Nutritional composition of Finnish semi-domestic reindeer (*Rangifer tarandus tarandus*) spring forage intake

Analysis for the assessment of current captive reindeer diets (Rangifer tarandus)

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Final thesis research report for
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Abstract

The aim of this study was to investigate the nutritional composition of spring forage plants consumed by semi-domesticated reindeer (*Rangifer tarandus*) on natural pastures in northern Finland. This study was conducted in order to contribute to the development of standards for the assessment of the current captive reindeer diets. In captivity, the absence of proper nutrition causes numerous health problems in reindeer, due to little being know about their nutritional requirements. Information about natural diets can be derived from field research, quantitative data on forage plant nutrient composition and utilization, which can help towards development of optimal diets for captive animal management. By means of microhistological (faeces) analysis, the botanical composition of reindeer winter and spring diet was examined. Nutritional composition of spring forage plants was determined by means of chemical analysis (Weende, van Soest, and mineral analysis). Captive reindeer diets were assessed with feed rations retrieved from literature and with diet samples collected from four zoos in The Netherlands. The botanical composition of the diet provided a general overview of forage intake for both seasons, and showed lichen to be predominant in winter and (early) spring. Chemical composition of spring forage plants showed lichens to be low in proteins and minerals, however relatively high in ether extract. Conversely, birch, graminoids and dwarf shrubs were a source of protein and minerals. The diets offered to captive reindeer varied between the zoos, in which two zoos provided a single diet year round, whereas the remaining two zoos made use of cyclic feeding. Cyclic feeding is a recommended practice for reindeer as it changes the composition of diets through the seasons, and thereby reflecting the natural dietary fluctuations. It is therefore recommended that knowledge on natural forage plant intake and its nutritional composition, as well as natural foraging behaviour, is to be included in captive diet assessments.

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1 Problem description

Nutrition is one of the most critical components of animal management (Allen, 1996) as it is integral to longevity, disease prevention, growth and reproduction (Dierenfeld, 1997). The absence of proper nutrition causes numerous health problems and nutritional disorders (Hatt, 2000, Kleiman et al., 2010). The nutritional needs of many zoo animals are still not completely understood, and unique nutrient requirements and metabolic adaptations for most species have yet to be determined (Dierenfeld, 1997, Kleiman et al., 2010, Ullrey, 1995). Nutrition of wild species is often based on related domestic species that have known requirements and nutritional values for feeds (van Soest, 1996). Feeding programs based on the knowledge of domesticated livestock dietary models do offer a basis of, and insight into, nutritional requirements, however species-specific differences, e.g. unique metabolisms, behaviours, and physiologies, are not apparent in domesticated models (Dierenfeld, 1996) and therefore may significantly deviate from their wild counterparts (van Soest, 1996). Wild animals exhibit a wide range of morphological, physiological, and behavioural adaptations in order to acquire and utilize a diverse array of food (Oftedal and Allen, 1996) and temporal and spatial distributions of food resources shape the actual diet in the wild. Field research can yield important information about actual natural food items, amounts, type and, through deduction, the nutritional needs of the species (Meritt, 1980). Qualitative information on natural feeding habits, in combination with quantitative data on food nutrient composition and utilization, can provide direction for development of optimal diets for captive animal management (Dierenfeld, 1997).

Reindeer (*Rangifer tarandus*) are physiologically adapted to survive severe climatic conditions of the (sub)Arctic (Gaare, 1968, Skjenneberg and Slagsvold, 1979, White et al., 1981, Leader-Williams, 1988). Severe weather conditions are absent in captivity, however zoos continue to have difficulties maintaining a healthy population of reindeer (Ågren and Rehbinder, 2000, Cadée and Gotink, 2005). Incidents of juvenile mortality and compromised nutrition status of adults are a cause for concern among European zoos (Voith et al., 2003). Captive reindeer suffer from health problems, of which multiple, such as lactic acidosis and enterotoxaemia, are known to be caused by an inadequate diet containing high proportions of concentrate feed (Ågren and Rehbinder, 2000). Compared to other domesticated ruminants, little is known about the mechanisms of reindeer metabolism, and the nutritional requirements of the species. Existing knowledge regarding reindeer nutrition is not sufficient to properly determine a diet on which to sustain healthy captive populations. Even though it is unlikely that the ingredients of any animal's diet can be duplicated exactly in captivity, the best alternative is to determine the nutrients contained within the natural diet and provide the same proportions within a captive diet (Dierenfeld, 1996). The chemical composition and seasonal variability of reindeer forage plants has been extensively studied (Thomas et al., 1984, Nieminen and Heiskari, 1988, Klein, 1990), however such information is rarely related to diets currently provided in zoos (Dierenfeld, 1997).

This study will investigate the nutritional composition of forage plants consumed by semi-domesticated reindeer on natural pastures in northern Finland in order to contribute to the assessment of the current diets of captive reindeer. Previous studies have mainly researched the summer and winter diet composition (Danell et al., 1994, Mathiesen and Utsi, 2000, Nieminen, 1986, Nieminen and Heiskari, 1988), therefore this study will focus on spring diet composition. The outcome will add to the knowledge on reindeer forage plant composition, which will contribute to the assessment of current captive reindeer diets and the improvement of their welfare.

Research aim

The aim of this research is to gain insight into the nutritional composition of Finnish semi-domestic reindeer forage intake during spring, in order to contribute to the development of standards for the assessment of the current captive reindeer diets.

Main research questions

1. What is the nutritional composition of forage plants consumed by semi-domestic reindeer during spring in northern Finland?
2. How does the nutritional composition compare to current Dutch captive reindeer diets?

Sub-research questions

To reach the aim of this research, the main research questions have been divided into the following sub-questions:

1a. What is the botanical composition of the spring diet of semi-domestic reindeer grazing on natural pastures?

1b. What is the nutritional composition of forage plant species consumed by semi-domestic reindeer during spring?

2. What is the nutritional composition of the current diets of captive reindeer in Dutch zoos?

2 Literature review

2.1 The origin of the Finnish domestic reindeer

2.1.1 Taxonomy

Caribou and reindeer (*Rangifer tarandus*) occur in North America and Eurasia in both wild and domestic populations. In North America, domestic animals that originated from Eurasian stock are referred to as reindeer, and native wild animals are referred to as caribou. In Eurasia, wild and domestic animals are both referred to as reindeer (Cronin et al., 2003). In general, caribou are larger, more difficult to handle and more migratory. Caribou breed 2-4 weeks earlier than reindeer and not all females have antlers (Cronin et al., 2003, Reimers, 1993). There are several subspecies of reindeer and caribou recognized (Bergerud, 2000). These subspecies can be categorized based on three ecological groups:

- <u>Continental tundra ecotype</u>: Eurasian tundra reindeer (*Rangifer tarandus tarandus*), Alaska caribou (*Rangifer tarandus granti*) and Canadian barren ground caribou (*Rangifer tarandus groendlandicus*). Characteristics: appear to have longer and more slender antlers.
- <u>Woodland ecotype</u>: Eurasian forest reindeer (*Rangifer tarandus fennicus*) and North American woodland caribou (*Rangifer tarandus caribou*). Characteristics: larger body size and long legs, but short and heavy antlers.
- <u>Arctic ecotype</u>: Svalbard reindeer (*Rangifer tarandus platyrhynchus*), Peary caribou (*Rangifer tarandus pearyi*) and the extinct eastern Greenland caribou (*Rangifer tarandus groenlandicus*). Characteristics: small body size and short rostrum (Flagstad and Røed, 2003).

Figure 1 shows the distribution of the subspecies; the tundra reindeer, forest reindeer and Svalbard reindeer occur in Eurasia, while the barren ground caribou, Peary caribou, Alaska caribou and woodland caribou occur in North America (Cichowski et al., 2004).

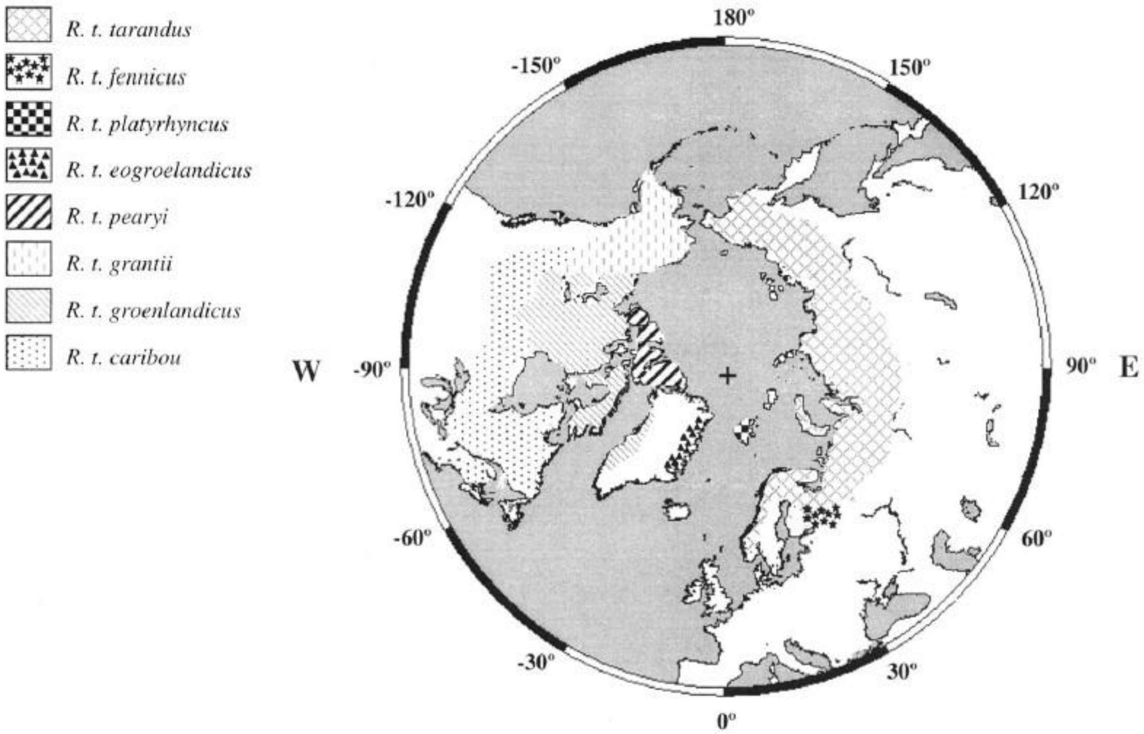

Figure 1 Distribution map of the different subspecies of reindeer (Flagstad and Røed, 2003)

2.1.2 Population and distribution

The *Rangifer tarandus* has a northern circumpolar distribution in tundra and taiga zones of northern Europe, Siberia and North America (figure 2). Reindeer are native to Canada, Finland, Greenland, Mongolia, Norway, the Russian Federation, Svalbard, Jan Mayen and the United States. Reindeer appear in Arctic and sub-Arctic areas and inhabit taiga woodlands, tundra and open mountainous lands (Nowak, 1999).

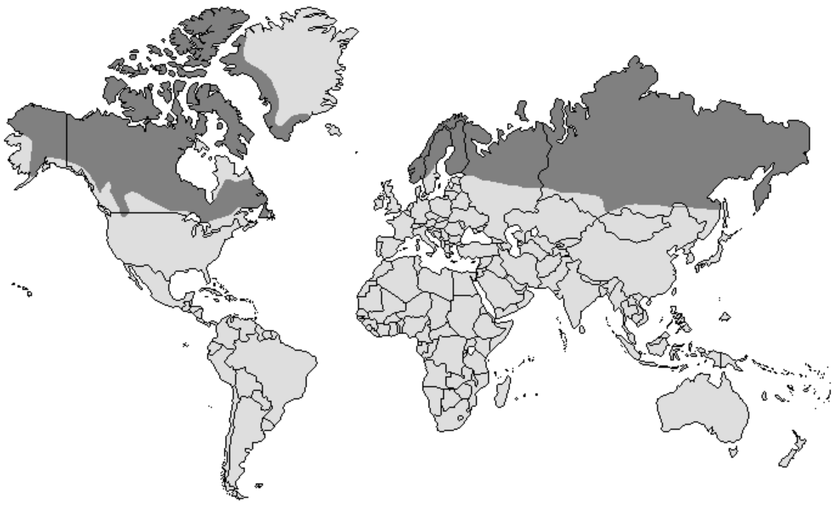

Figure 2 Global distribution of *Rangifer tarandus* shown in dark coloured patterns (Whitehead, 1993)

In Finland, the population is divided into two isolated eastern and western subpopulations. Finnish forest reindeer (subspecies *Rangifer tarandus fennicus*) were driven to extinction in the early 1900s, however have started to recover as a result of animals moving in from Karelia (Russia) and from some reintroduced captive bred stock. Forest reindeer remain rare in Finland; approximately 1.200 in the eastern subpopulation and 1.000 individuals in the western subpopulation. The Finnish population trend is difficult to determine, as the population in eastern Finland has expanded rapidly from circa 40 reintroduced individuals in 1980 to circa 1.200 today, whereas the western subpopulation has declined from circa 1.800 to circa 1.000 during 2001-2006 (in last year's prior to 2001 population had been increasing) (Henttonen and Tikhonov, 2008, Koubek and Zima, 1999).
Major threats to the reindeer in Finland are loss of habitat, mainly through logging. Furthermore, sporting activities in winter increase the disturbance of this species in some areas of Finland. The major natural predators of reindeer are bears (*Ursus arctos*) and wolves (*Canis lupus*) (Henttonen and Tikhonov, 2008).

