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Ungulate-driven forest-steppe vegetation changes in enclosures

Aleksandr P. Berber[1],

Artūras Kibiša[2*]

[1] *'Zhivaya priroda Kazakhstana', Building 6, Microrayon 6, Temirtau 101400, Karaganda Region, Kazakhstan*

[2] *Faculty of Forest Sciences and Ecology, Vytautas Magnus University Agriculture Academy, Studentų St. 11, 53361, Akademija, Lithuania*

Ungulate enclosures are commonly established for wildlife observation and conservation, recreational hunting, meat, and material production. In this study, we analyse the 'Elen' hunting estate located in the forest-steppes of Kazakhstan. Our main objectives were to determine the richness and abundance of herbaceous and woody vegetation within the enclosures. Additionally, we aimed to evaluate damages inflicted by ungulate browsing and grazing. Our results reveal that dominant tree species in the forests of the 'Elen' estate are Scots pine, silver birch, and downy birch. Within the herbaceous vegetation cover, we identified 107 grass, sedge, and herb species, majority of them belonging to the Asteraceae, Poaceae, Fabaceae, and Rosaceae families. Our analysis indicates that ungulates significantly impact forest-steppe vegetation in the enclosures. On average, 29.4% (20–100%) of trees and shrubs and 17.1% (15.6–81.8%) of herbaceous vegetation were damaged. The results of this study provide valuable insights for determining the optimal ungulate population size within the enclosures and contribute to the preservation of forest-steppes vegetation.

Keywords: ungulates, enclosure, food resources, tree-shrub vegetation, herbaceous vegetation, grazing, browsing, forest-steppe

INTRODUCTION

In recent decades, worldwide development of multi-purpose wild ungulate breeding in fenced enclosures has been on the rise. The main drivers of establishing hunting estates are meat and material production, recreational hunting, wildlife observation and conservation (Piasentier et al., 2005; MacMillan, Phillip, 2008; Martínez-Jauregui et al., 2016; Watts et al., 2017).

In June 2017, an amendment to Kazakhstan's legislation regarding the conservation, reproduction and use of wildlife' opened the door to the establishment of enclosed hunting estates, game reserves, and hunting farms.

As selection of feeding areas and sources are contingent on food availability, quality and abundance, enclosures restrict natural ungulate foraging behaviour, (Gordon, Prins, 2008). Consequently, high feeding pressure in enclosures can lead to changes in vegetation composition, diversity, and biomass. However, previous studies on vegetation browsing and grazing provide inconclusive results. Some

* Corresponding author. Email arturas.kibisa@vdu.lt

authors observed a decrease in biomass, while others report an increase (Grime, 1973; Miller et al., 1992; Gough, Grace, 1998; Olff, Ritchie, 1998; Stohlgren et al., 1999; Horsley et al., 2003; Côté et al., 2004; Suzuki et al., 2013; Hegland et al., 2013; Habeck, Schultz, 2015). Furthermore, a few studies determined that ungulates have no influence on vegetation cover within enclosures. According to Holtmeier (2015), red deer browsing can increase diversity of vascular plant species. In contrast, Horsley et al. (2003) propose that increasing cervid abundance decreases the number of plant species. It is important to note that negative effects on the diversity and abundance of herbaceous vegetation are commonly observed (Russell et al., 2001; Rooney et al., 2004; Stockton et al., 2005). In temperate forests, ungulates also reduce vegetation diversity in enclosures (Rooney et al., 2004; Rooney, 2009; Begley-Miller et al., 2014; Řepka et al., 2021).

Regardless of the purpose behind establishing an enclosure (conservation of rare and endangered animals, a hunting estate, a game reserve, a safari park, etc.), it is evident that fulfilling basic needs of animals, particularly for food and water, is paramount. Majority of the grasses and sedges within Poaceae and Cyperaceae families exhibit high grazing tolerance (Coughenour, 1985; Kirby, 2001; Horsley et al., 2003; Rooney, Waller, 2003; Côté et al., 2004; Collard et al., 2010). Conversely, Kirby (2001) pointed out that the abundance of Poaceae family species decreases with more intense grazing pressure. Additionally, ungulate grazing can increase abundance of the ruderal and nitrophilous species (*Urtica dioica, Angelica sylvestris*, *Filipendula ulmaria*) (Grime et al., 1988; Chytry, Danihelka, 1993; Crampton et al., 1998; Boulanger et al., 2017; Vild et al., 2018).

