SEASONAL VARIATION IN WEIGHT OF FUNCTIONAL SEGMENTS OF THE GASTROINTESTINAL TRACT AND ITS CONTENTS IN YOUNG MOOSE (*ALCES ALCES*)

Åke Pehrson[1], R. Thomas Palo[2], Hans Staaland[3] and Peter A. Jordan[4]

[1]Department of Wildlife Ecology, Swedish University of Agricultural Sciences, Grimsö Wildlife Research Station, S-730 91 Riddarhyttan, Sweden; [2]Department of Animal Ecology, Swedish University of Agricultural Sciences, S-901 83 Umeå, Sweden; [3]Department of Biology and Nature Conservation, Agricultural University of Norway, Box 5014 , N-1432 Ås, Norway; [4]Department of Fisheries and Wildlife, College of Natural Resources, 200 Hodson Hall, 1980 Folwell Ave., St.Paul, MN 55108-1036, USA

ABSTRACT: Quantitative seasonal variation of biomass among segments of the gut wall and associated contents of moose has not been previously reported. From a sample of 6- to13 -month old moose collected in southcentral Sweden, gastrointestinal tracts were divided into nine functionally distinct segments. Each segment was measured for live weight and length of the wall, and wet and dry weight of the contents. Dry matter digesta was greater in winter than in summer within all segments except the small intestine. Live weight of the wall and its weight relative to other segments was significantly greater in the rumenoreticulum and abomasum during summer than in winter. Weight variations by season and among segments of the tract are discussed in terms of nutritional strategies and adaptations.

ALCES VOL. 33 (1997) pp.1-10

For herbivorous mammals, choice and processing of food are constrained by metabolic requirements and by the anatomy and physiology of the digestive tract (Demment and Van Soest, 1985; Hofmann, 1973; Janis, 1976; Owen-Smith, 1988; Renecker and Hudson, 1990). Alimentary size scales to body mass as $M^{1.03}$ (Demment and Van Soest, 1985); whereas metabolic requirement scales as $M^{0.75}$ (Kleiber, 1975). One consequence will be that a larger animal is more adapted to a high fiber/low quality diet.

Changes in length and biomass of segments of the intestine in association with seasonal changes in diet and energy requirements has been shown in a number of vertebrates including small rodents, mallards (*Anas platyrhynchos*) and gallinaceous birds (Gross *et al.*, 1985; Hammond,1993; Kehoe *et al.*, 1988; Moss,1983).

Moose (*Alces alces*) experience major seasonal fluctuations in the nutritional quality of woody plants, their primary food. During the 3-6 months of plant growth, high-nutrient, readily digestible leaves are eaten. In contrast the same plants plus conifers offer only low-nutrient, high-fiber forage often with relatively high levels of defensive compounds during 6-9 months of plant dormancy (Bergström and Hjeljord, 1987; Cederlund *et al.*, 1980). In association with winter, there is a simultaneous decrease in body weight, metabolic rate and activity, and probably near cessation of growth in the moose (Regelin *et al.*, 1985; Renecker and Hudson,1989; Schwartz *et al.*, 1987). To date there has not been a quantitative description of changes in mass of the gut and its contents, nor a discussion of how such changes may relate to the sharp seasonal differences in forage quality as well as to growth, reproduction, and energy metabolism in general.

We hypothesized that each functional segment along the digestive tract of moose should show fluctuations in size and contents that can be related to the marked seasonal differences in fiber and levels of nutrients in their natural forages. Furthermore, such fluctuations should represent adaptive physiological responses to these normal seasonal changes in forage quality.

From a sample of young moose collected in different seasons, we weighed and measured each functionally separate segment of the gastrointestinal tract. In addition, we weighed the mass of the contents of each portion. The findings are discussed in relation to changing diet quality over the seasons, and to the feeding strategies of the moose.

STUDY AREA

Grimsö Wildlife Research Area is located in the southern part of the boreal forest zone in southcentral Sweden (55°5'N, 15°5'E). The 140 km² research area consists of fairly flat, forested land with elevations 75 - 150 m above sea level. Coniferous forest covers about 72%, with dominant trees being Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) and subdominants being birch (*Betula* spp.) and aspen (*Populus tremula*). The ground layer is dominated by dwarf shrubs, mainly bilberry (*Vaccinium myrtillus*), lowbush cranberry (*Vaccinium vitis-idaea*), and heather (*Calluna vulgaris*). The area is interspersed with boggy and swampy wetlands covering 18%, and lakes and rivers 4%. There is little arable land in the form of a few small farms (about 3%). For description of forest management and climatological characteristics see Cederlund *et al.* (1991).