2.2 Nutritional ecology and digestive physiology

2.2.1 Digestive system

Fermentation in herbivores occurs in large fermentation compartments as a part of their digestive tract. Due to this fermentation process, such herbivores (including reindeer) are called fermenters. Fermenters are divided into two distinct groups; the ruminants (cranial fermenters) and the hindgut digesters (caudal fermenters). Reindeer are cranial fermenters (or ruminants), which means that these animals have the ability to efficiently digest and extract energy from cellulose and hemicelluloses, and can utilize bacterial protein produced in the fore stomach. However, this group does not have the ability to utilize dietary hexose sources directly. The small intestine is the only place in the digestive tract where simple sugars and amino acids can be absorbed. (Bowen, 1998) The reindeer is classified as an intermediate feeder, between bulk and roughage feeders and concentrate selectors (Hofmann, 1989, van Soest, 1994) with a digestive system (figure 3) adapted to their rich summer diet (high crude protein and mineral content) and poor winter diet (low crude protein and mineral content) (Sundset et al., 2007). The length of the intestines is approximately 25 m; one third of the intestines consists of the large intestine and two thirds of the small intestine. The mean capacity of the reticulum and rumen is approximately 30,06 litres and weighs approximately 11,5 kg. The coiled colon is assumed to reflect the different ways of developing a large intestine of appropriate physiological length. (Westerling, 1970).

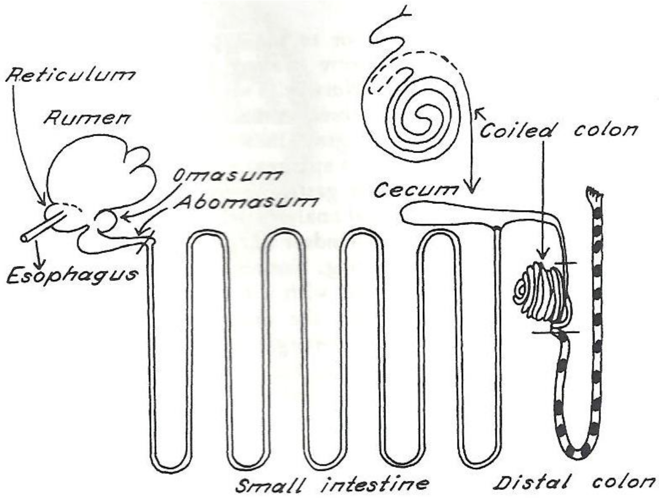

Figure 3 The alimentary tract of the reindeer (Staaland, 1984)

Reindeer have a high voluntary food intake in summer, but a low intake in winter, which forms a cyclic pattern (figure 4) (Mathiesen et al., 1999).

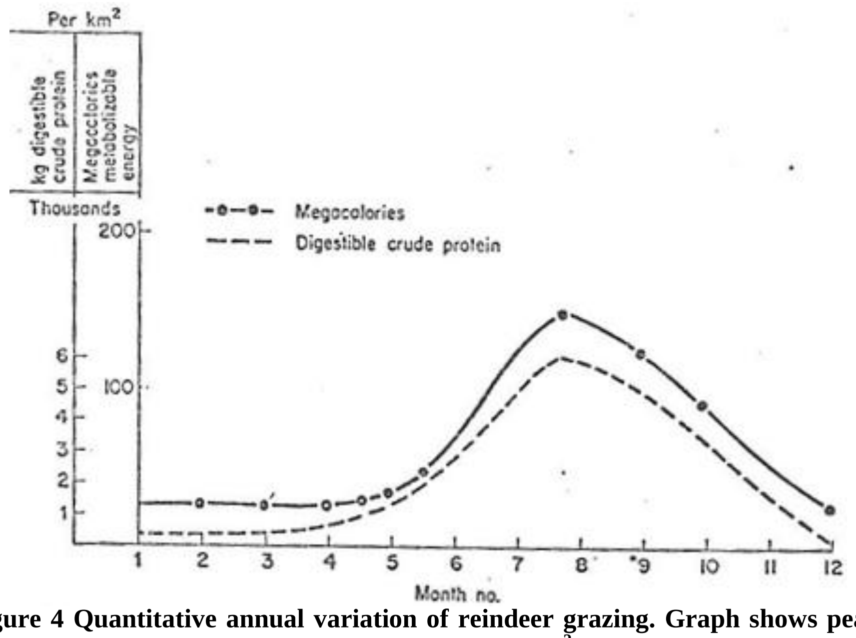

Figure 4 Quantitative annual variation of reindeer grazing. Graph shows peak of megacalories and kg digestible crude protein per km^2 during August (Steen, 1968)

In winter, reindeer select a mixed diet of lichens and vascular plants, which are low in protein and minerals and high in carbohydrates. However, in summer, reindeer select high quality vascular plants, which are high in protein and minerals and contain more starch and cellulose then winter feeds (Aagnes et al., 1995, Asplund and Nieminen, 1989). This mixed winter diet increases protein intake, which results in improved growth conditions for rumen bacteria.

(Aagnes et al., 1995) Thus, appetite and forage plant availability influence the digestion in the winter season (Mathiesen et al., 1999).

After food intake, four salivary glands (parotid, mandibular, sublingual and buccal) produce saliva. Saliva supplies alkalic substances to buffer the production of Volatile Fatty Acids (VFA), lactate and maintain the pH of the rumen close to 6.5. The mandibular glands secrete mucus and hypotonic buffer. Parotid glands secrete tannin-binding proline rich protein, which makes reindeer more tolerant for tannin in their diet. In summer, the parotid and mandibular glands are significantly greater than in autumn and winter, which is related to the quality and quantity of forage plants eaten. Big salivary glands in summer suggest a high rumen microbial fermentation (high dry matter intake). (Mathiesen et al., 1999) Moreover, saliva secretion is greater in summer (0.66 kg/kg $BW^{0.75}$) than in winter (0.5 kg/kg $BW^{0.75}$).
In winter the mineral component of reindeer saliva dry matter contains mainly potassium and is low in sodium. However, sodium is very important for the reticulo-rumen functions. Approximately 40% of the sodium secreted in the saliva can be reabsorbed in summer in the fore stomach; this percentage is up to 80% in winter. For potassium this is 60% in summer and 80% in winter. (Chalyshev, 1998)

After being swallowed, the food passes back and forth between the reticulum (1) and rumen (2) (figure 5). The bacteria in the rumen break down cellulose and other cell wall constituents in plants. These ruminal bacteria are essential for reindeer as they could not survive on a diet of plants and lichens without the bacteria in the rumen. (Dieterich and Morton, 1990) The dominant population of microorganisms in the rumen of the reindeer consists of anaerobic bacteria (*Bacteria*), methanogens (*Archaea*), ciliates and anaerobic fungi (*Eucarya*). The composition and quantity of ruminal microorganisms is influenced by the passage rates of fluid and particles through the digestive tract. Diet and the availability of the substrate for fermentation are important factors.
During the breakdown of complex plant parts by microorganisms in the rumen, Short Chain Fatty Acids (SCFA), CO_2 and CH_4 are formed. Energy-rich SCFA (e.g. acetate, butyrate or propionate) support approximately 70% of the daily energy requirement of the animal. In winter, when reindeer mainly feed on lichens, the animals maintain a high SCFA production. (Mathiesen et al. 2005) And due to this lichen diet the rumen pH is slightly acid (6.7 pH). Conversely, when reindeer mainly feed on hay or grass the rumen is on the alkaline side. (Westerling, 1970)

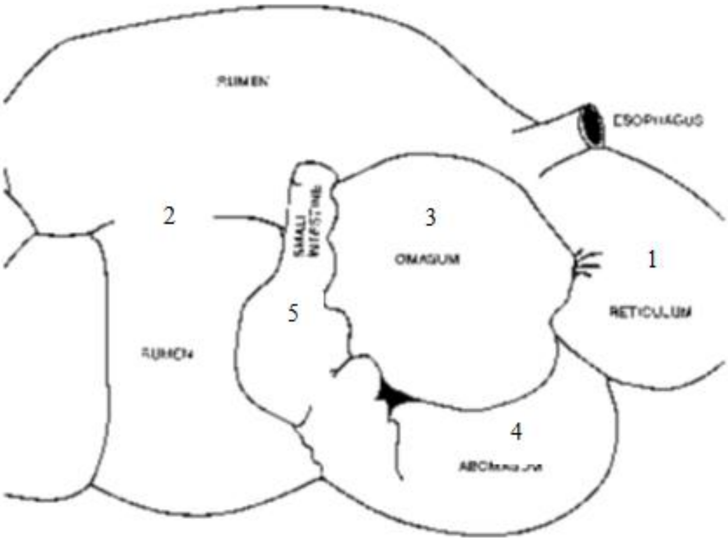

Figure 5 Ruminant stomach of the reindeer. Numbers in figure represent as following: reticulum (1), rumen (2), omasum (3), abomasum (4), small intestine (5) (Dieterich and Morton, 1990)

Usnic acid is a naturally occurring compound found in common lichens, such as *Cladonia*, *Usnea* and *Cetraria*, which protects lichens from damage by solar radiation. Usnic acid functions as a defence against pathogens and herbivores. Lichens are toxic for most herbivores (e.g. elk and sheep) at high doses. However, reindeer have the ability to consume a pure lichen diet. This indicates that reindeer have adapted to manage the otherwise toxic usnic acid from lichens. Recent research has shown that usnic acid was not present in reindeers' faeces, urine, rumen, liver or kidneys after being fed a lichen diet, which indicates complete disappearance from the gastrointestinal tract. (Sundset et al., 2010) The enzyme lichenase, which is produced by specific rumen micro-organisms, stimulates the digestion of lichenin and is the most active enzyme in acid solution. Reindeer use these specialized microorganisms in the rumen to handle lichen substances which are absent in other mammalian herbivores. (Westerling, 1970, Palo, 1993)

After being passed back and forth between the reticulum and rumen, food which is still harsh and indigestible, is brought back to the mouth and re-chewed. After being swallowed again, the food continues through the rumen and reticulum to the omasum (3). In the omasum, the food is further grinded and water is absorbed by the body. (Dieterich and Morton, 1990)
After three to four hours the grinded food passes the abomasum (4), where the food is further broken down by digestive juices and the food particles continue their way to the small intestine (5). The majority (85%) of the reindeers' feed leaves the fore stomach within four days, while the rest can remain in the reticulo-rumen (rumen and reticulum) for approximately 13 days. When the food leaves the abomasum, the nutritional content of the particles is absorbed and directed to the liver, which converts the particles into products used to produce energy for the rest of the body (e.g. maintaining body heat, reproduction, body and antler growth). Lastly, in the lower part of the intestine, the undigested part of the food is formed as pellets or faecal droppings which are passed outside the body. (Dieterich and Morton, 1990)

Water excretion
Reindeer have a high rate of water turnover and fluid balance is controlled by fluid intake and excretion. As a result, reindeer have a special kidney function; the kidney has a low medulla and is limited to concentrate urine or to excrete solute load (water content). Also, the reindeers' kidney is resistant to antidiuretic hormone (ADH). Ruminants can re-use their urea for microbial protein synthesis in the fore stomach. Reindeer can effectively use the restriction of urea losses through reducing the glomerular filtration rate (filtering of fluids from kidneys' glomerular vessels into Bowman's capsule) and increase the relative tubular urea reabsorption. This ability is useful for reindeer, since their diet consists of green vascular plants in summer and lichen in winter, which contains approximately 75-90% water. Thus reindeer have the ability to excrete surplus water without losing solutes. (Valtonen and Eriksson, 1977)

2.2.2 Energy and protein requirements

Nutritive requirements of reindeer are based on limited indoor experiments. Two requirement standards were produced by the USSR and Sweden. In table 1, the Swedish standard nutritive requirements of reindeer, according to Steen (1968), are given.

Table 1 Standard nutritive requirements of the average reindeer living in a free environment (Steen, 1968)

Per day	Female		Male	
1. Full production (summer/early autumn)				
Megacalories	7.0		9.5	
Megajoules	29.28		39.75	
Digestible protein (g)	315		425	
	Summer	Winter	Summer	Winter
2. Maintenance only (rest of the year)				
Megacalories	3.3	5.1	5.1	6.2
Megajoules	13.82	21.35	21.35	25.96
Digestible protein (g)	115	(150)	150	(190)

During the green (growing) plant period (summer/autumn) these requirements are most likely met. However, during the winter these requirements cannot be fulfilled. Previous research showed that the lichen diet in winter lacks in protein and minerals and has a negative nitrogen balance. Only during good lichen grazing conditions in winter, the animals can store fat, which is used as a surplus energy for production. Reindeer have a productive period during summer and early autumn, whilst the remaining seasons are for maintenance or sometimes even starvation periods. (Steen, 1968)

The requirement standards in Sweden differ in some respects from the USSR. Table 2 shows a comparison of the nutritive requirements developed by the USSR and Steen (1968). The biggest difference is that Steen (1968) considers winter for maintenance only, while the USSR consider this season for needing more energy and food due to the low temperature and energy needed for digging for food. Contrary, Steen (1968) believes that reindeer in summer have high nutritive requirements for maintenance and production (grow, gain strength and increase body weight for the winter). (Westerling, 1970)

Table 2 Comparison of nutritive requirements per 100 kg body weight (Westerling, 1970)

Per day	USSR	Sweden
1. Production & maintenance (summer)		
Megacalories	6.4 – 8.0	10.4
Megajoules	26.78 – 33.47	43.51
Digestible protein (g)	45 – 50	462.5
2. Maintenance only (winter)		
Megacalories	9.6 – 11.2	7.2
Megajoules	40.17 – 46.86	30.12
Digestible protein (g)	100	212.5

2.2.3 Physiology

Basic physiological functions (such as survival, growth and reproduction) are modulated by seasonal changes, the availability and quality of forage plants, and the reindeers' ability to utilize the plant carbohydrates and proteins. Growth and survival are dependent on seasonal climatic factors. From late October until early May the light intensity remains below twilight, whereas from mid-June until July the sun never sets. These seasonal changes in temperature and daylight have an influence on the seasonal physiology of reindeer, including appetite and reproduction. (Pösö, 2005, Mathiesen et al., 2005)

