

Increased mass of reticulo-rumen tissue and contents with advancing age in Svalbard reindeer

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Abstract

Little is known about the effect of age on digestive processes in wild cervids. One potentially important mechanism is that tooth wear alters the occlusal surface topography, causing gradual loss of functionality. Mastication efficiency is crucial to digestion processes among ruminants, as a larger particle size is associated with longer retention times and potentially reduced digestion efficiency. Using data from 49 adult Svalbard reindeer *Rangifer tarandus platyrhynchus* females, we investigated whether the mass of reticulo-rumen (RR) contents and tissue and the amount of back fat showed age-related changes. Older animals had higher RR content mass than younger individuals. This is consistent with the prediction that altered particle size due to decreased mastication efficiency led to increased rumen retention time either through increased RR capacity or filling. Additional data on RR particle size distribution were available for a subset ($n = 30$). The correlation between the proportion of small particles (< 1.0 mm) and RR contents was much weaker than the correlation between age and RR contents. This suggests that additional factors apart from particle size contribute to the age-related pattern in RR content mass. The mass of RR tissue in older animals was higher than that in younger animals. This possibly reflects an adaptation to the higher organ fill. The amount of back fat decreased with age, suggesting that alterations in digestion-related processes are not sufficient to compensate for reduced mastication efficiency in Svalbard reindeer. Our results present one possible link between foraging, digestive processes and life-history patterns.

Introduction

Ruminants are especially well adapted to digest plant carbohydrates such as cellulose and hemicellulose. This is essentially achieved through the action of symbiotic microbes in the rumen (e.g. Van Soest, 1994, chapter 12). The microorganisms are, on the other hand, inefficient in reducing forage particle size (Spalinger & Robbins, 1992). Mechanical degradation through mastication processes is therefore crucial to facilitate microbial decomposition and hence digestion efficiency. Wear of dental tissue is an inevitable consequence of this process, and has led to the evolution of lesser or larger degrees of hypsodonty and molar complexity (in terms of enamel–dentin infoldings and infundibuli) among all ungulate species (Janis, 1988; Janis & Fortelius, 1988). Despite these adaptations, wear has been found to cause a gradual reduction in chewing efficiency (Lanyon & Sanson, 1986b; Skogland, 1988; Kojola *et al.*, 1998; Perez-Barberia & Gordon, 1998; Veiberg *et al.*, 2007). However, there have been few empirical

examinations of the relationship between age and reticulo-rumen (RR) function, which may be affected if mastication efficiency or other factors related to digestive efficiency change with age. An exception is in koalas *Phascolarctos cinereus*, where it has been shown that individuals with more worn teeth used a longer time to feed, chewed more and had larger particles in the stomach compared with individuals with better teeth (Lanyon & Sanson, 1986a,b; Logan & Sanson, 2002a,b).

The mechanisms involved in selective retention of RR particles are a combination of passive processes related to filtering and particle properties, and active turnover of RR fill through rumen wall contractions (Lechner-Doll, Kaske & Engelhardt, 1991; Van Soest, 1994). The reticulo-omasal orifice represents the bottleneck for flow of digesta from the RR to the omasum. For a long time, the reticulo-omasal orifice was considered the single mechanism for selective retention, but this has been repeatedly disproved (e.g. Lechner-Doll *et al.*, 1991). The fully opened reticulo-omasal orifice diameter is recognized to far exceed the threshold size