Moose consume leaves and twigs of deciduous browse, mainly birch, aspen, mountain ash (*Sorbus aucuparia*) and willows (*Salix* spp.), together with forbs and some grass during the summer. During winter, pine is the dominating food species with a minor contribution from deciduous browse. During spring and fall, dwarf shrubs constitute a considerable portion of the moose diet (Cederlund *et al.*, 1980).

MATERIALS AND METHODS

The data presented are from collections of immature moose harvested as part of the population-regulation program at Grimsö. They ranged from 6 to 13 months of age. Due to the hunting regulations we had to restrict our sampling to young animals in order to acquire material from the entire year. Technically all animals were treated in the same manner. They were brought to the laboratory within 45 minutes of death and then the digestive tracts were removed immediately. Carcasses (whole body mass minus head, skin, lower legs, kidneys and viscera) were weighed to the nearest kg. When relating gastrointestinal measurements to body mass, it is preferable to use carcass mass as denominator since it is unaffected by variations in the numerator. All measures on fresh material were made within 3 hr of post mortem. We have no indications that sampling time throughout the day in any case influenced the amount of gastrointestinal contents. During summer moose were collected during the night, while winter animals were collected during a few hours before noon.

In the following we are dealing with three data sets.

<u>1. Entire sample:</u> Originally 99 animals harvested between 1986 and 1992 were available. From all these animals contents and tissue weights of the rumenoreticulum together with carcass mass were recorded. The entire sample was used for analyses of eventual sex-related differences. Based on the local food habits analyses by Cederlund *et al.* (1980), that showed a shift from dormant season to growing season forage in early May and then the reverse in the shift of September - October, we separated this sample into summer animals (n=17) and winter animals (n=82).

2. Small sample: We studied 8 individuals in more detail. These animals were collected in June 1986 (n=3), November 1986 (n=3), February 1987 (n=1) and April 1987 (n=1), thus comprising 3 summer and 5 winter animals. The digestive tract was cut into its nine functionally distinct segments (Fig. 1). For measurement of the tract wall, the rumen and reticulum were not separated. Contents of each segment were removed and weighed (±1 g), then sub sampled (treating rumen and reticulum separately) for dry matter and for mineral levels (Staaland *et al.*, 1992). The emptied walls of each segment were weighed (±1 g). Length (±1 cm) of each segment was measured by first freeing the mesenteries and then laying the segment straight without stretching.

3. Large sample: Since 3 animals in one group is such a low number and can create statistical problems, we wanted to make comparisons with the data available from the entire sample, i.e. contents and tissue weights of the rumenoreticulum. This was done in order to improve and verify the interpretation of the smaller sample. The larger sample was stratified in terms of mean carcass mass, variation in carcass mass between individuals, and the distribution of animals collected in different winter months to identify and select individuals comparable to those in the smaller sample. This resulted in a sample consisting of 12 summer and 12 winter animals. In the following this is referred to as the large sample.

When adjusting organ measurements by body mass and, as in our case, to analyse for seasonal differences, one should ordinarily use an Analysis of Covariance to adjust for the differences in body mass. Since our material is too limited this is not possible and we prefer to use a non-parametric test for our small sample. Therefore, the 3 summer and 5 winter animals from this sample are compared to each other using a two-tailed Mann-Whitney U-test.