Seasonal changes in hormones

Adaptation to the variation in temperature and food availability requires metabolic changes, which are initiated and maintained by hormones. The presence and absence of daylight affects the reindeers' physiology through the pineal gland and its hormone, melatonin. This hormone plays a role in the regulation of reproduction, fur growth, thermogenesis, body mass and immune function. Melatonin is produced during the dark period in the winter. The daily rhythm of a reindeer disappears during the Arctic summer, but returns again in autumn. The absence or presence of melatonin enables reindeer to distinguish day from night and regulate sleep cycles and the circadian rhythm. The duration of the melatonin pulse allows reindeer to distinguish short days from long days', and the direction of the change is used to recognize seasons. (Pösö, 2005)

Besides melatonin, thyroid hormones, insulin and leptin also indicate seasonal changes. Thyroid hormones quantity increases when the temperature is low, which plays an essential role in the regulation of basal metabolic rate. Thyroid hormones T3 (triiodothyronine) and T4 (thyroxine) concentrations change per season, but also according to the feeding pattern of the individual reindeer. Leptin has effects on appetite, thermogenesis and reproduction, and it plays an essential role in the regulation of body energy homeostasis. In reindeer, leptin decreases during winter and by food deficiency. Lastly, insulin is one of the essential hormones which regulates metabolism, and in reindeer, levels of insulin decrease during winter. (Pösö, 2005)

Seasonal changes in energy balance

In winter, reindeer have a negative energy balance. Due to changes in concentration of the hormones melatonin (increase) and leptin (decrease), appetite is reduced during this season. The availability and quality of food, and demand for energy for heat production, contribute to the negative energy balance. As a result, energy reserves built up during summer need to be utilized in order to survive. This survival strategy is used, because the availability of forage plants cannot be predicted at the beginning of the winter. This strategy is based on economic and controlled use of energy stores; approximately 85% of energy is stored in body fat under the skin or around internal organs and bone marrow. The remaining 15% is body protein. Survival chances are also increased through adequate insulation (fur coat) and decreasing time spent moving. (Pösö, 2005)

Circannual changes in lipid metabolism

Lipid reserves are at a maximum in October and reach their lowest point between April and June. Lipid build-up is determined by the balance between lipolysis and lipogenesis (Kersten, 2001). Lipolysis and lipogenesis are regulated so these processes are not active simultaneously. During winter, the lipogenesis process rate is low, whereas during summer this rate is high. During fat reserve usage, the rate of lipolysis is controlled and the use of fatty acids in tissues (e.g. muscles) decreases. Only during severe starvation the rate of lipolysis increases adequately to give rise to an increase of ketone bodies. After the starvation, only the protein mass is maintained and used for energy production. (Pösö, 2005)

Seasonal changes in protein metabolism

Lichen, reindeers' main winter feed, is low in nitrogen (< 1% dry matter) in comparison to green vascular plants (> 1% dry matter). Feed intake is reduced in winter (due to hormone influences) and the diet exists mainly of lichens, which results in a negative nitrogen balance in winter. Pregnant females have to catabolise own tissues to produce amino acids, which are needed for growth of the foetus and later for milk proteins. In winter, a decrease in urea concentration is seen, because urea is recycled to the rumen. Increased urea concentration in urine indicates severe starvation and the use of body protein as an energy source. Body protein mass is greatest in October (during winter approximately 29%) and lowest in late spring. (Pösö, 2005)

2.2.4 Natural diet

Reindeer are highly adapted to their native habitats of Arctic tundra and taiga lands (Dieterich and Morton, 1990). The food habits of free-ranging reindeer are similar throughout the northern Arctic (Kelsall, 1968). Their natural diet consists of approximately 250 species, though 106 species are most important, which consists of lichens, grasses, herbs, woody species, mushrooms, shrubs and horsetail (Skuncke, 1958).

The reindeer diet undergoes a notable seasonal variability due to climatic extremities. Food selection of herbivores is dependent on availability and quality which vary among plant species and with the seasons (Danell et al., 1994). Reindeer follow the annual cycle in forage quality and quantity, and therefore their annual dietary cycle reflects this relationship (Klein, 1990). A hypothetical model, set up by Klein (1990), depicts the relationship of reindeer diet and their annual physiological cycle and seasonal changes in the environment.

In general, their diet changes from being high in carbohydrates and lichen-dominated during winter (Heggberget et al., 2002), to protein-rich and dominated by herbs, shrubs and grasses during summer (Nieminen and Heiskari, 1988, Klein, 1990, Gaare and Skogland, 1975).

Reindeer are physiologically adapted to the annual dietary changes by alterations in rumen bacteria composition in order to properly digest lichens (Pösö, 2005). The body mass of reindeer fluctuates annually as a consequence of seasonal food availability and quality and body maintenance and reproduction (see figure 6a,b).

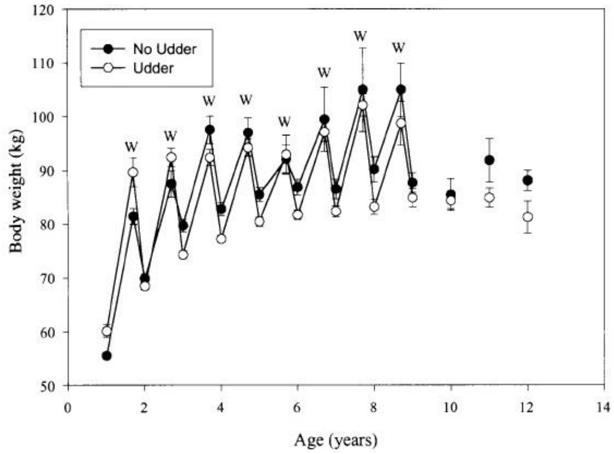

Figure 6a Summer and winter (mean) body weights of female reindeer based on presence or absence of an udder during summer handling ('W' indicates winter weights). Note body mass fluctuations between winter and summer. (Finstad and Prichard, 2000)

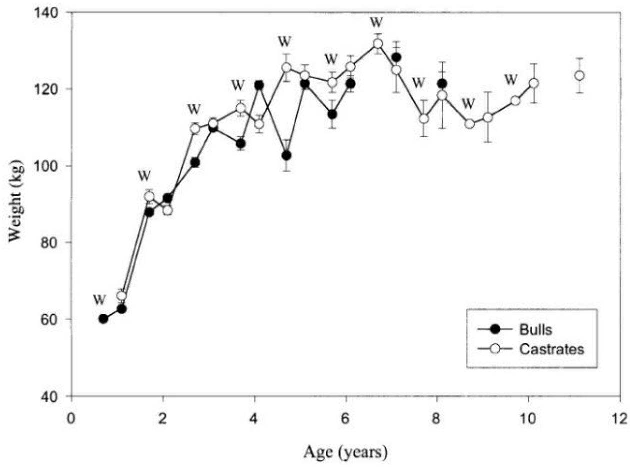

Figure 6b Summer and winter (mean) body weights of bull and steer reindeer in Western Alaska ('W' indicates winter weights). Note body mass fluctuations between winter and summer. (Finstad and Prichard, 2000)

Seasonal weight fluctuations are observed in both female and male reindeer (Leader-Williams and Ricketts, 1982, Finstad and Prichard, 2000). Females tend to be lighter in summer than in winter, whereas males are heavier in summer than in winter (Finstad and Prichard, 2000). This difference is occurs as a result of increased expenditure of resources during early spring and summer to maintain faetal development and lactation. In contrast, males expend body reserves during rut in the autumn and early winter (McEwan, 1968). Their annual diet coincides with the physiological cycle of reindeer with stagnated growth and body maintenance during winter, and high nutritional demands for protein to support growth and lactation during late spring and summer (Klein, 1990, Van der Wal et al., 2000). During summers' selective feeding, reindeer are able to increase the digestibility of their ingested forage and their total dry matter intake, thereby considerably increasing their daily intake of metabolisable energy (White, 1983).

2.2.5 Seasonal variability

The annual cycle is determined by the seasons, which in northern Finland are defined as listed in table 3.

Table 3 Definitions of season duration in northern Finland (FMI, 2011)

	Duration
Spring	Early May – end June
Summer	End June – mid-August
Autumn	End August – mid-October
Winter	Mid-October – early May

A description of seasonal reindeer body condition and forage intake is listed in table 4. Reindeer food intake varies seasonally in an annual cycle and is characterized by plant availability and quality. In late spring, as the snow begins to melt, reindeer actively seek out fresh green vegetation as the new forages appear. Reindeer tend to follow new emerging plant growth, which is of high nutritional value, and move into new areas as the emergence of new growth proceeds along climatic gradients (Klein, 1970, Skogland, 1980).

During the summer months forage is abundant and the diet consists of a wide variety of plants including shrubs, sedges, heaths, grasses, and lichens. As the deciduous forages mature and become fibrous, reindeer select increasing amounts of lichen. This transition continues through late autumn, when lichens become the predominant forage food. Throughout winter and early spring when forage is often in short supply, lichens are consumed extensively. Reindeer are unique in their ability to survive on lichens during long winter grazing period (six to eight months) (see figure 7).

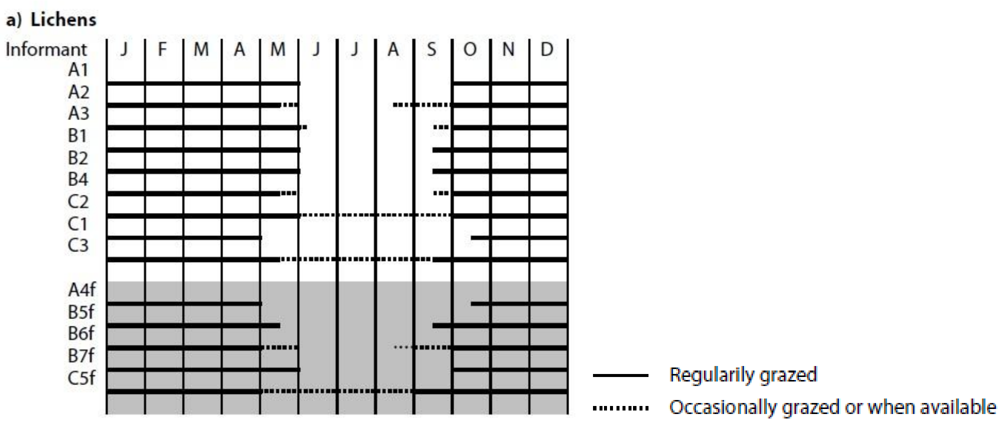

Figure 7 Seasonal use of lichens by semi-domesticated reindeer (based on interviews with 14 reindeer herders in northern Sweden (each horizontal line represents one informant)). (Inga, 2007) Note the seasonal decrease during summer season when other, more qualitative, forage is available.

In figure 7 is shown that reindeer consume lichens regularly during most seasons, especially during winter months, when other forage is unavailable. Lichens are low in mineral and protein content, but rich in soluble carbohydrates, which are used as a source of maintenance energy. For reindeer, lichens are highly palatable and easily digestible, however due to low mineral and protein content, a mixed diet is needed to ensure uptake of essential nutrients (Nieminen and Heiskari, 1988, Nieminen and Helle, 1980).

Adequate forage intake during winter is important for the survival of reindeer due to the extreme cold temperatures during winter, which requires higher energy demands for thermoregulation (Holleman et al., 1979). During spring and summer, the availability of nutritious forage is particularly critical to female reindeer for calving and lactation. Reindeer with access to high-quality forage produce more milk (Chan-McLeod et al., 1994) and recover faster from winter loss of body condition (Chan-McLeod et al., 1994, Adamczewski et al., 1987).

Table 4 Summary of seasonal variation of reindeer body condition and behaviour, forage plant intake and grazing usage of habitat.

