier and White 1998). Reindeer were fed grain-based pellets and lichens that were freely available, while caribou had free-grazing and a grain-based diet. Much of their active time was spent eating, and rumination took place when the animals were resting between feeding sessions. For reindeer, time spent ruminating between meals was shorter in summer (28 minutes per ruminating session) than in winter (47 and 54 minutes in December and March, respectively). Since the frequency of activity and rest was higher in summer, the resulting total time for ruminating (not reported) probably did not differ much between seasons. Captive reindeer offered different diets ad libitum (Nilsson et al. 2006b) ruminated 16–26% of their time, and this did not differ between diets (lichens, silage and pellets in different combinations) once the animals had been adapted.

Experiments with reindeer equipped with esophageal fistulas (Trudell and White 1981) and foraging on different natural vegetation showed that about 10 g dry matter is usually regurgitated each time and chewed for about a minute before being swallowed again.

The utilization of forage in ruminants depends on a range of anaerobic bacteria, ciliate protozoa, fungi and methanogenic archaea (previously classified as bacteria) that are present in the rumen and hindgut. These microorganisms have the capacity to digest the different carbohydrate fractions in the forage and make them available to the host. The microbial flora differs between environments in both quantity and composition, and changes with season and diet (Mathiesen et al. 2005). Bacteria that generally dominate in summer are more adapted to using soluble carbohydrates, while cellulolytic bacteria dominate more in winter.

It is well documented that the digestive system of *Rangifer* is poor at handling large quantities of fibrous forage (Aagnes et al. 1996). Rapidly increasing live body mass in animals fed hay or silage...
may actually be a sign of failure of cellulolysis and subsequent accumulation of forage in the rumen (Olsen et al. 1995). Svalbard reindeer, which need to survive on a very poor-quality diet in winter, are known to host relatively more cellulolytic bacteria compared to Rangifer in other environments (Mathiesen et al. 2005, Orpin and Mathiesen 1990).

Animals of the Rangifer species are unique in their ability to utilize lichens as their main forage at times when the availability and quality of vascular plants is poor. The polysaccharides of lichens contain glucose linkages that differ from those in starch and cellulose (Culberson 1969), and specific bacterial enzymes are required for breaking these. In addition, secondary phenolic compounds, including usnic acid, which is toxic to fungi and many Gram-positive bacteria, are found in several of the lichen species that are eaten by reindeer (Ingolfsdottir 2002). However, rumen microbes in reindeer seem to tolerate usnic acid (Palo 1993), and novel species of usnic acid resistant bacteria (Eubacterium rangiferina) have been identified by Sundset et al. (2008). Sundset et al. (2010) showed that even when reindeer were provided with relatively large amounts of usnic acid, no traces were found in rumen fluid, urine or faeces. The authors conclude that usnic acid is degraded by rumen microbes, explaining the ability of reindeer and caribou to fully utilize lichens. Detoxification of usnic acid, alternatively microbial resistance, was further confirmed by research showing that rumen bacteria and methanogenic archaea populations did not change significantly when usnic acid was added to the rumen content (Glad et al. 2014). Rumen bacteria from reindeer have also been shown to be resistant to other phenolic secondary compounds that are present in lichens (Glad et al. 2009).

The adaptation to lichens has been further demonstrated by measurements of in vitro digestibility of lichens, showing that digestibility (of Cladina spp.) was higher (70%, compared to 63%) in rumen fluid from lichen-fed reindeer than from reindeer on other diets (Wallsten 2003). It was also evident that lichens were poorly digested in rumen fluid from cattle (11% digestibility), while the digestibility of vascular plants did not differ depending on rumen fluid donor (cattle or reindeer). The importance of adaptation to lichens was confirmed by Nilsson et al. (2006a), who found that rumen content from lichen-fed reindeer contained more bacteria that could be cultured on media with lichens as the only energy source, compared to rumen content from reindeer fed diets without lichens (pellets and grass silage).

Bacterial species that are attached to the rumen wall differ from those in the rumen fluid (Cheng et al. 1979), and include, for example, ureolytic bacteria, which may be important for recycling nitrogen and producing ammonia that can be further used for protein synthesis by other rumen bacteria.

The concentrations of total protozoa in the rumen of reindeer has been reported to range from 130 to 250 × 10⁴, which is higher than in other domestic livestock investigated (5.2 – 44.5 × 10⁴) (De la Fuente et al. 2006). Westerling (1970) investigated the ciliate fauna of semi-domesticated reindeer in Finland and found that it differed substantially from that found in domestic livestock like cattle and sheep. The composition of ciliate species was also shown to vary with season (Orpin and Mathiesen 1990, Westerling 1970). Dehority (1975) reported that domesticated reindeer in Alaska had similar ciliate species to domestic livestock, while the ciliate flora of wild caribou was more similar to that found in wild and semi-domesticated Eurasian reindeer. Based on several studies, Mathiesen et al. (2005) conclude that ciliate fauna is probably not primarily linked to host species, but rather to diet and possible isolation of host populations.

Methanogenic archaea are a group of microorganisms that produce methane and other by-products, and have received growing attention during recent years. Archaea were earlier defined as bacteria but have their own evolutionary history and are now regarded as a separate domain. Methanogens have not been investigated much in reindeer. Thus far, studies on Svalbard and Norwegian reindeer (Sundset et al. 2009a, Sundset et al. 2009b) suggest that their numbers are relatively small (10⁷–10⁸ cells/g rumen content) compared to that reported for cattle (up to 1.34 10⁹ cells/g) (Denman et al. 2007). This might indicate lower methane emission from reindeer compared to cattle, at least with regard to reindeer free-grazing on natural ranges.
In addition to bacteria, methanogens and protozoa, the rumen also hosts anaerobic fungi with the capacity to utilize, for example, cellulose (Mathiesen et al. 2005). It seems that these fungi have a higher capacity to invade plant tissue than many bacteria, and thus that they are important for the breakdown of fiber in the rumen.

Microorganisms utilize carbohydrates in the food eaten by the animal to produce carbon dioxide, methane and energy-rich volatile fatty acids (VFA): mainly acetic, butyric and propionic acid. All are highly absorbed across the rumen wall (72–82%) (White and Gau 1975) and their net energies may constitute up to 60–80% of metabolizable energy intake (Annison and Armstrong 1970). The production and concentration of VFA in the rumen can be used as an indicator of rumen activity and forage quality, and they are considerably reduced in poor diets or during starvation. Nilsson et al. (2006a) found a 56% reduction in the VFA concentration in the rumen (from 110 to 48 mmol/l) of reindeer calves after a period of 9 days with restricted feed intake. Due to reduced volume of rumen content, the total VFA decreased to 34% of the original level. Reindeer calves that had been starved for four days showed even lower VFA concentrations of 14–37 mmol/l (Aagnes et al. 1995).

The absorption of VFA depends on the total rumen surface. Westerling (1975) found that the reindeer rumen mucosa changed according to diet. This was later confirmed by studies on reindeer calves by Josefsen et al. (1997), who found that the size and density of rumen papilla changed with season, so that the total rumen surface (or surface enlargement factor, SEF) in late summer (September) was almost double that in late winter (April). Most of the observed decline occurred by November. The effect of diet quality (and not quantity) was demonstrated in a feeding experiment, using silage with different digestibility (content of soluble carbohydrates versus cellulose), where high digestibility was shown to be positively correlated with high SEF. The mechanism behind this difference is the concentration of VFA in the rumen content that stimulates the growth of rumen papilla (Sakata and Tamate 1979).

