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ANIMAL AND HUMAN PHYSIOLOGY

Transformation of Food Lignocellulose Compounds in the Digestive Tract of *Saiga tatarica*: Functional and Comparative Aspects

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Abstract—Comparative analysis of chymus transformation have been carried out in *Saiga tatarica* kept at the Center for Wild Animals of Kalmykia, as well as in four wild *Bovidae* species: the Siberian ibex *Capra sibirica,* the East Caucasian tur *C. cylindricornis*, the chamois *Rupicapra rupicapra,* and the bighorn sheep *Ovis canadensis*. The size composition of cellulose fibers and the nutrient content were studied in different parts of the digestive tract and in feces of 12 animals. It was found that the relative cellulose value in the saiga rumen was higher than in other *Bovidae* species, whereas in feces it was lower. The most effective cellulose fiber reduction in the digestive tract was observed in the East Caucasian tur, while in the Siberian ibex it was the least effective. It was shown that in *S. tatarica* successful fiber reduction depended not only on the dental apparatus, but also on the enzyme system of the species.

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INTRODUCTION

Over the past two decades, studies of the use of fibrous food particles by herbivores and the characteristics of transformation of these fragments during digestion have become of particular interest. Significant data have been published on the size and distribution of dietary fibers in the digestive tract of wild mammals depending on their food specialization, body size, and structure of the digestive tract (Nigren and Hofmann, 1990; Sokolov et al., 1995; Clauss et al., 2001, 2002; Hummel et al., 2008; Fritz et al., 2009, 2010; Zharova et al., 2011; Naumova et al., 2012). According to some researchers, the main role in size reduction of food particles on a large scale is given not to microbial fermentation, but rather to the effectiveness of the dental apparatus during the initial and repeated (rumination) chewing. The contribution of the digestive process to fiber reduction in cattle was 17% (McLeod and Minson, 1988). It was found that the size of plant fibers excreted with feces depended on the body weight and on the specific features of animal nutrition.

Due to the functional significance of transformation of the fiber sizes and the chemical composition of the chymus in herbivores, we used a similar approach to study digestion in saigas in comparison to other ruminants. Saigas were the only representative of antelope that lived in Europe and the only potentially massive species of ungulates that inhabited arid landscapes (steppe, desert, and semi-desert) of the vast Eurasian continent. According to the IUCN Red List (2018), saigas are recognized as Critically Endangered (CR) species.

The aim of our study was to evaluate the efficiency of the dental apparatus and the contribution of digestion to the reduction of cellulose fibers in saigas in the course of the chymus transformation and to compare these characteristics with those of free-ranging representatives of bovids.

MATERIALS AND METHODS

Samples of food, rumen contents, and feces of saigas *Saiga tatarica* were obtained from animals kept at the Center for Wild Animals of the Republic of Kalmykia that died as a result of accidental mechanical injuries. Samples from four individuals were studied: two males and one female (all 7.5 months old) and one two-year-old female (nos. 1–4). Material for other *Bovidae* species was obtained as a result of licensed winter hunting in the Russian Federation: the Siberian ibex *Capra sibirica* and the East Caucasian tur *C. cylindricornis* (three individuals for each species) and one individual each of the chamois *Rupicapra rupicapra* and the bighorn sheep *Ovis canadensis*. The adult specimens of bovids had noticeably different average body mass (Sokolov, 1979; Danilkin, 2005). Saigas were close in weight to chamois and the East Caucasian tur (up to 50 kg), while adult individuals of the Siberian ibex and the bighorn sheep were twice as large.

