Comparative aspects of volatile fatty acid production in reindeer (*Rangifer tarandus tarandus*) in northern Norway and on South Georgia

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Abstract: Dietary influence on pH and volatile fatty acids concentrations and production rates in the rumen and distal fermentation chamber (DFC) was investigated in Norwegian reindeer (*Rangifer t. tarandus*) on South Georgia in summer (SG), and in northern Norway in late summer (NS) and winter (NW). Mean [standard deviation (*s*)] ruminal pH was similar in SG reindeer (6.46, s = 0.13) and NW reindeer (6.45, s = 0.19), but significantly different from NS reindeer (6.87, s = 0.08)($P < 0.05$). Mean DFC pH in SG reindeer (6.92, s = 0.12) and in NS reindeer (6.70, s = 0.16) did not differ significantly. In NW reindeer DFC pH (6.26, s = 0.20) was significantly lower than in the SG and NS animals ($P < 0.05$). Mean ruminal concentration of volatile fatty acids (VFA) was 92.4 mM (s = 13.3) in SG reindeer, which was significantly larger ($P < 0.05$) than in NS (71.5 mM, s = 10.2) and NW reindeer (73.3 mM, s = 9.7). In DFC mean VFA concentration was 51.3 mM (s = 11.7), and 48.8mM (s = 14.5) in SG and NW reindeer respectively, and significantly less than in NS reindeer (86.7mM, s = 5.4) ($P < 0.05$). Mean daily ruminal VFA rate of production was 246.4 kJ/kg $BM^{0.75}$ in SG reindeer, compared to 195.6 kJ/kg $BM^{0.75}$ in NS and 193.4 kJ/kg$BM^{0.75}$ in NW reindeer. Mean daily VFA rate of production in DFC was 8.3 kJ/kg $BM^{0.75}$ in SG reindeer compared to 6.2 kJ/kg $BM^{0.75}$ in NS and 3.0 kJ/kg $BM^{0.75}$ in NW reindeer. The summer pastures on SG and NS were of moderate quality in terms of ruminal VFA production. In winter in northern Norway when forage quality was assumed to be low, both ruminal and DFC pH were low. The high fermentation rate in winter was probably due to easily digestible carbohydrates in the lichens eaten. DFC seems to be of minot impottance in these reindeer in terms of VFA energy yield.

Key words: fermentation, grasses, lichen, VFA, woody plants.

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Introduction

In northern Norway semi domesticated reindeer (*Rangifer t. tarandus*) migrate 150-350 km seasonally between inland pastures where they eat lichens, woody plants and some dry grasses in winter, to coastal summer pastures where graminoids and herbs are selected to a greater extent. Lichens which consist of fungi and algae are chemically and structurally very different from vascular plants. The chemical composition of lichens consists of as much as 75% lichen hemi-cellulose, including xylan and lichen starch lichenins in addition to small amounts of cellulose and protein, while woody plants in winter are highly lignified (Person *et al.,* 1980; Mathiesen *et al.,* 1999b). Early in this century semi domesticated Norwegian reindeer were introduced to the sub-Antarctic island of South Georgia where they now eat mainly grasses all year round, indepen-

dent of lichens and woody plants (Leader-Williams, 1978; 1988). The reticulo-rumen (RR) and distal fermentation chamber (DFC = *caecum* and *ansa proximalis coli*) of reindeer harbour microorganisms which ferment plants to energy-rich volatile fatty acids (VFAs), including acetate, propionate and butyrate (Orpin *et al*, 1985; Mathiesen *et al*, 1987; Aagnes *et al.*, 1995). The VFAs are absorbed across the reticulo-rumen and DFC wall and supply as much as 70% of the daily energy requirement in domestic animals (Annison & Armstrong, 1970; Hungate, 1966). In many domestic ruminants the concentration and the size of the VFA pool in the reticulo-rumen may be correlated to the rate of production of VFA and reflect food quality (Leng & Brett, 1966; Leng *et al*, 1968, Weston & Hogan, 1968). Only few data on ruminal carbohydrate fermentation rates are available from wild ruminants (White & Gau, 1975; White & Staaland, 1983; Lechner-Doll *et al.*, 1991; Boomker, 1995; Sørmo *et al*, 1997). In Svalbard reindeer (*R. t. platyrhynchus*) ruminal VFA production rate was low in winter when the animals were eating poor quality grasses and mosses. In summer, when these animals forage on a high quality diet, ruminal VFA production contributed more than 78% of their resting metabolic rate in summer (Nilssen *et al*, 1984; White & Staaland, 1983; Sørmo *et al*, 1997). In view of the extremely different diets of reindeer on South Georgia and in Norway, ruminal and DFC carbohydrate fermentation were evaluated by investigating the pH, rate of production and concentrations of VFAs using the zero-time technique originally described by Caroll & Hungate (1954).