Food needs to be degraded into small enough particles before it can proceed further through the digestive system. The threshold size seems to be general for most ruminants and ranges from 1 to 4 mm (Lechner et al. 2010). The rumen retention time of particles and rumen liquor declines with increasing intake of digestible dry matter (Lechner et al. 2010, White and Trudell 1980). Particle retention time was reported to be 23–69 hours in lichen-fed reindeer (Aagnes and Mathiesen 1994), while it was only 10.8 hours in Alaskan reindeer consuming early summer pasture (White and Trudell 1980). Turnover time of the liquid component of rumen contents is less than that for particles and is inversely related to dry matter intake (Lechner et al. 2010, White and Trudell 1980). Lechner et al. (2010) found that the rumen retention time in reindeer was shorter than in muskoxen (a grazer), but longer than in moose (a typical browser), though all species showed a similar relative pattern with regard to retention of different sized particles.

The caecum, together with the proximal part of the colon, represent the distal fermentation chamber (DFC) where cellulolytic bacteria take care of undigested cellulose that escaped the rumen, thereby further improving the digestibility of the consumed forage. As in the rumen, VFAs are absorbed into the blood to be used as an energy source by the animal. It has been observed that as much as 17% of the total VFA is produced in the DFC of Svalbard reindeer in winter (Sørmo et al. 1997), and the corresponding production rate of reindeer fed commercial pellets or lichen-based diets was 20% of the rumen production rate (White and Gau 1975).

In the distal colon, water is absorbed and faecal pellets are formed. Rangifer produce small faecal pellets that are usually relatively dry in winter when food is limited, but are more soft and “clotted” on lush summer pastures, or when the reindeer are fed grain-based diets (pellets).

Reindeer and caribou can obviously be sustained on poor ranges during winter, where their ability to digest lichens and tolerate anti-digestive substances like usnic acid give them an advantage compared to other herbivores in the same environment. However, in summer they need to compensate for the restricted nutrient intake with rapid growth and replenishment of body reserves. As their ability to digest fiber is limited, they require a highly digestible diet that enables them to process a large enough volume of forage with the necessary nutrients for synthesis of fat and
protein. The possibility for selective grazing is then a key issue, as demonstrated by White (1983) and stressed later in this chapter. The limited capability of *Rangifer* to digest fiber is an important consideration when feeding reindeer, as accumulation of undigested forage in the rumen may subsequently lead to starvation.

Although reindeer and caribou are clearly very well adapted to utilizing lichens, there seems to be a limitation in their ability to use lichens as the only, or major, dietary component. Several feeding experiments show that reindeer have a lower total DM intake when fed only lichens or a major share of lichens, compared to when fed other diets (Jacobsen et al. 1981, Nilsson et al. 2000). These experiments also revealed that reindeer fed lichen-diets did not eat enough to maintain their body mass, even though the diets were offered ad libitum, while reindeer fed other diets increased in body mass. The reason for this is unclear, though it might be linked to a lack of necessary nutrients (nitrogen and minerals) for the gastrointestinal microbes, or may indicate that some substances in lichens (e.g. the secondary compounds discussed on p. 112) reduce the animals’ appetite.

### 3.3 NUTRITIONAL PHYSIOLOGY AND NEEDS

Reindeer and caribou are highly adapted to the seasonal variations in availability and nutrient content of forage typical of their Arctic and Sub-Arctic ranges. Long winters with limited daylight, constant snow cover and limited access to forage through occasional icing events, is a challenge that the species has evolved to cope with through evolution, and which has shaped life history timing and anatomical, physiological and metabolic adaptations. *Rangifer* have, for example, several adaptations for saving energy during winter (Tyler and Blix 1990). Heat loss is minimized by thick fur and heat exchange mechanisms in the legs and nose (Folkow and Mercer 1986). The energy necessary for locomotion is reduced by anatomical attributes like large hooves, long legs and cost effective gaits (Fancy and White 1987). The sharp edges and size of the hooves makes digging in snow effective (Fancy and White 1985a). Antlers on females is a unique feature among *Cervidae*, enhancing the social rank of *Rangifer* females in late winter, when the males have already lost their antlers, making the females superior in the competition for forage (Barrette and Vandal 1986, Espmark 1964) and allowing their offspring to share feeding sites.

Seasonality of food availability and quality has selected for a high capacity to store energy and protein as fat and muscle tissue. Fat and protein are regained during periods with higher forage abundance (summer and autumn) in response to body reserves lost during periods of low nutrient intake (winter). Negative energy balance and consequent weight loss in winter is often considered a regulated process for *Rangifer* (Tyler et al. 1999, White et al. 2014) and should be regarded as dependent on nutrition but not necessarily be described as malnutrition. In most environments with low or moderate *Rangifer* densities, available forage in winter is sufficient to maintain the reproductive capacity and survival of populations, often through millennia. Reproductive output is, however, seasonally variable via adjustment of conception rate (Cameron and Ver Hoef 1994, Reimers 1983), rate of foetal growth in the final trimester (Bergerud et al. 2008, Reimers 2002) and variability in weaning date (Russell et al. 2005). Body fat and muscle tissue serve as supplements to available forage and in females provide a regulated reserve for terminal gestation and the initiation of lactation. In addition, fat and muscle reserves provide insurance against mortality during potential periods of acute starvation. Adaptations that minimize N loss in winter assist in this process.

Timing of the reproductive cycle of *Rangifer* follows annual patterns of snow-melt and forage availability, demonstrating plasticity with respect to seasonal variation in forage availability and quality (Cameron et al. 1993, Flydal and Reimers 2002).

### 3.3.1 ENERGY AND PROTEIN FOR MAINTENANCE, THERMOREGULATION AND ACTIVITY

The allocation of energy and protein (nitrogen) for maintenance, activity, reproduction, growth and body reserves in *Rangifer* has been described in detail by White, Russell and co-workers.
(Russell 2011, White et al. 2014), with most based on the NRC *Nutrient Requirements of Small Ruminants* (NRC 2007).

Irrespective of season, a certain minimum of energy and nutrients is needed for base requirements to keep the animal alive (maintenance). This includes the basal metabolism, plus added cost for maintenance activity (e.g., foraging) and sustaining body temperature. It has been speculated whether reindeer and caribou lower their basal metabolic rate (BMR) in winter as an adaptation to save energy. However, observed seasonal differences in resting metabolic rate are related to food intake before measurement of energy expenditure, confusing estimation of seasonal effect (Nilssen et al. 1984b, Tyler and Blix 1990). White et al. (2014) assumed a constant daily BMR of 293 kJ/kg\(^{0.75}\) for *Rangifer* in winter when modeling energy expenditure. Taking the efficiency of use of metabolizable energy in forage into consideration, daily maintenance requirements for sedentary reindeer and caribou were calculated to be 493 kJ/kg\(^{0.75}\) and 560 kJ/kg\(^{0.75}\), respectively.