Therefore, maintaining a balance between the ungulate population and the available food resources within fenced enclosures is crucial for preserving natural ecosystems. In this paper, our main objectives are to (1) identify woody and herbaceous vegetation richness and cover in the 'Elen' hunting estate and (2) determine ungulate browsing and grazing pressure in enclosures.

MATERIAL AND METHODS

Study area

The 'Elen' hunting estate is located within the Otradnensky forest enterprise, in the Bulandinsky district of Akmola region, Republic of Kazakhstan (Fig. 1). The region is situated in the temperate zone with dry, continental climate (Rachkovskaya, Bragina, 2012). The terrain is

Fig. 1. Location of the studied forest-steppe enclosures

mostly plains with undulating hills and mountains known as the Kazakh Hummocks.

The study area is located within the forest-steppe zone characterised by steppes, plains, meadows, and marshes alternating with forests (Rachkovskaya, Bragina, 2012). During winter, the snow cover can last from 140 to 165 days, with the snow depth of up to 40 cm.

The hunting estate covers a total land surface area of 8769.3 hectares. The enclosures are inhabited by a variety of wild ungulates, including moose (*Alces alces* Gray), maral (*Cervus elaphus sibiricus* Severtzov), Siberian roe deer (*Capreolus pygargus* Pallas), European fallow deer (*Dama dama* L.), wood bison (*Bison bison athabascae* Rhoads), and wild boar (*Sus scrofa* L.) (Table 1).

The land cover consists of pine, birch, and aspen forests, occasional clearings, swamps, and the infrastructure of the estate (Fig. 2).

Field surveys and data analysis

We surveyed herbaceous vegetation in different land cover types, including open landscapes and forests, in the enclosures of the 'Elen' hunting estate in July 2021. To determine the quantity of forage based on the grazing and browsing accessibility, we assessed the aboveground biomass of understory vegetation and undergrowth. We used Otradnensky forestry management plans and cartographic enclosure maps (Otradnensky management plan, 2012).

The data on herbaceous vegetation was collected and analysed using common methodologies (Petkov et al., 2017; Olsen et al., 2017; Bjerkeet et al., 2021). A diagonal walking route was planned within the study area. In different land cover types, we arranged 1 m^2 plots (1 × 1 m) inside the enclosures and outside of them for control. The plots were placed every 25 m. The number of plots varied from 4 to 15

Table 1. **Number of animals in the 'Elen' game reserve in 2021, per 1000 ha**

Species	Game population in 2021, animals/1000 ha
Moose (*Alces alces* Gray)	113
Maral (*Cervus elaphus sibiricus* Severtzov)	130
Siberian roe deer (*Capreolus pygargus* Pallas)	402
Wild boar (*Sus scrofa* L.)	119
Wood bison (*Bison bison athabascae* Rhoads)	63
European fallow deer (*Dama dama* L.)	90
In total:	917