for particle passage. This emphasizes that other mechanisms, such as density dependency of outflow (Lechner-Doll *et al.*, 1991), may be of significance to the processes responsible for selective RR particle retention in ruminants. RR filling is determined partly by the physical characteristics of the feed, which also affects digesta passage (Conrad, 1966). In seasonal environments, forage quality (mainly fibre content) is suggested to be responsible for increases in both RR capacity (Lechner-Doll *et al.*, 1990; Holand, 1992) and retention time (Lechner-Doll *et al.*, 1990; Holand, 1994), representing a strategy for improving the utilization of low-quality feed (Lechner-Doll *et al.*, 1991). While seasonal changes in forage quality are known to cause numerous physiological adaptations along the entire digestive system of ruminants, potential alterations of digestive processes induced by irreversible changes in chewing efficiency have not been documented. Given that tooth wear reduces mastication efficiency, one possibility is that RR turnover processes would become slower as a consequence of increased average particle size. It is also possible that there may either be compensation through increased chewing investment (Gross *et al.*, 1995; Perez-Barberia & Gordon, 1998) or changes in other aspects of the digestive process (e.g. increased dimensions of parts or of the entire digestive tract).

In this study, we analyse the relationship among the weight of RR tissue, RR contents and age in Svalbard reindeer *Rangifer tarandus platyrhynchus*. In a previous study, we found a correlation between increased tooth wear and reduced proportion of small (< 1.0 mm) rumen particles with increasing age in Svalbard reindeer (Veiberg *et al.*, 2007). Based on this, we make predictions for correlations between these factors. We test whether there is (1) increased mass of RR contents with age. This might be expected if the RR retention time increases with age due to a reduction in mastication efficiency (and a subsequent increase in the particle size) under the assumption of a constant intake level. We also test whether the (2) mass of RR tissue increases with age, which would indicate that the RR had increased in volume, been reinforced or both. Finally, we address the potential consequences for the energy budget predicting (3) reduced amounts of energy reserves (back fat) with increasing age. Other studies have reported reduced body mass with increased age (Mysterud *et al.*, 2001; Weladji *et al.*, 2002); this likely reflects a decrease in fat, but we are not aware of studies showing this with direct measurements of fat.

Materials and methods

Study area

Data were collected from two areas, Colesdalen/Reindalen (77°57'N, 15°30'E) and Sassendalen (78°15'N, 17°20'E), in Nordenskiöldland, Spitsbergen, Svalbard. The region is characterized by wide valleys surrounded by steep mountains and glaciers. Helicopter surveys conducted annually

during the summers since 1992 indicate that the reindeer population size in both areas is roughly ≈ 700 (Governor of Svalbard, unpubl. data). Hunting pressure is generally low and there are no large terrestrial predators present in the area.

Detailed vegetation mapping has only been carried out in the Colesdalen/Reindalen area, but the productivity and the distribution of dominating vegetation communities in the two areas are believed to be similar. The vegetation is diverse and ranges from polar desert with an extremely low plant cover to relatively dense *Dupontia* marshes. Ridge communities largely remain snowfree during winter, contain very few species and are characterized by the presence of *Dryas octopetala* and *Salix polaris*. Extensive heathland areas (*Luzula* heath) occur, which are dominated by *Luzula confusa* and *S. polaris*, and in wetter places also *Alopecurus alpinus* (*Luzula*–*Alopecurus* heath). On shallow slopes, patches of graminoid vegetation are found, with a relatively high density of grasses, including *Poa alpigena*, *Poa alpina*, *Festuca cryophila* and *A. alpinus*. Wet moss vegetation is characterized by *A. alpinus* and a relatively high density of *Equisetum arvense*. *Dupontia* marshes hold numerous species but are dominated by *Dupontia* spp. and *Eriophorum scheuchzeri* (Van der Wal *et al.*, 2000a).

Data material

RR were collected from 49 adult Svalbard reindeer females (Sassendalen and Colesdalen/Reindalen) harvested for scientific purposes between 20 and 24 October in 1994, 2002 and 2003. Based on an extended dataset of females shot in late October between 1994 and 2006, growth in body mass ($n = 248$) and jaw length ($n = 239$) was found to cease at 3 years of age (Fig. 1a and b). This age was used as the threshold age for being classified as an adult. We had data from a single male only, which we therefore discarded. Information on RR particle size distribution was available only for a subsample of 30 females included in a previous study (Veiberg *et al.*, 2007), in which the method for RR particle fractioning is also described.

