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ECOLOGY

Forage Availability to Saigas (*Saiga tatarica*) and Their State on Steppe Pastures with a Different Ratio of Graminoid Plants and Forbs

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Abstract—An interfaced analysis of change of forage vegetation, nutrition of saigas (*Saiga tatarica*), and their state in the steppe regions of Russia is performed. It is noted that the percent of graminoids has increased considerably and the proportion of forbs has decreased in the vegetation of current pastures, which has had a negative impact on the nutrition and state of saigas. It is shown that the lower nutritional value of graminoids has caused a decrease in the digestibility of forage used by saigas and does not provide the physiological requirements of the animals. It is established that modern steppe pastures, where gramineous communities prevail, are of little use or absolutely unsuitable for the stable existence of saiga populations. Only separate dwelling places with an abundance of forbs continue to provide adequate nutrition for saigas and well-being for their local groupings.

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INTRODUCTION

Modern climatic changes and the reduction of anthropogenic pasture impact in the steppe regions of Russia and Kazakhstan have caused drastic changes in the plant cover, which have been expressed in mesophytization of vegetation, as well as in domination of graminoids in plant communities, and, generally, in steppification of subarid and arid regions (Myalo and Levit, 1996; Zolotokrylin, 2003; Neronov and Chabovskii, 2003; Novikova et al., 2004, 2010; Zolotokrylin and Vinogradova, 2007; Larionov et al., 2008; Dzapova et al., 2013). These transformations resulted in the absolute domination of graminoids and the visible reduction of participation of forbs (in our case, grass and subshrub species, except for graminoids and sedges) in the vegetation of steppe zones by the late 1990s. It seems likely that such a radical transformation of the plant cover has had a negative impact on the forage quality of pasture vegetation and nutrition, as well as on forage availability and the state of herbivorous animal populations. Forbs are considered to surpass graminoids in nutritive value; in particular, the leaves of most of pasture forbs species are richer in the content of proteins and, in general, in the diversity of nutrients synthesized in the plant, compared with gramineous plants. Moreover, the majority of graminoids are characterized by a lower digestibility due to the high concentration of lignin and silica in their plant tissues (cell walls), which restrict digestibility efficiency and perform protective functions in pasture plants in relation to their consumers (Van Soest and Jones, 1968; Holechek, 1984; McNaughton et al., 1985; Kolesnikov and Abaturov, 1997; Abaturov, 2005; Massey and Hartley, 2006; Massey et al., 2007).

Nonetheless, the reaction of the pasture mammals themselves to the above-mentioned vegetation transformations remains unclear. It is only known that mammals with a different morphology of the digestive system do not react to gramineous and forb forages in the same way. Horses, which are characterized by hindgut fermentation of consumed forage eat rough forage plants successfully and even prefer them, including graminoids. Forbs are more attractive for ruminant ungulates with complex four-chamber stomach (Hofmann, 1991; Menard et al., 2002; Pozdnyakova et al., 2011). Thus, it has long been observed that feather grasses, which are one of the most widespread steppe graminoids, are better eaten by horses, less eaten by sheep and cattle, and they are eaten to the least extent by camels (Larin et al., 1950). It is apparent that the latter category also includes saigas, which have always avoided eating not only feather grasses, but also any other graminoids in experiments based on feeding with a set of different species of plants, as well as in field experiments with a free range (Abaturov et al., 1982, 1998, 2005). The different reaction of animals to forbs and gramineous forage plants is also confirmed by recent materials on earlier era mammal nutrition. According to these data, the gradual decay and extinction of rich Pleistocene megafauna (mam-

moths, rhinoceroses, bison, etc.) took place due to a change from forbs vegetation of ice–age tundra–steppe pastures to the less nutritious gramineous vegetation after glacier melting (Willerslev et al., 2014).