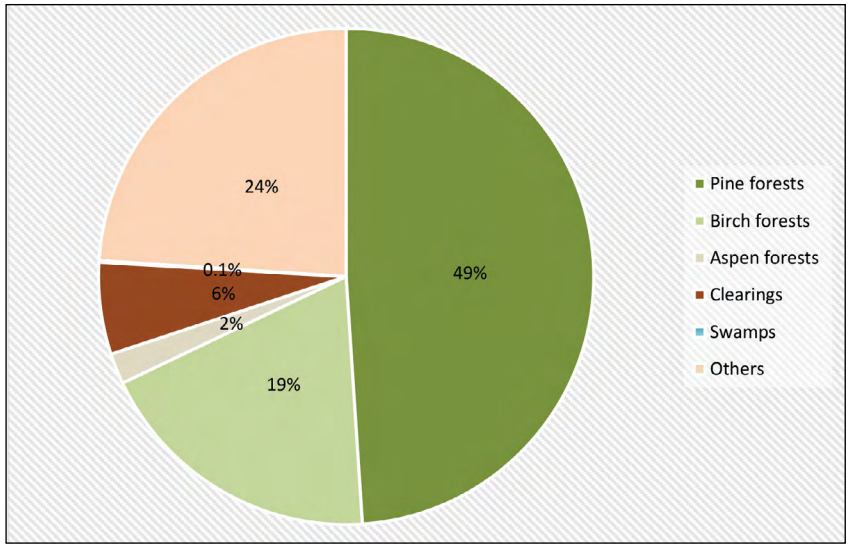

Fig. 2. Distribution of different land cover types in the 'Elen' hunting estate, % (Otradnensky management plan, 2012)

among different land cover types depending on the evenness of the distribution of herbaceous vegetation. In total, 22 sites were examined, covering 220 surveyed plots (126 inside the enclosures and 94 control). The damage to herbaceous vegetation was assessed by cutting vegetation layer 5 cm above the soil surface. Collected vegetation was sorted by species.

Vegetation samples were air-dried in a dry and well-ventilated room. The dried samples were weighed (with accuracy of 0.1 g) to determine the average weight for each species within the respective plot. We analysed and compared the composition of herbaceous species, quantitative attributes of plots, and species and systematic groups. The collected samples were identified using plant identification guides commonly used in this region. (Isachenko, 1961; Illustrated guide to the plants of Kazakhstan, vols. 1, 2, 1969; Gorchakovskiy, 1987; Kupriyanov, 2020). To assess the grazing pressure on herbaceous vegetation, we compared biomass between areas inside and outside of the enclosure, selecting plots with identical conditions separated by a fence.

Browsing (e.g., browsed shoots) of young trees and shrubs was assessed visually. In this study, we analysed trees under five years old with diameter at breast height of >1 cm. The size of damaged areas was measured to 1 m^2 accuracy. To determine the height of the apical (dominant) shoot, measurements were taken with an accuracy of 0.01 m, extending from the soil surface to the apex of the damaged shoot. These measurements were taken to determine the damage sustained prior to the current growing season. At the beginning of a new growth period, several of the damaged trees and shrubs grew a new dominant shoot from the buds closest to the tip of the damaged shoot. These shoots were cut at the base of the renewal bud, and their length was measured in millimetres. By measuring the new growth of shoots after damage, we can assess the ability of trees and shrubs to recover, determine the growth dynamics, the amount of regenerated biomass, and the effect of ecological conditions. Collected shoots were air-dried and weighed with an accuracy of 0.1 g, separating stems and leaves.

RESULTS

Forest cover

Most of the enclosures are covered by forests (Table 2). Over 60% of the forest cover consisted of coniferous Scots pine (*Pinus sylvestris* L.).

Table 2. **Composition of tree and shrub species in the forests of the 'Elen' hunting estate**

Species	Forested area, %	Forested area, ha
Trees		
Scots pine (*Pinus sylvestris* L.)	60.9	3654
Silver birch (*Betula pendula* L.) and downy birch (*Betula pubescens* L.)	23.4	1404
Aspen (*Populus tremula* L.)	2.6	156
Ash-leaved maple (*Acer negundo* L.), Siberian elm (*Ulmus pumila* L.), Siberian crab apple (*Malus baccata* (L.)	0.57	34.2
Shrubs		
Tatarian honeysuckle (*Lonicera tatarica* L.)	11.5	690
Willow (*Salix*)	0.2	12
Siberian pea-shrub (*Caragana arborescens* Lam.)	0.8	48
Thicket shadbush (*Amelanchier spicata* (Lam.) C. Koch) and golden currant (*Ribes aureum* Pursh.)	0.03	1.8
Total	100	6000