Material and methods

Study areas

Studies on South Georgia (54-55°S, 33-38°W) were carried out in January and February 1990 (summer) in Husvik Harbour, where the vegetation differed markedly from that normally encountered by reindeer in Norway. Swards of grasses such as *Deschampsia antarctica, Phleum alpinum,* and *Poa annua* occur locally in wet areas surrounded by large areas of tussock grass, *Paridiochola flabellata* (Lindsay, 1973; Leader-Williams *et al*, 1987).

Our "summer" studies were carried out on the island of Reinøy in northern Norway (69 (N, 21 (E) in the middle of September 1994 (late summer/early autumn). The vegetation on Reinøy is dominated by graminoids and herbs, with an abundance of willow and birch. The winter studies in northern Norway were carried out in February and March 1991 close to Kautokeino (69°N, 23°E) where birch, shrub forest, lichens and heather heaths dominated (Johansen & Tømmervik, 1990).

Animals

On South Georgia (SG) six adult non-lactating female reindeer (77.2 kg BM, $s = 3$) were shot while grazing. Rumen fermentation was investigated in all animals, and DFC fermentation was investigated in three of them. On the summer pasture (NS) in Norway four non-lactating adult females (78.5 kg BM, $s = 6$) were killed for the rumen investigations, and three of them were used in the DFC fermentation experiments. Nine adult females (59.0 kg BM, $s = 15$) were killed on winter pasture (NW) for the rumen experiments, and six of these were used in the DFC fermentation rate studies.

In vitro *ruminal and DFC VFA production*

The zero-time *in vitro* fermentation method was used to calculate the VFA concentration at the time of death and the VFA production rates in rumen and DFC contents (Caroll & Hungate, 1954; Hungate *et al*, 1961; Hungate, 1966; White & Staaland, 1983; Olsen & Mathiesen, 1996; Sørmo *et al*, 1997). The method includes collection of rumen and DFC fluid using standard methods to avoid oxygen contamination (Orpin, 1982; Orpin *et al*, 1985). In NS reindeer the rumen and the DFC of individual animals were emptied into separate prewarmed thermos flasks (10 L and 5 L, respectively) which were sealed, weighed and incubated for 60 min at 35-39 °C. In SG and NW reindeer the rumen and DFC were left in the abdominal cavity for 60 min after death during the incubation and the digesta contents were then weighed. The contents were mixed thoroughly prior to sampling. A sub-sample of rumen contents (100 g) was sieved through two layers of muslin. Ten ml of filtered rumen fluid and 1 ml of DFC content were subsequently collected using a syringe. All samples were collected *in duplo.* Five ml 0.5 M HCl were added to 10 ml rumen filtrate, and 2.5 ml 0.5 M HCl to the DFC content which was then frozen in plastic tubes (-20 °C). Samples for VFA concentrations measurements taken from individual animals immediately after death and then at intervals during the incubation period. The production of VFA in 24 h was calculated on the basis of the amount produced during the 60 min incubation period. The total rumen and

Table 1. Mean (s = standard deviation) body mass, ruminal fluid volume, volatile fatty acid (VFA) concentrarion pool size and production rate in reindeer (*Rangifer t. tarandus*) on South Georgia in summer (SG) (n = 6), northern Norway in late summer (NS) (n = 4) and in winter (NW) (n = 9).

					VFA production			
Location	Body mass (kg)	Fluid volume (ml)	VFA concentration (mM)	Pool size (mmol)	(mM/h)	(mM/h·L)	(mM·L/kg $BM^{0.75}$/d)	(KJ/kg $BM^{0.75}$/d)
SG	77.2	9877.8	92.4	925.0	23.4	225.9	207.7	246.4
s	3.1	1446.6	13.3	234.3	5.6	49.9	43.9	52.1
NS	78.5	7556.0	71.5	554.9	25.2	195.5	175.5	195.6
s	5.6	1065.0	10.2	89.5	7.8	80.6	66.4	74.7
NW	59.0	6413.9	73.3	461.0	24.2	157.5	171.8	193.4
s	14.6	2005.7	9.7	126.0	9.6	85.7	70.1	77.5

Table 2. Mean (s = standard deviation) body mass, fluid volume of distal fermentation chamber (DFC), volatile fatty acids concentration (VFA), pool size and production rates in reindeer (*Rangifer t. tarandus*) on South Georgia (SG) in summer (n = 3), in northetn Norway in late summer (n = 3) (NS) and in winter (n = 6) (NW).