RESULTS

Test for sex-related differences

Rumenoreticular contents and tissue

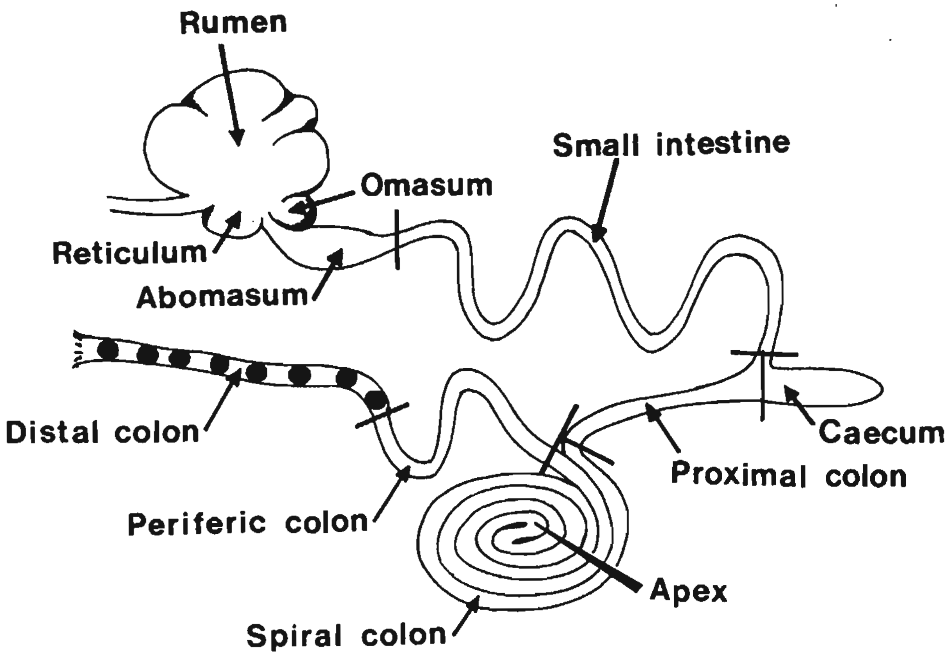

Fig. 1. Demarcation of the functional segments of the moose gut that were individually measured in this study.

weights were compared between sexes in the entire sample (n=99) using covariance analyses with carcass mass as the independent variable. Neither when checked for summer (11 males/ 6 females) nor winter (43 males/39 females) animals were any differences detected between the sexes (P>0.22 in all cases). Therefore, in the following both sexes are treated together.

Large sample

Biomass distribution of digesta

Rumenoreticula of both winter and summer animals contained around 24 kg wet material (Table 1). Due to the fact that winter animals had considerably lower carcass mass than summer animals (t=3.17; P=0.004), rumenoreticular contents in immature winter moose constituted 37% of their carcass mass while the corresponding figure for summer moose was significantly lower, 29% (t=4.28; P=0.0003).

Mass of rumenoreticular tissues

The reverse condition of biomass distribution was true for rumenoreticulum wet tissue mass, where summer animals had considerably heavier rumenoreticulums compared to the winter animals (t=4.49; P=0.0001). This was true even when related to body weight (t=4.22; P=0.0004).

Small sample

Biomass distribution of digesta

The three summer animals had a carcass mass of 83.7 ± 10.8 kg (x ± SD). The corresponding figure for the five winter animals was lower (68.0 ± 6.4) and the difference was statistically significant (p=0.025, two-tailed Mann-Whitney U-test). This created a difference between winter and summer animals in rumenoreticular contents relative to their carcass mass. Rumenoreticular contents constituted 32.4% in winter moose and 26.1% in summer moose (Table 2). Even though this difference was not statistically significant, the figures were similar to what we found in the larger sample. Therefore, we assume that differences in contents between seasons for other parts of the gastrointestinal tract that we recognized in the small sample are realistic. This is further stressed if we compare the figures calculated on rumenoreticular dry matter contents where the differences are significant both in the large (Table 1) and the small sample (Table 2).

In relation to carcass mass both omasum and abomasum contained significantly more digesta in winter than in summer, both calcu-

Table 1. Rumenoreticular (RR) content and tissue weight in immature moose during winter and summer. Data from the large sample investigated.

	Winter (n=12)	Summer (n=12)	P-value[1]
Carcass mass (kg)[2]	66.6 ± 12.0[3]	83.2 ± 13.5	0.004
RR content, wet weight	24.6 ± 5.5	23.8 ± 3.5	0.68
% of carcass mass	37.0 ± 6.0[4]	28.9 ± 2.6	0.0003
RR content, dry weight	4.05 ± 0.91	3.25 ± 0.38	0.01
% of carcass mass	6.11 ± 1.08	3.95 ± 0.31	0.0001
RR tissue, wet weight	2.25 ± 0.30	3.59 ± 0.96	0.0001
% of carcass mass	3.42 ± 0.35	4.27 ± 0.60	0.0004

[1] Differences are examined with unpaired t-test

[2] Whole body weight with head, skin, lower legs, kidneys and viscera removed

[3] Mean weight ± SD

[4] Mean ± SD

Table 2. Content and tissue weight of segments of the digestive tract in immature moose during winter and summer. Data from the small sample investigated.