It is important to assess the reaction of phytivorous mammals and, in particular, saigas (*Saiga tatarica*), i.e., the typical dwellers of steppe and desert regions, to the modern transformation of the plant cover of steppes. It is noteworthy that the above-mentioned transformation of the steppe vegetation coincided with a deep depression of saiga populations with respect to time and scale, which also started in the 1990s throughout the steppe and semidesert zone and has been continuing for the past two decades over almost the entire area inhabited by saiga. This depression is traditionally explained by poaching, which increased in the same years (Milner-Gulland et al., 2001). It is clear that the given changes of the natural environment which, along with poaching, have an influence on the present number of saigas, should also be noted when identifying the reasons for such a long-term depression. However, the role of this factor has not yet been assessed.

The purpose of the study is to find out the extent of the influence of the present transformation of vegetation of steppe regions on nutrition peculiarities and state of saigas inhabiting these regions.

FRACTION OF GRAMINOIDS AND FORBS IN PASTURE VEGETATION AND IN THE DIET COMPOSITION OF SAIGA

Let us compare the nutrition and the state of the saiga population in pasture ecosystems with the different participation of forbs and graminoids in the plant cover from the example of saigas of the northern part of the Caspian Lowland. It is the change of forbs into gramineous communities that expressed the modern massive change of the plant cover of this region in the most visible form. It should be recalled that the Northern Caspian region is the traditional dwelling place for saigas for the whole observable period. In the second half of the 20th century, the number of saigas in this region, as well as on their whole dwelling area, was high (*Saigak*, 1998; Lindeman et al., 2005; Bliznyuk, 2009), but in the late 1990s, a catastrophic recession took place. The number of animals decreased approximately from 200000 to 15000 individuals in 1998–1999 in the northwestern Pre-Caspian area alone (Kalmykia) (Bukreeva, 2005). Currently, it remains on the same level or has even decreased. The same is characteristic of almost the entire area including the steppes and deserts of Kazakhstan, the southeast of the European part of Russia, and partially Uzbekistan and Turkmen. It was during this period that the massive change from pasture forbs to gramineous vegetation communities took place in the steppe part of the saiga range.

The materials of the research on the forage resources, nutrition, and state of the saiga population in the Northern Caspian region, which has been conducted by us from 1996 to the present, are used for comparison. Note that we made an interfaced assessment concerning the state (species composition and aboveground mass) of the pasture vegetation, as well as the composition of the diet and digestibility of the forage consumed by the saigas, and the state (body weight dynamics) of the individuals in the population (Abaturov et al., 1998, 2005; Larionov et al., 2008). The composition and state of vegetation on the pasture were assessed by consideration of the aboveground phytomass on standard travelled areas; the composition of plants eaten by saigas, as well as their ratio in their diet, was determined using microhistological cuticular analysis residues of plants in feces., as well as direct visual count of plants bites by tame saigas during their free range. The digestibility of the diet was determined using an indirect method based on the ratio of indigestible natural markers in the consumed forage (in the diet) and feces, i.e., lignin and organogenic silicon (Abaturov et al., 2003).

The northern part of the Caspian Lowland is an area of dry steppes and deserts. Xerophytic-forb communities (*Kochia prostrate*, *Tanacetum achilleifolium*, *Artemisia pauciflora*, *A. lerchiana*, etc.) were a zonal type of vegetation on its major area until the 1990s, including a significant participation of steppe graminoids: wheat grasses, feather grasses, fescue, etc. (*Stipa* spp., *Festuca valesiaca*, *Agropyron pectiniforme*, *A. fragile*, *A. desertorum*, etc.) (Dzapova, 2008). The range of phytivorous mammals played an important role in the formation of vegetation, as a result of which ruderal annual plants (*Ceratocarpus arenarius, Descurainia sophia*, *Lepidium perfoliatum*, *Bassia sedoides*, etc.) were important in vegetation communities.

At that time, forbs constantly prevailed among phytocenoses. As early as in the mid 1990s (1996), the forbs accounted for more than 60% of aboveground the phytomass in the lowlands of Northern Caspian region, the percentage of gramineous plants did not exceed 40% (Fig. 1).

