The quality of the forage eaten by Norwegian reindeer on South Georgia in summer

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Abstract: The chemical composition and digestibility of plants selected by Norwegian reindeer (*Rangifer t. tarandus*) on the sub-Antarctic island of South Georgia (SG) were investigated in the austral summer and compared with two qualities of standard grasses of *Phleum pratense* of European origin. *Paridiochola flabellata, Poa pratense, Poa annua, Deschampsia antarctica,* and *Phleum alpinum* collected on SG contained 14.8, 17.6, 22.8, 16.1 and 10.1% respectively of crude protein of dry matter (DM). *Aceana magellanica* also collected on SG contained 19.8% of crude protein and 18.8% of water-soluble carbohydrates (WSC) of DM, while the tussock grass *P. flabellata,* contained as much as 29.3% of WSC of DM. Total plant cell-wall contents (CWC), including cellulose, hemi-cellulose and lignin in *P. flabellata, P. pratense, P. annua* and *P. alpinum* were 53.2, 49.6, 41.7 and 40.4% of DM respectively, while *A. magellanica* contained only 17.5% of DM CWC. The lignin concentrations of plants analysed varied between 1.2 and 3.2% of DM. Mean *in vitro* dry matter digestibility (IVDMD) of selected plants ranged from 70% in *P. flabellata* to 83% in *P. alpinum* after 48 h incubation in rumen fluid from these reindeer. In contrast, the IVDMD of the poor and high quality standard grass *Phleum pratense* were 54% and 73% of DM, respectively. The forage eaten by reindeer on SG in summer was of high quality, with low lignin content, moderate protein concentration and high degradability in rumen fluid.

Key words: digestion, *Rangifer.*

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Introduction

The first description of South Georgia and its flora was made in 1775 by Captain James Cook when he discovered this island, 200 km south of the Antarctic convergence, in the Atlantic Ocean (54-55°S, 35-38°W). He wrote in his journal: «The wild rocks raised their lofty summits till they were lost in the clouds and the valleys laid buried in everlasting snow. Not a tree or shrub was to be seen, not even big enough to make a tooth pick» (Cited after Beaglehole, 1961). The plant communities and plant species on this island have since been investigated by Greene (1964), Lindsay (1973), Kightley & Lewis Smith (1976), Walton & Lewis Smith (1980), Pratt & Lewis Smith (1982), Leader-Williams & Ricketts (1982), Leader-Williams (1988), and Mathiesen *et al.* (1999). The flora consists of few grasses and rushes and there is a lack of trees, shrubs and true woody plants. One dominant plant species is *Paridiochola flabellata,* a winter green coastal tussock grass with high biomass and productivity, which does not occur in the northern hemisphere. Swards of the grasses of *Deschampsia antarctica, Phleum alpinum* and *Poa annua* occur locally on wet areas surrounded by the tussock grass. There were originally no terrestrial herbivore vertebrate species on the island, but large colonies of penguins and seals come ashore to nest and breed. In 1911 and 1925 22 Norwegian reindeer (*Rangifer tarandus tarandus*) were successfully introduced by whalers from Norway (Olstad, 1930; Bonner, 1958; Leader-Williams, 1978). In 1972-1976 their numbers had increased to almost 3000 in three distinct herds. The reindeer on South Georgia do not migrate between seasonal pastures and the density of animals might be as high as 22 reindeer per km^2 (Leader-Williams & Ricketts, 1982). In winter, these reindeer eat almost exclusively *P. flabellata,* since lichens are scarce (Leader-Williams *et al.,* 1981). *P. flabellata* is also an important forage plants throughout the summer, together with other highly preferred species such as *P. annua,* introduced with seeds in consecrated earth brought from churchyards in Norway, and the indigenous nurnet *Aceana magellanica* and the *D. antarctica* (Leader-Williams, 1980). High fibre concentrations of plant cell wall contents (CWC), such as cellulose, hemi-cellulose and lignin, low concentrations of nitrogen available for microbial synthesis and low concentrations of easily digestible energy sources are important factors which may limit the ruminal digestion of forage plants in ruminants (Ørskov, 1992; van Soest, 1994). This study was carried out in order to investigate the nutrient value and ruminai degradability of selected plants eaten by reindeer on South Georgia in summer.