	Biomass in kg ± SD		% of carcass[1] mass ± SD		
	Winter n=5	Summer n=3	Winter n=5	Summer n=3	s/ns[2]
Rumenoreticulum					
contents wet weight	21.8 ± 3.6	21.8 ± 1.7	32.4 ± 6.6	26.1 ± 2.1	ns
contents dry weight	3.3 ± 0.47	2.7 ± 0.22	5.0 ± 0.91	3.2 ± 0.56	s
tissue wet weight	2.5 ± 0.14	4.8 ± 0.26	3.7 ± 0.38	5.8 ± 0.47	s
Omasum					
contents wet weight	0.73 ± 0.14	0.34 ± 0.12	1.10 ± 0.31	0.40 ± 0.10	s
contents dry weight	0.16 ± 0.05	0.06 ± 0.03	0.25 ± 0.09	0.07 ± 0.04	s
tissue wet weight	0.23 ± 0.04	0.31 ± 0.04	0.34 ± 0.09	0.37 ± 0.06	ns
Abomasum					
contents wet weight	1.2 ± 0.34	0.93 ± 0.41	1.81 ± 0.50	1.09 ± 0.32	s
contents dry weight	0.16 ± 0.04	0.11 ± 0.04	0.24 ± 0.06	0.13 ± 0.06	s
tissue wet weight	0.41 ± 0.07	0.81 ± 0.10	0.61 ± 0.14	0.97 ± 0.08	s
Small intestine					
contents wet weight	4.4 ± 0.60	4.7 ± 0.64	6.6 ± 1.4	5.7 ± 1.1	ns
contents dry weight	0.43 ± 0.04	0.50 ± 0.06	0.66 ± 0.13	0.60 ± 0.05	ns
tissue wet weight	1.3 ± 0.17	1.9 ± 0.18	1.89 ± 0.28	2.24 ± 0.11	ns
Cecum					
contents wet weight	1.4 ± 0.29	0.65 ± 0.18	2.1 ± 0.38	0.78 ± 0.24	s
contents dry weight	0.20 ± 0.04	0.08 ± 0.02	0.29 ± 0.05	0.10 ± 0.02	s
tissue wet weight	0.09 ± 0.02	0.11 ± 0.02	0.13 ± 0.03	0.13 ± 0.03	ns
Proximal colon					
contents wet weight	1.1 ± 0.41	0.49 ± 0.04	1.65 ± 0.80	0.59 ± 0.04	s
contents dry weight	0.14 ± 0.06	0.06 ± 0.01	0.22 ± 0.12	0.07 ± 0.02	s
tissue wet weight	0.14 ± 0.02	0.18 ± 0.01	0.22 ± 0.06	0.22 ± 0.04	ns
Coiled colon					
contents wet weight	0.98 ± 0.13	0.80 ± 0.09	1.49 ± 0.29	0.97 ± 0.21	s
contents dry weight	0.14 ± 0.02	0.10 ± 0.02	0.21 ± 0.05	0.12 ± 0.04	s
tissue wet weight	0.25 ± 0.03	0.35 ± 0.02	0.38 ± 0.06	0.42 ± 0.05	ns
Periferic colon					
contents wet weight	0.69 ± 0.12	0.68 ± 0.20	1.0 ± 0.17	0.80 ± 0.16	ns
contents dry weight	0.13 ± 0.03	0.10 ± 0.02	0.20 ± 0.04	0.12 ± 0.01	s
tissue wet weight	0.18 ± 0.03	0.28 ± 0.08	0.27 ± 0.05	0.33 ± 0.07	ns
Distal colon					
contents wet weight	0.91 ± 0.18	0.24 ± 0.05	1.4 ± 0.22	0.28 ± 0.03	s
contents dry weight	0.23 ± 0.06	0.04 ± 0.01	0.31 ± 0.06	0.05 ± 0.01	s
tissue wet weight	0.44 ± 0.04	0.44 ± 0.09	0.66 ± 0.10	0.52 ± 0.08	ns
Total gastr. int. tract					
contents wet weight	33.2 ± 4.9	30.6 ± 2.1	50.0 ± 8.9	36.7 ± 2.2	s
contents dry weight	4.9 ± 0.51	3.7 ± 0.29	7.3 ± 1.1	4.4 ± 0.36	s
tissue wet weight	5.5 ± 0.23	9.1 ± 0.61	8.3 ± 0.79	11.0 ± 0.65	s