Season	Body condition / behaviour	Intake	Grazing resources
Spring	Most reindeer are in a compromised condition after the winter season, and spring diets compensate for limited nutrient intake of the winter months. Tussock cotton grass flower buds and early inflorescences are extremely important to milk production and survival of reindeer calves on the calving grounds in spring due to their low lignin content (3,3 %) and high crude protein content (18 %) (Griffith et al., 2002). During late spring plant foods become more abundant and are of increasing nutritional value (Dieterich and Morton, 1990).	Snow disappears and lichen intake decreases to a minimum. Plant selection shifts to available fast-growing green plants; green shoots and other vegetative parts of grasses, shrubs, and sedges. First emergence; sedges (*Carex* spp.), followed by shrubs, of which most preferred bilberry (*Vaccinium myrtillus*). Shoots, new spring buds and young leaves of shrubs and forage trees (e.g. birch (*Betula* spp.) and willow (*Salix* spp.)) are preferred due to high protein levels (Mårell et al., 2006, NRC, 2007). Dry heaths and wet grassy meadows (*Dupontia fischeri*, *Dryas integrifolia*, *Eriophorium angustifolium*) are extensively fed on.	Wet boggy areas are avoided due to mosquitoes and other stinging insects (Dieterich and Morton, 1990). Female reindeer seek areas where snow melts and vegetation growth starts early, e.g. southern slopes (Danell and Nieminen, 1997, Skjenneberg and Slagsvold, 1968). In mountain herding districts males may stay in the lowlands, where green forage appear earlier (Danell et al., 1999, Skjenneberg and Slagsvold, 1968, Skogland, 1989).
Summer	Body weight increases and body condition improves (Dieterich and Morton, 1990). Reindeer follow new emerging plant growth rapidly; selective feeding on high quality food to store minerals and proteins to restore depleted body reserves of nutrients and accumulate fat, to increase chances of survival in winter (Nieminen and Heiskari, 1988, Staaland, 1984). In midsummer, plants attain peak nutritional content and quality, and reindeer attain peak body condition for winter survival (Klein, 1970, Klein, 1990).	Forage plants consist of grasses (*Carex aquatilis* and *Dupontia fischeri*), sedges (*Eriophorum angustifolium*, *Carex microglochin*, *C. rubestris*, *C. rofunda*), shrubs (*Salix spp*, *Vaccinium myrtillus*), glandular birches (*Betula glandulosa*, *B. nana*). Important willow species are *Salix lapponum*, *S. lanata*, *S. hastate*, *S. herbacea*. Most prominently consumed tree species: dwarf birch (*Betula nana*), mountain birch (*B. tortuosa*), downy birch (*B. pubescens*), aspen (*Populus tremula*), and grey alder (*Alnus incana*). (Kurkela, 1976) During midsummer, horsetail (*Equisetum* spp.) and bogbean (*Menyantes trifoliate*) are consumed. Lichens make up 20 % of the summer diet (White, 1983) and they are eaten selectively and preferred when moist (White and Trudell, 1980).	Area usage shifts to open forests (mountainous birch forest) and wetlands with early growth of palatable vegetation (Danell and Nieminen, 1997, Skjenneberg and Slagsvold, 1968). Midsummer, grazing areas are higher mountains or on plains and heaths, where the wind makes heat and insects less troublesome (Skjenneberg and Slagsvold, 1968, Skarin et al., 2010).
Autumn	The condition of male reindeer can attain weights up to 200 kg before the rut, but much of their body resources are lost during the 2-3 weeks of rutting, when males are pre-occupied with gathering and fighting for their harems (Skjenneberg and Slagsvold, 1979). Forage plant selection shifts from grasses and sedges to leafy green plants. Quality of available plant species decreases due to increasing fibre levels and decreasing protein levels (van 't Hof, 1993). However crude fibre content in grass and sedge hays is efficiently used by reindeer for digestibility. Fungi are highly important for nutrition and vitamins (Nieminen and Heiskari, 1988) (Kitti et al., 2006) as they are high in protein, fat and minerals. Lichen intake increases to 20-50 % as snow starts to cover pastures and other plants decrease in quantity.	Green leafy parts of woody perennials: bearberry species (*Arctostaphylos alpine, A. rubra)*, bog blueberry (*Vaccinium uliginosum*), sub-Arctic rhodondendron (*Ledum decumbens*), black crowberry (*Empetrum nigrum*), Lapland rosebay (*Rhodondendron* sp.) (Nieminen and Heiskari, 1988). White mountain avens (*Dryas integrifolia*), several *Salix* spp, and various herbs and forbs (*Pedicularis* sp.) (Dieterich and Morton, 1990). Most important mushrooms: *Boletus* spp., *Polyporus*, *Helvella*, *Calvatia* sp., *Bovista nigrecens* (Kurkela, 1976)	Early autumn grazing lands are birch forests and marshlands for access to grass and herbs (Skjenneberg and Slagsvold, 1968). Mid autumn main grazing in lower mountains, while the vegetation withers and its nutrient content declines (Skjenneberg and Slagsvold, 1968) and in sparse forests and marshlands.
Winter	Body condition is often poor by the end of winter due to low nutrient intake of low-quality forage (Van der Wal et al., 2000). Diet composition is influenced by restricted forage availability due to snow cover (Bjørkvoll et al., 2009). Limited feed availability becomes critical when ground vegetation is unavailable due to deep snow cover or ice crust formation. Effect of snow/ice limits feed intake which results in inadequate nutrition and may lead to complete starvation. (Nilsson, 2003) Body substance decreases due to the very low protein, ash and fat content and high crude fibre of lichens.	Lichens (mostly *Cladina* spp., *Cladonia* spp., and *Cetraria* spp.). On dry and barren sites in northern Finland, *Cladonia stellaris* is predominant (Helle and Aspi, 1983). Lichens can make up 50-80% of winter diet under good pasture condition (Kumpula, 2001). Wintergreen plants; forest wiregrass (*Deschampsia flexuosa*), cotton grass (*Eriophorum* spp.), horsetails (*Equisetum* spp.), sedges (*Carex* spp.). Occasionally consumed; shrubs (*Empetrum* spp. and *Vaccinium* spp.), bogbean (*Menyanthes trifoliate*), marsh cinquefoil (*Comarum palustra*) and arboreal lichens *(Alectoria* and *Bryoria* sp.) (Boertje, 1990, Mathiesen et al., 2000, Nieminen and Heiskari, 1988).	Early winter grazing takes place in forest and marshland for green vegetation, due to snow on ground in open areas (Skjenneberg and Slagsvold, 1968, Warenberg et al., 1997). Mid winter main grazing is in forest areas. Older sparse forests are preferred as grazing grounds (Roturier and Roue, 2009, Inga, 2007, Kumpula and Colpaert, 2007). Late winter, old forests rich in arboreal lichens are essential.

2.2.6 Ex-situ diet

The dietary requirements of reindeer for many nutrients have not been specifically determined (Fuller, 2004). Current information available on the diet of Eurasian tundra reindeer and Forest reindeer in Dutch zoos has been based on a thesis research project of 2005 (Cadée and Gotink, 2005), which is based on chemical analysis of diets in six zoos (Aqua Zoo Friesland, Burgers' Zoo Arnhem, Dierenrijk Europa Mierlo, Kasteelpark Born, Kerkrade Zoo, Ouwehands Zoo Rhenen). The content was analysed for dry matter, ash, minerals, crude fibre, neutral detergent fibre, acid detergent fibre and acid detergent lignin.

However, diets fed to wild animals in captivity should meet the nutritional needs of the animals and should take into account variability in digestive physiology and natural feeding behaviour. Providing appropriate quantities and quality of required nutrients is critical to avoid nutrition-related diseases. Many diseases observed in captive wildlife are the result of dietary nutrient deficiencies; the animal’s inabilities to synthesize, transport, or metabolize specific nutrients; and excessive dietary intake or absorption of nutrients. (Kleiman et al., 2010) Animals that are stressed due to being immune compromised, such as by poor nutrition, concurrent diseases are more likely to get infection or are less able to fight off infections (Bartlett et al., 2009). Lactic acidosis, enterotoxemia, wet belly syndrome, laminitis, splenomegaly are examples of conditions often seen under poor nutrition (conditions described in more detail in appendix III).

3 Methods

3.1 *Study site*

The Riista- ja Kalatalouden TutkimusLaitos (RKTL) (in English: Finnish Game and Fisheries Research Institute (FGFRI)) assesses, compiles statistics and predicts fishery and game resources, and maintains the diversity of fish populations. This organisation aims to produce scientific information for sustainable use of natural resources and to help maintain biodiversity through research and aquaculture. The institute is part of the Ministry of Agriculture and Forestry. (RKTL, 2011)

To obtain information about all the Finnish game and fishery resources, the organization is divided into different units at different stations throughout Finland. The Game and Reindeer Research unit is important for this research. This unit studies game and reindeer populations, their habitats and husbandry. (RKTL, 2011)

The Game and Reindeer Research unit is located at the Reindeer Research Station, located near Kaamanen (69° 3' 0" North, 27° 0' 0" East) (see figure 8). This station has various studies conducted by researchers from Finnish and foreign universities and other organisations. Those studies focus on pastures, population dynamics and herding. Studies of the economy of reindeer husbandry are in cooperation with the Finnish Game and Fisheries Research Institute socioeconomic and aquaculture research programs. The aim of these researches is to advance their knowledge and to share newfound ideas in an effort to sustain and improve reindeer husbandry in Finland. (RKTL, 2011)

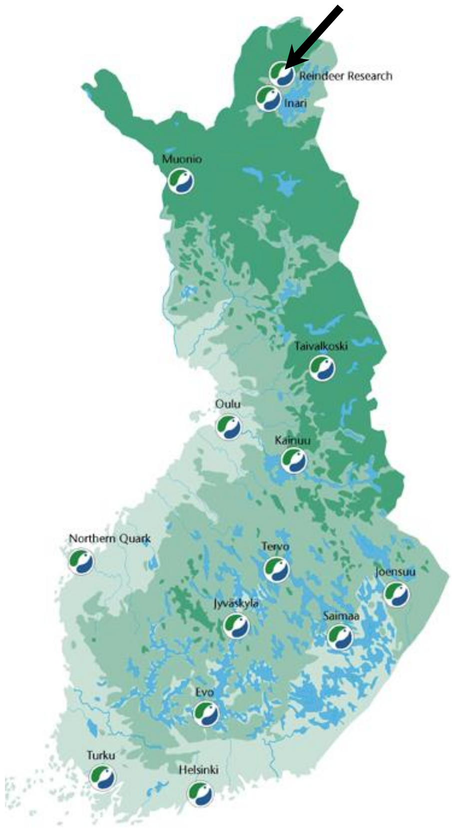

Figure 8 RKTL has stations throughout Finland, located near clients and research sites. The arrow shows the location of the Reindeer Research Station in Finland. (RKTL, 2011)

3.2 *Research population*

The reindeer study population is located approximately 30km from the Reindeer Research Station (near Kaamanen, Finland) on the Muddusjärvi winter range. The semi-domestic reindeer herds graze freely on natural pastures, however do receive supplementary feed during winter and spring season. The supplementary feed type and quantity varies between herders, but commonly consists of pre-dried silage, commercial feed pellets and optional dried lichen and dried sedge. The Reindeer Research Station does not keep reindeer, however cooperates with Kutuharju; a large experimental field station located at a distance of 20 km. Kutuharju covers 43 km^2 of natural pasture with approximately 200 adult reindeer owned by the Reindeer Herders' Association (Lauvergne and Nieminen, 2010, Kumpula, 2011). The Reindeer Research Station is located central to Sámi reindeer herding areas and several reindeer herding cooperatives, where reindeer graze on either purely natural pastures or are provided with supplementary food in winter (Kumpula, 2011).

3.3 Working method

3.3.1 Overview

Field sampling was carried out at the study site (Muddusjärvi winter range) during spring throughout May 2011, which consisted of forage plant sample collection and faecal sample collection. Forage plant species were determined and collected based on existing knowledge and previous research at the study site. Of each collected plant species, the nutritional content was analysed following the Weende-analysis, van Soest analysis and mineral content (calcium, magnesium and phosphorus) at the Van Hall Larenstein laboratory, The Netherlands. Faecal samples were collected at the study site to determine what traces of plant groups can be found within the spring diet of reindeer. The results of the microhistological analysis of spring faeces were compared to results of previously collected winter faecal samples (2007-2008) to determine whether differences in plant group proportions could be found within and between these seasons. Reindeer herders provide their reindeer with different supplementary feed throughout the seasons, therefore interviews were held with local herders to determine what additional feed reindeer herds receive during spring. The results of forage plant nutritional content was compared to the nutritional content of diets of captive reindeer herds kept in six Dutch zoos, of which a comparative analysis was made, to assess current reindeer zoo diets.

3.3.2 Data collection

Data collection consisted of the following three components: botanical composition of the reindeer diet (I), analysis of the nutritional composition of the in-situ diet (II), and comparative analysis of the nutritional content of the ex-situ diet as described in literature (III).

I. Botanical composition reindeer diet

Microhistological analysis of faeces was used to determine the proportions of plant groups[1] (lichen, arboreal lichen, grass/sedge, shrub and moss) that make up spring diet (botanical composition) of reindeer. For comparisons, winter faecal samples were also analysed, using similar methods, to determine whether any changes exist in plant group proportions between seasons.

Faecal sample collection

Spring faecal sample collection was limited to fresh faeces, because of probable plant part damage in older samples caused by insects, bacteria or fungi (Ward, 1970). Fresh samples were collected either after observations of defecating individuals or by recognition the characteristic strong odour, layer of mucus and no signs of dehydration (Barja et al., 2007). The number of pellets within a sample varied depending on availability, however faecal consisting of less than five pellets were not collected. The samples were stored in a freezer (-20°C) to eliminate the possibility of spoiling faecal samples which may reflect in the results.

Faecal preparation and microhistological analysis

Faecal samples were prepared following the methods of Hansson (1970) and Viro & Sulkava (1985) (see Appendix I). Three subsamples were made of each faecal sample, and of which each subsample five microscopic window views were randomly chosen for analysis. In each

[1] For practical purposes of this thesis, the term ‘plant’ also includes lichens.

view, relative proportion of each visible plant group (lichen, arboreal lichen, grass/sedge, shrub, moss, others) was calculated (see Appendix II).
Spring faecal samples (n=17) collected during this study were compared to winter faecal samples (n=6) collected between December 2007 and April 2008 at the study area. Winter faecal sample collection method differed from collection method used for spring. During winter collection, reindeer feeding craters were used to collect approximately 500 grams fresh faeces of multiple reindeer (6-10 individuals) which was mixed together to create pooled faecal samples. Five subsamples were made of each faecal sample, of which from each subsample, ten windows were randomly chosen for analysis. Faecal collection method differed between seasons. However, this was disregarded for analysis due to number of collected samples to represent each season.

Faecal statistical analysis
For purposes of statistical analyses, measurements of plant groups lichen and arboreal lichen were combined. Statistical analyses that were performed (based on mean values derived from microhistological analysis):

- <u>Independent samples t-test</u> to determine whether significant differences exist for plant group proportions between seasons (spring and winter);
- <u>Multivariate ANOVA</u> to test whether there are significant differences in plant group proportions throughout spring collection period (early, mid, late).

