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ECOLOGY

# Phytomass Utilization and Deposition of Feces by Ungulates on Steppe Pastures of Eastern Mongolia

**B. D. Abaturov[a], I. A. Dmitriev[a], L. Jargalsaikhan[b], K. Z. Omarov[c]**

[a]*Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Leninskii pr. 33, Moscow, 119071 Russia*

[b]*Institute of Botany, Mongolian Academy of Sciences, Jukovyn Gudamzh 53, Ulaanbaatar, 210351 Mongolia*

[c]*Caspian Institute of Biological Resources, Russian Academy of Sciences, ul. Gadzhieva 45, Makhachkala, 367025, Russia*

*e-mail: abaturov@sevin.ru*

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**Abstract**—The amount of phytomass removed by a complex of livestock (horses, cattle, sheep, and goats) and wild ungulates (Mongolian gazelle *Procapra gutturosa* Pall.) grazing in plain and mountain pastures of eastern Mongolia has been estimated by taking account of feces deposited by these animals. The results show that at an animal density of up to 30 head/km$^2$, the total annual amount of feces reaches 140 kg/ha (dry weight), with the greater part (up to 90 kg/ha) being deposited by horses. The contribution of Mongolian gazelles in some pastures reaches 20-40 kg/ha per year. Decomposition of feces proceeds very slowly, with the annual loss of their weight averaging only 9–12%. This is evidence for gradual accumulation of nondecomposed matter in the soil. The removal of phytomass by the complex of ungulates, calculated from the amount of feces with regard to their annual loss and forage digestibility, varies in different grazing areas from 240 to 400 kg/ha (25–60% of the total aboveground phytomass). The greatest amount of phytomass is utilized by horses, reaching 200 kg/ha (13%), and Mongolian gazelles utilize up to 86 kg/ha per year. In the growing season, ungulates remove no more than 11–16% of the total aboveground phytomass. It is concluded that the impact of total ungulate stock does not impair the productivity of vegetation in the pastures studied.

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## INTRODUCTION

To understand specific features of steppe ecosystem functioning and estimate the state and productivity of their vegetation under the grazing impact of livestock and wild ungulates, it is necessary to know the degree of trophic load on the vegetation and, primarily, the amount of phytomass removed by these animals. Otherwise, it is impossible to determine the real productivity of vegetation in pastures, their carrying capacity, and the potential (acceptable) animal population density. However, the quantitative assessment of trophic phytomass removal is a difficult task, as no methods used for this purpose can be regarded as absolutely reliable.

In particular, the phytomass utilized by animals is determined from the amount of feces (undigested plant remains) excreted by them. This method was successfully used for the first time to estimate forage consumption by moose in the Lapland Nature Reserve (Semenov-Tyan-Shanskii, 1948). Later, it was applied in studies on phytomass consumption by moose populations in taiga forests, and by saigas and horses in steppes of Kazakhstan and the Kalmyk Republic (Kuznetsov, 1975, 1976, 2002; Abaturov, 1984). It is also important that this method allows the daily ration (food consumption) of one animal to be determined by taking account of feces excreted per day (Semenov-Tyan-Shanskii, 1948; Kaz'min and Smirnov, 1992; Abaturov et al., 1995, 2003).

The results presented below were obtained in the course of long-term stationary studies on deposition of feces by a complex of livestock and wild ungulates grazing in steppe pastures of eastern Mongolia. Their purpose was to estimate phytomass utilization by grazing ungulates and their trophic impact on forage stocks in different types of habitats and in different seasons, to compare the patterns of phytomass removal by different species, and to reveal natural mechanisms limiting the consumption of vegetation by grazing animals.

## MATERIALS AND METHODS

**Study region and environmental conditions**. Studies were performed at the Tumentsogt Steppe Research Station of the Joint Russian–Mongolian Complex Biological Expedition between 2002 and 2006. The station is in the Tumentsogt somon (district) of the Sukhbaatar aimag (province), in the zone of typical steppes of eastern Mongolia. The main economic activity in the region is livestock raising, but part of its area has a protective status and is not exposed to grazing pressure.

Four stationary test sites were located in an area with a radius of about 100 km. They were chosen so as to reflect natural and economic diversity of the study region and had the following specific features:

(1) The Talyn Shand site (47°41′ N, 112°24′ E), an intermontane steppe valley with elevations of 920–970 m a.s.l. The level of economic activity (open-range livestock raising) is medium. As the site is within 15 km from the administrative center of the Tomentsogt somon, it is exposed to relatively strong anthropogenic influence (unrelated to grazing). Livestock population density varies within the range of 23–25 head/km$^2$.