As noted above, by the end of the 1990s, vegetation had transformation which was expressed in the expansion and absolute domination of gramineous communities in the plant cover. From 1983 to 2012, numerous forb communities in the plant cover of Kalmykia pastures, which mainly included wormwoods (*A. lerchiana* and *A. pauciflora*), leban (*Kochia prostrata*), and other plants, were changed by gramineous plants: feather grasses (*Stipa* spp.), wheat grasses (*A. fragile*), ephemeral plants (*Poa bulbosa*,), and annual plants (*Anisantha tectorum* and *Eragrostis minor*) (Dzapova et al., 2013). According to our data, the weight percentage of graminoids in the vegetation of the Black Lands of Kalmykia exceeded 90% in 2006 and 2007, while forbs accounted for less than 10% for the most of the year (Fig. 1). Therefore, the change in vegetation

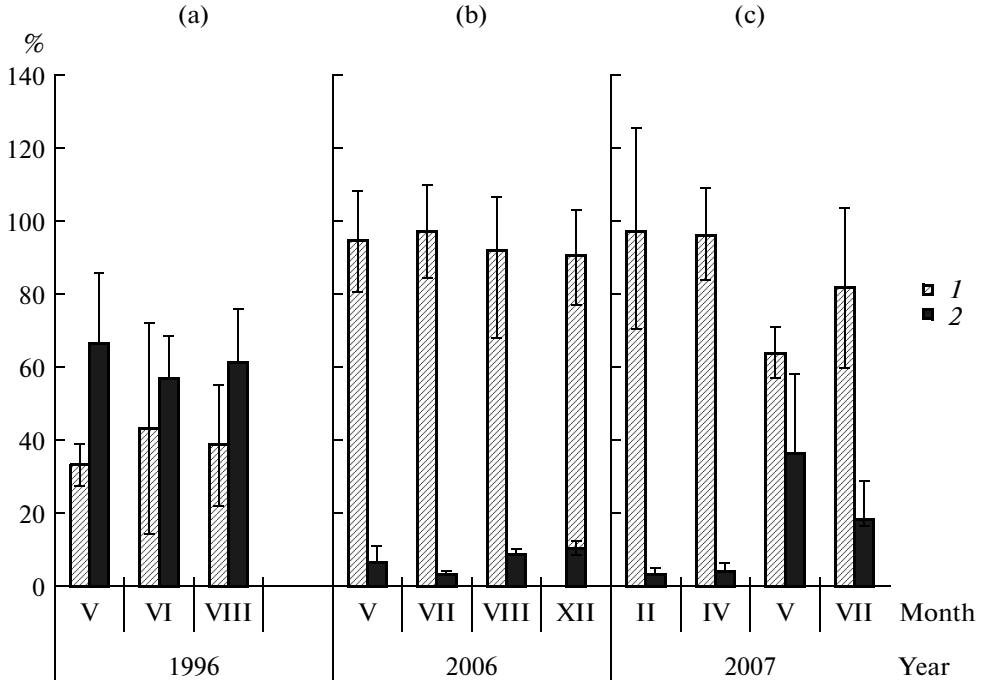

Fig. 1. The percentage (%) of graminoids (*1*) and forbs (*2*) in the aboveground phytomass of the pastures of the semidesert in the Northern Caspian region (a), the Black Lands of Kalmykia (b, c) (Abaturov et al., 1998; Larionov et al., 2008).

caused a sharp reduction in the volume of forbs in the phytocenosis that is preferred by saigas, as well as an increase of the percent of graminoids in it, including feather grass, which have lower nutritional value (Larionov et al., 2008).

The change in the aboveground phytomass composition had an influence on the nutrition of grazing saigas. By assessing the selectivity of nutrition during feeding, the tame captive saigas and using the direct visual counting of plants eaten in the field experiments with the grazing tame saigas, we established that, if there was a choice, saigas ate mainly forb species, generally pigweeds (*K. prostrate*, *Salsola laricina*, and *C. arenarius*), composite flowers (*Galatella tatarica* and *G. villosa, Artemisia* spp.), legumes (*Medicago romanica*), and almost never used graminoids (Abaturov et al., 1982, 1998, 2005).