					VFA production			
Location	Body mass (kg)	Fluid volume (ml)	VFA concen tration (mM)	Pool size (mmol)	(mM/h)	(mM/h·L)	(mM·L/kg $BM^{0.75}$/d)	(KJ/kg $BM^{0.75}$/d)
SG	78.7	885.3	51.3	46.0	10.6	9.4	8.5	8.3
s	3.7	91.3	11.7	13.5	2.9	2.6	2.2	2.1
NS	77.0	468.0	86.7	30.0	14.8	5.5	6.5	6.2
s	5.7	120.4	5.4	8.4	12.4	5.5	4.9	4.6
NW	50.8	414.2	48.8	20.3	5.6	2.2	2.9	3.0
s	8.7	52.7	14.5	6.6	2.4	0.8	1.3	1.4

DFC fluid volumes were found by determination of the dry matter content in the fermentation chambers and the total water VFA pool size was calculated. Time of death and time of sampling of rumen and DFC fluid were registered. The mean VFA concentration and rate of production in the rumen and DFC in the SG, NS and NW reindeer were calculated on the basis of regression line analyses of production rates in individual animals (Tables 1 and 2). Single VFA concentrations measured in rumen and DFC fluid subsequently after death within each group of the reindeer investigated are shown in Fig. 2. The slope of the curve represents the rate of production *in vivo* at the time at which the sample was collected from the animal. By extrapolating the regression lines to zero, we were able to determine the concentration of VFA in the fermentation chambers at time of death. Energy available from the VFA pool was calculated using the proportion of VFAs measured in the rumen and DFC of these reindeer and energy values of 874, 1534, 2190 kJ/mole for acetic, propionic and butyric acids, respectively, were obtained (Blaxter, 1962).

pH measurements

Ruminal and DFC pH values were measured directly in the fluid of the fermentation chambers in the animals or immediately after transfer to prewarmed thermos containers, and then at regular intervals until 60 min after death, using two calibrated portable pH meters (pHM 80 and pHM 201, Radiometer® Copenhagen) with combined pH electrodes (GK 2501c and pHC 2005). The temperature in the ruminal and DFC contents was kept at between 35 °C and 39 °C during the sampling period. Mean pH at t_0 and mean rate of pH changes in the rumen and DFC in SG, NS and NW reindeer were calculated from the regression line analysis of individual animals (Table 3). All single ruminal and DFC pH measurements within each group of ani-

Table 3. Mean (s = standard deviation) molar proportion (%) of acetate, propionate and butyrate and the acetate/propionate (A/P) ratio and pH in the ruminal and DFC contents (distal fermentation chamber), respectively, in reindeer (*Rangifer t. tarandus*) on South Georgia in late summer (SG) (n = 6) (n = 3) in northern Norway in summer (NS) (n = 4) (n = 3) and in winrer (NW) (n = 9) (n = 6).

		Acetate		Propionate		Butyrate		A/P		pH		pH/h	
		mean	s	mean	s	mean	s	mean	s	mean	s	mean	s
Rumen	SG	69.3	1.8	16.8	1.3	13.8	1.1	4.1	0.4	6.45	0.13	0.21	0.04
Rumen	NS	73.6	0.5	16.2	1.0	10.1	1.1	4.5	0.3	6.87	0.08	0.16	0.12
Rumen	NW	71.6	1.4	17.7	2.2	10.6	1.4	4.1	0.6	6.45	0.19	0.22	0.09
DFC	SG	85.2	1.1	12.0	1.2	2.7	0.4	7.2	0.9	6.92	0.12	0.05	0.034
DFC	NS	89.4	1.4	8.2	1.4	2.3	0.1	11.3	1.9	6.70	0.16	0.03	0.022
DFC	NW	81.9	0.8	13.6	0.4	4.3	0.5	6.0	0.3	6.26	0.20	0.09	0.091

mal investigated are also shown in Fig. 1. By extrapolating the calculated regression lines for changes in pH to zero time, the pH at time of death could be estimated. Changes in pH per unit time were used as an indicator of fermentation rate.

VFA analyses

Samples of ruminal and DFC contents were collected regularly at intervals of no greater than 15 min for 60 min after death. The VFA concentration was measured using a gas-liquid chromatograph (GLC) (Crompack CP 9000; Crompack Bergen op Zoom, Holland), and a CP SIL 8 CD column (Cromepack no 7452, 30 m, 0.2 mm ID) as described by Sørmo *et al.* (1994); Olsen & Mathiesen (1996), Olsen *et al.* (1997) and Sørmo *et al.* (1997).