Material and methods

Study area

This investigation was carried out in Husvik Harbour, South Georgia in January and February 1990 (summer), as part of the Norwegian Antarctic Expedition 89/90. Mean annual precipitation on South Georgia can be as high as 1200-2000 mm. Winter and summer seasons are clearly defined and the absolute range of temperatures is -19 to +24 °C. Summer snowfalls are frequent, and deep snow covers the vegetation at sea level for five to six months in winter. The severe climate on South Georgia relative to its latitude results from cold oceanic currents from the south. Permanent ice and snow covers 60% of the island. The vegetated grazing area in Strømnesbay used by one reindeer herd makes up 11 km^2 of a total ice-free area of 124 km^2. Seabirds and seals have a considerable effect upon this vegetation, enriching it around the colonies and even damaging it by trampling in densely populated areas (Walton & Lewis Smith, 1980).

Animals

All animals investigated (n=10) were female adults more than two years old, age based on annulation in the cementum of the first incisor teeth. The mean live body mass (BM) was 74 kg, the total gastrointestinal tract (GIT) comprised 27% of BM, while the rumen wet weight fill was 14% of BM (Mathiesen *et al.,* 1999). BM, less blood lost from the wound, were measured to 0.5 kg using a Salter model 235 scale. Three of these adult non-lactating reindeer were shot while grazing 0-5 km from the whaling station Husvik Harbour (licence given by the Governor of the Dependencies of Falkeland Island and South Georgia). The *post mortem* examinations, including sampling of rumen contents (2 L) were carried out in the field. The fresh rumen contents were transported to the laboratory in the former whaling station in a preheated (39 °C), anaerobic thermos-flask no later than one hour after the animals were shot.

Plant chemistry

Leaves of *P. flabellata, A. magellanica, P. pratense, P. annua, D. antarctica* and *P. alpinum* were collected in areas grazed by reindeer and dried for 17 h at 55 °C in the laboratory. Likewise, high and poor quality standard grasses of *Phleum pratense,* originally harvested by Tilley & Terry (1963) for dietary standards in domestic ruminants in Europe, were treated similarly to the plants collected on South Georgia and included in this investigation for comparative analysis. The dried plant material was subsequently milled to 0.8 mm size and transported to Norway for analysis of dry-matter content (DM), ash, minerals (P, Mg, Ca, K, Na), crude protein, true-protein, ether extract, water-soluble carbohydrates (WSC), fibre of the plant cell-wall contents, including cellulose, hemi-cellulose and lignin (CWC). DM was determined after heating a subsample of the preheated plant-material at 105 °C for 17 h. For the analysis of ash and minerals plant materials were ashed at 550 °C for 12 h. The ash was dissolved in *aqua regi.* After evaporation the dry residue was dissolved in HCl and diluted with deionised water. Sodium and potassium in solution were determined by flame photometry, and calcium and magnesium by atomic absorbtion spectroscopy (Perkin Elmer 306). Phosforus was determined according to Boltz & Howell (1978). Nitrogen was determined with the Kjeldahl method and converted to total crude protein by multiplication by 6.25 (Horwitz, 1980). True protein was determined according to Olsen *et al.* (1995) by boiling the plant material in water to remove the soluble protein and the remaining nitrogen was analysed by the Kjeldahl method. Ether extract was determined using the Soxhlet method and extracted with diethyl ether (Horwitz, 1980). WSC was determined by extraction of the plant samples in NaOH (Smith & Grotuleschen, 1966), de-proteinised with zinc sulphide/barium hydroxyde, and the WSC content analysed using the ferricyanide method (Furuholmen *et al.*, 1964). CWC fibres were analysed according to Van Soest (1963 a; b) and Goering & van Soest (1970). Neutral detergent fibre (NDF), acid detergent fibre (ADF) and acid detergent lignin (ADL) were determined directly. Hemi-cellulose was calculated as the difference between NDF and ADF, and cellulose was calculated as the difference between ADF and ADL. The energy contents of two sub-samples of each plants species collected were analysed according to Mortenson *et al.* (1994) using a bomb calorimeter MK 200 (Franz Morat KG, Eisenbach, Germany).