[1] Whole body weight with head, skin, lower legs, kidneys and viscera removed

[2] two-tailed Mann-Whitney U-test (s=significant, ns=non-significant)

lated by wet and dry weight (Table 2).

The small intestines contained wet digesta representing around 6% of moose carcass mass both in winter and summer animals. The cecum and all sections of the colon contained more material in winter than in summer, both on wet and dry basis, and calculated on absolute as well as relative figures. The only exception where the difference was not significant was the wet biomass amount in the periferic colon (Table 2).

Taken together, the wet contents of the entire gastrointestinal tract comprised 50% of the winter moose carcass mass while the corresponding figure for summer animals was 37% (P=0.025; Mann-Whitney U-test). The difference is even more evident if calculated on dry matter contents (Table 2).

Weight of the ruminant gastrointestinal tract and its contents generally varies directly with live mass of the animal. Our samples were too small and too varied for a reasonable regression analysis, but we did examine for digestive tract : body weight relationships. The content in all examined parts showed a tendency for a positive relationship with body mass, with omasal content as the only possible exception.

The digesta in rumen, reticulum, omasum, periferic and distal colon contained significantly less water during winter compared to summer conditions (Table 3). The tendency was similar in abomasum, cecum, proximal and coiled colon, while the small intestine seemed to hold similar amounts of water both in summer and winter.

Mass of gastrointestinal tissues

Rumenoreticular tissue mass weighed more and constituted a significantly larger part of the body mass during summer than winter (Table 2). Since these differences correspond well to what we found in the large sample (Table 1), we assume that other seasonal relationships in tissue mass throughout the gastrointestinal tract found in the small sample are realistic.

No significant seasonal difference was recognized for the omasum when tissue mass was related to carcass mass. The abomasum, on the other hand, constituted a larger part of the carcass mass in summer moose (Table 2).

No part of the intestines differed in relative tissue weight between winter and summer. When tissue mass for the whole gastrointestinal tract was tested against carcass mass there was a significant difference found, since tissue mass constituted a larger part of the summer moose compared to winter moose (Table 2). However, this difference was due to the heavier stomach compartments in summer animals. All tissues from the gastrointestinal tract showed a tendency towards a positive relation to body weight.

Length of intestines

Lengths of various parts of the intestines did not vary between winter and summer animals with the exception of distal colon (Table 4). Both in absolute length and when expressed as a proportion of total intestinal length, winter animals had longer distal colons than animals collected during summer. Even when length was expressed per kg body weight, only the distal colon differed significantly in length between winter and summer animals, with longer distal colons in winter. No differences in the results were found when body mass was transformed by its cube root in order to correct for the comparison between a one-dimensional and a three-dimensional variable (Weckerly, 1989).

DISCUSSION

For comparison with our data, there is little quantification of moose-gut contents in the literature. Furthermore, the studies available only deal with adult animals and gut contents are related to total body mass. To be able to compare our study with others it is possible to transform our data on carcass mass into whole body mass following the relationship between carcass and body mass given by Wallin *et al.* (1996).

Coady and Gasaway (1972) report that in moose rumenoreticulum wet contents in winter comprised 15.7% of total body weight which compares closely with our figures of 14.6 to 16.8% for the large and small sample, respectively. However, their comparable figure of 8.7% for summer was considerably lower than our finding ranging from 11.9 to 13%. This great discrepancy for summer data could not be ascribed to the fact that growing animals may need more food since a large unpublished material from our research area also shows corresponding figures for adult animals (Pehrson unpubl.).

