Forage quality thresholds for Saiga antelope in a semi-desert rangeland

Boris D. Abaturov & Andrey E. Subbotin*

ABSTRACT: Levels of digestibility and protein content necessary for maintenance, weight gain and lactation were estimated for Saiga antelope (*Saiga tatarica*). Estimates were based on results of digestion-balance trials using confined animals, and feeding trials involving tractable animals at pasture. Threshold parameters were estimated by regression of metabolizable energy intake and body weight gain, food digestibility and metabolic energy intake, protein content in food and the amount of consumed digestible protein. To meet maintenance requirements, food digestibility must be ≥ 59%, with protein content ≥ 7.7%. To meet requirements for growth and lactation, minimum digestibility must be 61–68%, with protein content ≥ 14%. When feeding on native semi-desert range, free-ranging Saiga antelope can meet these nutritional thresholds only through selective foraging. Therefore, when evaluating grazing capacity of Saiga habitat it is important to take into consideration that only a small portion of the total plant biomass is comprised of plants and plant parts of sufficient quality.

KEY WORDS: threshold levels, maintenance requirements, *Saiga tatarica*, body weight, energy in-take, protein content, diet quality, forage selectivity.

Boris D. Abaturov [abaturovbd@mail.ru, abaturov@sevin.ru], Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Leninsky prospect 33, Moscow 119071, Russia; Andrey E. Subbotin [andrey.subbotin@gmail.com], All-Russian Research Institute for Nature Conservation, "Znamenskoye-Sadki" Estate, Moscow 117628, Russia.

Критические уровни качества кормов у сайгаков на естественном пастбище в полупустыне

Б.Д. Абатуров, А.Е. Субботин

РЕЗЮМЕ: Определены уровни переваримости и содержания протеина, необходимые для поддержания жизнедеятельности, роста и лактации у сайгаков (*Saiga tatarica*). Оценки основаны на результатах балансовых опытов с использованием клеточных животных и опытов по питанию прирученных животных на пастбище. Критические параметры определены регрессионным анализом соотношения количества поглощенной обменной энергии и привеса тела, переваримости корма и количества обменной энергии, содержания протеина в корме и количества потребленного переваримого протеина. Для обеспечения поддержания жизнедеятельности переваримость должна составлять ≥ 59%, содержание протеина ≥ 7,7%. Для обеспечения роста и лактации минимальная переваримость составляет 61–68% при содержании протеина ≥ 14%. При потреблении кормов на естественном полупустынном пастбище свободнопасущимися сайгаками данные кормовые параметры могут быть обеспечены только избирательностью питания. Вследствие этого при оценке пастбищной емкости местообитаний сайгаков крайне важно учитывать, что только малая доля общей растительности массы включает в себя растения и их части, обладающие необходимым кормовым качеством.

КЛЮЧЕВЫЕ СЛОВА: критические уровни, требования к поддержанию жизнедеятельности, *Saiga tatarica*, вес тела, потребление энергии, содержание протеина, качество корма, кормовая избирательность.

Introduction

The tendency of ruminant herbivores to choose the more nutritious foods available to them is a widely known phenomenon. Even when food is abundant, it may not satisfy nutritional needs of animals if its quality is low (Bell, 1971; Robbins, 1983; Berry & Louw, 1982; Eisfeld, 1985; Abaturov & Magomedov, 1988; Owen-Smith & Cooper, 1989; Abaturov *et al.*, 1996; Cook *et al.,* 1996; Sinclair *et al.*, 2006). Data show that free ranging herbivorous mammals are fairly sensitive to changes in nutritional value of their plant food, especially with respect to its digestibility and protein content (Eisfeld, 1974, 1985; Mould & Robbins, 1981;

Sinclair *et al.*, 1982; Arnold, 1985; Regelin *et al.*, 1987; Jiang & Hudson, 1992; Cook, 1996). Nevertheless, the nutritional ecology of many wild ruminants remains poorly understood. Precise knowledge of forage availability, and especially its quality, is crucial for understanding mechanisms of animal distribution, movements, and forage use patterns, as well as reproductive performance of animals in free-ranging populations. Among Eurasian species, Saiga antelope (*Saiga tatarica* L.) are susceptible to nutritional deprivation based on their body allometry and productivity of their native habitats (Abaturov *et al.*, 1998). Here we present analyses of qualitative parameters, including forage digestibility and protein content that are relevant to assessing the suitability of habitats to support Saiga antelope. Conservation of Saiga antelope populations and proactive management of the species' habitat requires explicit knowledge of their nutritional requirements (Abaturov, 2007). In this paper we investigate nutritional thresholds, which managers can use to evaluate the suitability, or carrying capacity, of various semi-desert habitats in terms of their ability to meet the nutritional needs of this herbivore.

Study area

We analyzed the data obtained in the field researches conducted in 1978–1980; 1995–1996, and 2002–2004 at the Dzhanybek Biological Field Station of the Institute of Forest Science, Russian Academy of Sciences. The Station located in the Northern Precaspian depression on the Russia-Kazakhstan administrative border. The study area occupies a contemporary range of Saiga antelope and represents typical clay semi-desert landscape with a complex of three-component soil and vegetation cover (Gordeeva & Larin, 1965; Bol'shakov & Bazykina, 1974; Abaturov *et al.,* 1998). Thus the territory includes desert, semi-desert and steppe plant communities. The deserted communities occupy the basic portion of plain, with a total 28 plant species among which *Kochia prostrata*, *Poa bulbosa*, *Tulipa gesneriana*, *Leimus ramosus*, *Artemisia pauciflora*, *Salsola laricina* predominate. Semi-desert communities include 40 species. Key dominants here are *Agropyron desertorum*, *Tanacetum achilleifolium*, *Galatella villosa*, *G. tatarica*, *Limonium sareptanum*, *Tulipa biebersteiniana*, *T. biflora.* Steppe associations include 80 species of vascular plants with a key predominance of *Stipa capillata*, *S. Lessingiana*, *Festuca valesiaca*, A*gropyron cristatum*, alfalfa *Medicago falcate*, *Galium verum* and others steppe species.