Nitrogen requirements for maintenance are associated with urinary losses and faecal output of metabolic N, and increase with increasing energy intake. The nitrogen requirements of reindeer have been little investigated, but for growing lambs N requirements have been estimated to be about 1 g N (≈6 g protein) per MJ energy intake (Black and Griffiths 1975), while larger and older animals need relatively less.

Due to effective mechanisms for reducing heat loss, the excess heat produced by digestive processes and metabolism is usually sufficient to maintain body temperature even at low ambient temperatures. Apparent lower critical temperatures have been estimated to be as low as −50°C for Svalbard reindeer and −30°C for Norwegian reindeer in winter (Cuyler and Øritsland 1993, Nilssen et al. 1984b). However, these critical temperatures require a certain level of heat-producing basic metabolism and activity (Parker and Robbins 1985) and may be different in situations of starvation, for example. Extra energy will be required at ambient temperatures below the critical temperature, and Dryden (2011) suggests a net energy cost of 14.6 kJ/kg\(^{0.75}\) BW for each degree (°C) below the critical temperature, based on research on temperate deer species (red and white-tailed deer). The thermal costs for *Rangifer* are expected to be lower because of their thick fur and other effective heat conserving mechanisms. Accordingly, costs of conductance of 5.9 and 7.7 kJ/kg\(^{0.75}\) BW and °C for reindeer and caribou at low temperatures were reported by Parker and Robbins (1985).

The energetic costs of standing, foraging or walking on plane ground are just slightly higher than the costs associated with resting, while activities like running, walking uphill, and walking or cratering in snow may increase energy requirements substantially (Fancy 1986). White et al. (2014) used estimates of energy requirements for activity from different sources for modeling *Rangifer* energetics. Lying or standing were assumed to require less than 0.5 kJ/kg body mass (BM) per hour, while the energetic costs for eating, pawing and walking were assumed to be 2–4 kJ/kg BM per hour. The total daily energy requirement for maintenance in summer was estimated at 660 kJ/kg\(^{0.75}\), or about 17 MJ for a 75 kg reindeer, and was the sum of energy required for basal metabolism, minimum activity for foraging, for growth of hair and antlers and for hosting parasites. The requirement of N for maintenance was assumed to be proportional to the energy requirements and was estimated to be about 0.73 g N/MJ, which equals 12 g N (77 g protein) for a 75 kg reindeer. Daily N requirements for maintenance determined by McEwan and Whitehead (1970), 0.82 g/kg\(^{0.75}\), is theoretically achievable using a crude protein concentration in the diet of about 8.3% and a daily dry matter intake of 50 g/kg\(^{0.75}\) (NRC 2007, p. 98), though these levels are not always achieved in the wild.

The cost of walking, additional to that of standing, is 1.6 kJ/kg body BM per km (Fancy and White 1987), corresponding to 120 kJ/km for a 75 kg reindeer. Similarly, Nilssen et al. (1984a) showed that the energetic cost for locomotion increases linearly with speed, irrespective of season and ambient temperatures. Only when temperatures were below the lower critical temperature did energy expenditure not increase with movement rate, indicating that heat from exercise substituted for the extra energy otherwise needed for the animal to keep warm. Walking uphill increases energy expenditure. As an example, lifting one kg one meter was shown to cost 23 kJ (Fancy and White 1987). Part of this cost could, however, be recovered when the animal walks downhill.
Walking and cratering in snow result in increased energy requirements for activity in winter, compared to summer. The cost of walking in snow increases exponentially with sinking depth (Fancy and White 1985a), with a 100% increase (doubling) in the energy needed for locomotion at 30–40 cm snow depth (depending on crust or not). At 50 cm, the energetic cost may be five times as high as that of walking on bare ground.

The cost of cratering in snow increases with snow density and hardness. According to Fancy and White (1985b), the mean cost for cratering was 118 J per stroke in light snow without crust and 219 J per stroke in denser snow with a thin, hard crust. The resulting daily cost for cratering was estimated to be 1.2–1.5 kJ/kg and 2.3–2.9 kJ/kg BM for a caribou cratering in soft and dense snow, respectively.

Gotaas et al. (2000) summarized total daily energy expenditures in winter, which ranged from 617 to 830 kJ/kg^{0.75} BM for free-living reindeer, barren-ground caribou and woodland caribou (recalculated from W/kg). A similar value of 837 kJ/kg^{0.75} BM was reported by McEwan and Whitehead (1970) for reindeer in winter. Considerably lower daily energy expenditure for maintenance in summer (232 kJ/kg^{0.75}) was reported for penned non-lactating females (Chan-McLeod et al. 1994). The low energy requirements in the latter case may, however, be partly explained by the fact that the reindeer were fenced and fed, thus not having to expend much energy on foraging.

### 3.3.2 Costs for Reproduction and Growth

Similar to many other large herbivores, *Rangifer* females depend on body stores of fat and protein for satisfying the extra energy and nitrogen needed for foetal growth and milk production (Barboza and Parker 2008, Taillon et al. 2013). This makes their reproductive success less sensitive to the irregular, and sometimes dramatic, variations in forage availability that are typical of their environment.

The energy costs for pregnancy are low during the first months. Boertje (1985) calculated (from published data) that the daily costs were 0.15 and 0.38 MJ in September–October and November–December, respectively, for a 110 kg caribou. This corresponded to 1% of the estimated total energy expenditure for a pregnant female. In January–February the daily cost increased to 0.97 MJ and in March–April to 2.41 MJ. This is in line with the rate of foetal growth reported by Roine et al. (1982), at only 1 g/d in mid-December, around 20 g/d in January–February and 100 g/d a month before parturition. Although foetal growth is remarkably linear at approximately 49 g/d between day 120 and 190 of gestation, both Reimers (2002) (reindeer) and Bergerud et al. (2008) (caribou) report large differences in terminal foetal growth (40–113 g/d) attributable to year and population effects, that likely act through the mother’s protein reserves. In line with this, White et al. (2013) estimated the tissue deposition for foetal growth at term gestation to be 14 g/d for protein and 2.1 g/d for fat. The gross energy content of this amount of fat and protein is about 300 kJ. Most of the extra energy required for gestation is lost as heat, however, and only a minor part (10–20%) is retained as new tissue (Robbins 1993, p. 200). Likewise, most maternal protein used over winter is not captured by the concept and White et al. (2013) speculated that extra protein must be mobilized to meet maternal and foetal glucose requirements through gluconeogenesis.

The daily energy needs for lactation are substantially higher than those for gestation. *Rangifer* calves in the Arctic are born before the start of green-up and females have very limited access to nutritious forage. Consequently, much of the energy and protein required for early milk production has to be mobilized from the female’s own body reserves. Experiments with reindeer and caribou fed a low nitrogen diet confirmed that lactating females continued to rely on body fat and protein during the first weeks of lactation (Barboza and Parker 2008). Similarly, Taillon et al. (2013) found that 88–91% of the nitrogen in milk protein was derived from female body reserves (Figure 3.3).