Forage plant collection
Forage plant species to represent spring diet were collected based on species availability, previous research and expert advice (Kumpula, 2011). Collected plant groups consisted of species of lichen, arboreal lichen, dwarf shrubs, graminoids, moss and birch. Plant parts were collected from a reindeers foraging perspective (Danell et al., 1994) which entailed specific plant parts (buds, leaves, branches) and new, green parts to be sampled that are primarily consumed (Crête et al., 2001, Mårell et al., 2006, Johnstone et al., 2002).

II. Nutritional composition of in-situ diet

Plant sample preparation and chemical analyses
Plant collection was followed by the removal of all waste material from each species and plant species were divided per plant part (e.g. lichens were divided into upper part containing the living top layer and lower part containing the dead thallus[2]). The samples were dried in ovens at 104°C for a minimum of 12 hours. The weight of each plant sample was recorded before and after drying to determine water content. Plant species were grinded as a final preparation for chemical analyses. The chemical analyses of all plant species were conducted at the laboratory at Van Hall Larenstein, the Netherlands, which included the Weende-analysis, van Soest analysis and calcium, magnesium and phosphorus analysis following the standard procedures of the Association of Official Analytical Chemistry (A.O.A.C., 2005). This study accepted standard deviations of 5-6% of mean values were accepted for all nutrients.

[2] Thallus is defined as a plant body that is not differentiated into stem and leaves and lacks true roots and a vascular system. Thalli are typical of algae, fungi, lichens, and some liverworts. (Simpson & Weiner, 1989)

III. Comparisons nutritional content between in- and ex-situ diets (III).

Zoos in The Netherlands provided the opportunity for current diet analysis of captive Eurasian tundra reindeer and forest reindeer (*Rangifer tarandus fennicus*). Captive reindeer rations were retrieved from literature (based on the thesis by Cadée and Gotink, 2005) and collected from the zoos: Aqua Zoo Friesland, Burgers' Zoo Arnhem, Dierenrijk Europa Mierlo, Gaiapark Kerkrade Zoo, Kasteelpark Born and Ouwehands Zoo Rhenen, for comparative analyses. The nutritional content of the captive reindeer rations were compared to the Finnish semi-domestic diet. Comparisons of feedstuffs were based on ingredients and nutritional value of captive diets and nutritional composition of semi-domestic reindeer.

4 Results

4.1 Botanical composition reindeer diet

Results of microhistological analysis of faeces indicate that reindeer forage on a range of plants in both spring and winter, and select a mixed diet divided into six principal plant groups: lichens, arboreal lichen, grass/sedges, shrubs, moss and other. Mean percentages of relative proportions (of microscopic window views) of the plant groups are listen in table 5. In the shift from winter to spring, the results show an increase in grass and sedge proportion and a decrease in shrub proportion. Additionally, the results suggest that lichen is the predominant forage plant species both in winter and spring.

Table 5 Mean percentages (%) and standard deviations (± s.d.) of six principal plant groups in spring (2011) and winter (2007-2008) derived from microhistological analysis of reindeer faeces. Percentages are based on the relative proportions of plant groups of the total microscopic window view.

	Lichen	Arboreal lichen	Grass/sedge	Shrub	Moss	Other
Winter	39.57 ± 11.07	0.30 ± 2.25	10.29 ± 3.86	32.55 ± 9.77	14.73 ± 8.17	0.12 ± 0.18
Spring	44.64 ± 12.23	2.74 ± 0.40	17.85 ± 7.44	21.93 ± 7.84	15.25 ± 4.81	0.03 ± 0.12

The results of faecal samples collected during winter (2007-2008) and spring (2011) were compared to determine differences in plant groups consumed within and between the seasons. For all statistical analyses, plant groups ‘lichen’ and ‘arboreal lichen’ were joined together. Plant group ‘other’ is left out, because of the low mean proportion (0.03-0.12 %) found in the faecal analysis. In the first statistical analysis, independent samples t-test showed significant increase for plant group proportions grass/sedge ($p = 0.020$) and a significant decrease for shrub ($p = 0.009$) between seasons winter and spring (see figure 9 and table 6). No significant increase of decrease was found for lichen ($p = 0.538$) or moss ($p = 0.920$).

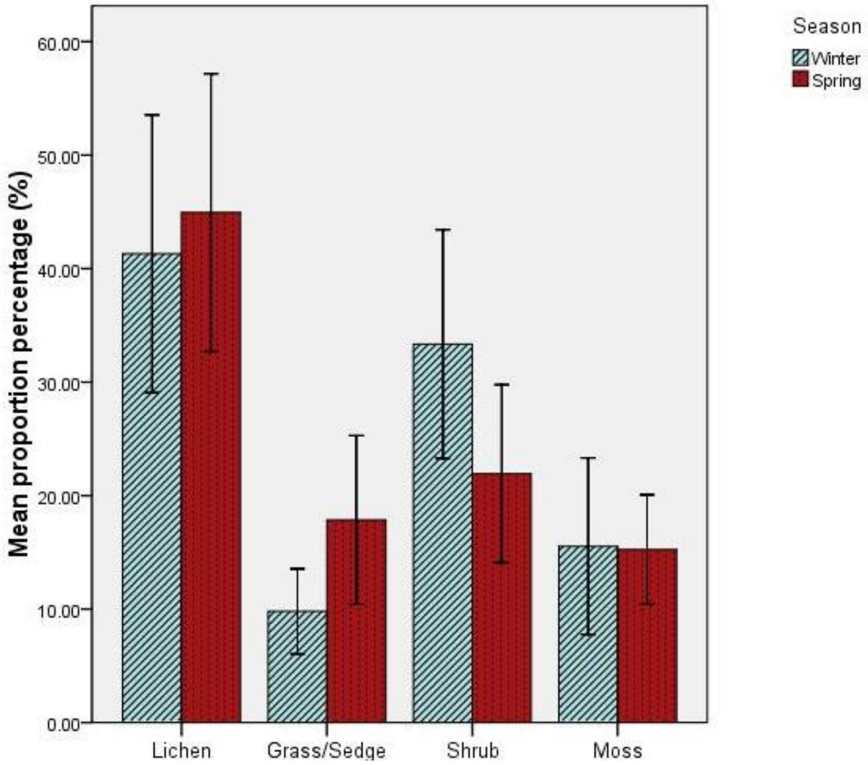

Figure 9 Microhistological analysis of reindeer faeces collected during winter 2007-2008 and spring 2011. Graph shows mean relative proportions (%) and standard deviations (± s.d.) of different plant groups found between seasons, with significant increase for grass/sedge (p=0.020) and significant decrease for shrub (p=0.009). Plant groups ‘lichen’ and ‘arboreal lichen’ groups were combined, and plant group ‘other’ were excluded from all analyses.

Table 6 Mean relative proportion (%) and standard deviation (± s.d.) of the four plant groups in winter (2007-2008) and spring (2011) derived from microhistological analysis of reindeer faeces (figure 10).

	Lichen	Grass/sedge	Shrub	Moss
Winter	41.32 ± 12.23	9.80 ± 3.76	33.36 ± 10.07	15.53 ± 7.78
Spring	44.95 ± 12.22	17.86 ± 7.43	21.94 ± 7.84	15.26 ± 4.81

Multivariate ANOVA was performed to calculate potential differences in plant group proportions between spring collection time (early, mid, late). Spring collection time is divided by early (1 May-10 May), mid (11 May-20 May), and late (21 May-30 May). Between early and late spring collection periods, a significant decrease was found for lichen (F=4.449, df=2, p=0.032) and increase in grass/sedge (F=20.457, df=2, p=0.000) (see figure 10 and table 7). There were no statistically significant differences in proportions for shrub (F=1.383, df=2, p=0.283) or moss (F=0.922, df=2, p=0.420). Due to small sample size within winter season (n=6), no tests were performed to analyse within winter collection time differences for all plant groups.

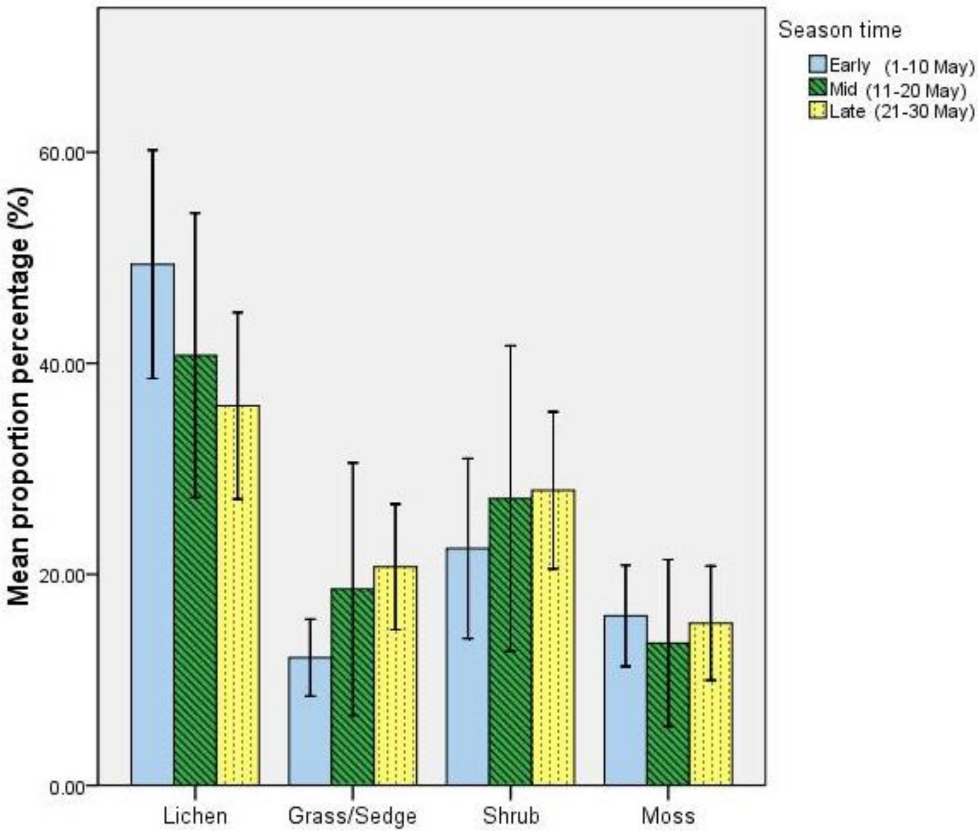

Figure 10 Microhistological analysis of reindeer spring 2011 faeces. Graph displays relative proportions (%) and standard deviations (± s.d.) of different plant groups for different times in spring season (early, mid, late). Significant shifts in plant proportions during spring were for decreased lichen (p=0.032) and increased grass/sedge (p=0.000). Plant groups 'lichen' and 'arboreal lichen' groups were combined, and plant group 'other' were excluded from all analyses.

Table 7 Mean relative proportion (%) and standard deviation (± s.d.) of the four plant groups throughout spring season (early, mid, late) derived from microhistological analysis of reindeer faeces (figure 11).

	Lichen	Grass/sedge	Shrub	Moss
Early spring	49.38 ± 10.83	12.10 ± 3.64	22.45 ± 8.53	16.08 ± 4.80
Mid spring	40.75 ± 13.48	18.60 ± 11.96	27.18 ± 14.47	13.48 ± 7.91
Late spring	35.97 ± 8.85	20.70 ± 5.95	27.96 ± 7.44	15.37 ± 5.41

4.2 Nutritional composition reindeer forage plants

Forage plant samples comprising of lichens (*Cladina stellaris*, *C. rangiferina*, *C. mitis*, *Cladonia uncialis* and *C.* spp.), arboreal lichen (*Bryoria fuscescens*), dwarf shrubs (*Vaccinium vitis-idaea*, *V. myrtillus* L., *Empetrum nigrum* ssp. *hermaphroditum*), graminoids (*Eriophorum vaginatum, Carex rostrata*, *Deschampsia flexuosa*), moss (*Pleurozium schreberi*) and birch (*Betula pubescens*) were collected to represent reindeer spring diet. The total weight of all collected plant material is listed in table 8. It was aimed to collect ≥230 grams dry plant material, of which ≥23 grams (10 %) was used for representative results for all plant species.

Table 8 Total weight of all plant material (n=23), collected throughout May 2011, before drying (b.d.) and after drying (a.d) in grams (gr).

Plant group	Species	Plant part	Weight b.d.(gr)	Weight a.d.(gr)	DM (%)
Lichens	*Cladina rangiferina*	Upper part	264.32	125.20	43.68
		Roots	157.99	61.17	35.29
	Cladina mitis	Upper part	227.88	103.94	41.76
		Roots	154.56	54.86	31.00
	Cladina stellaris	Upper part	277.62	96.93	31.57
		Roots	214.62	69.63	29.01
	Cladonia spp.	Upper part	76.46	44.42	54.08
		Roots	59.10	30.90	48.86
	Cladonia uncialis	Upper part	218.76	94.46	40.58
		Roots	124.67	47.13	35.01
Arboreal lichen	*Bryoria fuscescens*	Whole thalli	83.36	74.49	82.94
Dwarf shrubs	*Vaccinium vitis-idaea*	Upper part	514.14	273.04	51.66
	Vaccinium myrtillus L.	Upper part	415.98	199.15	45.24
	Empetrum nigrum spp. *hermaphroditum*	Upper part	475.96	217.60	44.61
Graminoids	*Eriophorum vaginatum*	Heads	283.65	57.34	17.68
		Stem	362.79	81.63	19.92
		Grass	34.00	13.75	35.53
	Carex rostrata	Green shoots	470.90	155.31	29.73
	Deschampsia flexuosa	Green shoots	159.40	36.11	18.56
	Deschampsia cespitosa	Green shoots	96.30	27.60	25.87
Moss	*Pleurozium schreberi*	Whole thalli	610.51	105.02	11.51
Birch	*Betula pubescens*	Buds	142.12	41.20	26.96
Other	Waste	Mixed plant parts, soil	134.42	56.85	38.79

All collected plant species were chemically analysed to determine the nutritional value of the species during spring season. Nutritive values were determined through analysis for dry matter, water, organic and inorganic matter, nitrogen (N), crude protein, ether extract, crude fibre, acid-detergent fibre, neutral-detergent fibre and minerals calcium, magnesium and phosphorus. Results are listed in table 9; mean values are shown as percentages (%) of dry matter with standard deviations (±) of 5-6%.