Material and methods

The groups of 2 to 6 tractable Saiga antelopes have been trialed in these studies. We used these animals to examine the nutritional ecology of Saiga via two approaches. The first approach involved direct estimates of nutrition relations using traditional digestion-balance trials during which the animals were fed rations of known composition while held captive in balance cages libitum (Fig. 1). The second approach was based on using fecal bags on free-ranging animals on native pasture (Fig. 1). The 3 animals were permanently employed in 13 digestion-balance trials of 6 different diets. The 2 animals were employed in 9 grazing trials in 4 differing habitats and all of the year-round seasons. Detailed descriptions of research methods were provided in the previous publications (Abaturov *et al.*, 1982, 1997, 2003).

Digestion-Balance Trials

Studies in digestive-balance cages allowed us to estimate daily food consumption and digestibility of different diets of known botanical and chemical compositions. These diets were comprised of *Kochia prostrata*, *Agropyron* species (sowing), a combination of forbs that are common on areas frequented by saiga in May and July, leaves of elm (*Ulmus pumila*), mix of grasses and dried alfalfa with ground barley grain. In the course of each experiment animals were periodically weighed to record any changes in their body weight. Each trial lasted 5–11 days, with an additional preliminary period of 2–3 days to allow for animal adaptation to each new diet. Animals were fed ad libitum. Non-fed forage and feces were gathered and dried at 90ï Ñ to constant weight.

Grazing Trials

Grazing trials were conducted during different seasonal periods to reflect changes in plant phenology: early spring, when the first sprouts of plants appear (April 12–17); late spring, when ephemerous and ephemeroid plants desiccate (end of May); early summer, when vegetation is at its maximum development (June 19–25); mid-summer, when the majority of steppe gramineous plants and forbs desiccate (July 20–30); late summer, when active growth of the predominant plant species (*Chenopodiaceae*, *Euphorbiaceae*, *Leguminosae)* proceeds (August–September); autumn, when nearly all plant growth has ended (end of September); and in winter, when only senescent plant biomass was available (December 5–10). Prior to each grazing trial the experimental animals were allowed to adapt to the experimental pastures over a period of 3–5 days. Each grazing trial lasted 4–6 days, during which the experimental animals were observed at pasture continuously and permanently, and each 10 minutes the type of their activity (grazing, rest laying, walking) has been registered.

The number of animals observed in each separate trial, varied from 1 to 2. During each observation period, the experimental animal was tethered but allowed to graze freely within the experimental area of 1130 m^2 in size. The ranging area has been rotated to exclude overgrazing for 3–4 times a day.

Botanical composition of grazed diets was determined by visual counts of the number of experimental

A

B

Figure 1. Trials of nutritional ecology of tame Saiga antelopes: A — in balance cages, B — free-grazing in native pasture with fecal bags.

animals bites took from each plant species. Bite counts were conducted during the entire ranging period from a distance of 2–3 m (Fig. 1). Botanical composition of diet was calculated on the proportion of total bites attributed to each species.

In the course of each grazing trial animals were weighed daily at the same time of day.

Estimation of Intake and Dietary Quality

Daily food consumption (C, g/animal, dry matter) was calculated as

$F \times 100 / (100 - D)$, where

F is the daily portion of feces (g/animal, dry matter), and D is the coefficient of dry matter digestibility (%). Daily amount of feces was determined using fecal bags. We inferred digestibility of saiga diets from the ratio between the concentration of inert substances in food and in feces (Gallup *et al.,* 1945; Streeter, 1969), using Organogenic Silica and also lignin in plant matter as the inert indicators. Concentration of the inert substantes in a diet was calculated taking into account a share of each plant species consumed in the diet and the content of inert substantes in them. The digestibility of dry matter (D, %) and separate nutrients (D', %) were calculated as $D = (1 - v/f) \times 100$; $D' = 100 - (100 \times v/f \times a/d)$, where v and f are silica and lignin concentration in food and in feces respectively, and a and b are investigated nutrients concentration in feces and in food, respectively. Silicon and lignin excreted in feces of saiga antelope comprises 97.4–99.5% of the total silicon consumed with forage and 93.0–98.3 of the total lignin consumed (Abaturov *et al.,* 1997). We analyzed organogenic silicon with acid hydrolyses using HNO_3, which excludes silicon in plant food that originates from soil and dust (Kolesnikov & Abaturov, 1997). Chemical composition of nutrients in forage plants and feces was determined by standard methods (Instruction for zonal agrochemical laboratories analysis of forage and plants) (Anon., 1968).

Energy value of food was estimated by multiplying the amount of different nutritional components by their energy equivalent: protein — 18.9 kJ, lipids — 39.0; carbohydrates — 17.6. To convert digestible energy into metabolic energy we used a conversion coefficient of 0.87 (McDonald *et al.*, 1969; Kaloshnikov & Kleimenov, 1985).

In this study we defined the metabolic energy requirement for maintenance to include energy expenditure in resting and grazing activities at zero weight balance (i.e., maintenance of energy equilibrium of free existence) was estimated by regression analyses of daily metabolic energy intake (kJ/kgBW$^{0.75}$) on daily weight gain of an animal (g/kgBW$^{0.75}$). Digestibility parameters for different energy needs (grazing activity, weight gain, lactation) were estimated by regression analyses of daily consumption of metabolic energy (kJ/kgBW$^{0.75}$) on digestibility of forage dry matter (DMD%).

Minimum nitrogen requirements for maintenance were calculated as the sum of fecal metabolic nitrogen and endogenous urinary nitrogen. Metabolic fecal nitrogen was calculated by regression of dietary protein content (%) on the amount of apparent digestible protein in the consumed forage (g/100g of forage, after Robbins, 1983). Endogenous urinary nitrogen was assumed equal to 0.12g/kgBW$^{0.75}$ (Agricultural Research Council, 1965; Eisfeld, 1974; Robbins *et al*., 1974; Robbins, 1983; Schwartz *et al.*, 1987). Protein requirements for growth and lactation of saiga antelope were assumed equal to those of domestic sheep (Agricultural Research Council, 1965; MacDonald *et al.*, 1969). Threshold levels of protein concentration in forage were estimated by linear regression of daily intake of digestible protein (g/kgBW$^{0.75}$) on dietary protein content (%).