Deciduous tree species were less prevalent, covering less than 40% of the total forest area. The most common deciduous tree species were silver birch (*Betula pendula* L.) and downy birch (*Betula pubescens* L.). Aspen (*Populus tremula* L.) and other planted tree species, including ash-leaved maple (*Acer negundo* L.), Siberian elm (*Ulmus pumila* L.) and Siberian crab apple (*Malus baccata* (L.) Borkh.) were less common. Willows (Salix) covered approximately 0.2% of the forest area, mainly along the shores and swamps. Tatarian honeysuckle (*Lonicera tatarica* L.) was dominant in the shrub layer, while Siberian pea-shrub (*Caragana arborescens* Lam.) covered only 0.8%. Thicket shadbush (*Amelanchier spicata* (Lam.) C. Koch) and golden currant (*Ribes aureum* Pursh.) were planted in 0.02–0.04% of the forested areas.

Ungulate damage to young trees and shrubs

During browsing surveys, we observed that young trees frequently sustained damage to their apical dominant shoots, often at a relatively low height. Ungulate damages had high variation between the different tree and shrub species (Table 3). The browsing pressure was most significant in the young coniferous forest as 80% of Scots pine trees were damaged over the dormant season. The highest biomass, measuring 9.8 kg/m^2, was observed in Scots pine stands. In comparison, the biomass of Siberian pea-shrub was over two times lower, while the biomass of Tatarian honeysuckle was four times lower.

Measured browsed height of apical shoots of trees and shrubs ranged from 24 to 235 cm. The average height of damaged trees was 84.9 ± 26.7 cm. During the dormant season, browsing primarily affected young trees, while mature trees were not damaged. Young coniferous species covered 7% of the forests, while young deciduous tree species – 9%.

Ungulate damage to herbaceous vegetation

During the growing season, biomass of the herbaceous vegetation was measured and compared in different land cover types (Table 4). The highest biomass of herbaceous vegetation was observed in hayfields, and the lowest in swamps and pastures. Compared to hayfields, herbaceous vegetation biomass was more than three times lower in Scots pine, birch, and aspen forests.

A total of 107 herbaceous species representing 63 genera and 23 families were identified in the study area. Diversity of herbaceous species in the enclosure was as follows: the Asteraceae family was represented by 22 species, the Poaceae family by 15, Fabaceae by 13, and Rosaceae by 11. Within the Poaceae family, 12 genera were identified, while the Asteraceae family had 10 genera. The Fabaceae family consisted of nine genera, and the Rosaceae family included five genera. Notably, the Cyperaceae family, particularly the *Carex* genus, had the highest number of herbaceous species (seven species) followed by the Asteraceae family, genus *Artemisia*, which had six herbaceous species identified. In the Rosaceae family, genus *Potentilla* accounted for five herbaceous

Table 3. **Area cover, biomass, and browsing damage to different tree and shrub species during the dormant season in the 'Elen' hunting estate**

Species	Area, ha	Biomass, kg/m^2	Browsing damage, %
Scots pine	256	9.8	80%
Aspen	213	4.6	33%
Willows	17.3	2.4	30%
Tatarian honeysuckle	939.7	2	25%
Siberian pea-shrub	64.8	4.2	30%
Golden currant	2.0	no data	100%
Other shrubs	1027.1	1.5–4.5	20%

Table 4. **Biomass of herbaceous vegetation in different land cover types in the 'Elen' hunting estate**

Land cover type	Land cover area, ha	Herbaceous vegetation biomass, g/m²	Herbaceous vegetation biomass, t/ha	Biomass distribution, t
Pine forest	4270	49.2	0.49	2092.3
Birch forest	1640	47.7	0.48	787.2
Aspen forest	180	46.9	0.47	84.6
Clearings	500	43.4	0.43	215
Hayfields	730	186.9	1.86	1357.8
Pastures	110	37.5	0.38	41.8
Cultivated fields, fallow lands	290	60.5	0.61	176.9
Swamp	40	26.2	0.26	10.4
Others (roads, buildings, shooting range etc.)	1009	11.5	–	–
Total	8769			4766

species, while the Plantaginaceae family's Plantago genus included four species.