In vitro digestion

The mean dry matter *in vitro* digestion (IVDMD) of plants eaten by reindeer on South Georgia was determined by use of the two-stage method described by Tilley & Terry (1963) modified for field investigations according to Aagnes & Mathiesen (1995) and Olsen *et al.* (1995). On arrival in the field laboratory in Husvik Harbour, the fresh rumen contents were strained through two layers of muslin and degradability of collected plants was investigated in the filtrate. Quadruplicate samples of approximately 100 mg of the preheated material from each plant species collected and the two quality standard grasses (55 °C for 17 h, with known DM content) placed in prewarmed, preweighed Hungate anaerobic culture tubes fitted with screw cap and butyl rubber septum (2047/16-125 Bellco, Vineland, USA). Artificial saliva were made according to McDougall (1948) with the modification made by Aagnes & Mathiesen (1995). The saliva (9 ml) was added to the tubes under CO_2. One ml of rumen fluid was then added by syringe to each tube and incubated in a water bath at 39 °C for 6, 12, 24 and 48 h, subsequently. Each test tube was then further incubated at 39 °C for 48 h with HCl and pepsin-solution added. The tubes were then centrifuged at 300 g for 10 min, the supernatant removed and the tube containing the pellet was kept frozen until arrival in Norway. The pellets were then thawed out and resuspended in distilled water, washed and centrifuged until the supernatant was clear. Control tubes without plant material were included to determine the DM content in the rumen fluid. The IVDMD of each plant species was calculated as percent DM disappearance. The IVDMD data are expressed as mean and standard deviations.

Results

Plant chemistry

The chemical composition of selected plants eaten by reindeer on South Georgia in summer are shown in Tables 1 & 2. The crude protein content of the plants eaten by reindeer ranged from 10.1 to 22.8% of DM. The crude protein concentration of high- and poor quality standard grasses was 22.1 and 6.9% of DM. In contrast, the mean true protein content of *P. flabellata, A. magellanica, P. pratense, and P. annua* were 11.7, 16.3, 14.5 and 20.1% DM, respectively. The concentration of lignin in the plants investigated ranged from 1.2 to 3.2% of DM. The high and poor quality standard grasses contained 2.3 and 4.4% lignin of DM. The mean total contents of plant CWC in *P. flabellata, P. pratense, P. annua* and *D. antarctica* were 53.2, 49.6, 41.7, and 40.4% DM, while the poor and high quality standard grasses contained 67.5 and 59.4% CWC of DM. *A. magellanica* contained very low concentration of CWC (18% of DM) (Table 1). The gross energy densities of *P. flabellata, A. magellanica* and *P. annua* were 19 054, 18 129, and 18 844 (KJ/g DM), respectively. The ash content of the selected plants ranged from 3.1-8.3% of DM, while high- and poor- quality standard grasses contained 9.8 and 4.5% of ash of DM, respectively (Table 1). The mean concentrations of P, Mg, Ca, K, and Na in all plants collected were 0.3, 0.2, 0.4. 1.4, and 0.2% of DM, respectively (Table 2).

In vitro digestion

Data on the rate and extent of IVDMD of five selected plants from South Georgia and of two qualities of standard grasses, in Norwegian reindeer on South Georgia in summer are shown in Table 3. There was a inverse relationship between the level of plant CWC and the digestibility of plants after 6 h. All plant species collected on South Georgia were

Table 1. Mean chemical composition (% DM) of plants eaten by Norwegian reindeer on South Georgia in summer and of two qualities of standard grasses.

	% DM	Ash	Crude protein	Ether extract	Hemi-cellulose	Cellulose	Lignin	WSC
Paridiochola flabellata	41	3.1	14.8	3.2	25.7	24.3	3.2	29.3
Aceana magellanica	46	8.3	19.8	4.3	5.9	9.5	2.1	18.8
Poa pratense	42	8.3	17.6	2.8	28.4	20.0	1.2	19.9
Poa annua	37	8.2	22.8	4.0	25.2	15.1	1.4	-
Deschampsia antarctica[a]	54	4.4	16.1	3.1	-	-	-	-
Phleum alpinum	50	3.1	10.1	3.2	21.0	18.1	1.3	-
Phleum pratense[a]	-	9.8	22.1	3.4	31.9	25.2	2.3	4.9
Phleum pratense[b]	-	4.5	6.9	3.1	30.2	32.9	4.4	15.5

[a] High quality standard grass of *P. pratense.* [b] Poor quality standard grass of *P. pratense.*
DM: Dry matter; WSC: Water soluble carbohydrates.
- : nor measured.