Results

Botanical Composition of Diets

The composition of diet in traditional digestion-balance trials (in balance cages) as it was noted above, consisted of separate plant species (*Kochia prostrata*, sown *Agropyron*, leaves of elm), barley grain and their mixtures. In grazing trials free-ranging animals have actively chosen the most nutritious plants and their parts in all cases. Despite of the rich vegetation diversity of the grazing areas (more than 100 plant species) the composition of the diet in all cases and different seasons included only several species particularly *Kochia prostrata* (up to 60% of a diet), alfalfa (up to 28%), the *Galatella villosa*, and *G. tatarica* (up to 25%). In early spring these were sprouts of tulip (*Tulipa* spp.) (88%); in early summer in steppe associations these were *Potentilla bifurca* (67%); and in late summer — *Artemisia austriaca* (58%). Proportion of other species of forbs was less and did not exceed 10%. It is important to note, that gramineous plants in all grazing trials were practically absent in a diet (Abaturov *et al*., 1998, 2005).

Chemical Composition of Diets

In the digestion-balance trials, sown *Agropyron*, barley grain, and elm leaves had the highest nutritional value*,* while *Kochia* and hay were of lower quality (Tab. 1). Protein and energy content were greatest in the sown *Agropyron*. Crude fiber was lowest in barley and similarly low in the elm leaves. Ash was lowest in the barley ration. Crude fat was greatest in elm leaves.

In contrast to the nutrient differences observed among rations fed in the digestion-balance trials, apparent nutrient quality of diets observed during the grazing trials (Tab. 1). The highest protein content was recorded in the early spring grazing trial (18.4%), when animals foraged primarily on sprouts of tulip (Tab. 1). Digestibility varied substantially among diets, from 50% (*Kochia*) to 75–77% (forbs and grain mix, spring forbs shoots in case of free grazing) (Tab. 2).

Intake of Dry Matter and Energy

Intake of dry matter and energy varied considerably among diets and seasons (Tab. 2). Daily intake of dry

Table 1. Chemical composition of saiga consumed forage (% of dry matter).

Type of food	Date	Crude protein	Crude lipids	Crude fibre	*FE*	Crude ash	Energy (kJ/g)
Crashed barley grain	–	16.7	2.10	4.5	72.6	4.07	16.88
Alfalfa hay	–	12.5	3.09	27.6	46.9	9.14	16.84
Kochia prostrata	May	11.3	1.19	24.5	54.0	8.70	16.47
Sown *Agropyron* (juvenile greens)	May	21.1	3.37	24.1	51.4	10.5	19.00
Leaves of elm (*Ulmus pumila*)	August	12.8	5.22	8.4	68.3	13.7	17.35
Green herb in diet	April 12–17	18.4	2.70	27.1	46.8	4.84	17.53
	May 26–29	14.8	2.80	29.6	46.4	6.20	17.29
	June 2–6	14.3	2.70	29.8	46.0	5.64	17.37
	June 21–26	14.2	2.77	32.1	45.1	5.76	17.35
	July 27–30	12.6	2.60	30.5	46.9	7.42	17.04
	August 3–6	12.0	2.60	29.50	48.65	7.16	17.06
	August 28–31	12.7	2.54	32.9	45.7	6.16	17.22
	September 21–27	13.3	2.69	33.6	43.8	6.67	17.19
	December 1–4	13.4	2.59	30.1	48.0	6.03	17.29

matter in summer ranged from 45g/kg $(BW)^{0.75}$ in the case of sown *Agropyron,* up to 117g/kg $(BW)^{0.75}$ in the case of grain mixed with grass or hay in cage trials or in the case of forbs in grazing trials. It should be noted that low consumption of sown *Agropyron* occurred despite high digestibility of this forage (64–66%). *Agropyron* was not dried prior to feeding and thus contained high moisture content (up to 80%). The high moisture content in consumed forage contributed to gut fill, and to low dry matter consumption (Abaturov *et al.,* 1982). In summer, daily metabolic energy intake varied from 470 kJ/kg $(BW)^{0.75}$ in the case of *Kochia* in the cage trials, to 1270 kJ/kg $(BW)^{0.75}$ in the case of forbs in the grazing trials. In winter, daily intake of forage dry matter and metabolic energy were considerably lower than in summer (as low as 42.3 g/kg $(BW)^{0.75}$ and 380 kJ/kg $(BW)^{0.75}$).

Food Digestibility as an Indicator of Sufficient Energy Intake

To estimate maintenance energy expenditures and energy costs of weight gain, we analyzed the relationship between metabolic energy intake (*y*) and the amount of weight gain (*x*). Regression analyses showed that relationship between these two parameters is practically identical for confined and free-ranging animals, suggesting that animal activity and overall energy expenditure in the digestion-balance cages were fairly similar to those in the grazing trials that were conducted at pasture. Thus, the correlation between the amounts of daily metabolic energy intake and weight gain of animals can be presented in the form of regression equation $y = 10.46\ + 719.1$ (Fig. 2). According to the equation, saiga maintenance energy requirements at zero balance level in summer on the pasture equals 719 ± 34.2 kJ/kg $(BW)^{0.75}$. In winter, the slope of this relation is considerably lower: based on data from three winter experiments (in cages and on the pasture) it equals approximately 500 kJ/kg $(BW)^{0.75}$ (Tab. 2). In a review by Hudson and Christopherson (1985) estimates of maintenance energy at rest for 5 species (*Odocoileus hemionus*, *Capreoulus capreolus*, *Cervus elaphus*, *Alces alces*, *Rangifer tarnadus* and *Antilocapra americana*) varied in adult individuals from 523–655 kJ/kg$(BW)^{0.75}$ in summer to 476–597 kJ/kg$(BW)^{0.75}$ in winter. In case of Saiga antelope, setting the adjustment for foraging activity that varied between 1.18 and 1.24 (Abaturov *et al.*, 1998), expenditures of saigas for maintenance energy at rest appear to make close figures: 594 kJ/kg (BW) in the summer and 413 kJ/kg (BW) in the winter.

Thus, according to our experimental data, saiga's daily metabolic energy expenditure for maintenance at zero body weight balance, which reflects maintenance energy requirements of grazing animal, equals 0.72 MJ/kg $(BW)^{0.75}$ during the warm season and 0.50 MJ/kg

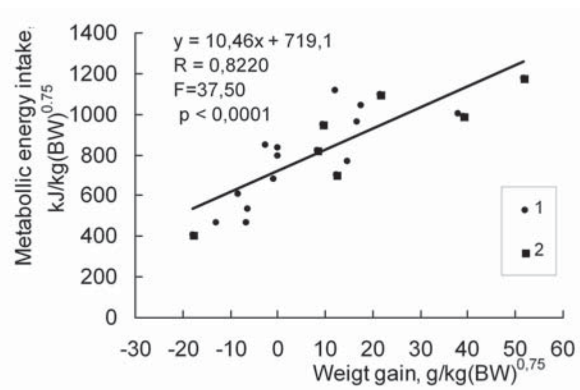

Figure 2. Relationship (y = bx + a) between daily metabolic energy intake (kJ/$kg^{0.75}$ body weight) and daily live weight gain (g/$kg^{0.75}$ body weight) of saiga based on data from experiments in warm season with animals in balance cages (*1*) and free ranging animals (*2*). Std. Error: a = 34.17, b = 1.70. P-level < 0.00001.