The distribution of herbaceous vegetation in different land cover types was as follows:

Pine forest. In total, air-dried herbaceous vegetation weighed 49.2 ± 17.4 g/m². The dominant family was Poaceae (29.1%), followed by the Apiaceae family (19.7%). The Rosaceae family exhibited lower abundance at 10.1%. Among the dominant vegetation was *Festuca valesiaca* from the Poaceae family, *Peucedanum* genus from the Apiaceae family and *Filipendula vulgaris* from the Rosaceae family, accounting for 7.9%. In total, 19 herbaceous species were identified, representing 18 genera across 11 families. The most diverse family was Asteraceae, with six species from five genera. The Rosaceae family was represented by three species from two genera, while the Fabaceae family included two species from two genera.

Birch forest. The total weight of air-dried herbaceous vegetation was 47.7 ± 14.8 g/m². The predominant species were *Peucedanum* from the Apiaceae family – 37.5%. The Poaceae family accounted for 35.0%, the Rosaceae family for 20.7%, and the Fabaceae family for 4.6%. The dominant species were *Rubus saxatilis* from the Rosaceae family (15.7%), *Poa pratensis* (14.7%), and *Phleum phleoides* (13.8%) from the Poaceae family. In total, 22 species from 21 genera and 8 families were identified. The families Rosaceae and Fabaceae exhibited the highest species diversity, with five species representing five genera. The Poaceae family included four species from four genera, while the Asteraceae family had four species from three genera.

Aspen forest. The total weight of the air-dried sample was 46.9 ± 15.0 g/m². The Poaceae family dominated, accounting for 56.1%, followed by the Rosaceae family – 34.3%. With 2.5%, the Asteraceae family had the lowest abundance. The most prevalent species were *Rubus saxatilis* from Rosaceae family (29.2%), and *Dactylis glomerata* (29.2%), *Phleum phleoides* (7.7%), *Alopecurus pratensis* (6.4%) and *Festuca valesiaca* (6.2%) from the Poaceae family. In total, 25 species representing 20 genera and 10 families were identified. The highest species diversity was observed within the Poaceae family, with six species from six genera, followed by the Asteraceae with five species from four genera, and the Rosaceae and Fabaceae with three species from two genera.

Non-forested areas encompassed a range of land uses, including arable lands, pastures, clearings, burnt areas, and other. Among these, the highest biomass of herbaceous vegetation was measured in the areas with planted currants (201.6 g/m²) and sea buckthorns (170.2 g/m²), as well as in the burnt areas (195.1 g/m²).

Grazing pressure

The biomass of herbaceous vegetation showed significant variation inside and outside of the enclosure, indicating that high grazing pressure was present inside of the enclosure (Fig. 3). In Scots pine forests, herbaceous vegetation was 15.6% lower inside than outside of it. In birch forests, herbaceous vegetation biomass was 15.9% lower inside than outside of the enclosure, in aspen forests 37.1% lower, in the clearings 22.1% lower. In swamps, observed grazing pressure was most severe. The biomass of herbaceous vegetation inside accounted to 18.2% of the total biomass outside of the enclosure. In the enclosures, swamps had 81.8% lower vegetation biomass compared to the outside areas. On average, the biomass inside of the enclosure exhibited a 17.1% decrease compared to the areas outside of the enclosure.

DISCUSSION

Our findings demonstrated the impact of ungulates on both woody and herbaceous vegetation within the enclosures. It is also important to recognise varying consumption rates among different ungulate species. Assessing the population size within the enclosures is a key element for the preservation of forest-steppe ecosystems. Danilkin (1999, 2002, 2005) studied the average consumption of herbaceous vegetation by different ungulate species in large enclosures (Table 5). According to these studies, the biomass of herbaceous vegetation of 4,766