Table 3. Water concentration in contents from various parts of the digestive tract of immature moose shot during winter (n=5) and summer (n=3). For the intestines, values are given as an average for the entire part.

	Winter	Summer	s/ns[1]
Rumen	84.6 ± 1.2[2,3]	87.7± 1.0	s
Reticulum	84.4 ± 1.8	89.4 ± 1.0	s
Omasum	78.1 ± 2.5	82.7 ± 1.7	s
Abomasum	86.6 ± 1.9	88.1 ± 1.4	ns
Small intestine	90.2 ± 1.1	89.3 ± 0.38	ns
Cecum	86.0 ± 1.3	87.6 ± 1.3	ns
Proximal colon	86.5 ±1.8	87.5 ± 1.6	ns
Coiled colon	85.7 ± 1.9	88.0 ± 1.1	ns
Periferic colon	80.3 ± 3.1	85.0 ± 2.1	s
Distal colon	74.5 ± 5.1	82.7 ± 2.6	s

[1] two-tailed Mann-Whitney U-test (s=significant, ns=non-significant)

[2] as a percentage of wet weight of contents

[3] mean ± S.D.

Hofmann and Nygren (1992a) give rumenoreticular contents of 20-35 kg for moose ranging in weight from 189-366 kg, thus heavier than our animals. This corresponds to around 10% of the whole body weight. Unfortunately Hofmann and Nygren do not tell during which season their material was collected. These data correspond with Kay *et al.* (1980) who reported that moose rumenoreticular contents, calculated as percentage of body weight, ranged from 8.0 to 11.4%. Their figures apparently came from Gasaway and Coady (1974), from 19 animals (yearlings and adults) collected in spring, summer and early winter in interior Alaska. Gasaway and Coady (1974) concluded that weight of female rumen content was greatest during winter and least during spring.

Table 4. Absolute and relative length of intestines in immature moose shot during winter (n=5) and summer (n=3).

	Length		% of total intest. length		
	Winter	Summer	Winter	Summer	s/ns[1]
Small intestine	203.0 ± 15.7[2]	253.3 ± 25.2	57.6 ± 1.9	60.4 ± 3.1	ns
Cecum	4.3 ± 0.56	6.0 ± 1.3	1.3 ± 0.17	1.5 ± 0.32	ns
Proximal colon	5.7 ± 1.7	5.6 ± 1.7	1.7 ± 0.50	1.4 ± 0.43	ns
Coiled colon	55.0 ± 6.2	62.7 ± 15.0	16.2 ± 1.8	16.0 ± 3.8	ns
Periferic colon	45.0 ± 7.5	60.7 ± 19.0	13.2 ± 2.2	15.4 ± 4.8	ns
Distal colon	39.2 ± 7.0	30.7 ± 1.2	11.1 ± 1.8	7.3 ± 0.40	s
Total intestines	352.2 ± 25.6	419.0 ± 15.1			

[1] two-tailed Mann-Whitney U-test (s=significant, ns=non-significant)

[2] dm, mean ± S.D.

In their review, following the classification by Hofmann (1973), Kay *et al.* (1980) calculated that the mean wet weight of forage needed to fill the rumenoreticulum was for browsers equivalent to 9.0% of body weight, for mixed feeders 11.5%, and for grazers 13.3%. These figures do not take into account seasonal differences in rumen fill. Independent of season, moose at Grimsö seem to have more material in their rumenoreticula than found in most other investigations and definitely more than concluded by Kay *et al.* (1980) for browsers in general.

Holand (1992) found that in winter, roe deer (*Capreolus capreolus*) in Norway had significantly more dry matter content in their rumenoreticula compared to summer conditions, and data from Grimsö (Pehrson unpubl.) also confirms this on a wet basis. From the studies referred to above and from our own investigation it is thus apparent that concentrate selectors in temperate regions can show seasonal variations in gastrointestinal fill with more digesta in winter animals. The seasonal differences could be explained by the higher digestibility in moose and roe deer summer food which allows a faster passage rate and thus a concomitant momentary lower rumen fill (Hofmann 1989, Holand 1992).