Table 2. Experimental nutrition parameters and weight gain of caged and free-ranging saiga antelope.

Forage composition	Date	Sex	Body weight kg	Weight gain, g/ animal/ day	Dige-sti-bility, %	Daily intake		
						Dry matter		Metabolic energy, kJ/ $kgBW^{0.75}$
						g/ ani-mal	g/kg $BW^{0.75}$	
Warm time of the year								
Steppe herbs and barley grain*	5/13–19	Male	34.2	164	75	1280	90.8	1118
	7/7–15	Male	34.7	250	68	1505	105.2	1046
Alfalfa hay and barley grain*	8/1–6	Female	22.4	150	64	843	81.8	767
	5/6–12	Male	32.8	229	73	993	72.4	962
	9/19–26	Male	39.4	–42.8	70	1253	79.8	853
	9/19–26	Female	32.2	0	68	952	70.4	797
Steppe herbs*	7/18–24	Male	32.0	–	54	1165	86.6	822
Sown *Agropyron**	5/12–20	Male	28.8	–102	64	637	51.4	611
	5/12–20	Female	25.5	–73	66	511	45.2	537
*Kochia prostrata**	6/13–18	Male	29.9	–14	53	1037	81.0	685
	6/1–7	Female	26.8	–80	52	744	63.0	470
	6/4–9	Female	23.0	–138	49	700	66.7	472
Elm leaves*	8/10–15	Female	27.3	0	57	948	79.7	839
Green herb in diet (free grazing)**	4/12–17	Female	20.0	–	77	986	104.2	1270
	5/26–29	Male	32.0	166	59	1060	78.8	704
	6/2–6	Male	35.0	562	68	1398	97.2	993
	6/21–24	Female	22.3	530	73	1054	102.7	1179
	7/27–30	Male	36.0	–262	51	796	54.2	409
	8/3–6	Male	41.0	150	56	1901	117.3	948
	8/28–31	Female	26.4	250	68	1207	104.1	1099
	9/1–27	Female	20.5	80	57	854	89.0	822
Cold time of the year								
Crashed barley and alfa alfa hay*	1/25–31	Male	36.3	4.8	71	702	47.4	504
	3/4–8	Male	34.5	20	71	699	49.2	521
Steppe herbs **	12/1–4	Female	27.2	–100	56	503	42.3	380

*Feeding in balance cages
** Grazing on natural range

$(BW)^{0.75}$ in winter. Based on regression equation showing relation between saiga weight gain and metabolic energy intake (Fig. 2) an animal uses 10.46 ± 1.70 kJ of metabolic energy per 1 gram of body weight gain in addition to energy expenditure for maintenance. It is important to mention that this value is different for saiga compared to other species. Thus for American elk (*Cervus elaphus*) it varies from 26 to 55 kJ/g depending on sex and season. It is lower than 16 kJ/g only for calves (Simpson *et al.*, 1978; Fennessy *et al.*, 1981; Suttie *et al.*, 1987; Jiang & Hudson 1992).

In wild populations of saiga, weight gain has been recorded only during the warm season (Bannikov *et al.*, 1961; Abaturov *et al.,* 1982). During five warm months (May through September), a yearling animal gains on the average 10 kg, i.e. about 65 g/individual daily (6g/ $kg(BW)^{0.75}$). Based on the equation in Fig. 2, cumulative energy expenditure (for maintenance requirements and growth) is 782 $kJ/kg^{0.75}$. If high quality forage is abundant, growth in body mass is usually more rapid. In our experiment with free ranging saiga antelopes, maximum daily weight gain in June was 530g/individual (51g/kg $(BW)^{0.75}$). In this case daily metabolic energy expenditure according to the equation was as high as 1252 kJ/kg $(BW)^{0.75}$. In August–September daily weight gain of 21 g/kg $(BW)^{0.75}$ required 984 kJ/kg of metabolic energy.

There is no data available on the energy required for daily milk production by saiga antelope. However, according to existing data for domestic sheep (Agricultural research council 1965; McDonald *et al.*, 1969) daily metabolic energy requirement of lactating females during the first 10 days of lactation is close to 1000–1020 kJ/kg $(BW)^{0.75}$. Hence, the energy expenditures for lactation are close to maximum energy costs of weight gain.

The amount of metabolic energy ingestion depends mainly on two parameters: the daily intake of food and on its digestibility. As food consumption is limited and is relatively constant, the amount of metabolic energy intake is affected mainly by digestibility, which depends on the quality of forage and varies over a wide

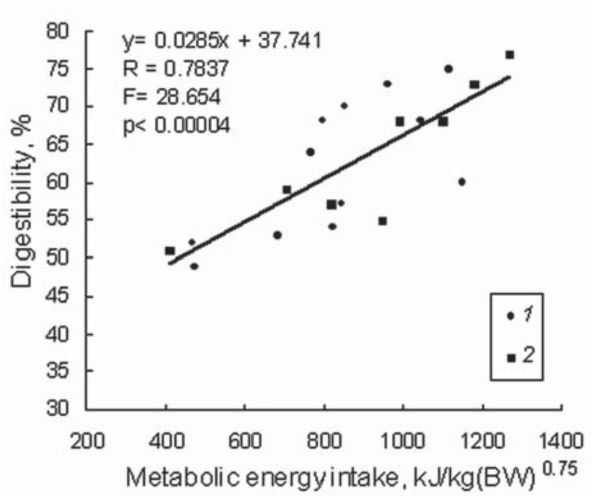

Figure 3. Relationship (y = bx + a) between apparent forage digestibility (% dry matter) and metabolic energy intake (kJ/kg$^{0.75}$ body weight). Data obtained in warm season in experiments with saiga in balance cages (*1*) and free ranging saiga (*2*). (*Agropyron* sp. excluded because its proportion in the ration was considerably lower than normal). Std. Error: a = 4.80, b = 0.005. P-level < 0.0001.

range. Relationship between ration digestibility (y) and metabolic energy intake (x) in our case can be presented in the form of the following regression equation: $y = 0.029\,x + 37.74$ (Fig. 3). According to the equation the maintenance energy requirements presented above (719 kJ/kg (BW)$^{0.75}$ without energy for growth) can be provided only at the forage digestibility level not lower than 59%. This level of digestibility should be considered critical level, providing maintenance level of energy intake and overall positive energy balance for grazing non-breeding animal. To provide for daily weight gain at 6g/kg (BW)$^{0.75}$, which during warm season requires daily metabolic energy intake of 782 kJ/kg (BW)$^{0.75}$, food digestibility should be not lower than 61% according to the above equation.