(2) The Toson Khulstai site (48°03′ N, 112°33′ E), a hilly steppe plain with elevations of 995–1070 m a.s.l. in the western part of the Toson Khulstai State Nature Reserve. As the site has the status of a specially protected nature area (SPNA), there is no economic activity except for illicit livestock grazing.

(3) The Zaan Shiree site (47°12′ N, 111°41′ E), mountain steppe near the Zaan Shiree volcanic summit with elevations of 1240–1300 m a.s.l. Economic activity (livestock grazing) is higher than in other sites, since it concentrates around the spring and the sole water well in the area. Livestock population density reaches 33 head/km$^2$. Within this area, we distinguished two groups of biotopes that were studied as separate sites: year-round pastures in the area with markedly broken topography (Zaan Shiree-1) and hayfields and winter pastures in relatively flat terrain (Zaan Shiree-2).

(4) The Bayan Khuree site (47°27′ N, 111°24′ E), the hilly undulating steppe near the Kerulen River valley, with average elevations of about 1110 m a.s.l. There are no permanent watering places, and economic activity is virtually absent. On rare occasions, free-ranging herds of horses graze in this area.

Permanent components of livestock in the study region are sheep, cattle, horses, and camels. Wild ungulates are represented by the Mongolian gazelle *Procapra gutturosa* Pall. Livestock population density was calculated on the basis of official statistical data on the numbers of animals and pasture areas in the administrative regions (somons) in which the test sites were located. In the Zaan Shiree site, it was also determined directly, from the actual numbers of animals and pasture areas used by them. The population density of Mongolian gazelles was determined by automobile route census within a 2 km strip (1 km on each side) followed by calculations of the area surveyed and the number of animals per unit area.

**An account of feces** deposited by each livestock species and gazelles per unit time (month or year) was taken in permanent plots established in each test site and thoroughly cleaned of older feces prior to the onset of our study (in September 2002). Their size varied from 100 to 2500 m$^2$. It was empirically estimated that, under local conditions, the optimal size providing for the occurrence of feces of all these species within each plot was 625 m$^2$ ($25 \times 25$ m). Over the study period, we collected and processed data on feces deposition in 20 plots with a total area of 9650 m$^2$.

The plots were surveyed once a month during the warm season (June–August). This allowed us to take account of feces deposited in different periods of the annual cycle, i.e., in the ten-month period conventionally designated as the winter grazing period; each month in summer, during the growing season (July and August); and throughout the annual cycle, from June of the previous year (the onset of active plant growth) to June of the current year.

Feces collected in the plots were weighed in an air-dry state. Aliquots of these samples were dried to a constant weight at 80–90°C, which allowed recalculation of air-dry weight to absolutely dry weight. This recalculation was subsequently performed using a factor of 7.2 reflecting moisture content in air-dry feces.

**Weight loss by deposited feces** under the combined effect of biotic and abiotic factors and, separately, their consumption by coprophages was estimated over the annual cycle. To this end, samples of fresh feces of Mongolian gazelles, horses, and cattle were exposed in a fenced area inaccessible to ungulates. The absolutely dry weight of each sample was determined as described above. In September 2002 and 2003, 13 samples of gazelle feces, 7 samples of horse feces, and 6 samples of cattle feces were exposed in this way. The samples were repeatedly weighed every following year in early June, to estimate weight loss over the winter–spring season, as well as at exactly one-year intervals (in August–September), to estimate total losses over the annual cycle. All calculations were made as per absolutely dry weight.

Losses of feces under effect of consumption by coprophages in the warm season were estimated by means of repeated weighing. Several piles of freshly deposited horse feces (about 10 piles) were weighed in place, and their aliquots were taken to determine their moisture content and absolutely dry weight. Subsequently, observations on their colonization by coprophages were performed. After a certain period of time (usually 10–15 days), when every pile dried up and remain “conserved” in this state, they were weighed again, with the results being recalculated per air dry weight. The difference between the results of the first and second weight measurements was regarded as the loss of feces to coprophages. Simultaneously, observations on colonization by coprophages of gazelle, sheep, goat, and cattle feces were performed.

On the basis of all these data, we calculated a coefficient for determining the weight of feces deposited during a certain period with account of its loss due to biotic and abiotic factors.

**Characteristics of vegetation in the plots** were determined simultaneously with taking inventory of feces. To this end, a complete geobotanical description was made (species composition, abundance, coverage, etc.) and phytomass stock was estimated by the hayharvesting method in 1 $m^2$ squares. The harvest was sorted into the green phytomass by species groups (grasses, sedges, legumes, shrubs, mixed herbs, and wormwood) and the necromass. The resulting fractions were dried in a thermostat to the absolutely dry state and weighed.