Table 2. Mean (standard deviation) mineral composition of plants eaten by Norwegian reindeer on South Georgia in summer (% DM).

	P	Mg	Ca	K	Na
Paridiochola flabellata	0.21	0.09	0.19	0.97	0.14
Aceana magellanica	0.33	0.38	1.07	0.97	0.25
Poa pratense	0.28	0.17	0.41	2.03	0.07
Poa annua	0.37	0.19	0.32	1.93	0.37
Phleum alpinum	0.19	0.12	0.06	1.11	0.06
Mean (*s*)	0.27 (0.06)	0.19 (0.10)	0.41 (0.35)	1.40 (0.47)	0.17 (0.11)

more thoroughly digested than the poor quality standard grass of *P. pratense, P. flabellata* and *D. antarctica* showed a similar pattern of digestion to that of the high quality standard grass. IVDMD of *P. annua, P. alpinum* and *A. magellanica* were higher than the high quality standard grass of *P. pratense* used (Table 3). The plant species were highly digested after six hours, which indicate that the diet on South Georgia contains high concentrations of nutrients that are easily soluble in the rumen of reindeer.

Discussion

The flora on South Georgia is poor in species because of the island's isolation and its extension south of the Antarctic Convergence. Plant seeds may have originally been brought to the island by birds. The vegetation is dominated by the tussock grass *P. flabellata* which seems to have been important for the survival of Norwegian reindeer. In winter, reindeer exclusively eat *P. flabellata,* but in summer only 20% of the rumen contents were *P. flabellata* (Leader-Williams, 1980; 1988; Leader-Williams *et al*, 1981). As much as 90% of the plant particles in the rumen content of reindeer on South Georgia in summer consisted of grasses (Mathiesen *et al.*, 1999). The energy density of *P. flabellata* (19 054 KJ/g DM) was higher than that of *Cladonia stellaris* (18 800 KJ/g DM), a lichen highly selected by reindeer in the northern hemisphere in winter (Nieminen & Heiskari, 1989). On South Georgia the reindeer have survived for almost one hundred year without this plant. Daily maintenance energy requirement of captive non-lactating *R. t. tarandus* females have been measured to 232 $KJ/kgBM^{0.75}$ (Chan-McLeod *et al.,* 1994). Therefore, the reindeer on South Georgia have a daily requirement of 57.5 g $DM/kgBM^{0.75}$ of *P. flabellata* with 70% IVDMD (Table 3) to meet their maintenance energy requirement in summer. On the basis of measurements of ruminal VFA productions rates and mean IVDMD of several plant species (77% of DM) (Table 3) we have calculated the food intake in reindeer eating a mixed diet on South Georgia in summer to 636 $KJ/kgBM^{0.75}$, which could be translated into a daily

Table 3. Mean (standard deviation) *in vitro* dry matter digestibility of plants selected by Norwegian reindeer on South Georgia in summer and of two standard plants digested for 6, 12, 24 and 48 h in fresh rumen fluid (n = 3).

	Incubations							
	6 h		12 h		24 h		48 h	
Paridiochola flabellata	40.6	(5.8)	47.8	(2.5)	58.9	(2.7)	69.6	(4.0)
Aceana magellanica	56.5	(6.5)	63.8	(3.5)	73.7	(1.7)	75.8	(2.6)
Poa annua	54.6	(4.0)	66.3	(7.5)	75.0	(1.3)	81.4	(1.6)
Deschampsia antarctica	45.3	(5.2)	55.2	(3.9)	68.8	(2.3)	77.9	(2.6)
Phleum alpinum	54.1	(6.6)	61.7	(4.1)	71.6	(5.8)	82.6	(1.8)
Phleum pratense[a]	42.5	(3.5)	49.7	(3.1)	63.9	(2.1)	73.2	(0.8)
Phleum pratense[b]	27.4	(6.3)	33.7	(7.5)	46.5	(5.4)	53.9	(1.3)