Higher metabolic energy requirements during lactation (1000–1020 kJ/kg$^{0.75}$) would accordingly require increase in food digestibility up to 67–68%. Thus in our case, the threshold level of forage digestibility for positive energy balance of adult (full grown) non-breeding saiga is 59%, and if growth and lactation energy requirements are included, it is above 61% and 68% respectively.

Provision with protein and threshold concentrations of protein in the forage of saiga antelope

Nitrogen requirements were evaluated using indices of protein consumption and digestibility obtained in our experiments with free ranging animals, and also in three cases of confined animals with feeding to leaves *Lactuca tatarica* and *Ulmus pumila* (Tab. 3). For ranging animals metabolic protein in feces was 4.797 ± 2.65 g /100 g of consumed food (Fig. 4). Consequently for an adult animal, consuming 1200 g of dry matter per day, daily metabolic protein content in feces was 57.6 g/individual or 9.22 g/individual (0.71 g/kg (BW)$^{0.75}$) of metabolic nitrogen. Combined with endogenous urine nitrogen (0.12 g/kg (BW)$^{0.75}$ per day) it amounted to 0.83 g/kg(BW)$^{0.75}$ of nitrogen (5.19 g/kg(BW)$^{0.75}$ of protein), which coincides to minimum daily nitrogen requirements of saiga for maintaining activity during the warm season of the year. These values are close to published estimates of nitrogen requirements (0.41–0.82 g/kg(BW)$^{0.75}$) for other ruminants (Robbins, 1983).

Energy costs of nitrogen for growth and weight gain adult animals are 2.5% per unit of weight gain (Agricultural research council, 1965). Taking into consider-

Table 3. Protein consumption and digestibility for saiga, 1996–2005 (reprinted from Abaturov et al., 1998, 2005).

Type of forage	Date	Content in dry matter, %		Digestibility, %		Daily consumption		
		diet	feces	apparent	true	diet protein,	digestible protein	
						g/anim.	g/anim.	g/kgBW$^{0.75}$
Green herb in diet (free grazing)**	4/12-17	18.4	15.0	81	100	181.4	181.4	19.19
	5/26-29	14.8	15.3	58	90	156.9	141.8	10.50
	6/2-6	14.3	14.6	67	100	199.4	199.4	13.85
	6/20-24	14.2	14.0	73	98	150.0	147.1	14.33
	7/27-30	12.6	14.6	43	81	100.1	81.2	5.52
	8/3-5	12.0	14.4	46	854	228.3	195.1	12.04
	8/28-31	12.7	14.1	65	92	153.3	141.3	12.12
	9/21-26	13.3	15.7	50	76	113.2	85.8	8.92
	12/1-4	13.4	11.2	63	89	67.2	60.0	5.00
*Lactuca tatarica**	8/2-17	17.3	17.8	54	74	130.5	97.1	9.93
Elm leaves*	- " -	10.5	11.0	54	88	110.3	97.2	9.94
	- " -	10.5	9.8	62	96	101.9	97.3	9.95

*Feeding in balance cages

** Grazing on natural range

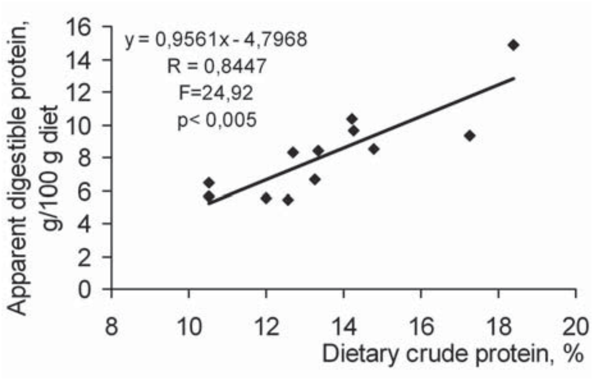

Figure 4. Relationship (y = bx + a) between dietary crude protein content (%) and its apparent digestibility (g/100g feed intake) for saiga. Std. Error: a = 2.65, b = 0.19.

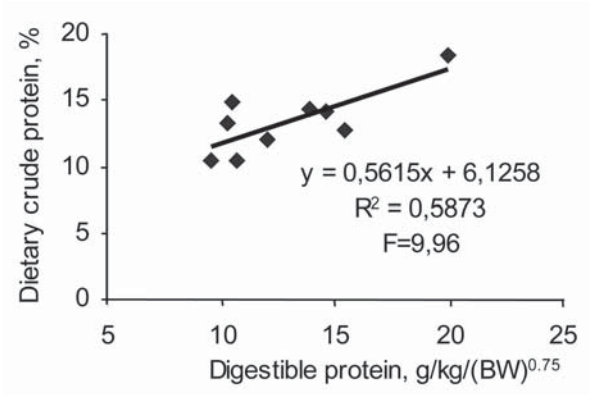

Figure 5. Relationship (y = bx + a) between dietary crude protein content (%) in free ranging saiga ration and daily consumption of digestible protein (g/kg$^{0.75}$ body weight). Std. Error: a = 2.07, b = 0.16.

ation the correction for biological value of dietary nitrogen, according to which only 70% of absorbed nitrogen is used effectively (Agricultural research council 1965; McDonald *et al.*, 1969; Robbins 1983), it is easy to calculate, that gain of 1 g of weight requires 0.0357 g of digestible nitrogen (0.223g protein). In our research when daily weight gain of grazing saiga in June, late August and in September was 530, 250 and 80 g/ind. respectively, cumulative digestible protein requirements for growth/weight gain only were 11.53, 4.80, 1.86 g/kg(BW)$^{0.75}$, and for both growth/weight gain and maintaining normal activity — 16.72, 9.99 and 7.05 g/kg(BW)$^{0.75}$ per day. At daily average weight gain throughout a year equal 65 g/individual, average requirements in digestibility protein should be equal 6.50 g/kg(BW)$^{0.75}$ per day.

