SEASONAL ADAPTATIONS OF MOOSE (*ALCES ALCES*) METABOLISM

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ABSTRACT: The experiments were conducted on two yearling moose (*Alces alces*) with rumen fistulas in July and October. Intake of digestible nutrients and energy was two times higher in July than in October when water balance was lower. Total volatile fatty acid concentration in rumen liquid decreased with a proportional change of increased acetate and reduced propionate and butyrate. Coincidentally, the level of volatile fatty acids in blood rose, and glucose and concentration of ketone bodies declined. The data suggest that metabolic adaptations for limiting heat loss in winter include inhibition of aerobic oxidation, enhancement of anaerobic glycolytic pathways of energy supply, and reduction of water exchange.

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There is a large seasonal variation in food consumption by moose (*Alces alces*) (Schwartz et al. 1984, 1985, 1987, 1988; Renecker and Hudson 1985; Regelin et al. 1985, 1987). Intake and expenditure of energy in winter decreases naturally in response to a decline in quantity, quality, and availability of forage. However, moose voluntarily reduce forage intake in winter even when offered high quality natural food ad libitum (Schwartz et al. 1984, 1988). Measurement of heat production (HP) in adult moose by Regelin et al. (1985) indicated that the highest levels of HP occurred in June, but HP remained high through September and then declined sharply in October. The mean summer HP was 1.5 times higher than the mean winter HP.

Similar patterns in consumption and digestibility of nutrients and energy have been demonstrated for moose in the Pechorskaya taiga (Kochanov et al. 1981, Kochan 1990, Weber and Chalyshev 1990, Weber et al. 1992). Investigations of gas-energy exchange (Chermnykh et al. 1980) showed that despite a decrease of heat production in winter, moose maintain thermal homeostasis. Moreover, earlier it had been established (Yazan and Kozhukhov 1964) that daily variation of moose body temperature is lower in winter than summer (1.4°C and 1.9°C, respectively). It is unknown how the decrease in metabolism and HP in cold seasons conforms to the increase in energy requirements associated with maintaining thermal homeostasis and locomotive activity. The purpose of my research was to study moose metabolism (digestibility of nutrients and energy, water exchange, rumen and intermediate metabolism) in summer and fall to understand the mechanism of physiological adaptation to changing conditions of the environment.

METHODS

Research was conducted with 2 yearling male moose (average weight of 153 kg in summer and 184 kg in autumn) with rumen fistulas at the moose farm at the Pechoro-Ilych Nature Reserve, Komi Republic. Nutritional balance trials were carried out in July and October. The animals were kept confined and fed fresh-picked forage daily. After acclimating for 26-30 days, food and water intake, fecal production, and urine production were measured for 6 continuous days.

Moose were offered forage twice daily in a quantity exceeding an amount they could consume (established during the acclimation period). The forage remains or orts were removed prior to the next feeding, their content and quantity measured, and subsequently subtracted from the fed amount to determine consumption. The animals drank water from a bucket installed in the feeding trough that allowed measurement of water consumption.

Feces and urine were collected in plastic bags fixed on 2 m sticks. This allowed us to safely approach the animals, minimize disturbance, and easily collect excrement. The excrement was weighed and subjected to chemical analysis. The water content, dry matter, carbohydrates, and energy in forage and feces were measured; their differences were used to estimate digestibility.

The summer diet included leaves of birch (*Betula pubestris*), aspen (*Picea obovata*), mountain ash (*Sorbus aucuparia*), willow (*Salix* sp.*)*, and fireweed (*Chamaerion angustifolium*) in a ratio of 3:25:20:5:47. The fall diet consisted of branches of willow, birch, pine (*Pinus sylvestris*), and cowberry bush (*Vaccinium vitis-idaea*) in a ratio of 23:30:17:30.

A rumen sample was taken 6 times daily every 4 hours starting at 0600 h. Contents were analyzed for cellulose, sugars, and volatile fatty acids (VFA). Blood samples taken from the jugular vein at the end of trial periods were analyzed for glucose, ketone bodies (acetone with acetoacetate and β-oxybutyrate), and VFA.

The concentration of VFA was determined with gas-liquid chromatography (Kochanov and Tulupov 1979); the concentration of cellulose after removal of lignin, hemicelluloses, and other substances was determined by oxidation with bichromate potassium in sulphoacid solution to carbonic acid and water. Further, the concentration of sugars was determined after their extraction with ferricyanic potassium using the volumetric method of titration (Pochinok 1976).

The amount of energy in forage and feces was determined by chemical oxidation (Khmylov 1953) with modification (Kochan 1982). The method was based on oxidation of substances with potassium bichromate in concentrated sulphuric acid, and subsequent conversion of the bichromate used to its oxygen equivalent and related caloric value. The Student *t*-test was used to determine statistical difference between seasons.