[a] High quality standard grass of *P. pratense.* [b] Poor quality standard grass of *P. pratense.*

DM food intake of 96 g/kgBM$^{0.75}$ (Mathiesen *et al*, 2000). *P. flabellata* contains high concentrations of easy fermentable fructans and WSC, which may influence its palatability for reindeer and support rumen microbial fibre metabolism and DM degradation rates (Gunn & Walton, 1976; Leader-Williams *et al*, 1981; Pratt & Lewis-Smith, 1982). *P. flabellata* has a high standing biomass, dominated by leaves with long swards, and the availability of green leaves of *P. flabellata* through the snow in winter could prevent reindeer from losing body mass to the same extent as when they feed on a lichen-rich diet in winter in Norway, or protein poor winter pastures on Svalbard (Leader-Williams, 1988; Aagnes & Mathiesen, 1994; Øksendahl, 1994; Sørmo *et al*, 1999). While lichen conrain less than 3% crude protein of DM (Person *et al*, 1980), *P. flabellata* contained moderate concentrations of crude protein (14.8% of DM), less than high quality standard grass of *P. pratense* used for domestic ruminants (22.1% of DM) (Table 1). The content of true protein relative to total crude protein content was high in the tussock grass, which indicate that nitrogen are adequately available and could be efficiently used for rumen microbial synthesis in the reindeer. Likewise, BM (74 kg) of female reindeer, two to eight-years-old, on South Georgia in summer, is similar to the mean BM (74 kg) of adult female Norwegian reindeer on summer pastures in northern Norway (Tyler *et al*, 1999). In summer, reindeer also select other grasses on South Georgia like *P. pratense, P. annua, P. alpinum* all introduced by whalers, and indigenous plants like *A. magellanica, D. antarctica* all of which have a low bio-mass and are covered by snow in winter, but have high contents of important nutrients like protein and minerals in summer (Tables 1 & 2).

A. magellanica is so highly preferred by reindeer on South Georgia, that it is mainly abundant in places were reindeer are unable to graze (Leader-Williams *et al*, 1987). This observation may partly be explained by its high content of protein (Table 1). In comparison with plants eaten by reindeer in Norway and on Svalbard, the protein concentrations of most plant species were of moderate quality, while easily digestible energy as WSC in summer was high (Table 1) (Staaland *et al*, 1983; Staaland & White, 1991). None of the plant species collected on South Georgia contained as much protein as *Oxyria digyna* (31.1% of DM) and *Polygonum viviparum* (26.3% of DM) from Svalbard in summer (Staaland *et al*, 1983). Ruminal digestion of CWC may be influenced by the availability of non-protein nitrogen, amino acids and carbohydrates in the rumen contents (Ørskov, 1992), but on South Georgia these nutrients seem to figure adequately in the forage of reindeer (Table 1).

The high contents of minerals such as Mg and Na of the plant species collected (Table 2), may be due to the fact that precipitation (as much as 2000 mm annually) is influenced by the Atlantic Ocean. Faecal fertilisation by seals and penguins which use the island for breeding could also affect the mineral concentrations of these plants. Likewise, Staaland *et al.* (1983) and Staaland & White (1991) found similar mineral concentrations in coastal forage plants in northern Norway and Svalbard.

The lack of true woody plants on South Georgia was also supported by our analysis of the plant CWC content, such as cellulose, hemi-cellulose and lignin (Table 1). The highly selected *A. magellanica* contained very low CWC concentrations, and plant CWC composition of tussock grass was similar to the high quality standard grass of *P. pratense,* and to