During the grazing trials, consumption of crude protein varied from 60 to 199 g/ind. (89 to 117 g/kg$^{0.75}$ body weight) per day and true digestibility of protein was from 74 to 100% (Tab. 3). In this case, correlation between daily digestible protein consumption (x) and dietary protein concentration (y) was fairly high (r = 0.81). It can be presented in the form of regression equation $y = 0.584\,x + 6.172$ (Fig. 5) According to the equation in order to provide a grazing animal with minimum amount of digestible protein (5.19 g/kg$^{0.75}$ body weight) required for maintenance protein concentration in plant forage needs to be not less than 9.2%. This particular value reflects the minimum (threshold) level of protein content in the food, necessary to sustain nitrogen balance of grazing saiga. If other needs (growth, shedding, pregnancy and lactation) are included this level must be higher: in June, when weight gain was up to 530g/ind. per day, daily digestible protein requirements (16.72 g/kg$^{0.75}$ body weight) could be satisfied only at 15.9% protein content in the ration. At the average level of annual weight gain, when requirements are 6.50 g/kg (BW)$^{0.75}$, protein content in the ration is not lower than 9.97%. During lactation period protein requirements increase significantly. During the first weeks of lactation according to data for domestic sheep (Agricultural research council 1965; MacDonald *et al.*, 1969), digestible protein requirements are 14.0 g/kg (BW)$^{0.75}$. In this case protein content in the forage needs to be not less than 14.3%.

Discussion

Our experimental data allow us to estimate minimum thresholds for energy and protein nutrition to support different levels of physiological demand, and to evaluate the sufficiency of various foods or diets based on forage quality parameters (digestibility, protein content) in the context of the saiga antelope's protein and energy demands (Tab. 4).

To provide for maintenance energy requirements (cumulative energy expenditure in a state of repose and during grazing) adult non-breeding animals need plant food with digestibility not lower than 59% and protein content not lower than 9.00%. Growth and reproduction require higher quality forage. To provide for growth, digestibility of forage should be not lower than 61% with protein content >9.80%. For reproduction and lactation, digestibility must be at least 68% with protein content at least 14.00%. These minimum thresholds are similar to those established for European roe deer. For roe deer, minimum estimated food digestibility and protein content for adult non-breeding animals was 60% and 5.5%, respectively, while for young growing animals the minimum digestibility was 75%, and for lactating females even higher (Eisfeld, 1974, 1985). According to our experimental data, nutritional value of most plant species grazed by saiga is lower than these thresholds. For *Kochia prostrata*, even during the peak of vegetation growth (in June), digestibility was only 49–52%, of mixed steppe forbs in May–June was 54% (Tab. 2). Thus, in our energy balance trials with confined animals feeding siaga with these forages in the form of whole-plants led to negative energy balance and weight loss. In contrast, free-grazing tractable animals that were foraging on the same plants species were selecting diets of substantially higher digestibility (60–

Table 4. Threshold parameters of forage quality for minimum energy and protein requirements of saiga antelope.

Componenets of energy and protein budgets	Requirements		Threshold parameters of forage quality	
	Metabolic energy, MJ/kg(BW)$^{0.75}$	Digestible protein, g/kg(BW)$^{0.75}$	Minimum protein content, %	Minimum digestibility, %
Maintenance of energy equilibrium of free existence	0.719	5.19	9.0	59
Maintenance of energy equilibrium of free existence and growth	0.782	6.50	9.8	61
Maintenance of energy equilibrium of free existence and lactation	1.002	14.0	14.0	68

77%) and positive energy balance. The high digestibility of grazed diets can be explained by the selective foraging behavior typical of saiga antelope. Free grazing saigas typically select only the most nutritious plants or parts of plants. For example, when feeding on plants of *Kochia prostrata* or *Galatella villosa,* they typically select tops of sprouts with flower buds or seeds. When feeding on *Limonium gmelinii* or *Salsola laricina*, and similar plants, they typically select for new lateral shoots and young leaves (Abaturov *et al.,* 1998).

It is obvious that these are parts of plants of higher nutrition value, characterized with high digestibility. Thus, in our experiments with free ranging animals when the main portion (60%) of the ration consisted of *Kochia prostrata,* selective grazing of only apex shoots still provided higher digestibility — up to 73% (Abaturov *et al.*, 1998). In the experiments with confined animals in cages, they were fed with whole plants of *Kochia prostrata* and in this case showed lower digestibility value of 51% (Abaturov *et al.*, 1982). The same pattern was observed with other plant species. In the environmental conditions of the pastures investigated, Saiga almost entirely avoided gramineous plants (Abaturov *et al.*, 1982, 1998, 2005). Their digestibility tends to be fairly low, and this explains why grasses are typically an insignificant component in the saiga's diet.

Crude protein is not apparently a nutrient likely to limit most populations of saiga antelope. In areas dominated by semidesert vegetation, where the main part of saiga population range is located, foliage of most plants is characterized by fairly high protein content throughout the year (about 14%) (Abaturov *et al.*, 1998). This is sufficient to meet protein requirements for maintenance, growth, and lactation (Tab. 4). Semidesert vegetation is diverse, includes both typical desert and steppe species, and has high diversity of plant forms including grasses, forbs, sub-shrubs and dwarf sub-shrubs, many of which vegetate all year round. Seasonal differences in phenological development among plants provide animals with green forage with high protein content almost throughout the year. This characteristic of semidesert vegetation sets it apart from other vegetations, particularly from steppe grass formations, which are dominated by grasses and forbs having short synchronous growing seasons. This is also typical of grassland (savanna) plant communities in Africa, where decrease (decline) of protein content in vegetation as low as 4–5% results in nitrogen deficiency in grazing animals (Sinclair, 1974; Arman & Hopcraft, 1975; Berry & Louw, 1982; Stanley Price, 1978; Abaturov *et al.*, 1995). This explains the fact that saiga distribution range is limited to the semidesert vegetation zone with only occasional occurrence of this species in the steppe zone.