Statistical analyses

The data were expressed as means and standard deviations (s). Significant differences were calculated by Student's t-test ($P < 0.05$) according to Johnson & Bhattacharyya (1992).

Results

Ruminal and DFC concentrations of VFA and pool size

The ruminal and DFC concentration of VFA in reindeer from different seasons and locations are shown in Tables 1 and 2 and Fig. 2. The mean ruminal concentration of VFA in SG reindeer (92.4 mM) was significantly higher than in NS (71.5 mM) and NW reindeer (73.3 mM) ($P < 0.05$) (Table 1). Mean DFC VFA concentrations in SG and NW reindeer were significantly lower than in NS reindeer ($P < 0.05$) (Table 2). Mean rumen fluid volumes were 127.8 ml/kg BM (s = 16.1), 95.7 ml/kg BM (s = 7.8) and 108.1 ml/kg BM (s = 14.0) in SG, NS and NW reindeer, respectively. These values were not significantly different. The mean fluid volume of the DFC in SG reindeer (11.3 ml/kg BM, s = 1.6) was significantly larger ($P < 0.05$) than in NS reindeer (6.2 ml/kg BM, s = 2.1) and NW reindeer (8.2 ml/kg BM, s = 0.7). The mean ruminal VFA pool size in SG reindeer (12.0 mmol/kg BM, s = 2.1) was significantly different ($P < 0.05$) from those of NS (7.0 mmol/kg BM, s = 0.9) and NW reindeer (7.9 mmol/kg BM, s = 1.6) (Table 3). The mean pool size of DFC were 0.6 mmol/kg BM (s = 0.2), 0.5 (s = 0.2), and 0.4 (s = 0.1) in SG, NS and NW animals, respectively (Table 2).

Ruminal and DFC pH

Mean values of ruminal and DFC pH in reindeer from different locations and seasons are shown in Table 3 and Fig. 1. Mean ruminal pH values in SG and NW reindeer were significantly different from those of NS reindeer ($P < 0.05$) (Table 3). Mean rates of *in vitro* pH changes in the rumen contents did not differ significantly between groups (Table 3; Fig. 1). The mean pH values in DFC in SG and NS reindeer were significantly different from NW reindeer (6.26) ($P < 0.05$) (Table 3). Mean rates of pH decrease in DFC content in SG, NS and NW reindeer were not significantly different (Table 3; Fig. 1).

Acetate, propionate and butyrate ratio

The mean ruminal acetate/propionate ratio varied between 4.1 and 4.5 in the groups investigated. The DFC acetate/propionate ratios in SG reindeer (7.2) and NW reindeer (6.0) were significantly different from that of NS reindeer (11.3) ($P < 0.05$) (Table 3).

VFA production rate

Mean rate of ruminal VFA production in SG reindeer (23.4 mM/h) did not differ significantly from