The number of hours with daylight around 78°N decreases rapidly in late October. Because both shooting and transportation needed to take place under daylight conditions, all animals were shot between 10:00 AM and 3 PM. Animals were gutted right after shooting, and the total weight of RR with and without contents was recorded with an accuracy of 0.1 kg. Adhering lymph nodes, discrete adipose tissue and the mesentery were removed before weighing. Back fat depth (mm) and animal dressed weight – that is live body mass minus head, skin, viscera, bleedable blood and metapodials – were recorded for all animals. Animal age was determined by sectioning incisors and counting cementum annuli (Table 1). The length of the lower jaw (mm) was recorded as a measure of skeletal size. The status of lactation was recorded in all females (20 lactating, 29 yeld). The entire dataset is listed in Appendix S1.

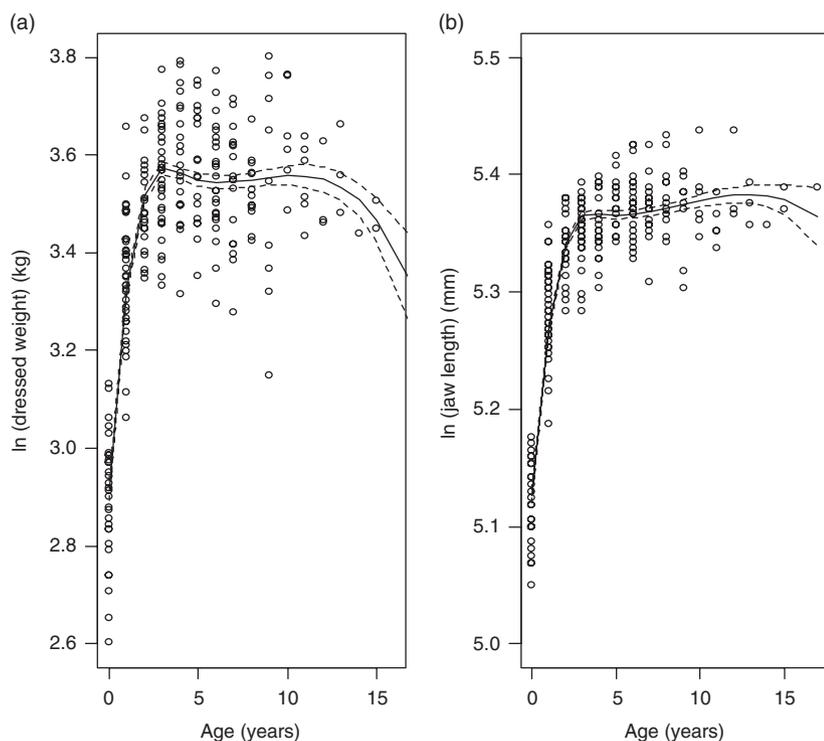


Figure 1 Relationship between age and (a) late October ln (dressed weight), $n=248$, and (b) ln (total jaw length), $n=239$, in Svalbard reindeer *Rangifer tarandus platyrhynchus* females ranging from 0 to 17 years of age. Lines are fitted using splines. Dashed, thin lines show standard errors.

Table 1 An overview of the age distribution, sampling location and year of sampling for the reticulo-rumen content material

		Age										
		3	4	5	6	7	8	9	10	11	12	
Sassendalen	1994	3	2	2	3	3	1	1	1			
	2002		2	2	2	1			1			
Colesdalen	1994				2							1
	2002	3	2	2			1		1	x		
	2003	6	3			2	2					
Total		12	6	9	7	6	4	1	3	x	1	

Statistical analyses

We first used general additive models (GAM) to investigate possible non-linearity in the relationship between the response variables and the predictor variables age and body mass. As visual inspection of GAM plots revealed no marked non-linearity; we continued to use ordinary linear models (LMs), enabling us to parameterize relationships. To account for possible confounding effects, we always entered the location (Colesdalen/Reindalen and Sassendalen) and the year of sampling (as a factor with three levels) in the models. We also considered the factors body size (jaw length or leg length), body mass and lactation status and their interactions. The variables body mass, body size, amount of back fat, RR content weight and RR tissue weight were (ln) transformed to make the relationship of the response variable more linear and to stabilize the variance. We used the

