SEASONAL VARIATIONS OF FOOD PARTICLE SIZE IN MOOSE

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ABSTRACT: We investigated digesta of 15 adult and 5 juvenile moose (*Alces alces*) from eastern and southern Finland over 12 months. We determined the proportion of food particle sizes at 2 ruminoreticular and 5 postruminal sites. Moose passed coarser food particles from the ruminoreticulum than grazing domestic ruminants. Presence of food particles >2 mm was lowest in winter and early spring when digestibility was low, and highest during vegetation growth (Jun-Sep), which coincides with greater forage selectivity. More than 50% of all samples from July to September consisted of coarse particles >4 mm. Sites of concentration of coarse particles changed, which suggested intermittent widening of the reticulo-omasal orifice. Moose are concentrate selectors and respond to the cyclic seasonality of their environment with foraging and digestive strategies that differ from grazing domestic ruminants.

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Moose are large concentrate selectors (tree and shrub foliage eaters, Hofmann and Stewart 1972) based on the morphology of their digestive system and feeding habits (Hofmann 1985, 1989, Hofmann and Hygren 1990a). Their evolutionary morphophysiological adaptation is distinguished by selective intake of plant material rich in cell contents (Renecker 1985, 1987), short food retention time (Schwartz *et al.* 1988) because of their relatively small and simple-structured ruminoreticulum with few delay mechanisms, large salivary glands (Hofmann 1988), with poor fiber digestion in the rumen (Hjeljord *et al.* 1982) but a very large caeco-colic (distal) fermentation chamber (Hofmann and Nygren 1990a).

During vegetative growth, when plant cell contents from leaves and fruit are abundant, the absorptive surface of the evenly papillated rumen mucosa enlarges; it reaches maximum size in summer followed by a gradual reduction of 30-50% during autumn and winter (Hofmann and Nygren 1990b). Winter rumen fill of moose in Alaska is about 30% less than summer fill (White 1984). We assume moose are adapted to variable seasonal nutrition and their digestive system is geared to a strategy that maximizes nutrient intake, growth, and the formation of fat deposits during summer and autumn.

Moose avoid fibrous food when possible (Renecker 19878). Fibrous foods pass quickly through the moose forestomachs mostly undigested, constituting part of the "ruminal escape" (Van Soest 1982) to undergo cellulolysis in the hindgut or rapid expellation. L.A. Renecker (pers. commun.) found large particles 8 mm in moose droppings in Alberta.

Moose have a relatively large reticulo-omasal orifice with numerous long papillae unguiculiformes arrayed like a sieve, which facilitates passage of large fibre particles but prevents unbroken leaves from passing.

McBride *et al.* (1984) suggested that long reticulo-omasal papillae in cattle (they are shorter than in moose) may prevent unruminated foliage from entering the omasal canal but allow ruminated particles to pass easily. In moose, large food particles can be found posterior to the ruminoreticulum, which suggests concentrate selectors have different digestive mechanisms based on specialized morphological adaptations (Hofmann 1973, 1988) than grass and roughage eaters (e.g., moose vs. cattle). Our objectives were to find out whether moose pass large food particles throughout the year in relation to changing

forage quality and availability, determine whether the outflow of such large particles is continuous and relate assumed changes in particle size to gastro-intestinal morphology.

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STUDY AREA AND METHODS

Moose were collected in eastern (63°N, 30°E) and southern Finland (60°30'N, 26°E) from natural forest habitats of mixed deciduous and conifer stands broken by moorland and heath. The period of sampling (1984-85) had low winter temperatures (ca. -40°C); a late, cold spring; and a hot (25-30°C), dry summer.

Eighteen moose (13 female and 5 male) were shot at regular intervals throughout the year during daylight, i.e. during or between feeding periods. Two adult females and one male calf were killed by vehicles and 2 females were killed by predators.

Ages of moose ranged from 2 months to 19.5 years, as determined by cementum annulae of the first incisor (Sergeant and Pimlott 1959).

Three moose were bled and the carcasses were transported within 1 hour to a laboratory. They were then measured, weighed, and dissected; weights were 195, 234 and 310 kg. The stomachs were infused with a 4% formaldehyde solution via esophagus and pylorus abomasi without distending. The ostium reticulo-omasicum was closed caudally by tight ligature to prevent flow of particles from and to the rumino-reticulum and omasum-abomasum. Similarly, the caeco-colon was moderately filled with formaldehyde via the ostium ileale and colon ascendens.