Table 9 Chemical analysis of reindeer forage plant species collected during spring (shown as percentages of dry matter (DM) with standard deviations (± s.d.)). Nutritional analysis included water, ash, nitrogen (N), crude protein (CP), crude fibre (CF), ether extract (EE), acid detergent fibre (ADF), neutral detergent fibre (NDF), calcium (Ca), magnesium (Mg), and phosphorus (P)).

Plant group	Species	Plant part	DM (%)	Water (%)	Ash %	N (%)	CP	CF	EE	ADF	NDF	Ca (%)	Mg (%)	P (%)
Lichens	*Cladina rangiferina*	Upper thalli	43.68	56.32	5.71 ± 1.57	0.32 ± 0.00	1.99 ± 0.03	47.42 ± 0.06	2.08 ± 0.08	26.64 ± 5.28	80.45 ± 0.93	0.10 ± 0.01	1.14 ± 0.11	1.55 ± 0.08
		Dead thalli	35.29	64.71	6.95 ± 0.30	0.30 ± 0.01	1.88 ± 0.04	48.25 ± 0.15	1.91 ± 0.18	23.85 ± 4.90	82.46 ± 0.00	0.08 ± 0.02	0.39 ± 1.00	1.16 ± 0.38
	Cladina mitis	Upper thalli	41.76	58.24	8.69 ± 0.57	0.28 ± 0.00	1.73 ± 0.01	47.59 ± 0.24	0.94 ± 0.07	18.97 ± 5.92	77.70 ± 0.01	0.12 ± 0.00	0.71 ± 0.06	1.70 ± 0.18
		Dead thalli	31.00	69.00	5.83 ± 0.11	0.26 ± 0.01	1.62 ± 0.04	47.10 ± 0.02	0.89 ± 0.05	19.66 ± 4.76	80.16 ± 0.71	0.08 ± 0.01	0.37 ± 0.07	1.42 ± 0.15
	Cladina stellaris	Upper thalli	31.57	68.43	5.83 ± 2.84	0.34 ± 0.01	2.12 ± 0.04	47.56 ± 0.38	1.78 ± 1.12	18.34 ± 0.67	75.40 ± 0.84	0.13 ± 0.00	1.23 ± 0.02	1.11 ± 0.06
		Dead thalli	29.01	70.99	2.99 ± 1.79	0.29 ± 0.01	1.83 ± 0.06	47.74 ± 0.04	0.40 ± 0.07	16.11 ± 0.85	75.92 ± 0.41	0.06 ± 0.00	0.40 ± 0.02	1.22 ± 0.28
	Cladonia spp.	Upper thalli	54.08	45.92	4.81 ± 0.57	0.40 ± 0.01	2.51 ± 0.01	47.93 ± 0.12	1.52 ± 0.04	12.02 ± 0.74	76.59 ± 2.10	0.10 ± 0.00	0.76 ± 0.04	1.13 ± 0.07
		Dead thalli	48.86	51.14	5.58 ± 0.30	0.39 ± 0.00	2.46 ± 0.02	47.47 ± 0.09	1.28 ± 0.18	23.81 ± 0.82	76.18 ± 0.12	0.12 ± 0.01	0.40 ± 0.05	1.37 ± 0.40
	Cladonia uncialis	Upper thalli	40.58	59.42	5.84 ± 2.11	0.29 ± 0.00	1.81 ± 0.02	48.40 ± 0.18	2.18 ± 0.28	10.06 ± 0.25	81.57 ± 0.79	0.08 ± 0.00	0.79 ± 0.06	1.45 ± 0.33
		Dead thalli	35.01	64.99	4.11 ± 0.16	0.29 ± 0.01	1.77 ± 0.04	48.53 ± 0.03	1.29 ± 0.04	9.33 ± 0.62	82.31 ± 0.57	0.05 ± 0.00	0.18 ± 0.02	1.48 ± 0.38
Arboreal lichen	*Bryoria fuscescens*	Whole thalli	82.94	17.06	1.02 ± 0.03	0.76 ± 0.01	4.74 ± 0.05	47.91 ± 0.07	2.58 ± 0.17	8.63 ± 0.67	55.86 ± 2.59	0.07 ± 0.00	0.85 ± 0.09	0.45 ± 0.10
Dwarf shrubs	*Vaccinium vitis-idaea*	Upper part	51.66	48.34	7.63 ± 3.26	0.74 ± 0.01	4.62 ± 0.04	47.92 ± 0.06	7.21 ± 0.04	44.81 ± 0.76	51.88 ± 3.02	0.40 ± 0.02	2.61 ± 0.22	1.04 ± 0.02
	Vaccinium myrtillus L.	Upper part	45.24	54.76	15.62 ± 1.02	0.66 ± 0.14	4.12 ± 0.88	45.96 ± 0.72	2.37 ± 0.09	41.44 ± 1.11	43.56 ± 1.08	0.89 ± 0.02	1.77 ± 0.04	1.47 ± 0.13
	Empetrum nigrum spp. *hermaphroditum*	Upper part	44.61	55.39	12.90 ± 0.08	0.74 ± 0.00	4.62 ± 0.01	48.33 ± 0.08	2.97 ± 0.08	46.18 ± 0.00	42.21 ± 1.56	0.61 ± 0.01	2.63 ± 0.07	0.91 ± 0.06
Graminoids	*Eriophorum vaginatum*	Heads	17.68	82.32	4.22 ± 0.03	2.60 ± 0.00	16.23 ± 0.01	47.66 ± 0.12	3.79 ± 0.74	23.12 ± 0.44	63.16 ± 0.30	0.12 ± 0.00	3.86 ± 0.01	3.50 ± 0.11
		Stem	19.92	80.05	4.21 ± 0.01	2.25 ± 0.03	14.08 ± 0.19	49.85 ± 0.23	2.63 ± 0.25	34.78 ± 0.07	65.48 ± 0.90	0.12± 0.01	3.66 ± 0.02	2.95 ± 0.17
		Grass	35.53	64.47	2.32 ± 0.01	0.99 ± 0.07	6.19 ± 0.42	46.90 ± 0.14	3.74 ±*	46.63 ± 0.66	72.79 ± 0.26	0.16 ± 0.00	1.85 ± 0.02	0.97 ± 0.02
	Carex rostrata	Green shoots	29.73	70.27	5.03 ± 0.37	1.31 ± 0.02	8.20 ± 0.14	47.50 ± 0.18	1.78 ± 0.05	36.53 ± 0.12	69.92 ± 0.11	0.17 ± 0.00	2.96 ± 0.00	1.62 ± 0.14
	Deschampsia flexuosa	Green shoots	18.56	81.44	8.36 ± 0.02	3.50 ± 0.06	21.88 ± 0.35	46.10 ± 0.19	4.73 ± 0.00	28.77 ± 0.32	59.23 ± 2.72	0.40 ± 0.00	4.29 ± 0.10	3.33 ± 0.04
	Deschampsia cespitosa	Green shoots	25.87	74.13	7.31 ± 0.08	2.36 ± 1.11	14.73 ± 6.96	46.31 ± 0.26	3.85 ± 0.09	31.51 ± 1.81	61.17 ± 1.53	0.25 ± 0.01	1.80 ± 0.23	3.05 ± 0.09
Moss	*Pleurozium schreberi*	Whole thalli	11.51	88.49	1.93 ±0.03	0.54 ± 0.00	3.35 ± 0.01	44.56 ± 0.06	3.83 ± 1.27	58.52 ± 1.12	84.63 ± 0.15	0.27 ± 0.03	3.93 ± 0.00	0.79 ± 0.11
Birch	*Betula pubescens*	Buds	26.96	73.04	9.94 ± 0.40	4.25 ± 0.00	26.53 ± 0.00	48.12 ± 0.90	8.85 ± 0.33	39.41 ± 2.46	40.34 ± 2.80	0.40 ± 0.00	4.06 ± 0.23	6.20 ± 0.30
	Waste	Mixed plant parts, soil	38.79	61.21	3.69 ± 0.72	0.80 ± 0.00	5.03 ± 0.02	47.19 ± 1.30	6.76 ± 0.08	55.38 ± 4.45	69.70 ± 2.65	0.35 ± 0.04	0.98 ± 0.13	0.82 ± 0.07

* value based on single measurement due to lack of plant material, therefore absence of standard deviation

4.3 Comparisons nutritional content between in- and ex-situ diet

The nutritional content of the Finnish semi-domestic reindeer spring diet was compared to Dutch captive reindeer rations. Comparisons of feedstuffs were based on ingredients and nutritional value of captive diets and nutritional composition of semi-domestic reindeer. Tables 10 and 11, show the nutritional composition of captive and natural diet.

Table 10 Nutritional composition of diets fed to semi-domestic reindeer in Dutch zoos and natural spring diet (% in DM)

	Ash	CP	CF	EE	ADF	NDF
Ex-situ						
Aqua Zoo	9.12	18.04	16.64	3.97	22.17	35.73
Burgers' Zoo	6.75	16.33	19.48	2.88	25.43	47.29
Dierenrijk Europa	8.15	14.95	19.29	2.97	26.49	46.71
Kerkrade Zoo	8.64	17.01	17.47	3.46	25.82	43.96
Kasteelpark Born	8.07	15.56	17.61	3.23	25.13	42.63
Ouwehands Zoo	9.04	14.78	13.77	5.28	19.04	33.69
In-situ						
Natural spring diet	**6.11**	**6.70**	**47.49**	**3.02**	**29.33**	**68.20**

The percentages of crude protein, crude fibre and NDF show some variation between the captive diets and natural spring diet. Especially crude protein content is more than twice as high, NDF and crude fibre are considerably lower compared to the Finnish semi-domestic reindeers' diet. Ash, ether extract and ADF have approximately the same percentage in the captive diets compared to the natural diet.

Table 11 Mineral content of diets fed in Dutch zoos and natural spring diet (% in DM)

	Ca	Mg	P
Ex-situ			
Aqua Zoo	1.40	0.67	0.36
Burgers' Zoo	0.77	0.31	0.35
Dierenrijk Europa	0.86	0.33	0.46
Kerkrade Zoo	0.91	0.33	0.42
Kasteelpark Born	0.97	0.47	0.37
Ouwehands Zoo	0.75	0.49	0.60
In-situ			
Natural spring diet	**0.22**	**1.81**	**1.77**

The mineral content of captive diet shows some variation in percentages in comparison to the natural spring diet. For both magnesium and phosphorus, the percentages in captivity are lower than the natural diet. Calcium, however, has a higher percentage in captivity than in the natural diet.

5 Discussion

Botanical composition of reindeer diet

This study determined the botanical composition of reindeer diets during spring (2011) and winter (2007-2008) by means of microhistological analysis of fresh faecal samples. The results indicate a shift from winter to spring diet in plant group proportion intake with an increase in grass and sedge proportion, and a decrease in shrub proportion. Lichen was predominant for both winter and spring diet, confirming the importance of this plant group for reindeer (Heggberget et al., 2002, Danell et al., 1994, Boertje, 1984, Thomas and Hervieux, 1986). Previous studies also determined that lichens are a major part of the reindeer's diet and are consumed continuously throughout the year (Holleman et al., 1979, Boertje, 1990, Wallsten, 2003).

Faecal samples for spring were collected during one month (May 2011), which differs from the three month winter collection period (December, February, April). This difference in collection periods may have resulted in a bias, which could have shifted plant compositions more towards reflecting an early spring reindeer diet. Taking into account this potential bias, it can be expected that faecal data collection, which would cover spring to early summer season, would show a clearer and more complete winter to spring shift in plant group proportions. Such a shift was found previously by Klein (1990), which reflected the reindeer's natural foraging behaviour, and showed a decrease in lichens, an increase in graminoids and shrubs, and no change in moss percentage.

Also, the number of sub-samples and microscopic window views differed for spring and winter faecal analysis, which may have influenced the mean values of plant group proportions by over- or underestimation. However, due to the relatively large number of faecal samples (pooled indv. winter n=6, single indv. spring n=17) analysed, this potential influence was not taken into account.

The results of this study's diet composition reflect reindeer foraging behaviour in relation to the plant availability of northern Finland. Reindeer tend to be selective grazers, preferring quality forage for maximum nutritional value (Pratt and Smith, 1982, Trudell and White, 1981). Based on the plant availability in northern Finland (Colpaert et al., 2003) and the relative proportions of plant groups found in faecal samples, reindeer are selective when foraging. Namely, the availability of lichen is much lower (15.4 % (Colpaert et al., 2003)) than their estimated intake (44.64 % in spring). New growth of dwarf shrubs in spring is selected by reindeer due to their protein content (Mårell et al., 2006, NRC, 2007, Kojola et al., 1995), however this is not apparent from shrub availability (28.6 % (Colpaert et al., 2003)), which is only slightly higher than intake (21.93 % in spring). Moss intake, however, tends to be sporadic and negatively correlated with lichen availability (Ihl and Barboza, 2007). This is apparent, as moss availability is much higher (41.4 % (Colpaert et al., 2003)) than estimated intake (15.25 % in spring). Mires/fens and wire grass (34.6 % and 16.0 %, respectively) are also actively selected during spring, however relatively low percentages of grass and sedges were found through faecal analysis (17.85 %). Despite this finding, an increase is apparent in grass and sedge when compared to winter proportion (10.29 %), which coincides with the new growth and green shoots in spring.