Indeed, the saiga diet on the plain dry steppe zone of the Caspian Lowland included mainly forbs in the past (1996), i.e., until the change in vegetation communities (Fig. 2). In that case, the percentage of graminoids in the diet was extremely low and did not exceed 2% during the entire warm period.

Quite a different pattern was observed after the transformation of pasture vegetation. The change in xerophytic subshrub vegetation in the Pre-Caspian Lowland plains to communities where graminoids prevailed resulted in a sharp change in the composition of plants eaten, as occurred, for example, in the pastures of the Black Lands of Kalmykia in 2006–2007, where graminoids prevailed in the composition of the saiga diet, in almost all seasons (Fig. 2). Their percentage in the diet, as a rule, was more than 50% and reached 70% in some seasons. It should be noted that, notwithstanding the extremely low participation of forbs in the aboveground phytomass of these pastures (<10%, Fig. 1), its percentage in the diet was only slightly smaller than that of graminoids and varied from 27 to 42% in different seasons. This indicates a high forage selectivity of saigas.

It is indicative that in the vast lacustrine–halophytic Aralsor basin, where the vegetation communities with dominance of forb wormwood–halophytic communities is widespread up to the present day, as distinguished from the surrounding plain areas, forbs prevail in the composition of the diet of the wild saiga population, which lives free here (>90%), and the percentage of graminoids does not exceed 15% (Fig. 2).

Therefore, when choosing forage, saigas give an obvious preference to forbs. When there is a choice, they exclude consumption of graminoids almost completely. They have to eat graminoids only if there is a strong domination of them in the pasture vegetation.

DIGESTIBILITY OF CONSUMED FORAGE AND VITALITY OF THE ANIMALS

As noted above, the differences in preferring forbs and graminoids are due to the different nutritional value of the both. Forb species are distinguished by a richer biochemical composition and high nutritional content, particularly the content of nitrogen com-

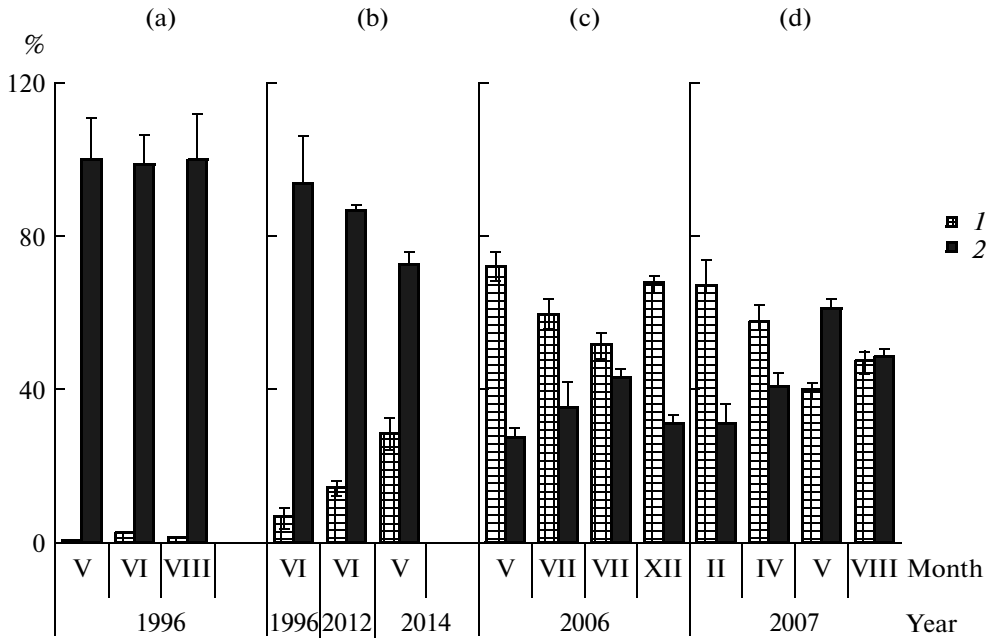

Fig. 2. Percentage (%) of graminads (*1*) and forbs (*2*) included in the saiga diet on the pastures of the semidesert in the Northern Caspian region (a), the Aralsor lacustrine–halophytic lowland (b), and the Black Lands of Kalmykia (c, d) (Abaturov et al., 1998; Larionov et al., 2008).