To avoid the effect of possible stratification on the fiber size composition in samples, the rumen content was mixed before sampling. In wild ruminants, we also

Table 1. Size composition of dietary fiber in the rumen and feces of saigas (%)

Animal no.	Sample	Sieve mesh size, mm				
		2	1	0.5	0.25	<0.25
1	Rumen	38.47	7.42	35.11	14.94	4.05
	Feces	0.58	3.47	45.09	38.15	12.72
2	Rumen	59.35	12.63	24.35	3.20	0.46
	Feces	1.96	3.92	47.06	33.33	13.72
3	"	0.86	12.00	61.71	9.71	15.71
4	"	0.66	3.62	45.72	39.47	10.53

sampled content from other parts of the stomach and intestines. The volume of the sampled material for different species was not equal, although the data obtained were of great interest due to the rare and protected status of the studied species as well as the hard-to-access areas of their habitats.

The digestive tract contents and feces were divided into six size fractions under running water on soil sieves with mesh sizes of 3, 2, 1, 0.5, and 0.25 mm. Particles passing through the last sieve were collected on filter paper. The obtained fractions were dried to constant mass, weighed to the hundredth place, and then the ratio of their masses was determined (Naumova et al., 1994). To assess the degree of reduction in size of the dietary fiber, the weighted average value was calculated by the formula

$$\bar{x} = \sum_{i=1}^{n} w_i x_i \Big/ \sum_{i=1}^{n} w_i ,$$

where x_i is the sieve cell size and w_i is the mass of the corresponding fraction.

Similar calculations were also performed for representatives of deer, the elk *Alces alces* and the red deer *Cervus elaphus* (six individuals of each species), on the basis of the available (previously processed) data on the size composition of fibers in the rumen, reticulum, omasum, cecum, colon, and feces. Chemical analysis of the food samples, rumen contents, and feces was performed at the Scrabin Moscow Academy of Veterinary Medicine and Biotechnology according to the generally accepted methodology (*Instruktsiya*..., 1968).

RESULTS AND DISCUSSION

Size Composition of Fibers

The ratio of different fiber fractions in the rumen varied significantly due to the periodic replenishment of the initially eaten food with that remasticated during rumination. In saigas, coarse and medium-sized fractions of the rumen predominated, and the content of small fibers was insignificant (<4%) (Table 1). In other bovids, the proportion of small fibers turned out to be larger (up to 25%) and the fraction of large fibers did not reach half of the total fibrous mass (Table 2). For convenience of comparison of the size composition of fibers in the content, the particles accumulated on sieves with the mesh diameter of 3 and 2 mm were assumed as large; the particles of 1 and 0.5 mm, as medium; and those of 0.25 mm and those accumulated on filter paper, as small. The results showed that in the rumen of the East Caucasian tur, the large-sized fraction of fibers predominated; it comprised ~50% of the total weight of the fibers. In the bighorn sheep, Siberian ibex, and chamois, this fraction on average amounted to <40% of all fibers. On the contrary, the mass ratio of small fibers with the length of 0.25 mm or less in these three representatives of bovids was significantly larger than in the East Caucasian tur. In the reticulum of the East Caucasian tur, as well as of the deer (Naumova et al., 2012), the ratio of fibers shifted slightly in favor of medium-sized fibers; however it still varied as in the rumen. In the omasum, the number of large fibers decreased sharply and the proportion of medium and small fibers increased. During rumination and fermentation in the rumen and reticulum, large fibers underwent significant reduction: due to the separator mechanism of the reticulo-omasal junction, only 5–10% of large fibers entered the omasum. In the *Bovidae* representatives with the exception of the East Caucasian tur, the omasum contained noticeably smaller fibers; the East Caucasian tur was characterized by the highest content of large fibers in comparison to other ruminants.

In the cecum, the ratio of the size fractions of the fibers stabilized, since no additional mechanical grinding of the food in the process of fiber reduction occurred and their size was reduced only by microbial fermentation. In the *Bovidae* representatives, the reduction of fibers was very significant, and the mass of the small fraction increased up to 80% of all fibers.