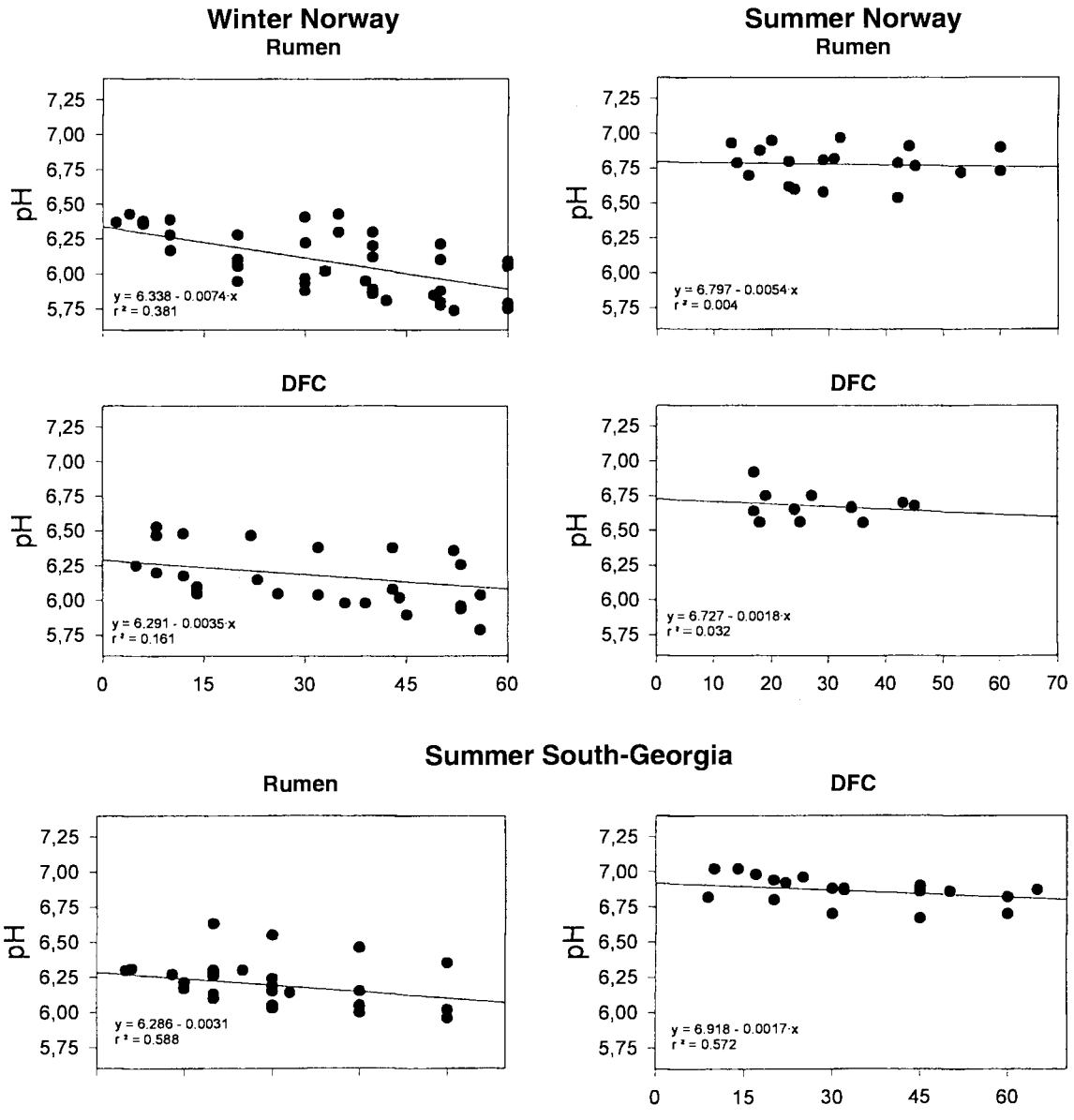

Fig. 1. All single pH measurements measured in each group of Norwegian reindeer (*Rangifer t. tarandus*) within one hour of death in the rumen fluid and distal fermentation chamber (DFC) content respectively on South Georgia in summer (n = 6) (n =3), northern Norway in late summer (n = 4) (n = 3) and northern Norway in winter (n = 9) (n = 6).

NS reindeer (25.2 mM/h), and NW reindeer (24.2 mM/h) (Table 1). The DFC VFA rate of production in SG reindeer (10.6 mM/h) was not significantly different from that of NS reindeer (14.8 mM/h) (Table 2). However, SG and NS reindeer had a significantly higher (P < 0.05) production of VFAs in DFC compared with reindeer in NW (5.6 mM/h, P < 0.05). Mean total ruminal VFA production was greater in SG reindeer (207.7 mM · L/kg $BM^{0.75}$) than in NS and NW reindeer (Table 1). In SG reindeer DFC fermentation comprised 3.4% of the total ruminal VFA production, compared with 3.2% and 1.6% in NS and NW reindeer, respectively. The energy available from VFA production derived from the fermentation of the plants eaten is shown in Tables 1 and 2.