Similar to many other cervids (Robbins 1993, pp. 205–6), reindeer and caribou produce concentrated milk with a high protein and fat content (around 8–12% protein and 10–20% fat) that changes
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During the lactation cycle (Gjøstein et al. 2004, Luick et al. 1974). Milk yield – determined using machine milking – was shown to vary substantially between individual female semi-domesticated reindeer, ranging between 595 and 1239 g/d (corresponding to an average of 8 MJ/d) at peak lactation around 3 weeks postpartum (Gjøstein et al. 2004). Milk intake in bottle-fed caribou calves was about 100 g/kg BM per day during the first month after birth, declining until weaning at the age of around 4 months (Parker and Barboza 2013). It should be noted that milk production is highly dependent on female condition and nutrient intake, and may be substantially reduced in years with poor forging conditions (White and Luick 1984). Likewise, in free-grazing reindeer milk production varies between individuals and between years, which is largely attributable to the female’s body reserves (White and Luick 1984). As the lactation period progresses, milk production declines, fat and protein content increases, and there is a decline in the concentration of lactose (Chan-McLeod et al. 1994, Gjøstein et al. 2004). However, the calf continues to suckle even when milk production is low, and complete weaning does not usually occur until the rut in autumn, 22–26 weeks postpartum (Gjøstein et al. 2004, Laviguer and Barrette 1992). There seems to be rather large variations, however, and lactation can sometimes be terminated early, or be extended through winter (Skjenneberg and Slagsvold 1968). Five weaning strategies have been documented for caribou (Russell et al. 2005, White et al. 2014).

Lactation imposes high energetic costs on a female with a calf. The daily energy requirements for maintenance were reported to be twice as high (457 kJ/kg0.75 BM) for a lactating reindeer or

FIGURE 3.3  Simplified example of energy allocation of a reproducing Rangifer female under satisfactory grazing conditions using figures derived from articles referred to in the text, mainly White et al. 2014, Russel et al. 1993, and Fancy 1986. Maximum female BM is set to 75 kg, and it is assumed that the female loses 15% of her BM from 15 November until 1 June. Birth date of the calf is set to 20 May, and birth weight to 5.5 kg. The maximum daily milk production is assumed to be 1.2 liters and occurs 1 week after calving. Weaning is set to 1 October. “Production” includes regaining of body reserves (fat and protein) as well as coat and antler production. Increased cost for activity during winter is mainly attributed to extra costs for walking and cratering in snow, while slightly increased costs from late June to early August are caused by higher activity because of insect harassment. Bottom line below zero implies that the animal uses body reserves and loses body mass. HIF is the heat increment of feeding (heat produced from digestion and metabolic processes), which may vary depending on diet and how the energy is used. Here a default value (30% of total metabolizable energy intake) has been used to estimate HIF.
caribou, compared to a non-lactating (232 kJ/kg⁰.⁷⁵ BM) (Chan-McLeod et al. 1994), resulting in a daily lactation cost of 7.6 MJ for a female weighing 110 kg (about three times the cost for late pregnancy). The amount of energy and protein allocated for lactation is, however, limited by the female’s own needs (White 1983, White and Luick 1984). In situations with low access to forage (e.g. at high population densities) Rangifer females are expected to adopt a “selfish cow strategy” (Russell et al. 1996) and use relatively more resources for regaining their own body reserves and for future reproduction, than for current milk production (Chan-McLeod et al. 1999). Since Rangifer calves are normally born before, or at the start of, vegetation growth, more body resources are required for gestation and early lactation in early breeders compared to late breeders. On the other hand, the calf will have more time to grow before autumn if born early.

Calf growth rates of around 300 g/d from birth to weaning have been reported for captive semi-domesticated reindeer (Gjøstein et al. 2004, Rognmo et al. 1983). This is in accordance with results from semi-domesticated reindeer on natural mountain ranges in Sweden (Ahman, unpublished results). White et al. (1981) report growth rates of between 295 and 350 g/d for caribou and reindeer in captivity (compiling results from several investigations); however, these values can be higher and more variable in caribou, e.g. between 380 and 440 g/d during the first 3 weeks and 193–344 g/d at 3 to 6 weeks for the Porcupine caribou herd (Griffith et al. 2002). Bottle-fed caribou gained 355 g/d on average until peak milk intake at age 30–40 days. This did not differ from the subsequent weight gain (351 g/d) that proceeded until weaning (Parker and Barboza 2013).

Higher weight gains (on average 428 g/d during the first month, and 454 g/d during the following months) were recorded for calves of caribou females kept on a high plane of nutrition (Parker et al. 1990). Daily energy costs were reported to vary substantially, but the energy for daily existence was reported to be 439 kJ/kg BM on average, corresponding to 923 kJ/kg⁰.⁷⁵ between 20 and 40 days of age. This was 1.7 times the estimated fasting metabolism for caribou calves at 3 months of age (536 kJ/kg⁰.⁷⁵ BM per day) (Luick and White 1983). Daily milk intake during the same period corresponded to about 10 MJ and 140 g protein per day, on average.

The costs of growth in Rangifer calves have been summarized by White et al. (1981), with an overall value reported to be 30 MJ per kg weight gain. As the calf grows, gradually more energy will be needed for maintenance, while at the same time milk production and intake decline. More of the nutrient intake will therefore have to be supported by foraging. Rangifer calves have been observed foraging from the available vegetation within a few days of birth (Espmark 1971, Skjenneberg and Slagsvold 1968). Even if milk is the main source of energy and nutrients during the calf’s first month of life, the size of the rumen gradually increases and the calf adapts to the utilization of forage. Knott et al. (2005) show that the relative size of the rumen of a 60-day-old Rangifer calf was almost as large as in the adult animal, and this coincided with increasing content of the gastrointestinal tract, similar to the content of the adult animal.

### 3.3.3 Mineral Requirements

Rangifer’s requirements have not been established for all essential minerals, but are generally believed to be similar to those of other deer species and ruminants in general. Skeletal growth, antler formation, hair growth and milk production may require specific nutrients, and dietary requirements thus vary with season, age and reproductive stage.

Calcium (Ca) is the main component of bone and teeth and is commonly discussed together with phosphorus (P), because of their ratio in the skeleton (Ca:P = 2:1). According to NRC (2007, p. 115) Ca balance in cervids is achieved at a daily intake of 73 mg/kg BM. The daily requirement of P is reported to be 20 mg/kg BW. Growing animals need substantially more, the recommended daily intake for a calf weighing 20 kg and growing 300 g per day being 5.6 g Ca and 4.0 g P. Antler growth increases the need for both Ca and P, and the requirements are related to antler size and growth rate. Moen and Pastor (1998) estimated the daily requirement for male reindeer at peak antler growth to be at least 25 g for Ca and 12 g for P.
Potassium (K) and magnesium (Mg) requirements are not available for cervids, but values for goats are recommended (NRC 2007, pp. 123–24). Daily maintenance requirements for these species can be calculated to be around 0.15 g K/kg BM and 0.02 g Mg/kg BM, respectively. For growing, pregnant and lactating animals, the requirements are higher. For animals on natural pastures the supply of K is generally sufficient. The natural winter forage for Rangifer is generally low in Mg, however, and there are several documented cases of deficiency (see section 3.4 of this chapter). Most vegetation is also low in sodium (Na) and salt hunger is consequently common among ungulates. Robbins (1993, p. 47) recommended 9 mg/kg BM of sodium, but Rangifer research indicates that a daily requirement at 3.2 mg/kg is probably more relevant for reindeer and caribou (NRC 2007, p. 121).