After filling, the 2 fermentation chambers were closed with intestinal forceps and fixed overnight in formaldehde baths. Random samples of 100-300 ml were taken the following day, without stirring organ contents, from the central region of rumen, reticulum, omasum, abomasum, ansa proximalis coli and caecum. Rectal contents were sampled immediately after eviscerating the animal and formaldehyde was added to stop the microbial activity.

Transportation of the remaining animals <1 hour was not possible. The same digesta samples were taken immediately after field dressing or dissecting the animal (2-5 hrs after death). With small amounts of formaldehyde added, the samples were transported in hermetically-sealed plastic bags or jars.

Fresh samples were weighed and sieved through tap water with a motorized sieve (Retsch Vibro, Retsch GmbH, West Germany) equipped with 0.5, 1, 2 and 4 mm steel wire-gauze screens. Sieving took 20 minutes, including automatic switch-off intervals. Subsamples were dried in a ventilated oven for 2 days at 60°C cooled in a desiccator with blue silics gel and weighed with a Sauter RL 200 top-loading balance. The 2 coarsest subsamples (2 and 4 mm) were studies under a binocular microscope to identify conspicuous food items.

RESULTS

During January and February (thick snow, low ambient temp.) pine (*Pinus silvestris*), juniper (*Juniperus communis*) and, to a lesser extent birch (*Betula* spp.), willow (*Salix* spp.) and aspen (*Populus tremula*) twigs were the main food items. From March to May (old snow melting, new snow falling for brief periods) also buds were selected increasingly. In June, birch and willow leaves increased in the diet. During an extended hot and dry period in July and August, leaves of birch, aspen, blueberry (*Vaccinium myrtillus*), fireweed (*Epilobium angustifolium*), yellow pondlilly (*Nuphar luteum*), and horsetail (*Equisetum* spp.) were the main food items in rumen contents. During September (rut; rain, mist and heavy winds), juniper, oat (*Avena*

sativa), fallen leaves, and herbaceous hay were eaten, in October (frosty mornings, first frosts during nights; leaves falling) blueberries, birch and aspen leaves, rowan fruit and leaves (*Sorbus aucuparia*), juniper and some pine. The latter 2 species increased after first snowfall late in October. Birch and willow twigs also were selected during November and December (thin snow cover, moderate frost).

Proportions of coarse food particles (> 2 mm) in ruminal and postruminal sampling sites were lowest in winter and early spring, especially in the postruminal digestive tract (Fig. 1). They were highest, both ruminal and postruminal, from June to October.

Coarse material of > 4 mm was found in 14 of 15 adults beyond the omasum; all 5 calves had postruminal particles > 2 mm.

The frequency of passage of coarse particles from the rumino-reticulum into the abomasum and intestine appears to be low in mid-winter and early spring, highest in summer and intermediate in autumn (Table 1). There are 2 different morpho-physiological compartments in the omasum: recessus interlaminares and canalis omasi. Coarser particles are supposed to pass only through the omasal canal. More than 50% of all samples had coarse particles (> 4 mm). Coarse particles dominated the rumen in 1 moose, the reticulum in 1, the abomasum in 4, the ansa proximalis coli in 4, the caecum in 1 and the rectum in 4. In contrast, coarse particles beyond the omasum were absent in only 1 moose.

Food was broken down less thoroughly in summer. Proportions of particles < 0.5 mm were smallest in summer but highest in mid-winter and relatively high in late autumn.

Five calves 2-7 months-of-age also were studied. The distribution of particle sizes in calves was similar to that of the adults, including occurrence of particles > 4 mm posterior to the omasum in a 2-months-old calf in summer.