**Amount of phytomass removed by grazing**. Phytomass consumption by each animal species ($C$, kg/ha dry weight) over a certain period was calculated by the formula

$$C = F \times K \times 100/(100 - D),$$

where $F$ is the amount of feces deposited by the animal over this period, kg/ha dry weight; $K$ is the coefficient of weight loss due to biotic and abiotic factors over the period of their accumulation ($K$ for the period of summer feeding is 1.0); and $D$ is the coefficient of phytomass digestibility, %. It should be noted that this formula is applicable only to the animals that graze in the open throughout the year (in our case, gazelles and horses). For the animals kept in pens for part of the day (cattle, sheep and goats), we used a more complex formula:

$$C = F \times K \times 100/[(100 - D)\, T \times 0.8],$$

where $T$ is the coefficient of grazing time budget (the factor 0.8 is used only for cattle in the winter feeding season). Coefficient $T$ was introduced because the feces that these animals left in pens could not be taken into account. On the basis of information on seasonal features of grazing and the pattern of pasture use by different kinds of livestock, which was obtained from local livestock keepers, this coefficient for sheep and goats was taken to be 2.0 in the winter feeding season and 1.5 in the summer season. Cattle have the same grazing pattern in winter, but they additionally receive hay, which accounts for approximately 20% of their daily ration. Hence, the above factor (0.8) was introduced in the formula for their winter feeding. In summer, coefficient $T$ for cattle is 1.0, as they graze virtually all day round. For horses and gazelle, $T = 1.0$ in all seasons, since they range freely on their grazing grounds all day round throughout the year.

Parameters of steppe vegetation digestibility by livestock were taken from the literature (Tomme et al., 1953, 1970), and these parameters for Mongolian gazelles were inferred from available data on saigas (Abaturov et al., 2005). Eventually, the values of digestibility coefficient $D$ used for calculations were as follows: Mongolian gazelle, $D = 62\%$; horse, $D = 50\%$; and cattle, sheep, and goats, $D = 60\%$.

**Proportion of phytomass removed by grazing**. For the summer feeding period, this proportion ($P$, %) was calculated by the formula

$$P = 100C/(M + C),$$

where $M$ is the total aboveground phytomass measured in the plot, and $C$ is the amount of phytomass removed over the period of interest, kg/ha dry weight.

The formula for the winter feeding period was as follows:

$$P = 100C/M,$$

assuming that the phytomass measured in early September is the total forage stock available to the animals over the whole winter period, until the onset of the next growing season.

## RESULTS

**Abundance of grazing ungulates**. The population density of Mongolian gazelles in the study region is markedly variable in time and nonuniform in space. Large aggregations of these animals, tens of thousands of head each, spread over their grazing grounds in small groups and permanently move over a vast area. This is why their abundance in the test plots varied widely, from zero to very high values. The highest abundance of gazelles over the study period was observed in Toson Khulstai, where their density in aggregations reached 37 head/$km^2$. In Zaan Shiree, gazelles were less abundant and rarely formed aggregations; in some years, they were virtually absent in summer. The smallest numbers of these animals were observed in Talyn Shand, where only 79 individuals were recorded along routes extending for a total of 723 km. According to local residents, herds of gazelles appear in Talyn Shand more often in winter than in summer. Thus, the size of groups, frequency, mode of presence, and, hence, population density of Mongolian gazelles were unstable, varying in different sites and in different periods from 0 to 37 head/$km^2$.

The abundance of livestock markedly differed from site to site, reaching the highest values (23–33 head/$km^2$) on pastures in Talyn Shand and Zaan Shiree. In the Toson Khulstai SPNA, virtually no livestock grazing takes place in summer (except for occasional groups of free-ranging horses), but horses and cattle graze there in winter, as follows from the presence of their feces. The density of horses and cattle in all sites (except Toson Khulstai) was similar, 4 to 5–6 head/$km^2$, whereas that of sheep differed markedly, from 14 head/$km^2$ in Talyn Shand to 25 head/$km^2$ in Zaan Shiree.

**Aboveground phytomass**. Assessments performed every month during the growing season showed that the aboveground phytomass in all plots was fairly uniform. In all years, the green (forage) phytomass stock usually varied within 500–1000 kg/ha, reaching 1400 kg/ha by the end of the growing season (in August) only in sites where no livestock grazed in summer (Zaan Shiree-2 and Toson Khulstai).