Trace elements are generally not limiting for free-grazing reindeer, and deficiencies have only been reported for copper. However, trace element requirements are relevant with regard to supplementary feeding and the composition of feed rations for Rangifer, and are therefore discussed in relation to feeding in Chapter 4, Feeding and Associated Health Problems.

### 3.3.4  **Retention and Use of Body Reserves**

Reindeer and caribou often lose around 10–20% of their body mass during winter, with some island or high arctic types losing even more (Couturier et al. 2009, Tyler and Blix 1990). The corresponding loss of protein may be as high as 29% (Gerhart et al. 1996a). However, Rangifer females seem to allocate as much of their body reserves as possible for foetal growth and instead use dietary energy and nitrogen for maintenance (Parker et al. 2005).

Protein and fat reserves have to be regained during the relatively short snow-free period, which requires sufficient quantity and quality of summer forage. The chemical energy in dry body protein is 23.6 kJ/g on average, while the energy in fat is about 39.5 kJ/g (Robbins 1993, p. 10). Protein generally contains about 16% nitrogen, yet muscle and other soft tissue contain a large proportion of water (normally at least 70%), which means that the nitrogen content will be about 50 mg and the energy content will be 7 kJ per gram of fat free muscle tissue.

The allocation of energy, protein and other nutrients from forage or body reserves at a given time depends not only on the supply of nutrients but also on the animal’s reproductive state and the time of year. Energy for maintenance, including, for example, the necessary activity involved in foraging, as discussed on pp. 116–117, evidently must be given a high priority in order to keep the animal alive, while there is a “choice” in the degree of retention or mobilization of energy and nitrogen for activity, body tissue or reproduction.

As earlier discussed, there is a trade-off between using resources for lactation and using them for direct growth and regaining body reserves. Although lactating females gain body mass considerably slower in summer than do non-lactating females (Chan-McLeod et al. 1994), there is evidence that milk production is limited when food resources are insufficient (White and Luick 1984).

Adult males lose a significant part of both their fat and protein (muscle) reserves in autumn, due to increased activity and little time spent eating during the rut. Some of this may be regained after the rut if foraging conditions are favorable, but there may be a risk that the body reserves will be insufficient for the animal to survive periods of poor foraging conditions during the following winter. Apparently, this is still an advantageous strategy for lifetime reproductive success (Barboza et al. 2004), and similar strategies are common for males of other polygamous species (Pelletier et al. 2009).

### 3.3.5  **Association between Nutrition and Parasites**

Reindeer and caribou can be plagued by a range of external and internal parasites (discussed in detail in Chapter 6, Parasitic Infections and Diseases). It is well known from research on domestic ruminants that, even in cases where they do not induce clinical symptoms, gastrointestinal parasites
may depress appetite, impair gastrointestinal function and increase endogenous protein loss, thereby negatively affecting the animal’s body condition (van Houtert and Sykes 1996). At the same time, poor nutrition may make the animal particularly susceptible to parasitic infections.

As pointed out in a review by Gunn and Irvine (2003), the nutritional implications of parasitism for wild and semi-domesticated ungulates have rarely been acknowledged in research. Their review focuses on gastrointestinal nematodes and confirms that findings regarding the importance of parasites for domestic ruminants also have relevance for wild ungulates, and that parasites should be considered further in relation to ungulate nutrition. Impaired appetite, and therefore poor weight gain, has been demonstrated as an effect of abomasal nematode infection in semi-domesticated reindeer in Norway (Arneberg et al. 1996), and experiments on Svalbard reindeer have shown that body condition was negatively affected by gastrointestinal parasites (Stien et al. 2002). Furthermore, anthelmintic treatment was shown to have positive effects on fecundity, and the effects were large enough to influence reindeer population density (Albon et al. 2002).

Hughes et al. (2009) found a negative effect of abomasal nematodes on body mass of barren-ground caribou, even at substantially lower parasite burdens than those observed in Svalbard reindeer (Stien et al. 2002). Caribou in Greenland are typified by high burdens of abomasal parasites as well as both warble and nasal bot fly larvae (Oestridae) in late winter/spring (Cuyler et al. 2012). However, pregnancy rates were high and body fat reserves were not fully depleted despite the high estimates of energy and protein costs imposed by these parasites. In addition, Hughes et al. (2009) found that oestrid larvae infections (measured in April) did not affect body mass significantly, but had a negative effect on back fat and were associated with a reduced probability of pregnancy. This might be a result of direct action of the parasite larvae in the body of the host, but may also be a delayed effect of heavy harassment by oestrid flies during the preceding summer, reducing the time that the animals can spend foraging. Ballesteros et al. (2012) found a significant effect of anthelmintic treatment of female reindeer in autumn on their body mass the following summer. Reproductive success of treated females did not, however, differ from that of untreated controls. It was assumed that the treated reindeer would be re-infected by intestinal parasites after the treatment and that the experiment would capture mainly the effect of oestrid larvae. Whether this was the case, however, is unclear.

### 3.4 NUTRITIONAL DEFICIENCIES AND STARVATION

#### 3.4.1 Deficiencies

As already mentioned, a negative energy and nitrogen balance is common for reindeer in winter. This is, however, something to which reindeer and caribou are adapted to via their capacity to accumulate body reserves in summer for later use, combined with their ability to effectively recycle endogenous nitrogen (Barboza and Parker 2006, Valtonen 1979). Moderate under-nutrition is thus not expected to cause significant loss of muscle tissue, although Soppela et al. (2000) found that a lichen-dominated winter diet may lead to a reduction in important serum lipids.

More specific deficiencies, in terms of lack of certain vitamins or minerals, are not very well documented among reindeer and caribou, magnesium (Mg) being an exception. Lichens contain only minor amounts of Mg compared to most vascular plants, and clinical illness due to Mg deficiency has been observed in reindeer grazing on lichen ranges in inner Finnmark, Norway (Hoff et al. 1993). Reindeer calves with clinical signs (they were paretic and ataxic) had extremely low levels of Mg in their blood (0.19 ± 0.18 mmol/l in blood serum, compared to an average of 0.82 in a healthy reference group), accompanied by a low calcium/phosphorus ratio (1.21, compared to 1.85 in the reference group) and greatly elevated levels of aspartate aminotransferase, creatine kinase and lactate dehydrogenase. Exceptionally low Mg levels (below 0.3 mmol/l) in blood serum have also been reported for Swedish reindeer in poor body condition in late winter (Åhman et al. 1986). In line with this, Ropstad et al. (1997) observed large variations both between herds and between
years in the concentrations of Mg (0.16–1.39 mmol/l), together with a large variation in calcium (Ca, 0.9–3.6 mmol/l) and phosphorous (P, 0.2–3.4 mmol/l), in blood plasma collected from reindeer in Northern Norway in winter. They also observed that the probability of a female being pregnant was positively correlated with the concentrations of Mg and Ca in plasma. Moderately low serum-Mg levels (0.67 mmol/l), alongside low serum levels of Ca and copper (Cu, 0.42 μmol/l), were observed in a reindeer herd with a subsequent high mortality rate (40%) in late spring, soon after sampling (Hyvärinen et al. 1977). The average Cu level in this herd was less than half of that observed in well-nourished herds, and Cu deficiency was believed to have contributed to the high mortality rate.