In saiga feces, the mass ratio of particle size fractions changed significantly in favor of smaller ones. Earlier from the example of many ruminant species, it was found that the ratio of the fiber size fractions in feces of different herbivorous mammalian species may differ significantly (Sokolov et al., 1995; Clauss et al., 2002; Zharova et al., 2011; Naumova et al., 2012). Comparison of the size composition of fibers in the cecum and feces in almost all cases showed that in the

Table 2. Size composition of fibers in different parts of the digestive tract and feces of bovids (%)

Part of GIT	Size composition of the fibers	Saiga	Chamois	Siberian ibex	East Caucasian tur	Bighorn sheep
Rumen	1	58.94	36.18	39.00	50.27	36.38
	2	29.73	38.53	33.42	36.56	37.81
	3	11.28	25.29	22.54	13.18	25.8
Reticulum	1	–	–	–	41.43	–
	2	–	–	–	33.86	–
	3	–	–	–	24.7	–
Omasum	1	–	3.8	3.78	7.58	5.18
	2	–	44.3	50.69	60.53	46.2
	3	–	51.9	45.54	31.89	48.64
Cecum	1	–	0.68	0.31	–	0.82
	2	–	22.45	21.21	–	39.77
	3	–	76.07	78.49	–	59.4
Feces	1	6.77	2.05	0.38	1.63	2.08
	2	49.90	33.56	23.46	50.76	49.47
	3	41.1	64.38	76.16	47.62	48.44

GIT, gastrointestinal tract; 1, large fibers (1–2 mm); 2, medium fibers (0.5 mm); 3, small fibers (0.25 and <0.25 mm); "–", no data (for Tables 2 and 3).

feces there occurred the increase in the relative mass of large fibers and the decrease of small fibers. In all the species studied, the proportion of small fibers increased significantly in the feces as compared to the rumen. The fact that insignificant amount of fibers may escape the cecum was also confirmed by the ratio of the size fractions of fibers in feces. In the feces of most animals, small fibers represented more than 50% of the total fiber. In saigas, the proportion of small fibers did not reach half of the mass of all fibers.

Chemical Analysis of the Chymus and Feces

As the food advanced through the digestive tract, there was a consistent decrease in crude fiber and the balance of other nutrients changed due to digestion. Hay offered to saigas at the Center for Wild Animals was characterized by a high crude fiber content (26.68%) and a low crude protein content (3.75%) and it was lower in quality if compared with green fodder. The green fodder of saigas grazing in different areas contained from 12 to 14.5% crude protein and from 9.5 to 32.9% crude fiber (Abaturov et al., 2005). The experimental feed of the East Caucasian tur contained from 9 to 12% of fiber, and the grasses in the grazing places contained 15.2% (Magomedov and Yarovenko, 1997).

The chemical composition of the contents of the rumen in ruminants quite naturally differed from the composition of the original food due to the microbiome functioning, but nevertheless reflected the quality of the consumed food. In the rumen, as a rule, the relative content of crude fiber, crude protein, and total nitrogen increased. This was caused by both rapid assimilation of nitrogen-free extractive substances, which were abundant in the original food of saigas, and microbial fermentation. The composition of the rumen content of the species studied was close to the initial food (Table 3). In wild-caught *Bovidae* representatives, the content of crude fiber in the rumen was significantly lower than that of saigas, and, accordingly, the content of crude protein and total nitrogen was higher.

The chemical composition of the feces was characterized by more significant transformations, as the fibers underwent cycles of microbial fermentation and endogenous digestion of food. In the feces of saigas in comparison with the rumen, the relative fiber content was almost half as much due to a slight increase in the content of the other components. Among the species studied, the fiber content in feces was noticeably higher only in the chamois. The other bovid species were close in this indicator to chamois, although in the rumen, the initial part of digestion, the species had significantly fewer lignocellulosic components than saigas.