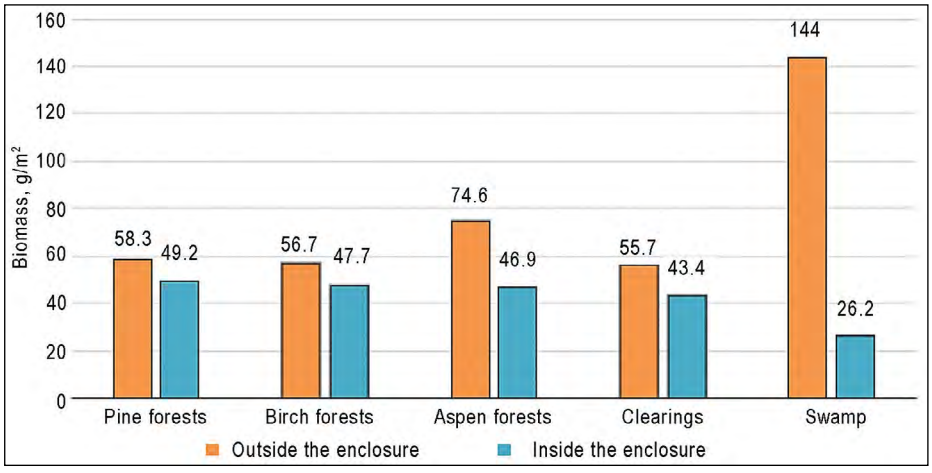

Fig. 3. Comparison of the biomass of herbaceous vegetation between different land cover types inside and outside of the enclosure, g/m²

Table 5. **Average consumption of dry mass of herbaceous vegetation by different ungulate species during the snowless period from April to October (214 days) in the enclosure (8.669 ha) (Danilkin 1999, 2002, 2005)**

Species	Average herbaceous vegetation consumption of an adult animal per day (dry forage), kg	Average herbaceous vegetation consumption during the snowless period, t
Moose (*Alces alces* Gray)	2.3	55.6
Maral (*Cervus elaphus sibiricus* Severtzov)	3.5	97.4
Siberian roe deer (*Capreolus pygargus* Pallas)	0.9	77.4
Wild boar (*Sus scrofa* L.)	0.33	8.5
Wood bison (*Bison bison athabascae* Rhoads)	10	134.8
European fallow deer (*Dama dama* L.)	1.1	21.2

tons within enclosure during the snowless period from April to October permits an increase in the herbivore population. On average, six ungulate species collectively consume 394.9 tons of herbaceous vegetation, which is 8.3% of the total enclosure biomass. However, to obtain more precise and comparable dry mass data, it's essential to use high-temperature drying methods or specialized equipment such as dryers or desiccators. Since we only air-dried the collected samples at room temperature, we could not determine the exact dry mass of the vegetation as an undetermined amount of moisture remained in the samples.

In comparison, our results indicated that, on average, the damage to different tree and shrub species within the enclosure accounts to 29.4%, ranging from 20% to 100%. During the dormant season, which spans from October to April, animals within the enclosures are provided with forage. It alleviates browsing pressure of tree and shrub shoots.

According to Erdös et al. (2018), Eurasian forest-steppes cover extensive areas across the continent. Based on several factors, including vegetation, physiognomic features, climatic and relief characteristics, the authors categorised forest-steppes. The 'Elen' hunting estate is located in northern Kazakhstan and the West Siberian geographical region identified as 'Region D'. Hence, for the purpose of comparison, we opted to consider the guidelines governing ungulate population densities in enclosures in both Kazakhstan and West Siberia (Table 6). In Kazakhstan, guidelines were developed to determine the optimal ungulate density, considering the quality of the habitat (Guidelines for the Conduct of On-Farm Hunting Management in the Kazakh SSR 1991). In the neighbouring West Siberian forest-steppes, the maximum ungulate density in the enclosures was determined by taking maximum, minimum, and economically sustainable ungulate population size into account (Order of the Ministry of Natural Resources and Environment of the RF 2020), although, there is no reference to the quality of the habitat. Comparing Kazakhstan and West Siberia, it is evident that the recommended ungulate densities differ significantly. However, these differences can be attributed to the way maximum population sizes were determined. In Kazakhstan, the guidelines focus on maintaining the optimal ungulate population, whereas in West Siberia, guidelines determine the maximum number of animals.