Akaike information criteria corrected for small samples, AIC_c (Burnham & Anderson, 2002) to select the most parsimonious LMs. The subset with available information on RR particle size distribution was used to run a correlation analysis between RR content weight and proportion of RR particles <1.0 mm. The proportion data were arcsine(sqrt) transformed.

All statistical analyses were conducted using the statistical software R version 2.5.0.

Results

Model selection resulted in identical models for both ln (RR tissue weight) and ln (RR content weight), containing the year, location and the first-order term of age (Tables 2 and 3). Supporting both predictions (1) and (2), both RR tissue and content mass increased with age (Fig. 2), but showed no relationship with body mass or body size (not even entering the best models). Animals sampled in Colesdalen/Reindalen showed a non-significant trend towards having less RR tissue than those from Sassendalen, and animals sampled in 2002 were found to have significantly less RR contents than in the reference year 1994. On both occasions, competing models ($AIC_c < 2$) included lactation status (Table 2). The 95% CI of the parameter estimates for lactation status overlapped 0, suggesting a minor effect if any ($\beta_{\ln(\text{RR tissue})} = -0.087$ [-0.212, 0.038]; $\beta_{\ln(\text{RR contents})} = -0.056$ [-0.175, 0.063]). For a subset ($n = 30$), we found that the correlation between age and RR contents was much stronger than the correlation between particle size and RR

Table 2 Results from model selection on the response variable ln (reticulo-rumen tissue weight) and ln (reticulo-rumen content weight) in the Svalbard reindeer *Rangifer tarandus platyrhynchus*

Year	Location	Age	Lactation	Ln (jaw length)	Ln (body mass)	Ln (body mass) × location	Ln (jaw length) × location	Age × year	Ln (body mass) × year	AIC _c	ΔAIC _c	AIC _c weights	Model likelihood
<i>(A) Tissue</i>													
x	x	x	x	x	x	x	x	x	x	2.196	18.199	0.0000	0.0001
x	x	x	x	x	x	x	x	x		-2.584	13.418	0.0005	0.0012
x	x	x	x	x	x	x	x			-5.578	10.425	0.0021	0.0054
x	x	x	x	x	x	x				-8.380	7.622	0.0083	0.0221
x	x	x	x	x	x					-10.752	5.250	0.0273	0.0724
x	x	x	x	x						-13.600	2.403	0.1132	0.3008
x	x	x	x							-15.603	0.399	0.3083	0.8192
x	x	x								-16.002	0.000	0.3764	1.0000
x	x		x							-14.339	1.663	0.1639	0.4354
<i>(B) Contents</i>													
x	x	x	x	x	x	x	x	x	x	-9.297	12.492	0.0009	0.0019
x	x	x	x	x	x	x	x	x		-12.889	8.900	0.0055	0.0117
x	x	x	x	x	x	x	x			-16.660	5.130	0.0363	0.0769
x	x	x	x	x	x	x				-17.310	4.479	0.0503	0.1065
x	x	x	x	x	x					-19.536	2.254	0.1530	0.3241
x	x	x	x	x						-17.965	3.825	0.0697	0.1477
x	x	x	x							-20.189	1.600	0.2121	0.4493
x	x	x								-21.790	0.000	0.4721	1.0000
x	x		x							3.946	25.735	0.0000	0.0000

The factors location (Sassendalen vs. Colesdalen/Reindalen) and year (1994, 2002, 2003) were always included to control for possible bias due to unbalanced sampling. The best models judged by the AIC_c are in bold.

AIC_c, Akaike information criteria corrected.