DISCUSSION

Diet

In accordance with the classification of diet types proposed by Hoffmann for ruminant mammals, all the *Bovidae* species studied grazing in mountain

Table 3. Chemical composition of the contents of the digestive tract and feces of the bovids (%)

Part of GIT	Nutrients	Saiga	Chamois	East Caucasian tur	Siberian ibex	Bighorn sheep
Rumen	Total nitrogen	1.84	3.21	2.91	1.96	1.94
	Crude protein	11.5	20.06	18.22	12.25	12.12
	Crude fat	9.12	13.82	9.76	11.66	9.08
	Crude ash	6.67	11.12	13.32	12.1	13.11
	Crude fiber	32.49	18.05	11.61	18.33	15.49
	WHyg	5.1	5.3	5.1	5.35	5.15
	NFES	35.12	31.65	41.9	40.31	45.05
Cecum	Total nitrogen	–	2.24	–	–	1.29
	Crude protein	–	14.0	–	–	8.06
	Crude fat	–	14.77	–	–	10.47
	Crude ash	–	14.75	–	–	22.57
	Crude fiber	–	21.64	–	–	17.06
	WHyg	–	5.4	–	–	5.18
	NFES	–	29.44	–	–	36.66
Feces	Total nitrogen	4.11	2.11	2.78	1.43	1.34
	Crude protein	16.29	13.2	17.37	8.95	8.37
	Crude fat	10.87	10.58	15.44	7.8	5.8
	Crude ash	12.59	13.34	14.55	19.68	20.46
	Crude fiber	18.1	28.8	17.91	13.11	17.58
	WHyg	5.38	5.15	5.29	5.27	5.25
	NFES	36.78	31.93	29.44	41.195	42.54

NFES, nitrogen-free extractable substances; WHyg, hygroscopic water.

meadows and steppes belonged to the intermediate feeding type consumers (Hoffman and Stewart, 1972; Hoffman, 1989). Browse forage was an integral part of the winter diet of Eurasian ruminants and an additional food for bovids, that during the winter season relied on green grass and grassland litter preserved under the snow (Danilkin, 2005). However, the division of herbivorous ruminants in accordance with their diet type into the three groups was very conditional and to a large extent depended on the food supply, which varied significantly due to annual and seasonal fluctuations. Among the species studied, the diet was better investigated in saigas and the East Caucasian tur (Abaturov et al., 1982, 1988, 2005; Magomedov et al., 1997; Larionov et al., 2008). Under experimental conditions of feeding these animals on a wide range of feeds, the choice fell on the most nutritious grass species. But at the Center for Wild Animals, saigas successfully existed on less nutritious feeds with a high fiber content (26.68%). The efficiency of digestion was related to the food quality: the higher it was, the better it was digested.

Size Composition of Fibers

Large-scale studies of the size composition of lignocellulose particles excreted with feces showed the relationship of this indicator to food specialization, body size, and the taxonomic affiliation of animals. It was found that the differences between ruminants of the three basic types of diet were most pronounced in large mammals with body weight of more than 70 kg: in the consumers of coarse food, the average size of the excreted fibers was smaller than in representatives of the other two groups, and in smaller ruminants these differences were not clear (Clauss et al., 2002). In addition, captivity also affected the size of food particles: in free-ranging ruminants, the average particle size was smaller than in captive individuals (Hummel et al., 2008). Unfortunately, published data may not always be used for comparative analyses due to differences in the details of the methodology. Despite the fact that many experts explain the differences in the size composition of the excreted fibers by the specifics of the dental apparatus rather than by the result of symbiotic digestion, there exist many indisputable