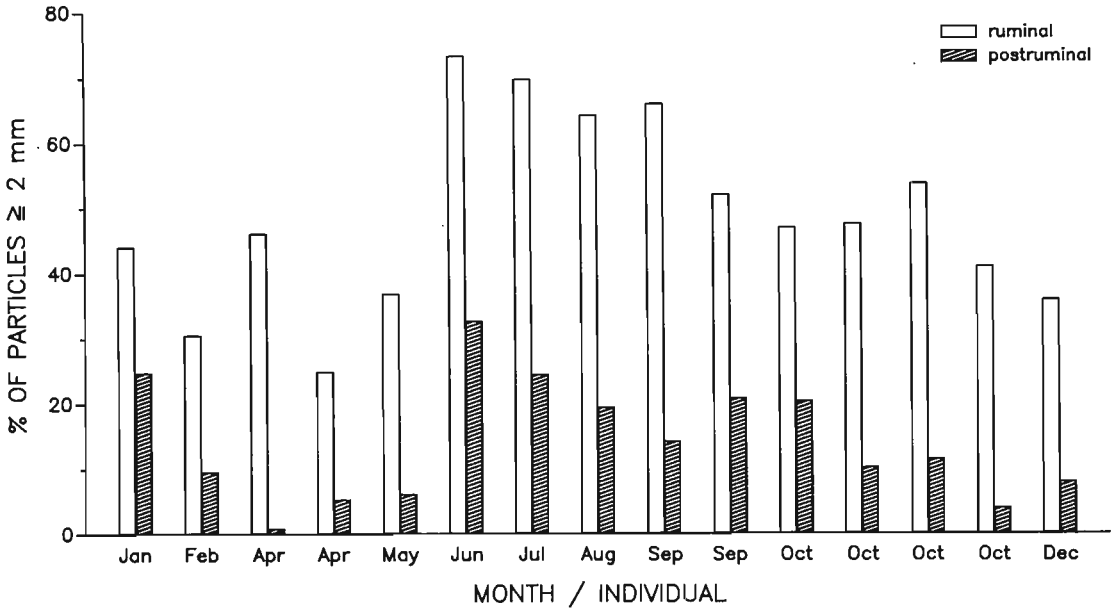

Fig.1 Proportion of coarse food particles > 2 mm in the digestive tract of moose (n = 15) collected over a 12-month period in Finland, 1984-85.

Table 1. Mean proportions of particle-size classes of moose digestive tract contents.

			Digestive compartments													
			Rumen		Reticulum		Omasum		Abomasum		Ansa prox. coli		Caecum		Rectum	
Months	*n*	Particle size	*x*	SD	*x*	SD	*x*	SD	*x*	SD	*x*	SD	*x*	SD	*x*	SD
Jan-May	5	< 0.5	35.1	8.6	36.6	7.1	68.2	14.4	65.7	14.7	74.8	20.0	77.6	12.6	77.8	12.9
		0.5-1.0	30.0	13.5	25.4	9.8	21.0	6.8	20.0	4.7	18.7	11.9	16.9	5.9	16.4	10.9
		1.0-2.0	11.3	8.2	16.2	6.3	8.4	6.6	6.9	4.7	3.3	5.3	4.7	6.1	3.2	4.9
		2.0-4.0	23.6	9.5	21.8	16.5	2.5	3.2	7.4	13.3	46.2	6.5	41.8	9.35	53.3	4.8
Jun-Aug	3	< 0.5	15.8	5.3	17.4	5.5	40.2	11.2	33.7	13.3	46.2	6.5	41.8	9.5	53.3	4.8
		0.5-1.0	14.4	1.7	14.7	2.3	30.8	2.9	31.7	2.7	32.7	9.96	38.1	1.9	30.0	4.2
		1.0-2.0	10.0	1.4	11.6	3.8	25.8	7.4	29.6	11.4	16.3	7.5	18.5	7.6	15.9	4.0
		2.0-4.0	59.8	5.7	56.3	2.2	3.2	1.5	5.0	3.8	4.8	5.7	1.6	0.8	0.8	0.7
Sep-Dec[a]	11	< 0.5	23.2	9.5	28.9	10.2	60.1	14.0	60.8	18.1	55.1	23.0	53.9	23.5	65.2	21.1
		0.5-1.0	20.8	9.8	22.0	8.4	24.9	7.6	24.0	7.8	35.5	21.5	34.8	15.6	20.3	9.0
		1.0-2.0	13.5	7.8	15.4	5.0	7.1	5.1	6.1	5.1	8.7	7.7	10.4	10.7	5.5	6.9
		2.0-4.0	42.4	20.1	33.7	19.3	7.9	13.3	9.1	20.9	0.7	1.3	0.9	1.6	9.0	19.1

[a]November sample not included due to a long chase before sampling.