Table 3 Parameter estimates and test statistics for the best linear model describing variation in (A) ln (reticulo-rumen tissue weight) and (B) ln (reticulo-rumen content weight) in female Svalbard reindeer *Rangifer tarandus platyrhynchus* 3 years and older ($n=49$)

	Parameter estimate	95% CI lower	95% CI upper	SE	P
<i>(A) Tissue</i>					
Intercept	0.4858	0.2452	0.7264	0.1194	0.0002
Age	0.0273	0.0022	0.0523	0.0124	0.0335
Year 2002 versus 1994	0.0669	-0.0731	0.2070	0.0695	0.3408
Year 2003 versus 1994	0.1178	-0.0708	0.3063	0.0936	0.2148
Location	-0.1254	-0.2722	0.0213	0.0728	0.0920
<i>(B) Contents</i>					
Intercept	2.0491	1.8223	2.2759	0.1125	0.0000
Age	0.0693	0.0457	0.0929	0.0117	0.0000
Year 2002 versus 1994	-0.1844	-0.3164	-0.0524	0.0655	0.0073
Year 2003 versus 1994	-0.0092	-0.1870	0.1685	0.0882	0.9172
Location	-0.0884	-0.2267	0.0500	0.0687	0.2048

Parameter estimates are given as least-squares estimates with standard errors and confidence intervals (CI). The reference levels for the factors location and year are Sassendalen and 1994, respectively.

content weight ($r = 0.666$ vs. $r = -0.298$). Two largely outlying data points creating non-linearity influenced the results markedly and were therefore excluded to obtain more reliable estimates.

As predicted, the amount of back fat decreased with age (Fig. 3). Apart from year and location, the best model only contained age and lactation status (Tables 4 and 5). A competing, simpler model only included age, while the first-order term of body size (jaw length) was included in two other competing models (Table 4). A significant between-

year variation was found, while sampling location had no influence on back fat deposits. A weak trend towards higher back fat measures for non-lactating relative to lactating females was found (Table 5).

Discussion

Numerous studies have addressed how variation in (often seasonally driven) plant quality and chemistry affects rumen retention times, as well as other digestive processes of

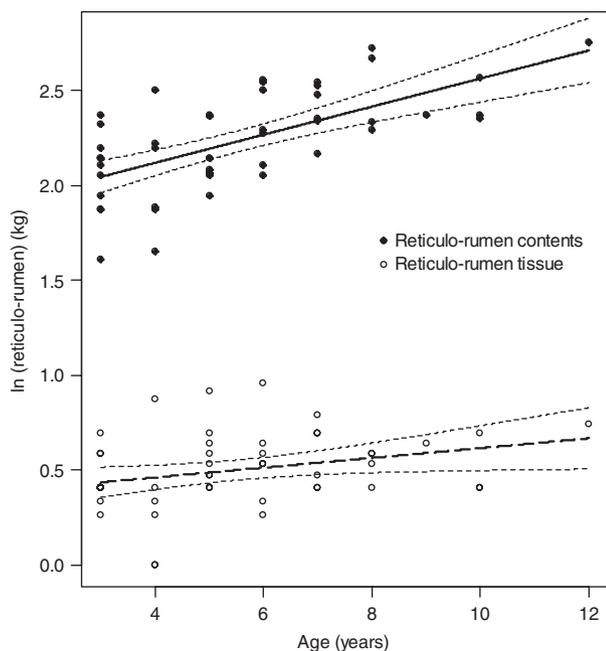


Figure 2 Changes in the mass of ln (reticulo-rumen contents) (filled circles, thick, solid line) and ln (reticulo-rumen tissue) (open circles, thick, long-dashed line) in Svalbard reindeer *Rangifer tarandus platyrhynchus* females between 3 and 12 years of age ($n=49$). Dashed, thin lines show standard errors. Values are not corrected for sampling location and year.