pounds (proteins). At the same time, graminoid leaves are characterized by an increased mechanical strength of tissues (sclerenchymas) and cell walls, which is due to the high content of lignin and silica saturating the cell wall and the mechanical tissues. The increased strength of the mechanical tissue impacts the digestion of ruminants in which the functioning of the four-chamber stomach requires maximum grinding of plant tissue, as well as additional time and energy for its chewing. In turn, the incrustation of the cell wall using silicon and lignin for strengthening restricts the availability of the cell contents and reduces the digestibility of the consumed forage. This is fully reflected in the efficiency of saiga nutrition; the direct dependence of the digestibility of consumed forage on the content of silicon in it is observed (Fig. 3).

Digestibility is the most important forage parameter of vegetation, on which the energy and material balances of the organism depend. There is a digestibility threshold below which the material and energy needs of the organism are not satisfied even in case of the maximum consumption of forage. Indeed, the assessment of the relation between saiga diet digestibility and daily body weight gains, which reflect animal energy balance, showed that they have this threshold when the forage digestibility coefficient is 56–59% (Fig. 4). However, such digestibility provides only the maintenance level of energy balance. With a lower digestibility, animal needs in forage are not satisfied, which is expressed in body weight losses in the given case.

The use of organism energy for other physiological needs (growth, molt, pregnancy, and lactation) increase significantly the requirements for the quality of forage (Abaturov, 1999; Abaturov and Subbotin, 2011). Plants with a digestibility of at least 61% is required for growth. During lactation, the positive energy balance is only reached in case of a high quality of forage with 68–69% digestibility.

It is clear that the forage quality of vegetation, as well as providing saigas with adequate nutrition and, in general, the suitability of the pasture for saigas, depends on the ratio of forbs included in the pasture vegetation and characterized by increased digestibility and graminoids with a low nutritional value inherent in them. Indeed, saigas that dwelled until recently on the lowland pastures of the Northern Caspian region with a domination of forbs, had a high digestibility coefficient of forages eaten by them, being 65–73% (Fig. 5). At that time, the saigas were provided with high-quality pasture forage meeting all organism physiological needs.

Quite a different pattern is observed in the modern pastures of the Northern Caspian region where gramineous vegetation communities prevail. The saigas dwelling on the pastures of the Black Lands of Kalmykia with domination of gramineous vegetations communities have to use mainly graminoids, i.e., forage with a lower nutritional value giving the forage diet a digestibility coefficient significantly lower than 60% almost in all seasons (Fig. 5). Such digestibility meets only the maintenance level of the energy balance and

does not reach the level that is necessary to provide for the main physiological functions (growth, reproduction, molt, etc.) and, therefore, cannot provide normal vitality for the population to a full extent.

It is important to note that a high level of provision with qualitative forage is characteristic of the modern grouping of saigas in the Aralsor lacustrine–halophytic basin. Here, forage digestibility is maintained at a high level (65–68%), which satisfies the main needs of the organism (Fig. 5). Under these conditions, saigas are in a viable state and maintain a high number. It becomes clear why it is on this geomorphologically restricted area where there is a constant local saiga grouping which is stable in number and survives even in the periods of deep depressions of the species (Bekenov and Grachev, 1998).

COMPARATIVE FORAGE SUITABILITY OF FORB AND GRAMINEOUS PASTURES

These data indicate the negative impact of the modern transformation of vegetation on saiga provision with adequate nutrition, which is due to the low nutritional value of graminoids that changed forbs in the steppe pastures. It is known that semidesert and dry steppe biotopes with domination of xerophytic dwarf semishrubs and forbs are mainly suitable for saiga habitation (Afanas'ev, 1960; Sludskii, 1963). The experimental range of saigas on the area with prevailing feather grass (*Stipa capillata*) was accompanied by losses of their body weight (240 g/individual per day), while positive weight dynamics was always observed in the forb pasture (Abaturov et al., 2005). Saigas avoid bunchgrass steppes communities, which are only used by them in spring and early summer, when forbs vegetate abundantly in these communities. The areas disturbed by human activity are also attractive for saigas: deposits, pastures, and outlets with prevailing weed ruderal vegetation (Lindeman et al., 2005; Abaturov, 2013). The modern general change of the arid subshrub plant cover, caused by climatic and anthropogenic factors, for steppe gramineous communities resulted in the above-described degradation of the forage quality of steppe and semidesert pastures, which obviously has become one of the most important reasons for the still continuing depressed state of the saiga population.