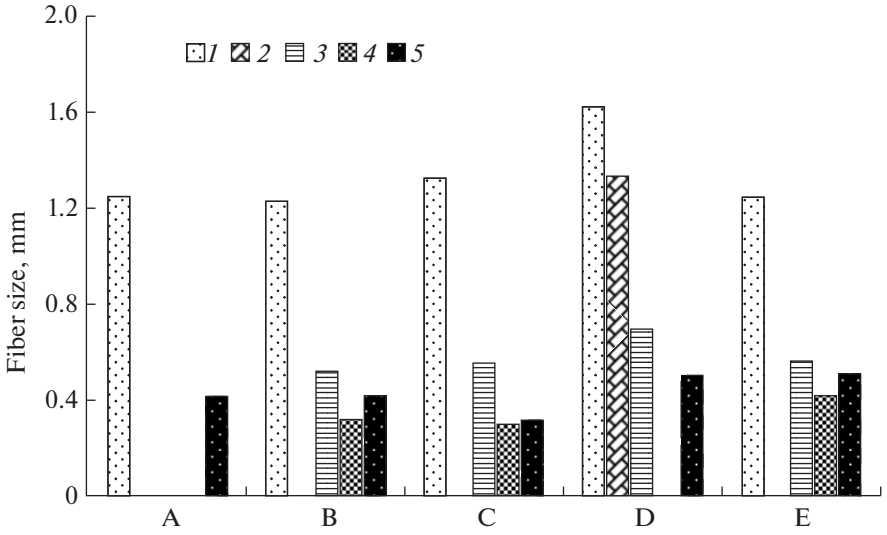

Fig. 1. Weighted average fiber sizes. *1*, rumen; *2*, omasum; *3*, cecum; *4*, colon; *5*, feces. A, saiga; B, chamois; C, Siberian ibex; D, East Caucasian tur; E, bighorn sheep (for Figs. 1 and 2).

facts of the high digestibility of lignocellulosic components by ruminants. It is also known that small fibers are more easily fermented by the microbiome than large ones. The dependence of the fermentation rate on the size of food particles in cattle was shown experimentally using *in vitro* and *in sacco* methods (Bjorndal et al., 1990). Due to unique material, although not always complete, we were able to trace the changes in the size of plant fibers in the digestive tract of several species of wild bovids and evaluate the contribution of the microbiome to the reduction of fibers.

The size composition of the fibers in the rumen reflects the total effectiveness of the primary and secondary grinding of food with teeth. It is clear that the ratio of large and small particles would vary depending on the stage of the initial chewing/rumination cycle during which an animal was taken, but the average fiber size generally reflects the efficiency of the dental apparatus. The difficulty of assessment of the effect of mechanical grinding of food and the effectiveness of fermentation is that in ruminants these processes are topographically combined. Fibers that have already undergone mechanical and microbial effects are introduced into the omasum, and their size also depends on the functioning of the separator mechanism, which selectively keeps large fibers in the rumen.

According to the body size (the average mean for the species), the studied ruminants were arranged in the following order (according to the decrease of the average body weight of the species): the Siberian ibex (100 kg), bighorn sheep (60–90 kg), East Caucasian tur (50 kg), chamois (50 kg), and saiga (40 kg). However, there were no obvious relationships found between fiber sizes and body weight. In the rumen, the largest fibers were found in the East Caucasian tur whereas the smallest were in saigas, chamois, and bighorn sheep (Fig. 1). These species were similar in body weight. This feature continued in the omasum, where the fibers that had already passed the stage of digestion in the rumen were introduced as a result of separation (selective retention of large fibers in the rumen). However, there were significantly more fibers with the length of <0.5 mm in the chamois than in the East Caucasian tur. No relationship was found between the relative fiber content of different size fractions in the omasum and the diameter of the opening between the reticulum and the omasum (reticulo-omasal junction). The diameter of this opening was 12 mm for the chamois, 10 mm for the Siberian ibex, and 8 mm for the bighorn sheep (Zharova et al., 2011).

The comparison of the average particle sizes in the rumen and feces of all the species showed a very large fiber reduction: in the Siberian ibex and East Caucasian tur, the fibers were 1 mm or more (~77% of the initial size), and in the other bovid species they were <1 mm (up to 70% of the original size) (Fig. 2). The reduction of fibers in the forestomachs occurred due to the action of three components: mechanical grinding, microbial fermentation, and separation. Even in the omasum, the size of the fibers was reduced almost by half. After the contents entered the abomasum and intestines, the role of the dental apparatus and separation in grinding of the contents may be neglected. Nevertheless, there was further reduction in particle sizes in the cecum and colon, resulting from alloenzymatic digestion and residual microbial fermentation. The lowest weighted average particle sizes in the cecum were found in the Siberian ibex and chamois. Calculations of the average fiber sizes in different organs of the gastrointestinal tract in deer gave similar results and demonstrated the dynamics of fiber size changes during digestion (Fig. 3).