**Feces degradation and weight loss**. It is logical to suppose that deposited feces lose weight due mainly to activities of coprophages. However, our observations show that feces of small ungulates (Mongolian gazelles, sheep, and goats) remain virtually unaffected

**Table 1.** Amounts of feces deposited in test sites by different ungulate species over the summer period (July–August) in different years, $\tilde{x} \pm S_{\tilde{x}}$

| Year | Test site | Number of plots | Month | Amount of feces, kg/ha dry weight | | | | Total |
|---|---|---|---|---|---|---|---|---|
| | | | | horses | cattle | seep and goats | gazelles | |
| 2004 | Talyn Shand | 2 | July | 0.9 ± 0.9 | 3.7 ± 3.7 | 0.5 ± 0.5 | 0 | 5.2 ± 5.2 |
| | | | August | 4.1 ± 0.1 | 10.7 ± 10.7 | 0.9 ± 0.7 | 0 | 15.8 ± 8.1 |
| | Toson Khulstai | 6 | July | 0 | 0 | 0 | 4.3 ± 1.3 | 4.3 ± 1.3 |
| | | | August | 0.7 ± 0.7 | 0 | 0 | 5.7 ± 2.5 | 6.4 ± 2.8 |
| | Zaan Shiree-1 | 4 | July | 3.1 ± 1.6 | 0.9 ± 0.7 | 7.8 ± 0.9 | 0.1 ± 0.1 | 11.9 ± 2.8 |
| | | | August | 6.5 ± 4.5 | 7.3 ± 6.8 | 4.2 ± 3.5 | 0 | 18.0 ± 9.8 |
| | Zaan Shiree-2 | 3 | July | 0 | 0.4 ± 0.4 | 0 | 0 | 0.4 ± 0.4 |
| | | | August | 0 | 0 | 0 | 2.2 ± 1.3 | 2.2 ± 1.3 |
| 2005 | Talyn Shand | 4 | July | 6.5 ± 2.6 | 1.9 ± 1.1 | 0.7 ± 0.2 | 0 | 9.1 ± 3.1 |
| | | | August | 19.1 ±13.4 | 0 | 1.4 ± 0.4 | 0 | 20.5 ± 13.5 |
| | Toson Khulstai | 6 | July | 0 | 0 | 0 | 4.8 ± 1.0 | 4.8 ± 0.1 |
| | | | August | 0 | 0 | 0 | 2.1 ± 1.5 | 2.1 ± 1.5 |
| | Zaan Shiree-1 | 4 | July | 8.8 ± 3.8 | 6.3 ± 3.1 | 5.3 ± 2.1 | 0 | 20.3 ± 3.0 |
| | | | August | 8.4 ± 2.3 | 10.0 ± 5.2 | 2.3 ± 1.3 | 0 | 20.6 ± 8.5 |
| | Zaan Shiree-2 | 3 | July | 0 | 0 | 0 | 1.4 ± 0.9 | 1.4 ± 0.9 |
| | | | August | 0 | 0 | 0 | 0 | 0 |
| | Bayan Khuree | 3 | August | 0 | 0 | 0 | 11.1 ± 5.0 | 11.1 ± 5.0 |

by coprophages: these relatively small (~1 cm), hard droppings scattered over the surface rapidly dry up and become inaccessible to them.

Feces of horses and cattle were colonized by a number of coprophages, including *Aphodius erraticus, A. burgaltaicus, A.* spp., *Onthophagus gibbulus, O. laticornis, O. marginalis,* and *O. olsoufieffi*. However, this process was neither ubiquitous nor constant in time: its peaks took place in late spring and early autumn, whereas in the driest and hottest midsummer period coprophages were much less active and virtually did not colonize feces.

An assessment of feces weight loss due to coprophages in late–August–early September showed that 6 out of 18 piles of fresh horse feces were not colonized by coprophages, and their weight remained unchanged. Moreover, in the piles processed by coprophages over the exposure period (15 days until the feces dried up and coprophage activity ceased), the average weight loss was also lower than the estimation error: from 242 ± 16.6 to 230 ± 18.9 *g* dry weight. Coprophages mainly destroyed the feces, transforming them into debris, while the proportion of the material they utilized (used as food) was undetectable at the given accuracy of measurements. Mammals (insectivores and small weasels) and birds also destroyed the piles in search of insects.

The total weight loss due to both biotic and abiotic factors in the first year after deposition (from September of the previous year to September of the current year) was smaller in the feces of Mongolian gazelles (and, apparently, of other small ungulates) than in the feces of horses and cattle: 14.4 vs. 17.1 and 18.6%, respectively. On the basis of these results, we made corrections in the formulas for calculating the weight of feces deposited over the annual cycle. The correction coefficient was taken to be 1.17 for Mongolian gazelles, sheep, and goats; 1.21 for horses; and 1.23 for cattle.

The destruction of feces in subsequent years slowed down. In general, its rate was very low: over three annual cycles (2002–2005), the weight of samples decreased by only 36.8% in Mongolian gazelles, 25.8% in horses, and 28.9% in cattle; i.e., the annual average weight loss was only 9–12%. The feces of gazelles, sheep and goats accumulate on the surface and remained undisturbed for many years. In the fenced area inaccessible to these animals for more than a decade, their old feces in the form of hard, uncrushable pellets abounded on the surface and in the upper soil layer.