Apparently, the negative reaction to gramineous forage is a widespread phenomenon among many species of herbivorous mammals. In a special experiment with comparative grazing of horses and sheep on a feather–wormwood pasture in Kazakhstan, the range of sheep, similarly to the above-mentioned experiment with saigas, was accompanied by a loss of animal body weight (Madiev, 1973). The sheep ate feather grass less well than the horses did, and, after the wormwood was eaten on the pasture, they quickly lost their body weight (107–126 g/individual per day). This experiment showed that the steppe habitats with domination of graminoids, such as feather grasses, have low suitability for constant habitation even by ruminants that are well-adapted to roughage, such as sheep.

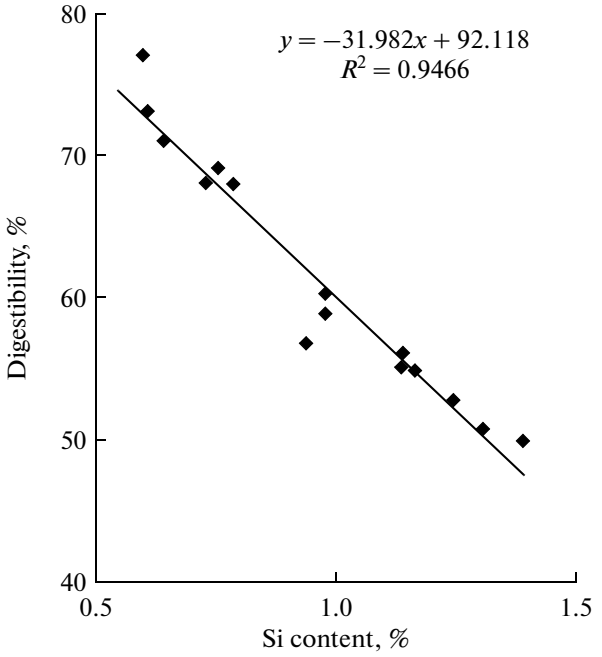

Fig. 3. Dependence of digestibility of eaten forage on the content of organogenic silicon in the diet of free-ranging saigas (Abaturov, 2005).

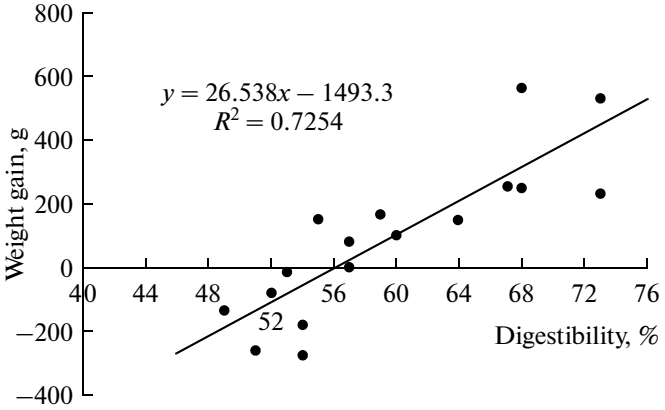

Fig. 4. Dependence of the daily weight gain of the saiga body on the digestibility of forage consumed (Abaturov and Subbotin, 2011).

It is noteworthy that, according to the recent research results, a similar reaction to the same change in the composition of pasture vegetation was inherent in the extinct representatives of Pleistocene megafauna in the arctic area of the Earth (Willerslev et al., 2014).