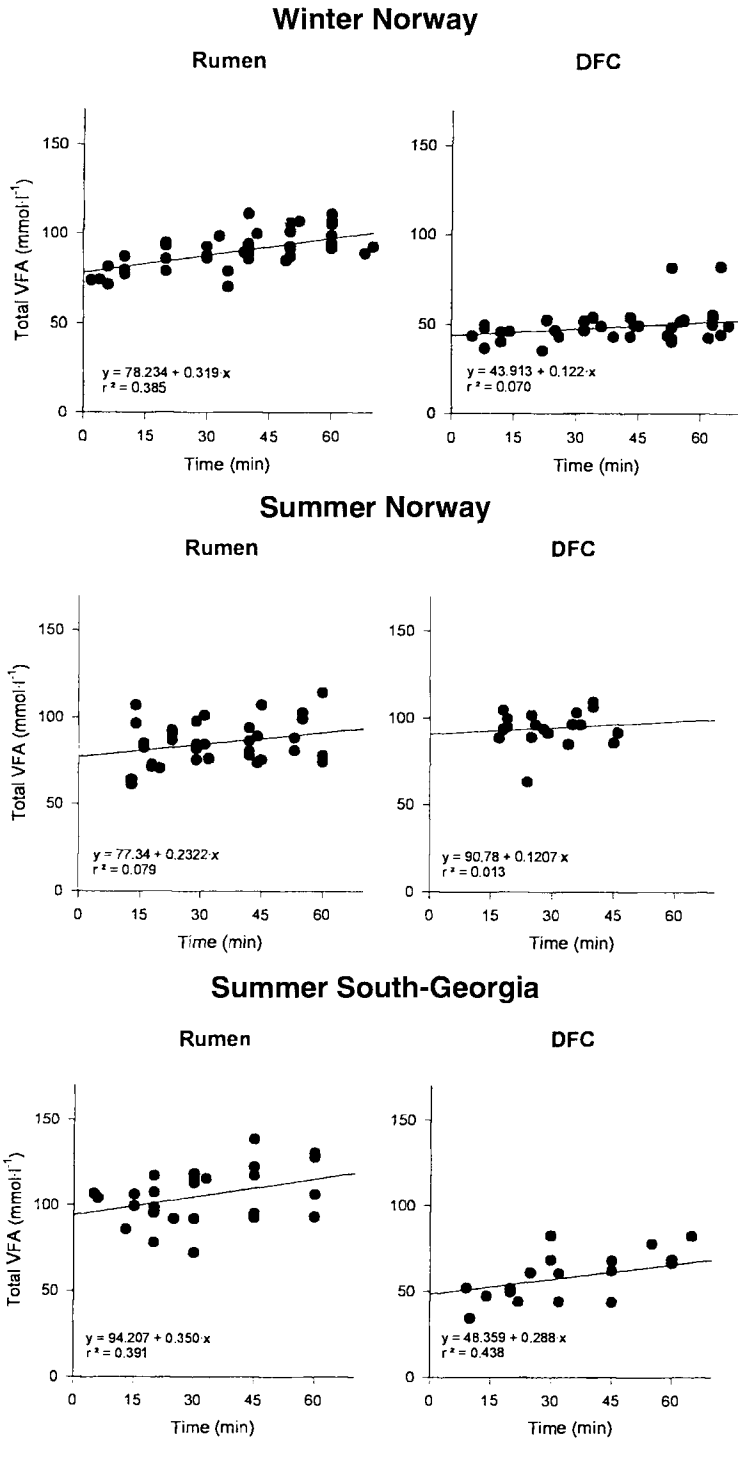

Fig. 2. All single concentrations of volatile fatty acids subsequently measured in each group of Norwegian reindeer (*Rangifer t. tarandus*) within one hour of death in the rumen and distal fermentarion chamber (DFC) content, respectively on South Georgia (n = 6) (n = 3), in northern Norway in late summer (n = 4) (n = 3) and in northern Norway in winter (n = 9), (n = 6).

Discussion

Ruminal and DFC pH

The pH of rumen fluid depends on the plant quality of the diet eaten, the rate and volume of salivary buffer secretion, and the rate of production and absorption of VFAs across the rumen wall (Church, 1983). The ruminal pH was similar in SG and NW reindeer despite the differences in dietary species and forage chemistry between these two locations (Table 3; Fig. 1). In SG reindeer as much as 90% of all plant particles in the rumen consisted of grasses, compared to 65% in NS and 21% in NW reindeer. In NS reindeer 11 and 17% of rumen particles were lichens and woody plants, respectively, compared with 35% lichens and 36% woody plants in NW reindeer. No lichens or true woody plants were found in the rumens of SG reindeer (Mathiesen *et al.*, 1999b). The similar pH in SG and NW reindeer could be explained by the large intake of highly fermentable forage on SG in summer, when their salivary secretion is assumed to be high. In winter appetite is assumed to be depressed in reindeer (Larsen *et al.*, 1985) and salivary secretion is therefore believed to be low. In accordance with this, the mass of salivary glands in reindeer decreased from summer to winter, supporting the explanation of reduced salivary buffer secretion in winter (Mathiesen *et al.*, 1999a). In NW reindeer, however, ruminal pH was lower than expected and positively related to the animals' intake of lichens. Ruminal pH in reindeer seems partly to reflect food quality. In reindeer fed poor quality fibrous timothy, ruminal pH was as high as 7.1, but fell to 6.3 when they were fed high quality timothy containing easily fermentable polysaccharides in winter (Aagnes *et al.*, 1996). Furthermore, in rein-