**Deposition of feces**. The pattern of monthly feces deposition in summer was extremely variable. The amounts of feces deposited by individual animal species in June and August markedly varied even in the same site (Table 1). In Talyn Shand, for example, the

**Table 2.** Amounts of feces deposited in test sites by different ungulate species over the autumn–winter–spring period (September–June) in different years, $\tilde{x} \pm S_{\tilde{x}}$

| Year | Test site | Amount of feces, kg/ha dry weight | | | | Total |
|---|---|---|---|---|---|---|
| | | horses | cattle | seep and goats | gazelles | |
| 2002–2003 | Toson Khulstai | 32.7 ±18.1 | 15.3 ± 1.9 | 0.7 ± 0.7 | 7.8 ± 1.4 | 48.6 ± 12.6 |
| | Zaan Shiree-1 | 117.2 ±14.6 | 3.6 ± 2.2 | 5.4 ± 1.6 | | 126.1 ± 15.9 |
| 2003–2004 | Talyn Shand | 58.0 ± 40.1 | 5.4 ± 3.9 | 6.9 ± 2.8 | 0 | 70.2 ± 46.8 |
| | Toson Khulstai | 7.0 ± 0.8 | 1.3 ± 1.3 | 0 | 20.8 ± 1.5 | 29.2 ± 2.1 |
| | Zaan Shiree-1 | 46.9 ± 15.6 | 15.2 ± 5.4 | 26.0 ± 5.5 | | 88.2 ± 24.4 |
| | Zaan Shiree-2 | 25.4 ± 2.7 | 38.5 ± 22.9 | 0 | 7.6 ± 1.9 | 71.6 ± 21.3 |
| 2004–2005 | Talyn Shand | 43.7 ± 12.2 | 10.8 ± 3.7 | 9.0 ± 2.7 | 0 | 63.4 ± 15.4 |
| | Toson Khulstai | 8.2 ± 6.6 | 1.0 ± 0.8 | 0 | 7.6 ± 2.1 | 16.91 ± 7.46 |
| | Zaan Shiree-1 | 39.9 ± 13.9 | 22.5 ± 9.6 | 16.6 ± 3.4 | | 79.0 ± 15.6 |
| | Zaan Shiree-2 | 90.2 ± 32.7 | 27.1 ± 15.3 | 0 | 19.6 ± 4.2 | 136.9 ± 41.9 |
| 2004–2005 | Bayan Khuree | 23.2 ± 23.2 | 0 | 0 | 32.4 ± 7.7 | 55.6 ± 16.1 |

amount of horse feces deposited in each of these months varied from 0.9 to 4.1 kg/ha in 2004 and from 6.5 to 19.1 kg/ha in 2005. In this case, such variation was explained by asynchronism in the use of pasture areas in each concrete period and also by the fact that the animals consecutively changed pasture areas as the vegetation was grazed off. In summer, the maximum monthly amounts of feces deposited by all ungulates, reaching 18–20 kg/ha, were usually recorded in Zaan Shiree-1 (as noted above, this site was characterized by the highest animal density), and the minimum amounts (0–1.4 kg/ha) were recorded in Zaan Shiree-2, in the area used for livestock grazing in winter. It is noteworthy that all feces deposited in summer in Toson Khulstai, the area with a protective status, belonged only to Mongolian gazelles. Their distribution in all years was relatively uniform, and their monthly amount varied from 2.1 to 5.7 kg/ha and was close to that of livestock feces in other pastures.

In the cold (nongrowing) period of the year (10 months), horses were far ahead of cattle and, especially, sheep and goat in the amount of feces deposited in pastures, as they remained free-ranging throughout the year. The amounts of horse feces in this period reached 90–117 kg/ha in different sites (except for the Toson Khulstai SPNA), compared to 20–40 kg/ha deposited by other kinds of livestock (Table 2). The amount of gazelle feces strongly varied in different years and in different sites, reaching a maximum of 30 kg/ha.

The annual amount of feces deposited by all ungulates in 2004 and 2005 reached 110–140 kg/ha in the mountain areas of Zaan Shiree, 82 kg/ha in the steppe valley of Talyn Shand, and only 28–36 kg/ha in Toson Khulstai, where the feces of Mongolian gazelles prevailed (18–27 kg/ha). In all sites except Toson Khulstai, horses accounted for the greatest proportion of feces (up to 90 kg/ha), and the contribution of gazelles amounted to 27 kg/ha.