Due to the different digestibility of various plant species, plant group proportions in faecal analysis may be over- or underestimated. Correction factors for reindeer have been developed previously (Dearden et al., 1975), however plant specific digestibility analysis will be needed to obtain correction factors useful for accurate and reliable results for this study population. Despite the probability of plant group over- or underestimation, true measurements and data were presented without alterations or modifications.

Previous research has found that for reindeer, faecal analysis usually overestimates mosses (Dearden et al., 1975) and occasionally shrubs (Boertje et al., 1985). Overestimations of shrubs is likely due to their low digestibility, except for *Vaccinium*, which may be underestimated as it is more digestible than other shrubs consumed by reindeer (Boertje, 1984). Lichen digestibility by reindeer is high (for some lichens; 69-77 % of dry matter) (Storeheier et al., 2002) and therefore likely to be underestimated when analysing faecal samples. However, Boertje (1984) found an overestimation for lichens during summer.
Microhistological analysis has been a topic of debate in literature as a method for determining botanical composition of herbivore diets (Alipayo et al., 1992, Bartolomé et al., 1995, Holechek et al., 1982a, Vavra and Holechek, 1980, Wam and Hjeljord, 2010, Boertje et al., 1985). Reliable determination of ungulate diet composition by means of microhistological analysis is difficult, as the results do not always correspond with the actual diet of the reindeer. (Kojola et al., 1995) Despite this, high similarities with the actual diet have also been reported by Casebeer and Koss (1970) and Johnson and Pearson (1981).
A previous study by Kojola et al. (1995) on the winter diet of semi-domestic reindeer in northern Finland showed high similarities to this study's results on winter composition. Kojola et al. (1995) found lichen to be predominant (>50 %), with similar dwarf shrubs percentage (16.5 %–22.9 %), and grass and sedge (6.3-10.1 %) proportion. Moss proportion, however, was estimated lower (7.8-10.7 %) compared to this study's findings. The high similarity of plant group proportions found between this study and previous research of diet composition suggests that faecal analysis is a suitable method for determining botanical composition of the reindeer diet throughout the seasons. Taking into account the under- or overestimation of plant group proportions, the advantage of faecal analysis is that it allows non-invasive sampling and permits practically unlimited sampling for free-ranging reindeer (Holechek et al., 1982b).

Nutritional composition reindeer forage plants
The diet of reindeer consists of a mixture of plants to achieve a balanced diet as some of the quantitatively most important forage species may be low in particular essential nutrients (Staaland and Sæbø, 1993). Lichens generally have low nutritional values (proteins, minerals (Olsen and Mathiesen, 1998, Scotter and Miltimore, 1973)) when compared to other reindeer forage plant groups. However, lichens are known to be rich in energy (Nieminen and Heiskari, 1988, Klein, 1990), highly palatable (Holleman and Luick, 1977, Danell et al., 1994), and are easily digested (Person et al., 1980) by reindeer. This study found lichens to be high in hemicellulose (NDF-ADF), and therefore easily digestible (Olsen and Mathiesen, 1998), and to be low for all other chemical components.
Lichen species were divided into upper and dead thalli to determine whether any distinct differences could be found for these parts. Higher values of ether extract and magnesium were found in the upper thallus compared to the dead thallus. Also, water content was slightly higher in the dead thallus (average 64.17 %) compared to the upper thallus (average 57.67 %). Arboreal lichen, an important winter forage when terricolous lichen availability is limited (Nieminen and Heiskari, 1988, Danell et al., 1994), had a higher crude protein content, the lowest ADF value (8.63 %) and lower NDF value (55.86 %) compared to other lichen species (ADF average 17.89 %, and NDF average 78.87 %). Also, arboreal lichen had the lowest mineral content (magnesium and phosphorus) compared to the other plant groups.
New growth of birch, graminoids and dwarf shrubs, which becomes available during spring, are highly digestible by reindeer and contained higher levels of crude protein (average of 4.25 %, 2.17 %, 0.71 %, respectively) and phosphorus (average of 6.20 %, 2.57 %, 3.42 %, respectively) (Mårell et al., 2006). This study found these plant groups to be generally higher in crude protein content, ADF, ether extract, calcium, magnesium and phosphorus. This

coincides with previous findings (Staaland and Sæbø, 1993) and that reindeer actively seek out new emerging plant growth for higher quality forage (Danell et al., 1994).
Moss is thought to be consumed sporadically (Ihl and Barboza, 2007), presumably due to its low palatability (Staaland et al., 1988) and poor digestibility (despite digestibility estimates ranging 0-48%) (Ihl, 2010, Staaland et al., 1988, Thomas et al., 1984). However, nutritional value for moss was slightly higher than lichen, with higher values for crude protein, ether extract, calcium and magnesium. Therefore, despite its low palatability and digestibility, even incidental intake of moss when foraging for lichen would be beneficial for reindeer.

Nutritional values of spring forage plants have not been determined previously, therefore, the comparisons were made based on winter and summer values. Snow melt at the study site did not occur until late May, resulting in relatively late vegetation growth compared to previous years (Kumpula, 2011). The developments of most vegetation, namely birch and *Carex rostrata*, was still in early stages by the end of the sampling period. The nutritional values found during this spring study were comparable to other studies' results of summer and winter forage plants collected in northern Finland.
Nutritional values of lichens for crude protein and ether extract were similar to previous research, however crude fibre was slightly higher (Nieminen and Heiskari, 1988, Nieminen, 1986). ADF values for lichens were higher in this study (ADF average 17.89 %) compared to results recorded by Danell et al (1994) (5-6 %) during winter. This shows that the hemicellulose content (NDF:ADF ratio) of lichens during this study was lower, indicating a higher potential digestibility compared to previous research. Mineral levels determined by Storeheier et al. (2002) during winter differed from findings in this study, namely calcium levels (0.2-2.1 %) were higher, magnesium (0.1-0.5 %) and phosphorus levels (0.3-0.9 %) were lower compared to the findings of this study. Crude fibre levels were generally higher in this study for graminoids and dwarf shrubs compared to values recorded during summer (Nieminen and Heiskari, 1988), which is generally not consistent with maturing plants from spring to summer. However, the higher fibre content may reflect late winter levels rather than early spring, thereby levels being higher when compare to summer levels. *Deschampsia fluxuosa* crude protein levels were higher during spring (21.88 %) when compared to levels found in summer (7.1-16.3 %) by Nieminen and Heiskari (1988), which reflects the decreasing protein content in maturing vegetation (Klein, 1990). Birch crude protein levels and ether extract were similar to levels found previously during summer (Nieminen and Heiskari, 1988). Nutritive values for moss corresponds with previous studies; high levels of NDF (Ihl and Barboza, 2007, Danell et al., 1994), high levels of ADF (Danell et al., 1994) and low levels of crude protein (Ihl and Barboza, 2007).

Commercial feed
The weak link in the nutritive chain of reindeer is winter (Steen, 1968). Winters can have a negative impact on reindeer populations mostly due to lack of energy intake as their primary food source (lichens) is covered by deep snow or ice crust (Boertje, 1990). Therefore, herders of semi-domesticated reindeer may supplement herds with extra feed when there are unfavourable snow conditions or insufficient winter pastures. The provision of artificial feed may be reflected in the results of the faecal analysis in this study. The natural diet of reindeer herds in Finland are supplemented with commercial reindeer fodders, which contain dry hay, grains, molasses and commercial feeds which are rich in digestible energy (Nieminen et al., 1987). Commercial pellets are based on mixtures of cereal grains, grass or alfalfa meal, and contain protein, cellulose, hemicellulose, lignin and water soluble carbohydrates (Storeheier et al., 2002). The nutritional composition of different commercial reindeer fodders used in Finland during winter and early spring are shown in table 12.

Table 12 Dry matter (DM), crude protein (CP), ether extract (EE), crude fibre (CF) and the minerals calcium (Ca), magnesium (Mg) and phosphorus (P) in different commercial reindeer pellets used in Finland during winter. (Nieminen and Heiskari, 1988, Raisio, 2006, Kinnusen Mylly, 2011)

	DM (%)	Ash (%)	CP (% DM)	CF (% DM)	EE (% DM)	Ca g/kg	Mg g/kg	P g/kg
Poroelo	86.8	8.4	10.9	18.3	4.4	12.5	2.6	7.5
Poroelo S	88.0	8.0	8.0	23.3	3.4	7.0	2.2	5.7
Poro-ennätys	90.0	11.2	16.7	19.9	4.3	20.7	5.2	7.5
Poro-rehu	88.0	8.8	10.9	19.2	4.5	13.9	3.0	7.3
Valtti	89.5	13.4	10.3	14.7	5.6	39.9	4.1	7.3
Poro-eväs	90.0	16.7	10.5	17.8	2.2	3.3	2.8	4.8
Poron-Herkku	88.2	8.8	13.1	13.5	6.9	15.5	8.5	9.4
Poron-Herkku 2	88.4	9.2	9.7	17.0	6.1	12.3	2.2	6.6
Tähti-Poro Artic	88.0	7.3	11.0	10.6	3.6	11.0	3.0	4.0
Tähti-Poro 2 Balans	88.0	7.0	11.8	8.7	2.9	10.0	3.0	5.0

In this study, herders provided their reindeer with *Poron-Herkku*, *Poron-Herkku 2* and *Tähti-Poro Artic*. Supplementary feeding of reindeer is important in Finland due to decreasing areas of original reindeer pasture lands and deteriorating quality of pastures due to other land use forms and intensive grazing (Helle and Kojola, 2006, Kojola and Helle, 1993). Supplementary feed has secured the survival of reindeer during winters and has resulted in reindeer population densities to double (and in some areas triple) in northernmost Finnish Lapland throughout 1990's compared to 1960's and 1970's (Helle et al., 1990). The seasonal use of supplementary feed shows to be an effective means of sustaining reindeer populations and a necessity for the reindeer herding industry.
Due to extra nutrient intake (reindeer pellets) in winter and early spring, it is possible that the reindeers' food intake pattern is adjusted to this supplemental feed. The reindeer may not eat the forage plants it would have eaten when the animals had not been offered commercial feed. This may result in an over- or underestimation of forage plants found in faecal samples and plants collected.

Captive diet and cyclic feeding
As a basic foundation of animal management, nutrition is fundamental for longevity, disease prevention, growth and reproduction. Animals use a wide variety of morphological, physiological and anatomical adaptation to obtain and consume foodstuff. (Dierenfeld, 1997) Nutritive forage of free-ranging reindeer has evolved based on complex chemical, temporal and spatial factors. Therefore, ingredients such as oats, wheat, corn and barley, which exhibit high fermentation rates by which acids are rapidly produced in the rumen, causes a pH change in the rumen. This pH change can result in several metabolic disorders, such as bloat, hoof overgrowth, laminitis, rumenitis, urolithiosis and gastro-intestinal tract obstructions. (McCusker, 2009) Many diseases observed in captive wildlife are the result of dietary nutrient deficiencies; this as a result of the animal's inabilities to synthesize, transport, or metabolize specific nutrients; and excessive dietary intake or absorption of nutrients. (Kleiman et al., 2010)
A pattern of cyclic growth, with rapid growth in summer and slow growth or weight loss in winter, seems typical for free-ranging reindeer (Dauphiné, 1976, Skjenneberg and Slagsvold, 1968, Reimers, 1983). Northern cervids in general share this cyclicity. This is evident in animals fed to appetite (ad libitum), and the food intake and fasting/resting metabolic rate declines in winter (Wood et al., 1962, McEwan, 1968, Nordan et al., 1968, Silver et al., 1969, Wandeler and Huber, 1969, Bandy et al., 1970, Gasaway and Coady, 1974, Pollock, 1974, Simpson, 1976, Nilssen et al., 1982). The cyclic pattern is an adaptation to seasonal changes in food quality and quantity, and reproduction. However, the pattern is not dependent on the

forage plant quality and availability, as research shows that this pattern also occurs when standard feed is offered ad libitum throughout the year. (Ryg, 1983) For example, in winter, the voluntary food intake is limited by the capacity of the reticulo-rumen and by the rate of disappearance of digesta (Heiskari and Nieminen, 1990). Keeping animals in captivity imposes unique nutritional conditions that are different from the ecological niches in which animals have evolved. Although captive wild ruminants have shown the ability to adapt to an artificial diet, 60-70% of captive ruminant mortality is caused by poor nutritional management and nearly 25% of these captive animals die from malnutrition. (Baker et al., 1998) Most captive reindeer are fed a single diet year round. Table 13 shows four different reindeer diets fed in the Dutch zoos: Burgers' Zoo Arnhem, Gaia Kerkrade Park, Artis Zoo Amsterdam and Blijdorp Rotterdam. The quantity (gr/reindeer) the reindeer receive may differ per season, but the nutritional composition of the diet stays the same.

Table 13 Food stuff of reindeer diets in four Dutch zoos (based on diets provided in 2011) (more detailed in appendix IV)

Zoo	Diet
Burgers' Zoo	*Year round:* Browser pellets, pulp, bran, calcium carbonate (chalk) & carrots Feeding times: 3x/day
Gaia Kerkrade Park	*Summer/ winter (quantities differ)*: Master pellets, pulp pellets, wheat bran, calcium carbonate (chalk), carrot, hay (short), dried leaves, branches, grass, salt licking blocks. Feeding times: 2x/day
Artis	*Apr-Oct/Oct-Apr (quantities differ)*: reindeer pellets, lucerne meal, bran, carrot, salt licking stone, calcium carbonate, totalin and vitamin E supplement Once a week: endive and chicory as enrichment Feeding times: 3x/day
Blijdorp	*Year round*: Horse pellets, browser pellets, grass pellets, pulp, bran, reindeer lichen, dried raspberry leaves, hay, lucerne with molasses and calcium carbonate (chalk) Feeding times: 2x/day

Burgers' Zoo and Blijdorp provide their reindeer with a single diet year round, whereas Artis has two feeding regimes (April-October and October-April). Their purpose, from winter until early spring, is for the animals to lose weight, which reflects their nature weight loss. The caretakers are informed of this transition, and that it is to be implemented gradually. The diet that Artis provides is used as a directive, which can be adjusted to the body condition of the individual reindeer. Gaia Kerkrade Park also has two feeding regimes (summer and winter); in the winter, their reindeer receive less food, while keeping the botanical composition of the diet the same. Lastly, Blijdorp is the only zoo which feeds their animals 'reindeer lichen', which is predominant in winter and spring in the natural diet of reindeer.