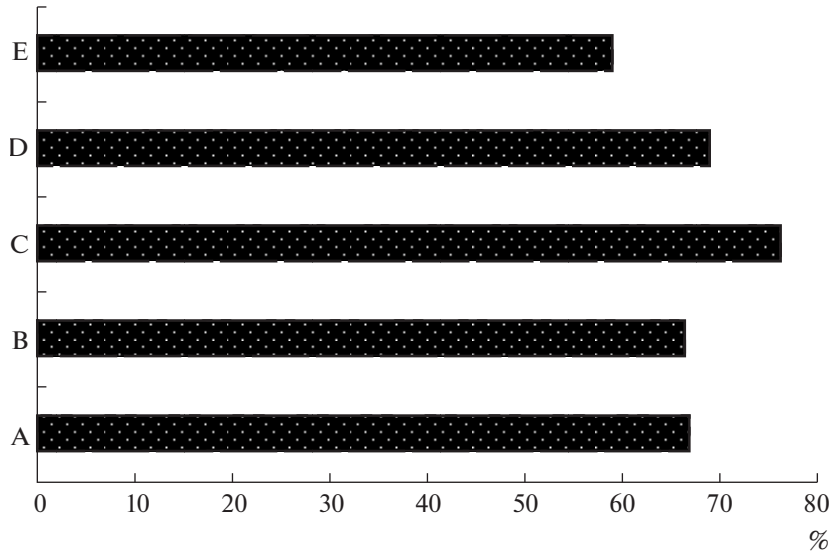

Fig. 2. Degree of fiber reduction over the full cycle of digestion, %. Calculated by weighted average values.

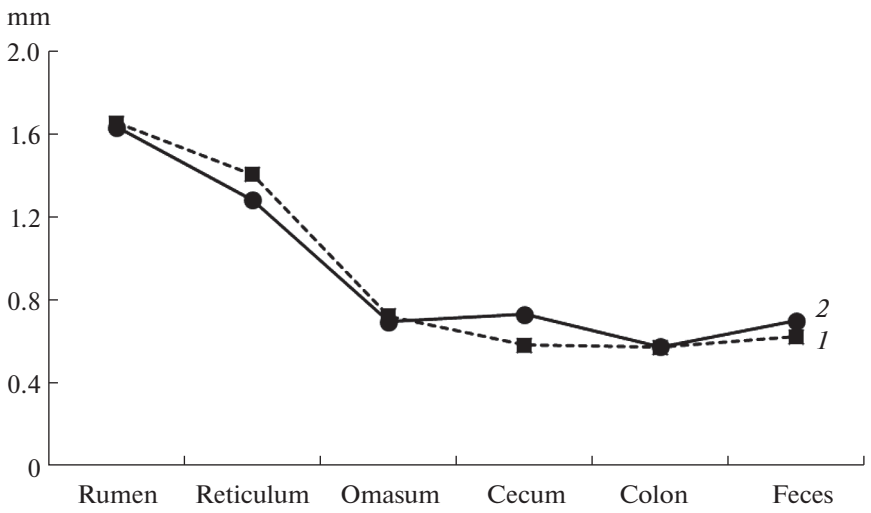

Fig. 3. Fiber reduction in the digestive tract of (1) maral and (2) moose, mm (weighted average values).