**The amount of phytomass removed**. The annual phytomass removal by all ungulate species (estimated from the amount of feces) varied in most sites within 240–400 kg/ha (Table 3), being markedly smaller (65–109 kg/ha) only in the Toson Khulstai SPNA, where livestock grazing was restricted. In Zaan Shiree-1, where the concentration of ungulates was higher, they utilized more than half of available aboveground phytomass (50–59%). In the Toson Khulstai SPNA, Mongolian gazelles utilized 4–13% of the phytomass, with total utilization (together with livestock) varying from 8 to 16%. Different ungulate species, including gazelles, more or less equally accounted for phytomass removal. In some cases (Zaan Shiree), the largest proportion of phytomass (19–23%) was removed by sheep and goats together with gazelles (being indistinguishable from each other, their feces were recorded together).

It was of interest to estimate the impact of ungulates on vegetation during the growing season. The removal of current vegetation (green phytomass) by the ungulate complex in summer proved to be insignificant in all cases. Its monthly (July and August) values varied from 0 to 9.5%, being higher (2.5–9.5%, or 20–53 kg/ha) in sites where livestock prevailed (Talyn Shand and Zaan Shiree). Green phytomass removal was almost absent (0–1.4 kg/ha) in winter pastures of Zaan Shiree-2, where summer livestock grazing was excluded. It was also insignificant (5.4–16.5 kg/ha, or 1.5–3.1%) in the Toson Khulstai SPNA, where only Mongolian gazelles grazed in summer. The absolute amount of removed phytomass in this site was considerable (22 kg/ha) only in August 2003, but its proportion relative to the total green phytomass was only 2.7%.

**Table 3.** Absolute (kg/ha, dry weight) and relative (%) phytomass removed from test sites by different ungulate species throughout the annual cycle, $\tilde{x} \pm S_{\tilde{x}}$

| Annual cycle | Test site | Phytomass removed (kg/ha) and its proportion of total above-ground phytomass (%), dry weight | | | | | | | | Total | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | horses | | cattle | | seep and goats | | gazelles | | | |
| | | kg/ha | % | kg/ha | % | kg/ha | % | kg/ha | % | kg/ha | % |
| 2003–2004 | Talyn Shand | 136.3 ± ± 87.2 | 11.6 ± ± 8.0 | 59.1 ± ± 32.8 | 7.4 ± ± 4.3 | 43.4 ± ± 15.9 | 4.4 ± ± 1.5 | 0 | 0 | 238.8 ± ± 123.7 | 24.9 ± ± 11.9 |
| | Toson Khulstai | 16.8 ± ± 2.42 | 1.8 ± ± 0.2 | 5.8 ± ± 5.8 | 0.7 ± ± 0.7 | 0 | 0 | 86.9 ± ± 8.7 | 13.0 ± ± 1.4 | 109.4 ± ± 11.1 | 15.9 ± ± 1.9 |
| | Zaan Shree-1 | 121.2 ± ± 35.2 | 11.3 ± ± 3.8 | 85.2 ± ± 28.6 | 10.6 ± ± 3.7 | 187.9 ± ± 33.3 | 23.1 ± ± 3.6 | * | * | 395.7 ± ± 82.3 | 49.9 ± ± 9.8 |
| | Zaan Shiree-2 | 55.3 ± ± 5.9 | 6.1 ± ± 0.7 | 164.7 ± ± 97.4 | 18.3 ± ± 10.8 | 0 | 0 | 22.6 ± ± 5.6 | 3.0 ± ± 0.7 | 248.0 ± ± 93.2 | 27.4 ± ± 10.4 |
| 2004–2005 | Talyn Shand | 154.0 ± ± 39.5 | 11.5 ± ± 3.5 | 57.5 ± ± 18.7 | 9.8 ± ± 2.5 | 59.8 ± ± 15.7 | 6.5 ± ± 1.7 | 5.7 ± 3.4 | 0 | 252.3 ± ± 54.2 | 31.2 ± ± 6.4 |
| | Toson Khulstai | 19.6 ± ± 15.8 | 2.3 ± ± 1.8 | 4.8 ± ± 4.3 | 0.6 ± ± 0.5 | 0 | 0 | 40.2 ± ± 7.6 | 4.4 ± ± 0.6 | 64.6 ± ± 18.8 | 8.1 ± ± 2.1 |
| | Zaan Shree-1 | 129.0 ± ± 34.3 | 12.9 ± ± 4.4 | 151.2 ± ± 49.5 | 21.3 ± ± 5.3 | 126.9 ± ± 22.2 | 19.0 ± ± 3.0 | * | * | 407.2 ± ± 59.6 | 58.6 ± ± 5.3 |
| | Zaan Shiree-2 | 214.3 ± ± 77.7 | 12.6 ± ± 4.7 | 129.5 ± ± 75.2 | 7.5 ± ± 4.5 | 0 | 0 | 61.1 ± ± 12.7 | 3.8 ± ± 0.6 | 404.9 ± ± 134.5 | 23.9 ± ± 8.1 |

Note: (*) In the Zaan Shiree-1 site, phytomass removal by Mongolian gazelles is included in data on sheep and goats.