The reindeer's natural diet consists of many different forage plant species, as is described in Table 4 in paragraph 2.2.5. Ranua Zoo, which is located in the north of Finland, attempts to follow these seasonal changes as much as possible. In summer, their reindeer are fed a diet of green grass, green leaves and some pellets. In autumn (September and October), they are offered mushrooms, as well as vegetables and fruit (i.e. apples or lettuce). In early winter, the reindeer receive lichens, pellets, dried hay and leaves. The nutritional quality of this winter diet is much poorer than in summer (Torvinen, 2001), which reflects natural winter diet consisting predominantly of lichens, which are low in mineral and protein content (Nieminen and Heiskari, 1988, Nieminen and Helle, 1980).

6 Conclusion

Semi-domestic reindeer that graze on natural pastures in Finland eat a wide variety of plants during spring. Forage plants in spring consist of lichens (*Cladina stellaris*, *C. rangiferina*, *C. mitis*, *Cladonia uncialis* and *C.* spp.), arboreal lichen (*Bryoria fuscescens*), dwarf shrubs (*Vaccinium vitis-idaea*, *V. myrtillus* L., *Empetrum nigrum* ssp. *hermaphroditum*), graminoids (*Eriophorum vaginatum*, *Carex rostrata*, *Deschampsia flexuosa*), moss (*Pleurozium schreberi*) and birch (*Betula pubescens*).

The average nutritional composition of these forage plant species during May 2011 was as following: 6.70% crude protein, 47,49% crude fibre, 3.02% crude lipid, 29.33% ADF, 68.20% NDF, 0.22% calcium, 1.81% magnesium and 1.77% phosphorus.

The average nutritional composition of diets of captive reindeer in the six Dutch zoos (Aqua Zoo Friesland, Burgers' Zoo Arnhem, Dierenrijk Europa Mierlo, Gaiapark Kerkrade Zoo, Kasteelpark Born and Ouwehands Zoo Rhenen) was: 16.11% crude protein, 17.38% crude fibre, 3.63% crude lipid, 24.01% ADF, 41.67% NDF, 0.94% calcium, 0.43% magnesium and 0.43% phosphorus.

With the development of standards for the assessment for the current captive reindeer diets percentages of crude fibre, crude protein, NDF and the minerals calcium, magnesium and phosphorus should be inspected. Percentages of crude fibre and crude protein are twice as high in captivity as in the natural spring diet. The percentage of NDF is considerably lower in captivity compared to the Finnish semi-domestic reindeers' diet. Both magnesium and phosphorus are in captivity lower than in the natural spring diet. Calcium has a higher percentage in captivity.

7 Recommendations

For further research on the nutrition of in-situ and/or ex-situ reindeer, the following recommendations should be taken into consideration. To prevent over- or underestimation of plant group proportions in faecal analysis, due to different digestibility of various plant species, plant specific digestibility analysis are needed to obtain correction factors useful for accurate and reliable results for the study population.

In order to follow the pattern of cyclic growth, with rapid growth in summer and slow growth or weight loss in winter, which seems typical for free-ranging reindeer, that the natural diet and its nutritional value in all seasons should be studied. It is important for the focus to remain on practical and feasible options for implementing this knowledge in zoos.

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Appendix

Appendix I – Preparation method micro histological analyses

1. Crush faeces mass with mixer, rinse with running water and strain mass through strainer with aperture of 0,125 mm. This will homogenize the sample and make identification easier.
2. Soak a small quantity of sample in 70% alcohol for approximately one minute.
3. Colour a small quantity of sample in 1% methylene blue for approximately 15 seconds. This will increase contrast of cell tissue and help to separate types of cell tissue.
4. Rinse with running water for 30 seconds and let dry for one minute.
5. Soak a small quantity of sample in 70% alcohol for one minute.
6. Quick rinse in 96% alcohol.
7. Take small sample of coloured mass of faeces and put on a micro slide, add few drops of Euparal mounting medium.
8. Spread sample to cover slide evenly and prevent sample build up, cover sample with cover slip.

(methods adapted from Hansson (1970) and Viro and Sulkava (1985))

Appendix II – Data sheet

Sample:	Date:
Subsample:	

View #	Lichen	Arboreal lichen	Grass/Sedge	Shrub	Moss	Others
1						
2						
3						
4						
5						

Sample:	Date:
Subsample:	

View #	Lichen	Arboreal lichen	Grass/Sedge	Shrub	Moss	Others
1						
2						
3						
4						
5						

Sample:	Date:
Subsample:	

View #	Lichen	Arboreal lichen	Grass/Sedge	Shrub	Moss	Others
1						
2						
3						
4						
5						

Sample:	Date:
Subsample:	

View #	Lichen	Arboreal lichen	Grass/Sedge	Shrub	Moss	Others
1						
2						
3						
4						
5						

Appendix III – Captive reindeer nutrition-related problems

Animals that are stressed due to being immune compromised, such as by poor nutrition, concurrent diseases are more likely to get infection or are less able to fight off infections (Bartlett et al., 2009).

Lactic acidosis

Ruminant lactic acidosis is a condition in which the ruminal fluid drops below pH 5. After ingestion of excessive quantities of highly fermentable feeds, there is an increase in number of bacterial species, which utilise the carbohydrate to produce large quantities of lactic acid. When large amounts of carbohydrate are present, lactic acid will be produced until rumen pH drops to 5 or less, which results in the destruction of lactic utilizing bacteria and rumen protozoa, and damage to the gastrointestinal tract. This causes acid accumulation, fluid influx into the forestomachs, increased osmotic pressure, dehydration and possibly hypovolemic shock. The lactic acid accumulation and associated osmotic changes are toxic to the rumen epithelium, and damage may result in bacterial and toxin leakage into the blood circulation. (NRC, 2007, Radostis et al., 1999) A microbial imbalance is caused by rapid diet changes to high concentrates, ingestion of large quantities of grain or readily fermentable starch, feed removal, underfeeding of effective fibre, restriction of feed intake during stress or voluntary feed aversion. Ruminal acidosis also occurred in reindeer during a rapid diet change of (experimental) re-feeding of starved reindeer (Sletten and Hove, 1990, Bøe and Jacobsen, 1981).

Enterotoxemia

Enterotoxemia or 'overeating disease', occurs in sheep, goats, deer and calves (Uzal and Kelly, 1998, Kummeneje and Bakken, 1973). Clostridial disease is a bacterial disease which can be caused by a sudden change of the diet or excessive amounts of high carbohydrate feed is ingested, specifically grain (Dieterich, 1993). The bacteria *Clostridium perfringens* of the lower digestive tract proliferates when there is an increase in undigested starch and carbohydrate levels (which are normally digested and metabolized higher in the digestive tract). Excessive bacterial growth and the production of lethal amounts of several very potent toxins are released into the intestinal tract and absorbed into the animal's system. (Dieterich, 1993) In reindeer, *Clostridium perifringens* was reported in the intestine and faecal samples associated with diseased animals (Kummeneje and Bakken, 1973) as well as in healthy animals (Aschfalk et al., 2002).

Wet Belly syndrome

Wet belly is a feed disorder known to occur occasionally in semi-domesticated reindeer in which the lower parts of the thorax and abdomen becomes wet due to intestinal fluids secreted from the liver, and it causes starvation or indigestion, and may indirectly even cause death (Fuller, 2004, Åhman et al., 2002). The exact cause is unknown, however it may be connected to malnutrition associated with supplementary feeding, as it has not been observed in grazing reindeer (Åhman et al., 2002). The induction of this disorder seems to be unrelated to any specific diet, but connected to insufficient energy intake (Nilsson, 2003, Nilsson et al., 2006).

Laminitis

Laminitis is an aseptic inflammation of the dermal layers inside the foot and can cause lameness in the animal (Joiner, 2008). Typically, laminitis is associated with high concentrate diets or with lush, succulent pasture high in protein and soluble carbohydrates (Cheeke and

Dierenfeld, 2010). Carbohydrate overload of the gut results in excessive microbial growth, which is the main contributing factor. Laminitis in reindeer has been observed in situations when animals were fed an exclusive diet of alfalfa (Dieterich, 1993).

Splenomegaly

A sudden death syndrome, known as splenomegaly, has occurred in ruminants, such as in sheep, goats, cattle and deer. Although the exact cause of this syndrome is unknown, it can affect well-condition domestic deer with intestinal haemorrhaging (Embury-Hyatt et al., 2005). Intestinal haemorrhage and splenomegaly syndrome is not directly associated with increased grain or a change of diet, however overeating or mild indigestion may also cause the intestines to become static, which prevents the normal flushing of toxic substances out of the system (Fleming, 1985). Any injury to the mucosa of the small intestine also may predispose to changes in the bacterial flora that result in clostridial overgrowt

Appendix IV - Dutch zoo reindeer rations

Burgers' Zoo

Forest reindeer (*Rangifer tarandus fennicus*)			
Adult no.	4		
Calfs no.	2		
Feeding times	3x/day		
Feedstuff	**Quantity (gr)**	**Quantity (gr)**	**Quantity (gr)**
Browser pellets	2000	2000	2000
Pulp	2000	2000	2000
Bran	500	500	500
Calcium carbonate (chalk)	20	20	20
Cold water			
Carrots	2000		
Total	**6520**	**4520**	**4520**

Gaiapark Kerkrade Zoo

Forest reindeer (*Rangifer tarandus fennicus*)			
Adult no.			
Calfs no.			
Feeding times	2x/ day		
Season	Summer	Winter	
Feedstuff	**Quantity (gr)/reindeer**	**Quantity (gr)/reindeer**	**Quantity (gr)/group**
Dierenpark pellets HE (Masters)	800	600	7200
Pulpbrok	800	600	7200
Wheat bran	150	150	1600
Calcium carbonate (chalk)	5	5	50
Carrot	300	300	3000
Hay (short)	Ad lib	Ad lib	Ad lib
Dried leaf (gedroogd blad)			1 bucket
Branches	Ad lib	Ad lib	Ad lib
Grass	On pastures	On pastures	On pastures
Salt licking blocks	On pastures	On pastures	On pastures
Total	**2055**	**1655**	**16350**

Artis Royal Zoo (Natura Artis Magistra)

Reindeer (*Rangifer tarandus*)			
Adult no.			
Calfs no.			
Feeding times	3x/ day (minimum)		
	Basis (Apr-Oct)	Winter (Oct-Apr)	Lactation
Feedstuff	**Quantity (gr)/ 100kg reindeer**	**Quantity (gr)/ 100kg reindeer**	**Quantity (gr)/100 kg reindeer**
Hay (only fine hay)	Small slice	Small slice	
Lucerne hay (1/4 of the hay can be lucerne)			
Fresh leaves with branches (fine) if in stock			
Reindeer pellets	700	400	
Lucerne pellets (mixed through pellets)	700	400	
Bran	500	500	
Carrot	400	400	
Endive (enrichment) 1-2x/week	Occasional crop		
Chicory (enrichment) 1-2x/week	Occasional crop		
Grass (fine) if in stock			
Salt licking stone	Ad lib	Ad lib	Ad lib
Calcium carbonate	10 gram	10 gram	10 gram
Totalin	10 gram	10 gram	15 gram
Vitamin E supplement			In consultation

Comments:

- Dried leaves can be fed
- Reindeer eats fine grasses as part of diet
- Feeding periods has to be gradually changed from basis to winter in a couple of weeks
- Reindeer have to lose weight in winter till the beginning of spring
- Vitamin E supplement, dosage of horse
- No fruit or sugary substances due to risk for acidosis
- Diet is a directive, adjust on basis of body condition

Rotterdam Zoo (Diergaarde Blijdorp)

Reindeer (*Rangifer tarandus*)			
Adult no.			
Calfs no.	0		
Feeding times	2x/ day		
Feedstuff	**Quantity (gr)**	**Quantity (gr)**	
Horse pellets*	300	1/3 cup	
Browser pellets*	125	1/8 cup	
Grass pellets	175	¼	
Pulp	600	½	
Bran	650	1 scoop, weigh!	
Reindeer lichen	50	One hand full mixed trough the food	
Dried leaves (raspberry)**	Ca 200	1/6 crate	
White hay (very fine!!)	Ca 200	0,3 slice	
Lucerne with molasses (Hartog)	50	One hand full	
Calcium carbonate (chalk)	15 of 30	1 (summer) or 2 (winter) scoops	
Total	**2365 - 2380**		

Comments:

- Fed in the morning after mixing. ¾ scoop for adults and ¼ scoop for young animals.
- ** Dried leaves is fed outside together with short, fine hay. If the feeders are empty in the afternoon, they are filled again.
- In the afternoon the animals get 1 ½ scoop pulp mixed with 3 scoops bran, ¾ lucerne pellets, 2 hands full reindeer lichen and 2 hands full Hartog lucerne. This mix is left to soak for 3 to 4 hours with water.
- Every animal gets 2 scoops of chalk (30 g) in the summer and 1 scoop (15 g) in winter.
- A salt licking stone should be available at all times.