It is important to emphasize that the thresholds of food quality estimated here apply only to the warm period of the year. During the cold period saiga, like other ungulates at high latitude, lowers its level of metabolism and forage consumption. Maintenance energy requirements in winter are 1.5 times lower, and maximum consumption (until satiation) of dry plant material is 2.5 times lower than in summer (Abaturov *et al.*, 1998). Therefore thresholds for food quality are different in winter. The quality of food in winter must be equally or even more important for sustaining positive energy balance. Substantial weight loss characteristic of saiga in winter (Bannikov *et al.*, 1961; Abaturov *et al.*, 1982; Lopatin *et al.*, 1987) indicates that energy balance is negative during this period of the year. In winter the energy balance of free ranging animals was negative when forage digestibility was 56% and forage consumption was at its maximum level for the winter period. Maintaining positive energy balance in winter is possible only at very high level of forage nutrition (Abaturov *et al.*, 1998). Indeed, energy balance of confined animals fed a grain and alfalfa hay mix (71% digestibility) was positive (Tab. 2).

Conclusions

Analyses of the state and quality of forage resources and their influence on the saiga population during the warm period of the year showed that only non-growing adult animals could maintain positive energy balance when digestibility of consumed plant material was as low as 59%. At or below this level of forage digestibility, animals cannot grow or accumulate fat. Therefore, providing plant resources above this level of digestibility should be considered critical to reproduction, lactation, and growth and survival of young in wild populations. Forage digestibility at 61% provides for positive energy balance and is sufficient to meet nutritional requirements for growth, but this level of digestibility is still insufficient to provide for reproduction, and particularly for lactation. To provide for all major components of the annual energy budget, including reproduction and lactation, the digestibility of consumed forage must be at least 68%.

To meet the saiga's protein demand for maintenance and growth, the content of digestible protein in forage must be at least 9.8%. Almost all semidesert plants are characterized with even higher content of crude protein throughout the year, and food quality in this relation is almost always above the critical threshold. Only during the lactation period, when protein requirements increase significantly to the critical level of 14.0%, may forage plants contain insufficient protein.

Thus, meet an individual's nutritional demand for growth, maintenance, and reproduction, plant forage digestibility must be at least 68% and forage digestible protein content must be at least 14%. Animals can survive on plants of lower digestibility (59%) and protein content (9.0%). However, diets this low in quality can only support maintenance and are inadequate for growth and lactation.

Given the selectivity of saiga when feeding, we conclude that normally only a portion of pasture plant mass is of necessary quality. This portion is usually not large and includes either single dominant species, or only certain parts of plants (tops, flower buds, inflorescences, new leaves and shoots). Many predominant species (majority of grasses for example) cannot be considered as forage plants of acceptable quality for saigas. Therefore, evaluation of forage availability for animals, and carrying capacity habitat should be based only on that portion of vegetation with digestibility and protein content above threshold levels, not on total standing crop biomass or even on live biomass.

ACKNOWLEDGEMENTS. Authors are very much grateful to Dr. Robert A. Riggs from Wildlife and Range Science of Boise Cascade Corporation for his valuable suggestions and general editing of the manuscript. We also thank Dr. William A. Wall of Sustainability, Inc. for his friendly notes and support of our work. Funding for this research was provided by the Russian Foundation for Basic Research (Grant 09-04-00125).

References

Abaturov B.D. 2007. The population of saiga antelopes in Russia and the Problems of its preservation // Herald of the Russian Academy of Sciences. Vol.77. P.462–469 [Translated from Vestnik Rossiiskoi Akademii Nauk. Vol.77. P.785–793]

Abaturov B.D. & Magomedov M.-R. D. 1988. [Food value and dynamics of food resources as a factor characterizing the state of populations of herbivorous mammals] // Zoologicheskii Zhurnal. Vol.67. No.2. P.223–234 [in Russian, with English summary].

Abaturov B.D., Kholodova M.V. & Subbotin A.E. 1982. [Intensity of food consumption and digestibility in Saiga tatarica] // Zoologicheskii Zhurnal. Vol.61. No.12. P.1870–1881 [in Russian, with English summary].

Abaturov B.D., Fekadu Kassaye, Kuznetsov G.V., Magomedov M.-R.D. & Petelin D.A. 1995. Nutritional estimate of populations of some wild free-ranging African ungulates in grassland (Nechisar national park, Ethiopia) in dry season // Ecography. Vol.8. No.2. P.164–172.

Abaturov B.D., Kolesnikov M.P., Likhnova O.P., Petrishchev B.I. & Nikonova O.A. 1997. [Use of plant forage lignin and silica as digestibility indicators for a quantitative estimation of food consumption by free-ranging saigas] // Russian Journal of Zoology. Vol.1. No.1. P.110–117. [Translated from Zoologicheskii Zhurnal Vol.76. P.104–113]

Abaturov B.D., Petrishchev B.I., Kolesnikov M.P. & Subbotin A.E. 1998. [Seasonal dynamics of forage resources and nutrition of saiga in natural semidesert pasture] // Uspekhi sovremennoy biologii. Vol.118. No.5. P.564–584 [in Russian, with English summary].

Abaturov B.D., Kolesnikov M.P., Nikonova O.A. & Pozdnyakova M.K. 2003. [Experience of quantitative investigation of nutrition in free-ranging mammals in natural habitat] // Zoologicheskii Zhurnal. Vol.82. No.1. P.104–114 [in Russian, with English summary].

Abaturov B.D., Larionov K.O., Kolesnikov M.P. & Nikonova O.A. 2005. [Providing of saigas (*Saiga tatarica*) with forage and their state in pastures with vegetation of different types] // Zoologicheskii Zhurnal. Vol.84. No.3. P.377–390 [in Russian, with English summary].

Anon. 1968. [Instruction for zonal agrochemical laboratories analysis of forage and plants] // Moscow: Izdatel'stvo "Kolos". 55 p. [in Russian].

Arman P. & Hopcraft D. 1975. Nutritional studies on East African herbivores. 1. Digestibilities of dry matter, crude fibre and crude protein in antelope, cattle and sheep // British Journal of Nutrition. Vol.33. P.255–264.

Arnold G.W. 1985. Regulation of forage intake. Bioenergetics of wild herbivores // Hudson, R.Y. & White, R.G. (eds.). Bioenergetics of wild Herbivores. Florida: CRC Press, Inc. Boca Raton. P.81–101.

Bannikov A.G., Zhirnov L.V., Lebedeva L.S. & Fandeev A.A. 1961. [Biology of saiga antelope]. Moscow: Izdatel'stvo literatury, zhurnalov i plakatov. 336 p. [in Russian].