## DISCUSSION

The rate of feces deposition depends on the numbers of grazing animals and reflects their trophic impact on the vegetation. In the study area, the smallest annual amount of feces (28–36 kg/ha) is deposited in the Toson Khulstai SPNA, which is protected from livestock grazing and, hence, is visited mainly by Mongolian gazelles. The maximum deposition rate (110–140 kg/ha per year) is characteristic of Zaan Shiree, where livestock population density is higher than in other sites.

Feces decomposition proceeds slowly, with weight loss over the first year after deposition varying from 14 to 19%, depending on animal species. It is noteworthy that weight loss by freshly deposited saiga feces in the Northern Caspian semidesert is similar, about 20% (Abaturov, 1984). The rate of weight loss decreases in subsequent years. Over three years, feces of different ungulate species have lost only 26–37% of their initial weight. It may be concluded that fecal organic mass accumulates with time in the steppe ecosystem. The feces gradually crumble into detritus particles that mix with the soil and accumulate there in a nondecomposed state, which is confirmed by the results of micromorphological soil analysis (Golovanov et al., 2004). Note that the rate of feces decomposition in areas with a humid climate is also slow. In taiga forests (Novgorod oblast), weight loss by moose feces over 4–6 years varied from 64 to 89%, and that in the Subarctic over four years reached only 53% (Malafeev and Kryazhimskii, 1990; Kuznetsov, 2002).

Parameters of phytomass removal by grazing undulates proved to differ depending on test site. In Toson Khulstai, Mongolian gazelles together with livestock annually consumed 65–109 kg/ha, or 8–16% of the total aboveground phytomass, with livestock accounting for only 2.5–2.9%. In other sites, both absolute and relative values of phytomass removal were markedly higher, ranging from 240–250 kg/ha (24–25%) in Talyn Shand (with gazelles accounting for only 3.8%) to 400 kg/ha (58%) in Zaan Shiree-1.

The low level of phytomass consumption in Toson Khulstai is due to the protective status of this site, which prevents grazing by livestock. The high level of consumption (relative to the total phytomass) by livestock in Zaan Shiree-1 is explained by the fact that the total phytomass of petrophytic plant communities prevailing in this mountain terrain is small, whereas the population density of livestock is higher than in other sites. In Talyn Shand and Zaan Shiree-2, as noted above, parameters of annual phytomass removal are almost half lower than in Zaan Shiree-1 but similar to each other (24–25%), irrespective of differences in the pattern of pasture use. In Zaan Shiree-2, all this phytomass is removed in the period of winter grazing, with more than half of it being consumed by horses and about one-third by cattle. Seasonal differences in the level of phytomass consumption are explained prima-

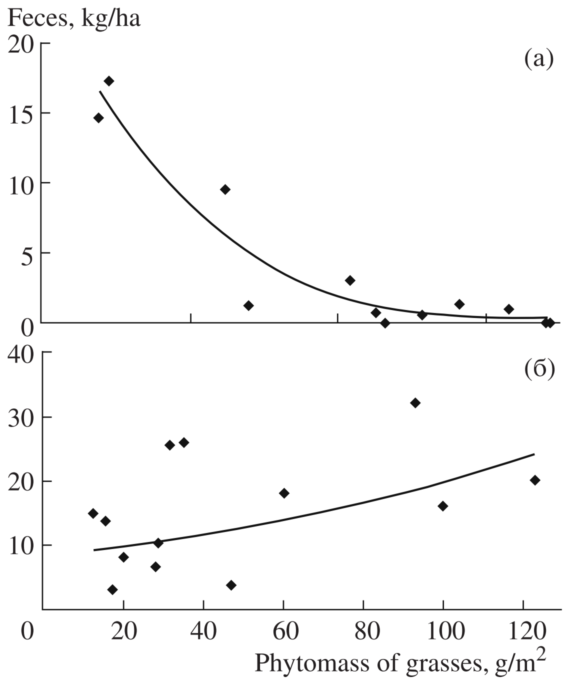


**Fig. 1.** The amount of feces deposited by Mongolian gazelles as a function of the phytomass of grasses in (a) summer and (b) winter periods, air-dry weight.

rily by the absence of permanent watering places, which is an obstacle to livestock grazing in summer but is counterbalanced by the presence of snow cover in winter. The population density of livestock in Talyn Shand is lower (23–25 head/km$^2$) and their distribution is relatively uniform, without any abnormal concentration of livestock farms in certain areas. The main consumers of phytomass over the year are horses (136–154 kg/ha, or 11-12%); then follow cattle (58–59 kg/ha, or 7-10%) and sheep and goats (43–60 kg/ha, or 4.4-6.5%).