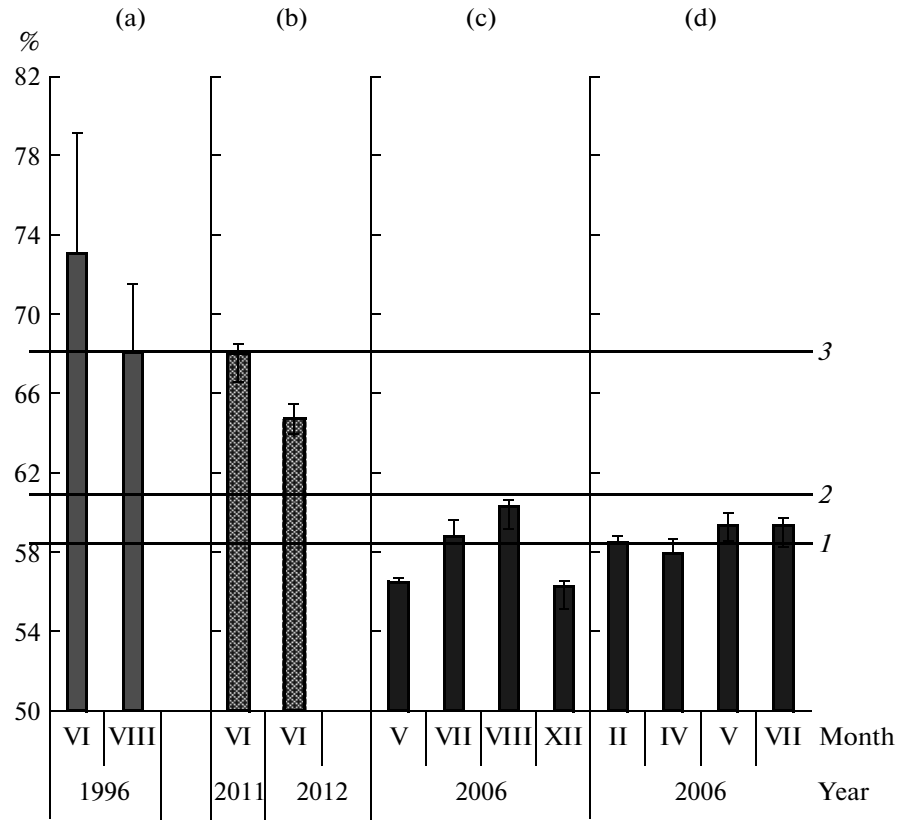

Fig. 5. Threshold levels of forage digestibility (*1–3*) providing the physiological needs of saigas, and actual digestibility (%) of the forage consumed by saigas on the pastures of the semidesert in the Northern Caspian region (a), the Aralsor lacustrine–halophytic lowland (b), and the Black Lands of Kalmykia (c, d). (*1*) Life maintaining; (*2*) growth; (*3*) lactation (Larionov et al., 2008; Abaturov and Subbotin, 2011).

A detailed analysis of the dynamics of plant cover for the last fifty thousand years, performed by the authors of this study, showed that the replacement of steppe tundra forb pastures, which are rich in species during the ice ages of the Pleistocene, by gramineous pastures with a low level of species diversity after deglaciation caused a gradual decay and extinction of the Pleistocene megafauna population: mammoth, woolly rhinoceros, and bison. The gramineous vegetation which replaced high-nutrient tundra–steppe forbs during the wet postglacial period did not provide adequate nutrition for these animals. As a result, the pastures became unsuitable for their stable habitation.

Therefore, at the end of the 20th century and at the beginning of the 21st century, under the impact of anthropogenic (the reduction of grazing) and climatic factors, as well as steppe fires which became common, the replacement of forb vegetation communities by gramineous plants in the steppe pastures within the main habitation area of saigas decreased significantly the availability of nutritious forage for the animals, had a negative impact on the vitality of saigas, and made these areas unsuitable or barely suitable for their stable habitation. Most likely, along with poaching rising during the same years, this caused a catastrophic decrease in the number of animals, as well as the continuing present depression of the population, which was reflected particularly sharply in the Russian part of the population in the northwestern regions of the Pre-Caspian Lowland (the Volgograd region and the Astrakhan region, Kalmykia).

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