Bell R.H.V., 1971. A grazing ecosystem in the Serengeti // Scientific American. Vol.225. P.86–93.

Berry H.H. & Louw G.N. 1982. Nutritional measurements in a population of free-ranging wildebeest in Etosha National Park // Madoqua. Vol.13. P.101–125.

Bol'shakov A.F. & Bazykina G.S. 1974. [Natural biogeocoenosises and conditions for their existing] // Rode A.A. (ed.). Biogeocoenotic fundaments for the development of Northern Caspian semidesert. Moscow: Nauka. P.6–34 [in Russian].

Cook J.G., Quinlan L.G., Irwin L.L., Bryant L.D., Riggs R.A. & Thomas J.W. 1996. Nutrition-growth relations of elk calves during late summer and fall // Journal of Wildlife Management. Vol.60, No.3. P.528–541.

Eisfeld D. 1974. Protein requirements of roe deer (*Capreolus capreolus* L.) for maintenance // XI Congress of International Union of Game Biologists. No.11. P.133–138.

Eisfeld D. 1985. Anspruche von Rehen an die Qualität ihrer Nahrung // XXII Congress of International Union of Game Biologists. Brussels. P.1027–1034.

Fennessy P.F., Moore G.H. & Gorson I.D. 1981. Energy requirements of red deer // Proceedings of New Zealand Society of Animal Production. Vol.41. P.167–173.

Jiang Z. & Hudson R.J., 1992. Estimating forage intake and energy requirements of free-ranging wapiti (*Cervus elaphus*) // Canadian Journal of Zoology. Vol.70. P.675–679.

Gallup W.D., Hobbs C.S. & Briggs H.M. 1945. The use of silica as a reference substance in digestion trials with ruminants // Journal of Animal Science. Vol.4. P.68-71.

Gordeeva T.K. & Larin I.V. 1965. [Nature vegetation of Caspian semidesert as forage reserve for livestock] // Moscow: Nauka. 160 p.

Hudson R.J. & Christopherson R.J. 1985. Maintenance metabolism // Hudson R.Y. & White R.G. (eds.). Bioenergetics of wild Herbivores. Boca Raton, Florida: CRS Press, Inc. P.121–142.

Kaloshnikov A.P. & Kleimenov N.I. 1985. [Standards and rations of livestock]. Moscow: Agropromizdat [in Russian].

Kolesnikov M.P. & Abaturov B.D. 1997. [Silicon forms in plants and their quantitative determination] // Uspekhi sovremennoi biologii. Vol.117. No 5. P.534–548 [in Russian, with English summary].

Lopatin V.N., Abaturov B.D. & Rossolovskiy S.V. 1987. [Mathematical model of energetic processes of saiga growth] // Zhurnal obshchei biologii. Vol.48. No.4. P.513–524 [in Russian, with English summary].

Magomedov M.-R.D.& Yarovenko Yu.A. 1997. [Intensity of consumption and digestibility of food in East Caucasian Tur (*Capra cylindricornis*)] // Zoologicheskii Zhurnal. Vol.76. No.2. P.243–250 [in Russian, with English summary].

McDonald P., Edwards R.A. & Greenhalgh J.F.D. 1969. Animal nutrition. Edinburgh and London: Oliver & Boid. 479 p.

Mould E.D. & Robbins Ch.T. 1981. Nitrogen metabolism in elk // Journal of Wildlife Management. Vol.45. No.2. P.323–334.

Owen-Smith N. & Cooper S.M. 1989. Nutritional ecology of a browsing ruminant, the kudu (*Tragelaphus strepsiceros*), through the seasonal cycle // Journal of Zoology. London. Vol.219. P.29–43.

Regelin W.L., Schwartz Ch.C. & Franzmann A.W. 1987. Effects of forest succession on nutritional dynamics of moose forage // Swedish Wildlife Research. Supplement. 1. Part. 1. P.247–263.

Robbins Ch.T., Prior R.L., Moen A.N. & Visec W.J. 1974. Nitrogen metabolism of white-tailed deer // Journal of Animal Science. Vol.38. No.1. P.186–191.

Robbins, Ch.T. 1983. Wildlife feeding and nutrition. N.Y.Æ Academic press. 343 p.

[Ruminants' requirements in nutrients and energy]. 1968. // Izdatel'stvo Kolos, Moscow. 414 pp. [in Russian]. Translated from Agricultural Research Council. 1965. The nutrient requirements of farm livestock. No.2. Ruminants, Technical reviews and summaries. London: H.M. Stationery Office.

Schwartz Ch.C., Regelin W.L. & Franzmann A.W. 1987. Protein digestion in moose // Journal of Wildlife Management. Vol.51. No.2. P.352–357.

Simpson A.M., Webster A.J.F., Smith J.S. & Simpson C.A. 1978. The efficiency of utilization of dietary energy for growth in sheep (*Ovis aries*) and red deer (*Cervus elaphus*) // Comparative Biochemistry and Physiology. Vol.69. P.1166–1175.

Sinclair A.R.E. 1974. The natural regulation of buffalo populations in East Africa. IV. The food supply as a regulating factor, and competition // East African Wildlife Journal. Vol.12. P.291–311.

Sinclair A.R.E., Fryxell J.M. & Caughley G. (eds.). 2006. Wildlife ecology, conservation and management. Oxford: Blackwell Publishing. 469 p.

Sinclair A.R.E., Krebs C.I. & Smith T.N.M. 1982. Diet quality and food limitation in herbivores: the case of the snowshoe hare // Canadian Journal of Zoology. Vol.60. P.889–897.

Smith S.H., Holter J.B., Hayes H.H. & Silver H. 1975. Protein requirement of white-tailed deer fawns // Journal of Wildlife Management. Vol.39. No.3. P.582–589.

Stanley Price M.R. 1978. The nutritional ecology of coce's hartebeest (*Alcelaphus buselaphus cocei*) in Kenya // Journal of Applied Ecology. Vol.15. P.33–49.

Streeter C.L. 1969. A review of techniques used to estimate the in vivo digestibility of grazed forage // Journal of Animal Science. Vol.29. P.757–768.

Suttie J.M., Fennessy P.F., Veenvliet B.A., Littlejohn R.P., Fisher M.W., Corson I.D. & Labes R.E. 1987. Energy nutrition of young red deer (*Cervus elaphus*) hinds and a comparison with young stags // Proceedings of New Zealand Society of Animal Production. Vol.47. P.111–114.