deer fed pure lichen *ad lib.* ruminal pH was 6.5 (Aagnes *et al.,* 1995). Thus, ruminal pH and its rate of changes in SG and NW reindeer may indicate high forage quality in terms of carbohydrate fermentation of plant materials (Table 3). The rumen contents of NW reindeer contained as much as 44.5% hemi-cellulose of organic dry matter (ODM), compared to 18.9% and 22.7% of ODM in SG and NS reindeer respectively (Mathiesen *et al.,* 1999b). In contrast, the high ruminal pH (6.9) in NS reindeer could be due to a combined effect of low rumen fermentation and high rate of salivary secretion in late summer in northern Norway. In NW reindeer the pH of the DFC content was low, compared to SG and NS reindeer which could indicate a high microbial fermentation rate. Likewise, in reindeer calves fed a pure lichen diet DFC pH was as low as 5.9 (Øksendal, 1994), while in Svalbard reindeer DFC pH was as high as 7.0 in winter when they were eating fibrous plants dominated by mosses (Sørmo *et al.,* 1997). We believe that the low DFC pH measured in NW reindeer could be related to the high proportion of lichens (35% of all rumen particles) in the diet and its unique carbohydrate chemistry (Mathiesen *et al.,* 1999b).

Concentration and production rates of VFA

In domestic ruminants the concentration and pool size of VFAs seem to be correlated with VFA production rates. High ruminal VFA concentration ought therefore to reflect high VFA production as determined by food quality and quantity (Hungate, 1966; Leng & Brett, 1966; Leng *et al.,* 1968; Weston & Hogan, 1968). This does not seem to be the case in Arctic ruminants with pronounced seasonal changes in food intake and large variations in plant quality (Sørmo *et al.,* 1997). In Svalbard reindeer the high ruminal pH seem to lower the absorption of VFA and was probably the reason for the high VFA concentration measured when VFA production rate was low in winter (Sørmo *et al.,* 1997). The pH in the rumen influences the ratio of dissociated and non-dissociated VFAs, while a low pH increases the proportion of non-dissociated VFAs and thus strongly influence absorption of VFAs (Dijkstra *et al.,* 1993). Likewise, in seasonal African domestic ruminants, Lechner-Doll *et al.* (1991) observed that dilution rates, rumen fluid volume and absorption rate influence VFA concentrations far more than the production rate. Weston & Hogan (1968) indicated that variations in diet and the physiological state of the animal could influence the blood supply to the rumen epithelium and result in changes in absorption rates, pool size and production of VFA relative to VFA concentration. The absorption of VFAs across the rumen epithelium of reindeer may also change seasonally due to changes in the relative size of the absorptive surface, due to atrophy of rumen papillae in winter (Josefsen *et al.,* 1996). Thus, the high VFA concentration in SG reindeer compared to those in NS and NW does not necessarily indicate better forage quality in terms of carbohydrate fermentation. The difference in ruminal VFA production rates, however, may well indicate differences in dietary quality (Table 1; Fig. 2). In the Svalbard reindeer ruminal VFA concentration was 89 mM and the production rate was 550 mM/kg $BM^{0.75}$/d in summer. Therefore the forage in SG and NS reindeer seems to be of moderate quality compared with the forage eaten by Svalbard reindeer (White & Staaland, 1983). Our results regarding ruminal VFA concentration and production rates in NS reindeer (Table 3) were similar to those obtained from reindeer grazing in Norway in summer (61 mM, 178 mM/kg$BM^{0.75}$/d) (White & Staaland, 1983). Svalbard reindeer have survived independent of lichens in winter, and VFA production was almost negligible when the rumen contained as much as 50% fibrous mosses and low levels of nitrogen (White & Staaland, 1983; Sørmo *et al.,* 1997; Sørmo *et al.,* 1999). In contrast to Svalbard reindeer, however, the high concentration and production rate of VFA in NW reindeer that eat lichen in winter, stress the unique character of the carbohydrates in lichen as an energy source for reindeer in winter. Seventy five percent of DM of lichens are digested by reindeer (Jacobsen & Skjenneberg, 1975). Furthermore, we believe that the energy released by lichens supports the microbial digestion of other less digestible plants in a mixed diet eaten in winter (Mathiesen *et al.,* 1999b).