ruminants (Heller, Cercasov & Vonengelhardt, 1986; Spalinger, Robbins & Hanley, 1993; Holand, 1994; Hummel *et al.*, 2006). Also, there is a rather extensive literature on senescence in ruminants (Williams *et al.*, 2006), and a few linking this to tooth wear (Loe *et al.*, 2003; Carranza *et al.*, 2004; Nussey *et al.*, 2007), but there has been limited focus on whether digestive processes are related to age. Our findings on Svalbard reindeer demonstrate that RR filling increases with age. This is consistent with the hypothesis that increased tooth wear and poorer mastication cause an increase in RR mass and possibly increased retention times. But, we cannot exclude that other mechanisms may be responsible for the demonstrated age-related changes. Indeed, for a subsample of individuals containing information on RR particle size distribution, we found that the correlation between RR contents and the proportion of small RR particles was weaker than the correlation between age and RR contents. Increased RR retention time is considered a central mechanism to increase the digestion efficiency of low-quality forage. Such a response may still be insufficient to fully compensate for the negative effects on the digestive processes caused by tooth wear-related reduction in mastication efficiency.

Van Soest (1994) stated that there is a strong relationship between body mass and gastrointestinal capacity in herbivores. Findings from experimental studies on dairy cows clearly support this relation, showing a positive correlation between body mass and dry matter intake (Kertz, Reutzel &

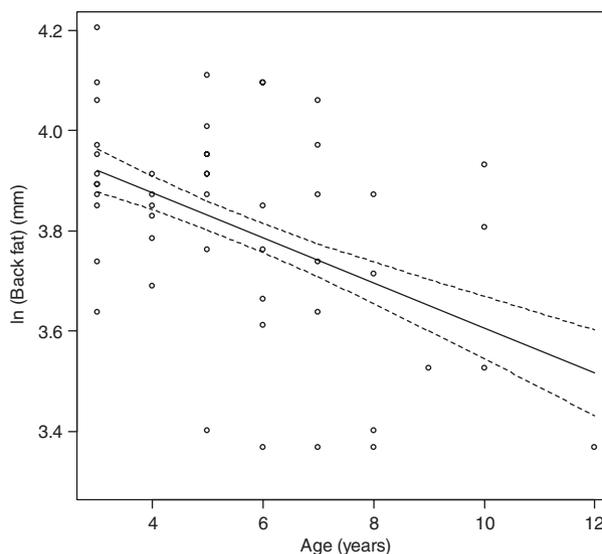


Figure 3 Relationship between age and ln (amount of back fat), $n=49$, in Svalbard reindeer *Rangifer tarandus platyrhynchus* females aged 3–12 years. Dashed, thin lines show standard errors.

Thomson, 1991; Maekawa, Beauchemin & Christensen, 2002; Johnson *et al.*, 2003; Galindo-Gonzalez *et al.*, 2007). Whereas these studies found no effect of number of lactations (an equivalent to age measures) on food intake, Hayirli *et al.* (2002) demonstrated that number of lactations was positively correlated with dry matter intake as a percentage of body mass in Holstein cattle. This finding demonstrates that age-related changes occur in the gastrointestinal tract.

In theory, selection of a higher quality diet is a possible strategy to counteract the negative consequences of reduced chewing efficiency. Such dietary improvements could either be attained through a training effect or through age-related domination of better food resources. As shown previously, diet quality did not change with age in Svalbard reindeer (Veiberg *et al.*, 2007), making it unlikely that older animals have access to better quality diet. Further, forage abundance is considered more limiting to energy gain in Svalbard reindeer than forage quality, even during peak primary production in summer (see Van der Wal *et al.*, 2000b).