Following the guidelines for Kazakhstan, the population of moose, maral and Siberian roe deer within the 'Elen' enclosures exceed the recommendations. The wild boar population is well-maintained, whereas the population densities of wood bison and European fallow deer are unregulated. The guidelines for West Siberia present a contrasting perspective: based on West Siberian guidelines, all ungulate species appear to have well-maintained populations.

Table 6. **Comparison of ungulate density within the 'Elen' estate enclosures and population size guidelines established in Kazakhstan and West Siberia, animals/1000 ha**

Species	Population density in the 'Elen' enclosures, animals/1000 ha	Population density guidelines, animals/1000 ha	
		Kazakhstan	West Siberia
Wood bison	7.3	–	20
Wild boar	13.7	20	20
Moose	13	6	18
Maral	15	10	40
European fallow deer	10.4	–	50
Siberian roe deer	46.4	20	80

CONCLUSIONS

In the 'Elen' hunting estate forests, the dominant tree species are Scots pine, silver birch, and downy birch. Other tree species such as aspen, ash-leaved maple, Siberian elm, and Siberian crab apple were also observed. Shrub species include Tatarian honeysuckle, willows, Siberian pea-shrub, thicket shadbush, and golden currant. The herbaceous vegetation is comprised of 107 herbaceous species from 63 genera and 23 families. Majority of herbaceous species were identified in the Asteraceae, Poaceae, Fabaceae and Rosaceae families.

In the enclosures, ungulate browsing and grazing significantly affects vegetation. The extent of damage to trees and shrubs ranges from 20% to 100%, with an average damage rate of 29.4%. The biomass of herbaceous vegetation in the enclosure is, on average, 17.1% (15.6–81.8%) lower than outside. Mitigation of grazing and browsing pressure during the dormant season necessitates implementation of regular ungulate feeding.

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Aleksandr P. Berber, Artūras Kibiša

KANOPINIŲ GYVŪNŲ SUKELTI MIŠKO-STEPIŲ AUGMENIJOS POKYČIAI APTVARUOSE

Santrauka

Aptvarai kanopiniams gyvūnams dažniausiai įrengiami laukinei gamtai stebėti ir apsaugoti, medžioklei, žvėrienos produkcijai. Šiame tyrime analizuojamas „Elen“ medžioklės ūkis, esantis Šiaurės Kazachstane. Pagrindiniai mūsų tikslai – nustatyti aptvare esančios žolinės ir sumedėjusios augmenijos įvairovę ir gausą. Tyrime atskleidžamas kanopinių gyvūnų poveikis skirtingoms augalų grupėms ir jų bendrijoms, taip pat ekosistemos dinamikai Kazachstano miškastepėje. Kartu siekėme įvertinti kanopinių gyvūnų skabymo ir ganymosi pasekmes. „Elen“ medžioklės ūkyje įrengtame aptvare vyravo paprastoji pušis (*Pinus sylvestris*), karpotasis beržas (B*etula pendula*) ir plaukuotasis beržas (*Betula pubescens*). Nustatytos 107 žolinės augmenijos rūšys, priklausančios miglinių (lot. *Gramíneae*), viksvuolinių (lot. *Cyperaceae*), astrinių (lot. *Asteraceae*), varpinių (lot. *Poaceae*), ankštinių (lot. *Fabaceae*) ir erškėtinių (lot. *Rosaceae*) augalų šeimoms. Tyrimas atskleidė, kad kanopiniai gyvūnai gerokai pažeidžia tiek medžius ir krūmus (vidutiniškai pažeista 29,4 % (20–100 %) sumedėjusios augalijos), tiek ir žolinę augaliją (vidutiniškai pažeista 17,1 % (15,6–81,8 %) augalijos). Šio tyrimo rezultatai suteikia vertingų įžvalgų nustatant optimalų kanopinių gyvūnų populiacijos dydį aptvaruose ir prisideda prie miškastepių augmenijos išsaugojimo.

Raktažodžiai: kanopiniai gyvūnai, aptvaras, mitybos ištekliai, medžiai ir krūmai, žolinė augmenija, skabymo ir ganymosi poveikis, miškastepė