Regardless of what set of factors influences seasonal changes in gut physiology, observations in this study clearly indicate such changes in moose. The greater weight of the rumenoreticulum organ in summer is undoubtedly related to both nutritional needs of that season and to the higher digestibility of forages available then; the weight increase is probably due primarily to an increase in papillae associated with increased absorptive capacity across that wall. Hofmann *et al.* (1988) and Hofmann and Nygren (1992 b) report that, as in other ruminants, the ruminal mucosa of moose increases during the season of high-digestibility forage.

Hofmann (1983, 1985) and Hofmann and Nygren (1992a) stress the importance of the distal fermentation chamber (cecum + proximal colon) in browsers and especially its seasonal variation in capacity with an increased volume during the dormant season. Our data confirm this since our moose in winter had considerably more material in the cecum and proximal colon than did the summer animals. This may indicate that a reduced food quality lowers passage rate, and that it is then necessary for the animal to improve the total utilization of the digesta by using the hindgut to a greater extent for assimilation and also possibly degradation of food. However, we were not able in our restricted material to distinguish any adaptation in the distal fermentation chamber in the form of increased volume indicated by e.g. greater organ length or tissue weight.

The same conditions were true for other parts of the large intestine. Organ weights did not differ notably between seasons even though the weight of contents was considerably higher in winter. This tends to suggest that the organ's function remains similar even as the amount of material contained therein varies. Likewise, as contents of the distal colon increased in winter, along with its length, the organ itself did not increase in mass. A reduced passage rate and increased organ length in winter may improve water resorption as indicated by the fact that compared to the rumen, dry matter concentration in the distal colon was about 40% higher during winter but only about 30% higher in summer. It may also be valuable in order to improve absorption of important nutrients (Staaland *et al.*, 1992).

From the abomasum to the coiled part of the colon there was a constant dry matter concentration of digesta throughout both summer and winter. In the other parts of the tract, dry matter concentration was distinctly higher in winter. Gasaway and Coady (1974) found rumen dry matter content in moose to vary from 10.8% in summer to 16.9% in early winter, values very similar to our findings.

To conclude, our investigation shows that there are seasonal differences concerning both amount of digesta and organ weight of the gastrointestinal tract of young moose. The amount of digesta in relation to body mass is greatest during winter in almost all parts of the digestive system. This is most certainly an adaptation to a lowered food quality during winter which demands a longer retention time in order to digest the food as efficiently as possible. The more easily digested summer forage, on the other hand, can pass through much faster and still be sufficiently digested, thereby allowing an optimized intake. Therefore, during the summer there is most likely a demand for an increased absorptive capacity of the digestive system. This could be achieved by increased length and maybe also increased number of papillae of the inner mucosa of rumen, reticulum and abomasum. We interpret this to be the reason why these organs were found to weigh more in moose during the summer as opposed to the winter.

ACKNOWLEDGEMENTS

We wish to thank Karin Åström for help with the laboratory work and Lars Jäderberg for drawing the figure. William Faber, Kjell Danell, Jon Swenson and a numerous amount of referees offered valuable suggestions for the manuscript. The study was funded by the Swedish Environmental Protection Agency and a private foundation (Olle and Signhild Engkvist stiftelser).

REFERENCES

BERGSTRÖM, R. and O. HJELJORD, 1987. Moose and vegetation interactions in Northwestern Europe and Poland. Swedish Wildl. Res., Suppl. 1:213-228.

CEDERLUND, G.N., H.K.G. SAND, and Å. PEHRSON. 1991. Body mass dynamics of moose calves in relation to winter severity. J. Wildl. Manage. 55:675-681.

______, LJUNGQVIST, H., MARKGREN, G., and F. STÅLFELT. 1980. Foods of moose and roe-deer at Grimsö in Central Sweden - results of rumen content analyses. Swedish Wildl. Res., Viltrevy 11: 169-247.

COADY, J.W., and W.C. GASAWAY. 1972. Rumen function and energy production of moose in Interior Alaska. Proc.N. Am. Moose Conf. Workshop. 8: 80-104.

DEMMENT, M., and P.J. VAN SOEST. 1985. A nutritional explanation for body size patterns of ruminant and non-ruminant herbivores. Am. Nat. 125:641-672.

GASAWAY, W.C., and J.W. COADY. 1974. Review of energy requirements and fermentation in moose and other ruminants. Le Naturaliste can. 101:227-262.