Prolonged rumen retention with age

The digesta normally occupies only a proportion of the total RR volume (Hofmann & Nygren, 1992), the rest being filled by gas and liquid. The degree of filling increases with the ingestion rate and fibre content of ingested forage (Van Soest, 1994). The mass of RR contents has also been found to change through the day (Weckerly, Bleich & Chetkiewicz, 2003). This is likely related to the distribution of feeding and rumination bouts through the day, as the mass of RR contents is expected to decrease with increasing time distance since the last feeding event. Apart from the limitations posed by the number of daylight hours (see 'Materials and methods'), time of shooting was not recorded more

Table 4 Results from model selection on the response variable ln (amount of back fat) in the Svalbard reindeer *Rangifer tarandus platyrhynchus*

Year	Location	Age	Lactation status	Ln (jaw length)	Ln (jaw length) × location	Age × year	Ln (jaw length) × year	AIC _c	ΔAIC _c	AIC _c weights	Model likelihood
x	x	x	x	x	x	x	x	-5.556	13.942	0.0003	0.0009
x	x	x	x	x	x	x		-11.711	7.787	0.0069	0.0204
x	x	x	x	x	x			-15.970	3.528	0.0579	0.1714
x	x	x	x	x				-18.684	0.813	0.2251	0.6659
x	x	x		x				-18.674	0.823	0.2240	0.6626
x	x	x	x					-19.497	0.000	0.3381	1.0000
x	x	x						-17.840	1.657	0.1476	0.4367

The factors location (Sassendalen vs. Colesdalen/Reindalen) and year (1994, 2002, 2003) were always included to control for possible bias due to unbalanced sampling. The best model judged by the AIC_c is in bold. AIC_c, Akaike information criteria corrected.

Table 5 Parameter estimates and test statistics from the best linear model describing variation in ln (amount of back fat) among female Svalbard reindeer *Rangifer tarandus platyrhynchus* 3 years and older ($n=49$)

	Parameter estimate	95% CI lower	95% CI upper	SE	<i>P</i>
Intercept	3.8135	3.5760	4.0511	0.1178	0.0000
Age	-0.0321	-0.0565	-0.0078	0.0121	0.0108
Year 2002 versus 1994	0.0604	-0.0805	0.2013	0.0699	0.3919
Year 2003 versus 1994	0.1681	-0.0119	0.3481	0.0892	0.0664
Location	0.0235	-0.1169	0.1640	0.0696	0.7370
Lactation status	0.1177	-0.0024	0.2377	0.0595	0.0545

Parameter estimates are given as least-squares estimates with standard errors and confidence intervals (CI). The reference levels for the factors location, year and lactation status are Sassendalen, 1994 and lactating, respectively.

accurately. Time of day therefore could not be controlled for in our analyses.

The variation in RR fill between years suggests that forage availability varies between years, subsequently affecting intake levels and RR filling. Because food availability represents a limiting factor to the energy gain in Svalbard reindeer (Van der Wal *et al.*, 2000b), increased RR fill within a given season and year is most likely due to increased RR retention time rather than increased intake rates. This allows a longer exposure of forage particles to rumen microflora, and leads to a more complete digestion (Demment & Van Soest, 1985; Lechner-Doll *et al.*, 1991; Hummel *et al.*, 2006). The actual mechanism behind this prolonged retention time is thought to be directly related to the physicochemical particle properties, and the longer time needed for RR particles to attain the properties coinciding with the criteria for reticulo-omasal orifice passage. Our results clearly support prediction (1) that the amount of RR fill increases significantly with age, but other mechanisms may explain such a pattern.

Ruminants can show plasticity in the size of all stomach compartments in response to alterations in the ingestion rate or forage properties (see e.g. Paloheimo, 1944; Lechner-Doll *et al.*, 1990; Domingue *et al.*, 1991; Freudenberg *et al.*, 1994; Barboza, Peltier & Forster, 2006). An increase in the amount of RR tissue may imply an advantage in terms of either increasing RR capacity (ultimately limited by the

capacity of the abdominal cavity, Conrad, 1966) or other aspects of RR morphology (such as increased papillation or RR muscle development). Our finding of an age-related increase in RR tissue is in agreement with prediction (2), and demonstrates that RR capacity or morphology most likely has been permanently changed, possibly as a consequence of decreasing mastication efficiency. We attempted to estimate the expected increase in RR contents as a response to increased RR tissue (corrected for other factors). Although the parameter estimate was positive, it was highly insignificant ($\beta = 0.0774 [-0.2187, 0.3736]$), emphasizing the need for more data. However, the slope for age-related increase in RR content weight was steeper than the slope for tissue weight (Fig. 2). This suggests that the increase in RR tissue can easily be explained by the increased RR content mass. On the other hand, the steeper slope of the latter indicates that its increase is larger than what could be explained by the increase in RR tissue mass alone. This supports the idea of an age-related increase in RR filling.