Our unique material did not allow us to analyze the factors affecting the transformation of the fiber sizes. The quality of food consumed by ruminants may vary significantly, which affected the size composition of the fibers excreted with feces. In particular, the average fiber size in early autumn (more nutritious food) and winter feces of the red deer (eight samples each) varied significantly and was 0.54 and 0.75 mm, respectively (Naumova et al., 2012). For the northern giraffes *Giraffa camelopardalis* (high-nutrient food consumers), the average fiber size in feces was larger in free-ranging individuals in comparison with captive ones, although for the cattle *Bos primigenius taurus* (coarse forage consumers), on the contrary, it was smaller (Hummel et al., 2008). It is possible to assume that the size composition of the fibers in the feces reflected the quality of food consumed at a particular time of the year. Among the bovids studied, the bighorn sheep and the East Caucasian tur were distinguished by the larger average fiber size in the feces, and the Siberian ibex, chamois, and saiga, despite the differences in their average body sizes, were characterized by the content of smaller fibers in the feces.

Nutrient Content

In the stomach of small rodents, chymus has similar nutritional value to vegetation consumed (Mago-

medov and Khashaeva, 1993); however, in the stomach of ruminants with well-developed microbiome, the ratio of nutrients changes to one degree or another in comparison with the food. According to the fiber content, the animals studied were arranged in the following order: saiga, Siberian ibex, chamois, bighorn sheep, and East Caucasian tur. Among the ruminants listed, the saiga was distinguished by the highest fiber content in the rumen (32.5%), and natural saiga food contained up to 33% fiber (Abaturov et al., 2005). The chemical composition of the food of the East Caucasian tur (Magomedov and Yarovenko, 1997) and the content of its rumen were also similar. Based on these facts and the ratio of the nutrients in the animals studied, we may assume that other *Bovidae* species were characterized by greater selectivity in the feeding behavior: they obviously preferred food with higher nutritional value.

In captive saigas of the Center for Wild Animals, the content of crude fiber in feces was almost half as less (up to 18%) in comparison with the rumen, while in the free-ranging animals, as well as in other representatives of the bovids, its value was similar or higher than that of the food and the rumen. Perhaps this was associated with permissible fluctuations in the level of fiber digestibility in saigas, from 46 to 66% (Abaturov et al., 2005; Ubushaev et al., 2012). Free choice of plants in natural environments led to significant variability of digestibility of dry matter by saigas (from 52 to 75%) depending on the nutritional value of the food consumed. The fiber content in feces to a certain extent correlated with its digestibility: with lower content in captive saigas (18%), its digestibility was higher (71%) (Ubushaev et al., 2012).

Differences between Species

Differences in the size composition of food particles in the feces of herbivorous mammals of high taxonomic ranks were usually considered as a function of body size, chewing progress, and food specialization (Clauss et al., 2002; Hummel et al., 2008; Fritz et al., 2009, 2010). Furthermore, it was found that the addition of granular feed to the diet of captive animals changed the ratio of the size fractions of fibers. Although the *Bovidae* representatives studied belonged to the group of mixed intermediate feeding type consumers, the most noticeable differences in the average particle sizes in feces were found between the Siberian ibex and the bighorn sheep (0.319 and 0.508 mm, respectively). The Siberian ibex was also characterized by the lowest fiber content in the cecum and feces and the most significant reduction in fiber size. The content of small fibers in the omasum and cecum was also higher in the Siberian ibex than in the bighorn sheep. The different degrees of fiber reduction in different species may be explained by three main factors: the quality of the consumed food, the degree of its grinding by teeth, and the duration of fermentation. A high content of small fibers in forestomachs accelerated fermentation (Bjorndal et al., 1990).

Saigas of the Center for Wild Animals differed from free-ranging saigas in terms of digestion, in particular, in the chemical composition of food and feces. Despite the introduction of forbs and alfalfa hay into their diet, which was less-nutritional than the pasture forage, saigas developed successfully under semi-free conditions. A significant decrease in the weighted average fiber sizes in feces in comparison with the rumen (from 1.25 to 0.416 mm) characterized the level of fiber utilization corresponding to the digestibility of dry matter (71%) and fiber (43.3%) (Ubushaev et al., 2012).

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