Deschampsia flexuosa in the northern hemisphere in winter (Danell *et al.,* 1994). In contrast, lichens eaten by the reindeer in the north in winter, contain high concentrations of hemi-cellulose (80% of DM), but not of cellulose, as determined by the van Soest fibre analysis (van Soest, 1963a; b; Person *et al.,* 1980). The most striking difference between the plants on South Georgia in summer and those eaten by reindeer in the north (Person *et al.,* 1980) was the low plant lignin content of all species investigated (Table 1). High concentration of lignin prevents ruminal microbial degradation and may increase ruminal retention of forage plants. The low concentrations of plant lignin (< 3.2% of DM) was also reflected in the rumen contents (5.0% of dry organic matter, OM) of these animals, which were considerably less than in the rumen contents from reindeer in northern Norway (15.1% OM) and Svalbard (25.5% of OM) (Mathiesen *et al.,* 1999; Sørmo *et al.,* 1999). The low plant lignin content and high rates of plant IVDMD in reindeer on South Georgia could explain why the rumen wet weight fill was small (14% of BM) relative to the total gastrointestinal system (26% of BM) (Table 3) (Mathiesen *et al.,* 1999). In Svalbard reindeer rumen wet weight content comprised as much as 20% of BM in winter when the animals are eating a highly lignified diet (Sørmo *et al.,* 1999). In terms of lignin concentration, the pastures on South Georgia have to be considered as superior, effecting the high degradability of plants in the rumen fluid and could facilitate a short ruminal retention time, and therefore a high daily food intake in these reindeer. Poor quality standard grass of *P. pratense* were similiarly digested in rumen fluid from reindeer on South Georgia and in rumen fluid from reindeer in Norway in summer and winter (Table 4) (Aagnes *et al.,* 1996). In the rumen fluid from Svalbard reindeer, however, the same standard grass was 10% DM more digested in winter (Mathiesen *et al.,* 1984) (Table 4). This high ability to digest poor quality plants in winter could be explained by adaptation of cellulolytic bacteria in the rumen of Svalbard reindeer when they eat a diet rich in CWC (Orpin *et al.,* 1985). Plant chemistry influence on the number, composition and efficiency of rumen micro-organisms in reindeer and could explain this difference in IVDMD. We have, however, not yet been able to discover major differences in the rumen microbiota between reindeer eating grass on South Georgia and lichen fed reindeer in Norway (Aagnes *et al.,* 1995; Olsen *et al.,* 1995; own obs.). IVDMD of plants collected on South Georgia was high (40-57% DM) already after 6 h ruminal incubation and 48 h enzymatic digestion (Table 3), which correlates with the high content of easily digestible nutrients, like protein and WSC in these plants (Table 1). Extent of digestion of *P. flabellata* after 48 h microbial incubation was similar to IVDMD of high quality standard grass of *P. pratense* (73% of DM) with known digestibility in sheep (71% of DM) (Tilley & Terry, 1963). The mean IVDMD of plants eaten by Svalbard reindeer in summer was as high as 74% of DM (*Alopecurus alpinus*) (Staaland *et al.,* 1983) and grasses such as *Poa arctica* gave an IVDMD of 70.7% of DM (Mathiesen & Orpin, 1985). The *in vitro* OM digestibility of *D. flexuosa* in rumen fluid from Swedish reindeer in winter was as high as 79% (Danell *et al.,* 1994), while in the Canadian Arctic the IVDMD of vascular plant in the rumen fluid of Peary Caribou ranged between 50-80% DM (Thomas & Kruger, 1980). The low lignin content, moderate content of protein, high WSC and mineral contents and high rate of digestion, all characterise a summer pasture for reindeer of high quality.

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Table 4. Mean (standard deviation) *in vitro* digestibility of two different qualities of standard grasses of *Phleum pratense* after 48 h incubation in rumen fluid from reindeer (*Rangifer t. tarandus*) on South Georgia in summer, reindeer in Norway (*Rangifer t. tarandus*) and in Svalbard (*Rangifer t. platyrhynchus*) in summer and winter.

	S. Georgia	Norway		Svalbard	
	summer	summer*	winter*	summer**	winter**
P. pratense[a]	73.2 (0.8)	62.2 (5.5)	74.8 (1.8)	71.3 (5.2)	74.0 (4.1)
P. pratense[b]	53.9 (1.3)	50.2 (6.6)	53.7 (2.6)	57.5 (3.4)	63.5 (3.8)
n	3	6	6	6	6

[a] High quality standard grass of *P. pratense.* [b] Poor quality standard grass of *P. pratense.*
*Aagnes *et al.,* 1996. ** Mathiesen *et al*, 1984.

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