Judging from concentrations determined in the liver, trace elements may vary substantially between Rangifer herds. Vikøren et al. (2011) found dramatic variations in liver concentrations of some trace elements (cobalt, copper, manganese, molybdenum, selenium and zinc) in wild reindeer from Norway, in which Cu varied more than 100 times (min 2.3 and max 289 μg/g dry weight). However, neither low nor high levels could be linked to any obvious clinical signs of deficiency or toxicity. Unlike moose and roe-deer from the same investigation, reindeer had sufficient concentrations of selenium in the liver.

Staaland et al. (1980) observed low levels of sodium (Na) compared to potassium (K) in reindeer saliva on winter ranges, suggesting insufficiency in Na that is a reason for the well-known salt hunger among Rangifer and many other herbivore species. Animals are clearly attracted to natural salt licks as well as, for example, roads that are salted for deicing, and Staaland and Hove (2000) point out evidence for a reproductive response to Na supplementation in an interior reindeer herd in Norway that exhibited Na deficiency.

Other than for magnesium and the above examples for copper and sodium, there are few documented cases of clinically significant mineral deficiencies in Rangifer. In many cases, even animals that have starved to death have not been reported as showing signs of specific vitamin or mineral deficiency, and, for example, the content of vitamin E and selenium in the liver of reindeer that died of starvation showed satisfactory levels (Josefsen et al. 2007). However, it is uncertain if lack of evidence for deficiencies is because they are generally uncommon, because the symptoms are difficult to detect or because deficiencies are simply not commonly investigated.

### 3.4.2 Starvation

Starvation is a relatively customary cause of death in Rangifer during severe winters, despite the fact that the species is adapted to large seasonal variation in nutrient intake. Lack of food will initially result in emptying of the gastrointestinal tract, depletion of glycogen reserves in the liver and use of easily accessible protein sources (Robbins 1993, p. 234). Body mass will drop as an effect of decreased gastrointestinal content and loss of water. In a second stage the animal will start to utilize body fat, at the same time reducing basic metabolism to save energy. This stage may continue for quite some time in an animal with plenty of fat reserves, and the decline in body mass will be rather slow. If the animal has no intake of nitrogen it will also have to utilize some body protein for maintenance and glucose synthesis. When most fat reserves have been used, protein will start to be utilized as an energy source. As lean muscle tissue contains only about 25% dry matter and protein contains about half as much energy as fat, the weight loss will be dramatic compared to when fat is used as the energy source. If depletion of protein reserves continues the animal will soon die from emaciation.

Results regarding the depletion of body resources in Svalbard reindeer demonstrated that both reindeer that survived and those that died had lost a substantial part of their total and lean body mass, and almost all their fat reserves during winter (Reimers 1984). However, although surviving reindeer had lost up to 97% of their body fat during winter, they still had a small amount remaining, while those that died had lost everything, including all bone marrow fat – the last fraction to be utilized.

Roffe (1993) investigated the cause of perinatal mortality in caribou calves, basing the diagnosis of emaciation on the appearance of fat tissue (reduced, firm and dark red, with histology indicating
lack of lipids in adipose tissue) and on lack of full functional development indicated by a missing, or poorly formed, urethra tube.

Josefsen et al. (2007) investigated 23 completely emaciated reindeer from different free-ranging herds in Northern Norway. The reindeer were found dead in late winter (March to May). All animals had very little lichen or leafy parts of grass in their rumen. Most of the rumen content was either stem parts of grasses, woody plants or mosses and litter. The animals had depleted fat reserves (shown by lack of visible fat in the abdomen), extremely low fat content in bone marrow (0.2–1.0%), and muscle mass also seemed considerably reduced. Eyes were sunken, a sign of dehydration. Common pathological findings were, for example, abomasal lesions (in 19 animals, 68%), a dark liver, excessive hemosiderosis in the liver and spleen and liver lipofuscinosis. The authors concluded that emaciation had arisen because of inadequate quantity or quality of food, although some of the animals had actually been offered supplementary feeds prior to death. In contrast to results by other authors (Westerling 1972, Ågren and Rehbinder 2000), Josefsen et al. (2007) did not observe that diarrhoea was indicative of starvation.

3.5 BODY CONDITION INDICATORS

There is often an interest in assessing the body condition of individual animals or whole populations in *Rangifer* research and management. A range of body condition indicators have been used or suggested for this purpose. Practical and logistical considerations often limit the methods that can be used.

Body mass is a straightforward measure of body condition, but must be related to age, sex and reproductive stage. Body mass is evidently affected by size, which complicates its use as a general indicator of body condition. Nonetheless, body mass may often be the most suitable indicator for measuring change in body condition in individual animals or within a population. For comparing individuals or *Rangifer* populations, a body size variable (e.g. back length or length of a specific bone) is generally needed as covariate in statistical analyses. Alternately, or in addition, a body condition score (1–5) based on that used in animal husbandry has been used to assess fat level (Gerhart et al. 1996b). When using body mass, it is also important to consider the amount of digesta. The rumen content represents a large part of the total body mass (typically 10–20%) and may vary considerably depending on feed intake. Ingesta-free body mass is consequently a better indicator of body reserves than body mass as such.

In Norway, Sweden and Finland, carcass weights of slaughtered animals are recorded in national databases for reindeer husbandry. This data has been used for describing variations and changes in general body condition of reindeer in relation to, for example, management, lichen resources and climatic factors, yet suffers from the same limitations related to animal size as does whole body mass or ingesta-free body mass. Fat and conformation classifications are standardized measures at reindeer slaughter in Sweden and are independent of size, therefore may be used in addition to carcass weight for accessing body condition (Olofsson et al. 2011).

Bone marrow fat, kidney fat and back fat are commonly used indicators of body fat reserves. Fat around the heart could be used in addition (Figure 3.4). Kidney fat, or kidney fat index, is probably the most well-used indicator of body reserves in ungulates. Kidney fat index is calculated by relating the amount of fat to the weight of the kidney. However, Serrano et al. (2008a) point out several weaknesses with using these kinds of indexes or quotas for statistical analyses, and recommend using the measure as such, while including the size measurement (in this case kidney weight) as a covariate in the statistical model. A muscle index – using the weight of a certain muscle in relation to bone length – was suggested by Tyler (1987b), and bone length was used in a multiple regression model to predict pregnancy rate in caribou (Gerhart et al. 1997). Such an index could have statistical limitations as shown for the kidney fat index.

As discussed in relation to starvation, bone marrow fat is a good indicator for assessing degree of emaciation. However, since bone marrow fat is one of the last fat reserves to be mobilized,
its concentration is not a very suitable measure of total fat reserves in animals of adequate body condition (Chan-McLeod et al. 1995). Nonetheless, Rehbinder and Nikander (1999, p. 66) suggested use of the following bone marrow fat contents for estimating the nutritional state of animals: >70% “good,” 30–70% “less good,” 5–30% “poor,” 2–5% “emaciated but possible to save,” <2% “inanition and the animal has no possibility of surviving.” Chan-McLeod et al. (1995) compared different variables for body mass and body composition that could be used for harvested caribou without access to specialized laboratories. They concluded that water content in indicator muscles, together with kidney fat index (left kidney), were the indicators of fat reserves in the caribou body that worked best across all seasons. Total marrow fat was suggested as a preferable alternative to percentage of fat in bone marrow, and back fat proved to be a good index in autumn only, when the animals were relatively fat.