While the main function of the RR compartment is to facilitate selective particle retention, and to be a fermentation chamber for microbial degradation, further enzymatic activity related to digestion and absorption of nutrients and water is localized to the omasum, abomasum and the lower tract. These parts of the digestive system may also show adaptations to variation in forage quality. Previous studies

have demonstrated a substantial variation in lower tract capacity between seasons (Staaland, Jacobsen & White, 1979; Weckerly, 1989). Within-season variation in forage quality has, on the other hand, not been found to cause similar alterations (Weckerly, 1989; Jenks *et al.*, 1994). In the cited studies and related investigations, proper age measures are generally lacking or not considered during analyses. Therefore, future studies should consider age as one of several factors influencing variation in gastrointestinal characteristics.

A penalty on the fat reserves

One interpretation of the age-dependent increase in RR content mass and tissue is that the RR retention time in Svalbard reindeer passively increases, and that a certain extent of compensation in terms of changes in RR morphology occurs. If this is a correct interpretation, what consequences does this have for the energy budget and individual performance? We found a marked decrease in the amount of fat with increasing age. (see also Stien *et al.*, 2002). The total amount of dissectible fat in Svalbard reindeer has been found to exceed 40% of late autumn dressed weight (Reimers & Ringberg, 1983). This represents a substantial amount of the energy needed through the winter (Tyler, 1987), and any reduction may have a huge effect on overwinter survival. Reduced amount of fat with increasing age may at least partly indicate reduced energy gain. This suggests that the demonstrated changes in RR mass and RR contents are inadequate to fully maintain digestion efficiency. From life-history theory, the terminal investment hypothesis predicts that animals spend more energy on reproduction with advancing age (e.g. Clutton-Brock, 1984). This relative increase in reproductive investment may thus amplify the consequences from any reduction in digestive efficiency, and may further reduce the amount of energy allocated to fat deposits.

Corrected for other factors, body size did not influence back fat deposits, suggesting that energy gain and allocation among adult females are mainly influenced by size-independent factors. Previous studies have shown that reproductive status has a marked impact on metabolic needs (Clutton-Brock, Albon & Guinness, 1989) and subsequently the size of energy storages (Stien *et al.*, 2002). Stien *et al.* (2002) found a significantly lower amount of back fat in lactating than in non-lactating females in the same Svalbard reindeer populations as in our study. This corresponds with the marginally non-significant trend in our material as well (Table 5).

Conclusion

To our knowledge, this is the first study to demonstrate that RR contents and tissue mass are altered with animal age in a wild cervid. Clearly, this study is open to alternate interpretations, but it is at least consistent with predictions derived from the well-documented pattern of changes in tooth wear and mastication efficiency with age. If this

interpretation holds, this represents one potential further link between foraging, digestive processes and life-history patterns. We recommend future studies also of other parts of the digestive system to include age as a factor.

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Supporting information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. The table gives an overview of the data material used in the analyses of the relationship between weight of reticulo-rumen tissue (RRempt) and contents (RRcont) ($N = 49$). All individuals are females. Area code 1 and 2 refers to Sassendalen and Reindalen/Colesdalen respectively. Lactation status is given by Y (yeld) and M (milk). Subcutaneous back fat (Subcut) is given in mm. Bm refers to animal dressed weight in kilos. Jaw is the total length (mm) of the lower jaw. Small particles refers to the dry weight proportion of RR particles < 1.0 mm ($N = 30$).

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