RESULTS

The moose consumed an average of 21.3 and 8.3 kg of wet forage daily in summer and fall. Daily dry matter intake was 6.6 and 4.2 kg, and daily gross energy intake was 129.7 and 72.0 MJ in July and October, respectively. Dry matter consumption and all nutritional parameters were lower in fall ($P < 0.001$), often by > 50% (Table 1). Intake of digestible dry matter and carbohydrates per metabolic weight in October was less than half that measured in July; digestible energy intake was 2.7 times lower in October (Table 1). The digestibility coefficients of dry matter, cellulose, and energy were higher in summer than fall; 69, 57.7, and 73.3% in July versus 56.9, 40, and 57.4% in October.

Table 1. Consumption of nutrients (g/kg BW $^{0.75}$) and energy (MJ/kg BW $^{0.75}$) by moose in summer and fall. Statistical difference ($P < 0.001$) between seasons indicated by *.

Nutritional Parameter	July	October
Dry matter	156.3 ± 9.5	84.2 ± 1.9*
Cellulose	27.6 ± 1.7	18.2 ± 0.3*
Sugar	19.5 ± 1.2	9.1 ± 0.2*
Digestible dry matter	108.8 ± 7.4	47.9 ± 1.6*
Digestible cellulose	15.9 ± 0.2	7.3 ± 0.4*
Digestible sugar	18.8 ± 1.1	8.7 ± 0.2*
Gross energy	2.98 ± 0.27	1.45 ± 0.03*
Digestible energy	2.2 ± 0.2	0.83 ± 0.02*

Table 2. Water exchange in moose (g/kg $BW^{0.75}$) in summer and fall. Statistical difference between seasons indicated by * ($P < 0.05$), ** ($P < 0.01$), and *** ($P < 0.001$).

Measurement	July	October
Intake with forage	333.3 ± 66.6	83.0 ± 1.2**
Intake in absolute form	107.6 ± 22.6	108.3 ± 10.8
Total intake	440.9 ± 21.6	191.3 ± 12.6***
Secretion with feces	128.8 ± 1.9	56.2 ± 5.6***
Urine secretion	163.4 ± 24.5	62.1 ± 8.1***
Approximate water retention	148.7 ± 20.3	73.0 ± 1.6**

Water intake changed relative to seasonal change in forage intake. Total water intake (net form and as forage component) per metabolic weight declined 57% in October relative to July ($P < 0.001$; Table 2). Fecal and urinary water output changed similarly. The approximate water balance or retention was 2 times lower in October than in July ($P < 0.01$; Table 2).

The seasonal change of diet quality influenced rumen metabolism. In October when forage was higher in fiber and lignin (more twigs than leaves), digestibility of cellulose was lower and subsequently its concentration in the rumen increased 15%, whereas, sugar level declined 25% ($P < 0.001$; Table 3). Mean VFA concentration in the rumen was 21% lower ($P < 0.01$) in fall than summer (Table 3). The proportion of VFA changed with an increase in acetic acid (up to 76% from the total of VFA), and declined in propionic acid (up to 14%) and butyric acid (up to 10%); the ratio of these acids in summer was 64:16:20 (Table 3).

Table 3. Concentrations of volatile fatty acids (VFA) (mmol/l), cellulose, and sugar (g/kg wet matter) in the rumen content of moose. Statistical difference between seasons indicated by * ($P < 0.05$), and ** ($P < 0.01$).

Item	July	October
Cellulose	22.7 ± 3.5	26.1 ± 0.1
Sugar	4.0 ± 0.1	3.0 ± 0.1**
Acetic acid	49.6 ± 1.3	47.2 ± 2.5
Propionic acid	12.8 ± 0.9	8.7 ± 0.2**
Butyric acid	15.8 ± 3.2	5.6 ± 0.6**
Total amount of VFA	78.2 ± 2.0	61.5 ± 3.4**

In October, glucose level in moose blood declined 45% ($P < 0.001$) compared to July (Table 4). Concentration of total ketone bodies in the blood in October was less ($P < 0.001$) than half that in July (Table 4). Conversely, the content of VFA in blood increased > 2 times ($P < 0.01$) that in October; propionate increased 3 times ($P < 0.001$), butyrate almost 5 times ($P < 0.001$), and acetate 2 times ($P < 0.01$) (Table 4).

DISCUSSION

Adaptations to cold seasons with limited forage resources include metabolic changes that aid thermal homeostasis; e.g., when energy intake is insufficient to meet requirements, the animal mobilizes fat from its body reserves. However, when nutritional intake is lower than the maintenance level in winter, heat

Table 4. Concentration of blood metabolites in moose during summer and fall. Statistical difference between seasons indicated by * ($P < 0.05$), ** ($P < 0.01$), and *** ($P < 0.001$).