GROSS, J.E., Z. WANG, and B.A. WUNDER. 1985. Effects of food quality and energy needs: changes in gut morphology and capacity of *Microtus ochrogaster*. J. Mammal. 66:661-667.

HAMMOND, K.A. 1993. Seasonal changes in gut size of the wild prarie vole (*Microtus ochrogaster*). Can. J. Zool. 71:820-827.

HOFMANN, R.R. 1973. The Ruminant Stomach, Stomach Structure and Feeding Habits of East African Game Ruminants. East African Monographs in Biology, Vol. 2. East African Literature Bureau: Nairobi, 354 pp.

______. 1983. Adaptive changes of gastric and intestinal morphology in response to different fibre content in ruminant diets. In : Fibre in human and animal nutrition. Royal Society of New Zealand, Bulletin 20:51-58.

______. 1985. Digestive physiology of the deer - their morhophysiological specialisation and adaptation. Pages 393-407 *in* K. Drew and P. Fennessy (eds). Biology of Deer Production. Royal Society of New Zealand, Bulletin 22.

______. 1989. Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. Oecologia 78:443-457.

______, and K. NYGREN. 1992a. Morphophysiological specialisation and adaptation of the moose digestive system. Alces, Suppl. 1:91-100.

______, and ______. 1992b. Ruminal mucosa as indicator of nutritional status in wild and captive moose. Alces Suppl. 1: 77-83.

______, SABER, A.S., Z. PIELOWSKI, and B. FRUZINSKI. 1988. Comparative morphological investigations of forest and field ecotypes of roe deer in Poland. Acta Theriologica, 33:103-114.

HOLAND, 0. 1992. Winter digestive strategy of a concentrate selector in Norway: the European roe deer. Can. J. Zool. 70:1331-1335.

JANIS, C. 1976. The evolutionary strategy of the Equidae and the origins of rumen and cecal digestion. Evolution 30:757-774.

KAY, R.N.B., V. W. ENGELHARDT, and R.G. WHITE. 1980. The digestive physiology of wild ruminants.Pages 743-761. *in* Digestive physiology and metabolism in ruminants. Y. Ruckebush and P. Thivend (eds.). Proceedings of the 5th International Symposium on Ruminant Physiology, Clermont-Ferrand.

KEHOE, F.P., C.D. ANKNEY, and R.T. ALISAUSKAS. 1988. Effects of dietary fiber and diet diversity on digestive organs of captive Mallards (*Anas platyrynchos*). Can. J. Zool. 66:1597-1602.

KLEIBER, M. 1975. The fire of life: an introduction to animal energetics. Krieger, Huntington, New York, 453 pp.

MOSS, R. 1983. Gut size, body weight, and digestion of winter foods by grouse and ptarmigan. The Condor 85:185-193.

OWEN-SMITH, R.N. 1988. Megaherbivores. The influence of very large body size on ecology. Cambridge studies in ecology, Cambridge.

REGELIN, W.L., C.C. SCHWARTZ, and A.W. FRANZMANN. 1985. Seasonal energy metabolism of adult moose. J. Wildl. Manage. 49:388-393.

RENECKER, L.A., and R.J. HUDSON. 1989. Seasonal activity budgets of moose in aspen-dominated boreal forests. J. Wildl. Manage. 53: 296-302.

______, and ______. 1990. Digestive kinetics of moose (*Alces alces*), wapiti (*Cervus elaphus*) and cattle. Animal Production 50:51-61.

SCHWARTZ, C.C., W.L. REGELIN, and A.W. FRANZMANN. 1987. Seasonal weight dynamics of moose. Swedish Wildl. Res. Suppl. 1:301-310.

STAALAND, H., PEHRSON, Å., JORDAN, P., and R.T. PALO. 1992. Seasonal variation of alimentary mineral and nitrogen pools in the moose. Comparative Biochemestry and Physiology, 102A:163-171.

WALLIN, K., G. CEDERLUND, and Å. PEHRSON. 1996. Predicting body mass from chest circumference in moose *Alces alces*. Wildl. Biol. 2(1):53-58.

WECKERLY, F.W. 1989. Plasticity in length of hindgut segments of white-tailed deer (*Odocoileus virginianus*). Can. J. Zool. 67:189-193.