Taillon et al. (2011) used a range of body condition indices (including body mass, a number of length measurements, chest girth, peroneus muscle mass, rump fat, kidney fat and bone marrow fat) for multivariate analyses in order to find a combined measure of body condition. For females, they identified a “body bulkiness index” that separated the heavy, round-bodied females from the light and lean ones. Whereas body condition of newborn calves was best described by body mass, a combination of mass and size measurements worked best for calves at weaning.

It is not only total fat that may change as result of poor nutrition, but also the proportions of individual fatty acids. Soppela and Nieminen (2001) observed a decline in oleic and linoleic acid in bone marrow fat as an effect of under-nutrition in adult female reindeer, while there was a decline only in linoleic acid in reindeer calves.

Thomas and Barry (2005) tested whether variation in antler mass correlated with changes in body mass, body condition and pregnancy rate, but concluded that this measure varied too much and was inferior compared to other body condition indicators.

Blood analyses can be used for measuring the nutritional state of live animals, and Soveri et al. (1992) found that blood serum parameters varied with diet and season in reindeer calves in winter.

**FIGURE 3.4** Fat around the heart is a useful indicator of Rangifer body condition: (a) Heart of an emaciated reindeer. (b) Heart of a reindeer in good body condition (Photo: Ulrika Rockström).
Säkkinen et al. (2005) measured blood constituents from free-ranging semi-domesticated reindeer and concluded that plasma total protein and albumin, and to some extent also globulin, may serve as nutritional biomarkers for reindeer, and that they reflect the nutritional composition of the animal’s diet. Total serum protein and serum triglycerides have also been found to reflect physical condition of Iberian wild goats (Serrano et al. 2008b).

Sample size often inhibits the assessment of temporal and spatial differences in body condition. In North America, initiatives have been conducted that involve aboriginal hunters providing their own assessment of body condition based on a number of quantifiable and qualitative indicators (Kofinas et al. 2004, Lyver and Gunn 2004). Protocols have been incorporated into monitoring activities in a number of jurisdictions.

### 3.6 EFFECTS OF NUTRITION ON POPULATION DYNAMICS AND MANAGEMENT

#### 3.6.1 Body Condition, Survival and Reproductive Success

It has been suggested that foraging conditions during summer are the main factor in determining growth rate and body size in *Rangifer*, and that conditions on winter ranges are important for survival, and thus for population density (Klein 1968, Reimers 1997). However, as discussed previously, enough summer forage is needed to accumulate sufficient body reserves to ensure survival during adverse winter periods with, for example, severe snow conditions.

It is frequently assumed that forage shortage, as such, is rarely problematic in summer. High animal density may, however, reduce the possibility for an individual animal to select plants with the highest nutritional quality and may thereby limit growth and the regaining of body reserves. For an individual animal, plant biomass can limit food intake on an instantaneous and daily basis, which is frequently the situation during spring green-up on Arctic ranges. Many plant species are of low palatability, preference or nutrient quality and thus selective feeding among the forage sward typifies the *Rangifer* feeding strategy. Selective grazing not only optimizes digestibility, but also boosts nutrient intake and retention to produce a multiplier effect. Consequently, White (1983) estimated a doubling in the rate of weight gain as result of a 14% increase in forage digestibility. At low or moderate animal densities, the limitations in forage intake and the possibility for selective grazing in summer are usually an effect of disturbances, the most important in many habitats being insect harassment. Detrimental effects of insect harassment have been described in several papers (Fancy 1986, Reimers 1980, Witter et al. 2012). Biting, stinging and parasitic insects are abundant in *Rangifer* habitats, where the most significant are the oestrid (warble and nasal bot) flies that force reindeer and caribou to move and seek windy and elevated areas (e.g. snow patches, if available) with little or no forage.

The rate of insect activity depends on the effective temperature, a combination of temperature and wind (Mörschel 1999), with oestrids requiring higher temperatures for activity than, for example, mosquitoes and black flies. Fancy (1986) estimated the energetic loss and subsequent negative effects on weight gain in *Rangifer* caused by warm summer days and the resulting insect harassment. Using data on observed temperature and wind during a single month (July 1981), he calculated that a lactating female was in a negative energy balance during most days within the observed period. Similarly, Reimers (1980) estimated negative effects of increased activity – because of insects – on reindeer productivity. This confirms that insect harassment is probably a key factor explaining temporal and geographical variations in *Rangifer* autumn body condition. It also implies that one of the more severe effects of global warming on *Rangifer* populations might be that of insect harassment.

As already mentioned, body condition at the onset of winter is expected to affect winter survival and be important for the animal’s ability to cope with periods of adverse snow conditions. Body reserves are especially crucial for calves during their first winter, and autumn body condition is also crucial for reproduction. Research on wild as well as domesticated *Rangifer* shows significant...
effects of female autumn body mass and fat reserves on conception rate and reproductive success the following year (Cameron and Ver Hoef 1994, Gerhart et al. 1997, Reimers 1983, Rönnegård et al. 2002). Eloranta and Nieminen (1986) found large effects of female autumn body mass on calving rate and calf survival in semi-domesticated reindeer, especially for young females. Differences in autumn body condition may thus explain a considerable part of the variation in reproductive rate that can be seen among and within reindeer and caribou populations.

Most Rangifer females over 1 year of age are fertile and ovulate at rut, and in sufficient nutritional conditions even juveniles may get pregnant (Tyler 1987a). However, raising a calf in the first year of life is expected to negatively affect a female’s future reproductive success, since she will probably not be able to invest enough in her own growth. Data from Norwegian wild reindeer showed that over a certain body weight threshold, most females were likely to get pregnant (Reimers 2002). Based on results from the Porcupine caribou herd, all females with a fat reserve of 12 kg or more would be expected to be pregnant. For non-lactating females, the corresponding fat content for a 100% pregnancy rate was around 7 kg (Gerhart et al. 1997). This is also in accordance with findings for captive caribou (Crête et al. 1993).

Rangifer females typically produce one offspring every year. Nevertheless, there are regions where female lifetime reproduction is very high and twins seem to be more common (Cuyler and Ostergaard 2005), at least in some years (Godkin 1986). Poor environments, on the other hand, where lactating females do not always succeed in regaining enough body mass during summer, may be associated with frequent reproductive pauses and alternate year breeding (Cameron 1994). It has also been shown that both the youngest and the oldest females are at higher risk of failing to produce a calf during a certain year compared to those at prime age (5–8 years old) (Rönnegård et al. 2002).

Some females exhibit a prolonged lactation (over the breeding season), which has been shown to be a factor that may reduce the probability of pregnancy at a given body mass (Gerhart et al. 1997). This might be a mechanism to support the survival of a calf when food resources are restricted, at the expense of not calving the following summer.

The timing of calving varies among Rangifer population and between years, and could be affected by nutrient supply and female body condition via effects on either conception date or gestation length. Cameron et al. (1993) observed that females that calved before a certain date (June 7) were significantly heavier both in the previous autumn and in the summer after calving. It has been observed that older, heavier females mate earlier than young and light females (Mysterud et al. 2009). There seems, however, not to be a direct effect of female autumn body condition on gestation length, and late breeders are shown to have generally shorter gestations than early breeders (Rowell and Shipka 2009). This actually counteracts some of the effects of female autumn body mass and timing of mating on calving date. On the other hand, poor nutrition during the latter part of pregnancy can extend the length of gestation and thus delay calving date (Cameron et al. 1993, Skogland 1983).