Blood Metabolite	July	October
Glucose, mmol/l	6.02 ± 0.42	3.30 ± 0.0***
Acetone + acetoacetate, mg/dl	2.35 ± 0.62	0.46 ± 0.05**
b-oxybutyrate, mg/dl	4.00 ± 0.80	2.00 ± 0.4*
Total amount of ketone bodies, mg/dl	6.35 ± 0.28	2.46 ± 0.45***
Acetic acid, mmol/l	0.64 ± 0.14	1.36 ± 0.173**
Propionic acid, mmol/l	0.03 ± 0.00	0.08 ± 0.002***
Butyric acid, mmol/l	0.01 ± 0.00	0.02 ± 0.001***
Total amount of VFA, mmol/l	0.67 ± 0.14	1.46 ± 0.182**

production declines. Therefore, to maintain thermal homeostasis, it is also important to reduce heat loss.

Reduction of heat loss in moose is aided by morphological specializations of the hair surface, skin, sweat, and fat glands (Sokolov and Chernova 1987), as well as physiological adaptations including reduction of lung ventilation and lower frequency and increased depth of breathing (Knorre and Knorre 1959, Chermnykh et al. 1980). However, physiological adaptations are based on biochemical changes because the amount of consumed O_2 and respired CO_2 depends on the level of the oxidation-reduction process. The decrease of the respiratory quotient to 0.7 in moose in winter (varies from 0.58 to 0.82; Chermnykh et al. 1980) points to the high use of fat reserves in energy metabolism, and also to incomplete oxidation of substances.

Decline of heat production in moose starts in October, as established by indirect calorimetry (Regelin et al. 1985), suggesting that inhibition of aerobic oxidative processes occurs in moose. The latter is confirmed by the data in this study, which indicated an increase of VFA concentration in moose blood in October, because the greatest utilization of VFA takes place in the tri-carboxylic acid cycle. It is known that the metabolic energy of VFA, mainly acetic acid, covers nearly 70% of the requirement of a ruminant organism. The rise of VFA level in blood when VFA production declined in the rumen indicates their lower utilization, because VFA and energy sources are predecessors of many important metabolites in the biosynthesis of fats, carbohydrates, and proteins.

Abatement of the intensity of oxidation-reduction processes leads to less production of main electron carriers (reduction form of NAD and FAD), and consequently, less required oxygen (main and finish electron acceptor) and lower ATP production. Lower ATP synthesis in winter is apparently explained by the reduction of ATP activity required for biosynthesis, given the dominance of metabolic activity associated with catabolism of energetic reserves (i.e., fat).

Increase of fat catabolism by moose in winter is expedient not only for the energy supply, but also to satisfy the water requirement that is not met by their seasonally lower intake of forage. Fat is the main source of endogenic water relative to carbohydrates and proteins; the amount of water produced by oxidation of 1 g of carbohydrate, protein, and fat is 0.55g, 0.41g, and 1.07g, respectively. The importance of endogenic water in reindeer during cold seasons was established by Cameron and Luick (1972) who showed that when body weight was maintained or reduced during winter and spring, total body water (percentage of body weight) increased, indicating appreciable loss in total body solids. Water possesses great heat capacity and heat conductivity. Therefore, lower water exchange (intake and excreta) in moose during winter is an adaptive mechanism to reduce heat loss.

Increased utilization of fat reserves for energy and water sources can occur only with an increase in glycolysis. Acetyl-CoA, formed as a result of fatty acids oxidation, enters the tricarboxylic acid cycle and is dependent on sufficient oxaloacetate formed by carboxylation of pyruvate (the product of glycolysis). The decline in concentration of ketone bodies in moose blood in October suggests some other use of Acetyl-CoA, because it is the main predecessor of ketone bodies.

I assumed that the inhibition of aerobic oxidation was compensated by the increased intensity of the anaerobic glycolytic pathway of energy supply for maintenance. The reduced blood glucose level in October (i.e, greater utilization than formation) was evidence of increased glycolytic intensity prior to winter. In summer, when consumption of nutrients, energy, and water are highest, VFA produced during rumen fermentation are efficiently used for production. This was indicated by the low VFA concentration in blood (significantly less than in October) and high glycemic level, pointing to intensification of gluconeogenesis. In fall, when there was reduced consumption of digestible nutrients and energy, and lower water retention, the total VFA concentration in the rumen decreased as their level in blood increased, while glucose and concentration of ketone bodies declined. These established changes suggest that metabolic adaptations of moose to limit heat loss during winter include reduction of aerobic oxidation, economical expenditure of body reserves, enhancement of the anaerobic glycolytic pathway of energy supply, and reduced water exchange.

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