DISCUSSION

Reduction of particle size by chewing and rumination in domestic ruminants increases rate of passage of digesta from the rumen, which in turn facilitates additional intake. In grazers (e.g., cattle and sheep), the size necessary to permit passage is considered to be about 0.5-1.0 mm (Pearce 1967, Poppi *et al.* 1980). Ulyatt *et al.* (1986) confirmed that little material > 2.0 mm is present in postruminal digesta of domestic animals and Sutherland (1988) suggested that floating and sinking particles in a grazer's rumen are differentiated by size at 1 mm. A floating ruminal digesta raft composed of larger particles delays, in grass and roughage eaters flux of larger particles to the omasum/abomasum (Deswysen *et al.* 1989). The omasum, especially its reticulo-omasal orifice and its canal, controls passage. There was no evidence that particls are broken down between the omasal leaflets. Their epithelium, in any case, is softer than cellulose structures.

Size reduction and the separation of food particles before passing through the reticulo-omasal orifice are responsible for the delay in transit of material through the rumino-reticulum, which is considered to be a biological disadvantage for ruminants compared to hindgut fermenters (e.g. perissodactyls (Janis 1976). This view suffers from its deductive generalization. Several African bovids that are either concentrate selectors or intermediate mixed feeders (Hofmann 1973) have different structural designs of their reticulo-omasal orifice and omasum compared to sheep and cattle. Furthermore, there is no or little stratification and raft formation in the rumen of forb, fruit, and foliage selecting ruminants. Similarly, cervids of these feeding types (e.g. white-tailed deer (*Odocoileus virginianus*), roe deer (*Capreolus capreolus*) and moose) have a comparatively larger reticulo-omasal orifice and, as has been shown, can be widened considerable on demand (Hofmann 1984, 1988).

Our results compliment those of Schwartz *et al.* (1984) who found food intake in moose

peaks in summer and is lowest in late winter, and of Renecker (1987) and Renecker and Hudson (1990). These results all point to a feeding strategy adapted to seasonally changing range conditions and forage availability. This adaptive strategy is different from domestic ruminants which, so far, have been models for most wild ruminants of the concentrate selector or intermediate feeding type.

In general , moose appear to have a relatively fast passage of fibrous plant material (Renecker and Hudson 1990, Schwartz 1990). Their large salivary glands ensure a high dilution rate of unstratified rumen contents, and their wide reticulo-omasal orifice probably permits rapid passage of particles > 1 mm, even > 2 mm (Hofmann and Nygren 1990a). Bacteria in the capacious distal fermentation chamber in the caeco-colon break down much of these structural carbohydrates, especially hemicelluloses,after passing through the acidic abomasum (Ulyatt *et al.* 1975).

The rumen of moose, with its wider openings and absence of a fibrous raft (Sutherland 1988) appears to lack the effective mechanisms for passage delay and particle separation found in sheep and cattle. Particles > 2 mm exceed 60-70% of digesta during periods of vegetation growth, when moose can afford to be extremely selective. Quick passage of relatively large particles from rumen and reticulum will clear these chambers in time for repeated intake.

Renecker (1985, 1987) observed maximum rates of forage consumption in moose in Canada in July, and short turnover times of alfalfa in summer, while aspen foliage was "propelled rapidly" through the rumen with a retention time of only 16 hours. Our results show about 20-30% of large particles in the postruminal portions of the tract between June and October, which coincides with the greatest opportunities for selective feeding. In contrast, during winter and early spring (delayed vegetation growth in 1984), rumen particle size was reduced (ca. 30-40% > 2 mm), while from February to May, postruminal particle size > 2 mm was < 10%. At that time, digestibility is only about 30%, and moose are least selective (Renecker 1985).

It becomes clear, therefore, that the foraging behavior and digestive strategy of moose is adapted to "an environment whose seasonality of climates and primary productivity is highly cyclic" (Jordan *et al.* 1971). this adaptation is based on specific morpho-physiological variations of the moose's digestive system (Hofmann and Nygren 1990a). Accumulation of coarse food particles found randomly distributed throughout the postruminal sites., suggests intermittent widening of the reticulo-omasal orifice for short clearing periods. The structural arrangement of this orifice which is modified seasonally, does not prevent coarser particles from passing through the omasal canal. The increase in particles < 0.5 mm during mid-winter implies increased rumination of forage, which is, by then, essentially more fibrous and less digestible. Also, food intake is reduced during this period. Both facts are reflected in a reduction of the mucosal surface of rumen papillae (Hofmann and Nygren 1990b).

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