VFA concentration and production rates in DFC

In NW reindeer the DFC size relative to the RR was small in comparison with the relative DFC size in SG reindeer (Mathiesen *et al.,* 1999b). The concentrations and production rates of VFAs in DFC were low in all groups investigated and were not positively correlated with the size of the DFC (Mathiesen *et al.,* 1999b). The pH of the DFC contents was low in NW reindeer (Table 3), and we assume that the proportion of non-dissociated VFAs

were high and consequently that absorption across the DFC wall would be high. This could explain the low VFA concentration recorded in NW reindeer. According to Ulyatt *et al.* (1975) the proportion of hemi-cellulose fermented in the large intestine is higher than that of cellulose, and we assume that lichen partially escape rumen digestion and becomes available for the bacteria in the DFC. Lichens consist mainly of hemi-cellulose including xylans (in β-1.4 and β-1.3 linkages) (Hale, 1961; Culberson, 1969; Person *et al.,* 1980), and it is likely that the high hemi-cellulose content in the rumen contents of NW reindeer would also influence fermentation in the DFC (Mathiesen *et al.,* 1999b). In Svalbard reindeer DFC content size was large (10% of rumen wet weight content) and positively correlated to the ammount of hemi- cellulose in the diet. No such relationship was found between DFC size and hemi cellulose in NW reindeer. The DFC to rumen ratio was only 1:16 in reindeer that were eating lichens in winter (Mathiesen *et al.,* 1999b). Eating a high quality diet with less fibrous food, Svalbard reindeer also had small DFCs, but in these animals as much as 17% of the total VFA produced originated from the DFC (Sørmo *et al.,* 1997; 1999). Fermentation and pH regulation in the DFC of ruminants are still poorly understood.

Energetics

Based on VFA production data we calculated the energy yield from the rumen fermentation employed by SG, NS and NW reindeer (Tables 1 and 2). Daily fasting metabolic rate in Norwegian reindeer was determined by Nilssen *et al.* (1984) to 112.32 kJ/kg BM. Resting metabolic rate in reindeer rose from winter (501.12 kJ/kg $BM^{0.75}$) to summer (736.13 kJ/kg $BM^{0.75}$) in accordance with the increase in daily food intake from 62.5 g/kg $BM^{0.75}$ to 134 g/kg $BM^{0.75}$. In domestic ruminants 50-70% of the daily energy requirement is supplied from the microbial production of VFA (Annison & Armstrong, 1970). Mean ruminal VFA production in SG reindeer was estimated to be 246.36 kJ/kg $BM^{0.75}$/d, which represents 33% of the resting metabolic rate measured in the summer animals. In reindeer in NS and NW ruminal VFA production rates were 26% and 38% less than the resting metabolic rates measured on different food intake in summer and winter, respectively. In the high Arctic the ruminal VFA production of Svalbard reindeer was as high as 575 kJ/$BM^{0.75}$/d summer, but was almost negligible in some areas in winter (White & Staaland, 1983; Sørmo *et al.,* 1997). The energy gain from VFA production in NW reindeer thus emphasises the importance of lichen in the diet of Norwegian reindeer in winter, when vascular plants are assumed to be poorly digestible. The unique carbohydrate chemistry of lichens seems to influence both ruminal and DFC metabolism in winter. We assumed that 50% of daily digestible energy passes through the VFA pool, and we know that the mean digestibility of plants eaten on SG in summer was 77% of dry matter (Mathiesen & Utsi, 2000). Thus, mean daily food intake in reindeer on SG was calculated to 636 kJ/kg $BM^{0.75}$. In summer the daily maintenance requirement of captive lactating female *R. t. granti* and *R. t. tarandus* was 457 kJ/kg $BM^{0.75}$, compared with 232 kJ/kg $BM^{0.75}$ in non-lactating females (Chan-McLeod *et al.* 1994), which is 1.4 and 2.7 times less than the daily food intakes of non-lacating female reindeer on South Georgia. Using data from Nilssen *et al.* (1984), we have calculated that our results are equivalent to 96 g DM/kg $BM^{0.75}$ daily food intake in SG reindeer. Daily dry matter intake in Svalbard reindeer in summer was 187 g/kg $BM^{0.75}$, using the same methods (White & Staaland, 1983).

The summer pastures on SG and NS were of moderate quality in terms of ruminal carbohydrate fermentation. Lichens in the diet of NW reindeer seem to stimulate ruminal fermentation when nutrient content is otherwise low in winter. Energy yield from rumen fermentation did not differ much between the SG, NS and NW reindeer. The VFA concentration and pH in the DFC was influenced by the different diets consumed, but VFA production was low regardless of diet, and seems to be of minor importance in these animals.

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