Phytomass removal by ungulates in the summer (growing) season is insignificant, no more than 11–16%, and has no serious impact on plant growth and productivity. Slight changes are observed only in the structure of plant communities, particularly in their species composition, as ungulates selectively consume their preferred forage plants. The total aboveground phytomass stock also decreases, but plant productivity remains unchanged.

Markedly higher parameters of phytomass removal are characteristic of the long nongrowing (autumn–winter–spring) period. However, winter-grazing ungulates consume mainly dead plants (necromass), thereby preventing their accumulation and consolidation into a mat, which obviously has a favorable effect on the state of steppe vegetation.

**Phytomass removal by Mongolian gazelles depends on the composition of grass stand and deserves special attention.** As Toson Khulstai is a state nature reserve, where economic activity is strongly restricted, Mongolian gazelles are the main consumers of plant production in this area. In the study period, the level of annual phytomass removal in this site varied from 4 to 13%, but we observed considerable scattering of values recorded in different plots. Thus, the pattern of pasture use by Mongolian gazelles proved to be extremely nonuniform in time and space. This phenomenon is explained primarily by differences in the composition of herbaceous cover between the plots. Mongolian gazelles prefer feeding on plants with easily digestible green parts (i.e., mixed herbs), whereas grasses are relatively poor forage for them. This is especially true of feather grasses (*Stipa grandis, S. sibirica, S. krylovii*) with their coarse, lignified generative shoot, which form the bulk of phytomass. Moreover, a dense grass stand impairs access to more wholesome food plants, thereby prolonging the time course of grazing. This was conclusively shown in studies on the feeding of steppe marmots (Ronkin and Savchenko, 2000). It can be seen that the amount of feces as an index of the total food consumption by Mongolian gazelles decreases with an increase in the phytomass of grasses (primarily feather grasses) in the test plots (Fig. 1a). In winter, however, this relationship is reversed (Fig. 1b): after the establishment of snow cover, grasses acquire the role of main forage, despite their low nutrient value (Bannikov, 1954).

No such relationships were revealed for Mongolian gazelles in areas regularly used for livestock grazing. In such pastures, horses and cows consume the bulk of feather grasses, thereby making other food plants more easily accessible to gazelles. In addition, regular grazing provides for continuous regrowth of vegetative plant parts, and this fresh phytomass is an easily digestible and nutritious forage. We have repeatedly observed gazelle herds grazing near livestock farms and, at night, mixed herds of grazing gazelles and cows. In such cases, the factor of easily accessible, high-quality forage supply obviously prevails over the factor of anthropogenic disturbance.

## CONCLUSIONS

The results of our study show that livestock and wild ungulates (horses, cattle, sheep, goats, and Mongolian gazelles) annually deposit up to 140 kg/ha of undigested plant remains (feces) in the steppe pastures of eastern Mongolia. Decomposition and mineralization of the feces under conditions of the steppe proceeds very slowly, with the annual loss of their weight under the combined effect of biotic and abiotic factors being no more than 9–12%. As a result, the fecal material gradually accumulates in the soil.

The rate of feces deposition characterizes the degree of grazing load and, taking into account parameters of forage digestibility, allows estimation of the amount of forage phytomass consumed by ungulates. In the study region, grazing load is insignificant: the annual phytomass removal is usually about 20–30%, increasing to 50–60% (400 kg/ha) in only a few areas. It should be noted that the greater part of this phytomass is removed in the nongrowing period, when ungulates feed mainly on dead plants (necromass). In the growing (summer) period, livestock together with wild ungulates consume no more than 11–16% of the total aboveground phytomass. Obviously, trophic activities of ungulates at such an insignificant grazing load do not impair plant productivity. On the contrary, the removal of necromass in winter has a favorable effect on the state of the pasture ecosystem.

Different ungulate species, including Mongolian gazelles, more or less equally account for phytomass removal. In the Toson Khulstai reserve, where the population density of gazelles is high, they consume a considerable proportion of phytomass (up to 13% per year).

At the current population density, both domestic and wild ungulates are quite sufficiently provided with forage on pastures of the study region, especially in the summer season. Apparently, the abundance of ungulates grazing on steppe pastures during the year depends on the winter stocks of vegetation. In other words, poor accessibility and low nutrient value of winter forage is the factor limiting the population density of ungulates and grazing load on vegetation in the steppe ecosystems studied.

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