Female nutrition during pregnancy affects foetal growth and early calf survival in Rangifer. Loison and Strand (2005) confirm that foetal growth rate is positively correlated with female body mass in wild reindeer. Skogland (1984) observed large differences in calf birth weight, calving date and calf survival depending on animal density and female body condition. Enhanced feed intake and an increased content of protein in the diet (13.7% crude protein compared to a lichen diet with 3.1% crude protein) were observed to have positive effects on foetal growth rate in domesticated reindeer (Rognmo et al. 1983). The same experiment also revealed a strong negative effect of a low protein diet on early calf survival, as five out of 17 calves on this diet died within 2 days of birth. This agrees with results from an experimental herd of semi-domesticated reindeer in Finland, where calves that were stillborn or died during the first day of life weighed 2 kg less at birth, than those that survived until autumn (Eloranta and Nieminen 1986). A similar effect has been deduced for caribou (Bergerud et al. 2008, Roffe 1993).

Energy and protein intake during pregnancy seem not to significantly affect the composition or energy content of the milk (Jacobsen et al. 1981, Luick et al. 1974, Rognmo et al. 1983),
while milk volume may be substantially affected (Jacobsen et al. 1981). Calf growth rate during the first weeks of life may vary between 150 and 400 g/d depending on the female’s milk production (White and Luick 1984). Delayed effects of female winter nutrition on early calf growth was also observed by Rognmo et al. (1983), who recorded an initial (first 3 weeks) weight gain of 290 g/d for calves of females fed only lichens prior to parturition, compared to 350 g/d for calves of females on an improved diet. However, the effect of winter nutrition disappeared by the time the calves were about 2 months old.

### 3.6.2 Nutrition and Population Dynamics

Fluctuations in population size regularly occur in wild as well as in domesticated *Rangifer* populations, and changes in forage availability are often seen as a main driver (Post and Klein 1999, Skogland 1983). High winter mortality, especially in young animals, sometimes occur because of icing and locked pastures (Chan et al. 2005). Even if reindeer and caribou have been shown to survive winter in habitats without lichens, persistent or long-term fluctuations in *Rangifer* population size are often linked to a gradual decline in lichen biomass due to high animal density on the ranges. Lichens grow slowly and overgrazed lichen ranges need to be protected from grazing over several years (maybe decades) in order to recover to optimal productivity. Lichens grow from the top of their branches and also need enough light and humidity to be able to grow. A heavily grazed and trampled lichen mat will have few branches to grow from, therefore having low density and height, and drying out quickly. Reindeer lichens (*Cladina* spp.) in northern Finland were shown to have a maximum annual production at 175 kg dm per ha (10 000 m²) on stands with about 2600–2800 kg dry matter of living lichen per ha (Kumpula et al. 2000). Substantially higher maximum growth rates, around 35%, were recorded at optimal conditions by Cabratic et al. (2010).

Dramatic population crashes have been observed in *Rangifer* populations the world over (Tyler 2010), one of the more spectacular being that of the introduced caribou population on St. Matthew Island, Alaska, happening in the winter of 1963–1964, when almost the entire population of 6 000 caribou died, and only about 40 animals survived (Klein 1968). During a 20-year period, after the introduction of 28 caribou on the island in 1944, the population had grown rapidly. Lichens, that had been abundant, were by that time almost eliminated, and during the years prior to the crash body mass and reproduction rate declined substantially.

Winter foraging conditions are important and complex with respect to forage abundance, snow characteristics and the variability of rain-on-snow and icing events. Nevertheless, summer forage and autumn body condition are crucial for determining the capacity of reindeer and caribou to cope with periods of food deficiency in winter. Regain of body reserves in summer decreases with age and is linked to tooth wear (Kojola et al. 1998), making older animals more sensitive to inadequate forage abundance and quality in summer. In winter, tooth wear is enhanced if the lichen availability is low and the animals have to eat alternative forage that is coarser than lichens. Worn teeth will reduce the animal’s ability to process and utilize both summer and winter forage, thereby limiting the potential for fat and protein accumulation.

It has been discussed to what extent body condition affects the risk that a reindeer or caribou will be killed by a predator. Top-down (predation) and bottom-up (food resources) mechanisms may, however act, and interact, in diverse ways in different environments and over time (Bastille-Rousseau et al. 2016, Mahoney et al. 2016). Fat reserves (marrow fat) did not affect the risk of being killed by predators among animals older than 1 year in a declining population of mountain caribou (McLellan et al. 2012), while there seems to be a negative correlation between calf body mass and risk of predation (Jenkins and Barten 2005) – although this relationship may differ depending on predator species (Nieminen et al. 2013).

In general, the most important influence of foraging conditions on population demographics is via the effect on recruitment rate. As previously stated, female body condition in autumn and over winter has significant effects on conception rate, foetal survival, timing of parturition, calf birth
weight and neonatal survival, while adult survival in herbivores generally shows little variation or density dependence (Gaillard et al. 2000). This is confirmed by findings on wild reindeer in Norway (Skogland 1990), where density-dependent limitation of winter forage did not influence adult survival, although calf survival the following summer was significantly affected. An outstanding difference for arctic barren-ground caribou is the finding that for some herds – after effects of recruitment by younger cohorts are accounted for – population declines can be linked to adult survival, especially as affected by icing events (Griffith et al. 2002).

### 3.6.3 Nutrition and Management of *Rangifer*

Controversy exists over whether factors limiting caribou and reindeer populations are related to predation and harvest, or to winter and summer habitat, and therefore if the population size of *Rangifer* should be regulated, rather than the number of predators. These contrasting approaches tend to reflect objectives and management efforts in North America, and particularly Alaska, where predator control represents a major tool used by management (Bergerud et al. 2008, Boertje et al. 1996, Mosnier et al. 2008), despite habitat fragmentation and industrial development having been shown to threaten survival of woodland caribou in Canada (Wittmer et al. 2005). In contrast, in Fennoscandia, long-term concerns over winter habitat loss and habitat fragmentation for both herded and wild reindeer have emphasized bottom-up approaches to management; much of it emphasizing the role of nutritional ecology (Colpaert et al. 1995, Olofsson et al. 2011). Predation is generally regarded to affect harvest rate (Hobbs et al. 2012) rather than population size, except in some exceptional cases (Åhman et al. 2014). Evolving approaches to management use resource selection analysis to assess habitat use (Johnson et al. 2004), and when combined with determination of cumulative effects, this can integrate top-down and bottom-up, as well as behavioural, factors. These may, either separately or in combination, affect recruitment and can be the basis for determining, for example, the influence of climate change (Bastille-Rousseau et al. 2016, Tyler et al. 2008). The future of reindeer and caribou management will require a thorough understanding of the interactions between environment and population dynamics through nutrition, as well as a wide-scale collation of data sets. “A glimpse of the future needs (to include) a different approach to sharing data and information to avoid fragmentation and to take advantage of electronic data such as networking the MERRA climate data sets” (Anne Gunn, 16th North American Caribou Workshop, Thunder Bay, Ontario, Canada, May 2016).

### REFERENCES


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