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UNGULATES IN THE ZALISSIA NATIONAL NATURE PARK: STATIONS OF EXISTENCE AND SEASONAL CHANGES IN BEHAVIOUR

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Abstract

The distribution and seasonal behavioural changes of ungulates in the Zalissia National Nature Park were investigated. In 2025, the two most numerous species were the red deer (932 individuals) and the sika deer (782 individuals); the populations of fallow deer (212 individuals) and European roe deer (187 individuals) were significantly smaller, while the Eurasian elk (30 individuals) and European bison (14 individuals) groups remained in a depressed state. The localisation of specific ungulate species within the park is linked to species-specific requirements for the foraging and protective properties of the habitats. The study of animal habitats was based on forestry methods, in particular on parameters of the forest site type—trophotope (soil fertility tiers), hygrotope (soil moisture regimes)—and on the dominant tree species, stand age group, understorey density, and ground cover density. The distribution of red deer covers the central, southern, and north-eastern parts of the Park, dominated by mature and maturing pine stands with a sparse lower layer of forest vegetation but decent grass cover; the site conditions type is fresh, fairly fertile pine–oak site (B_2). The sika deer occupies the north-western part of the Park, which is dominated by black alder swamp forests with dense undergrowth and rich herbaceous cover; the site conditions type is wet fertile oak–hornbeam site (C_4). The Eurasian elk occurs sporadically in small patches of deciduous forest or in dense deciduous undergrowth beneath a pine canopy in the north-east and south-east of the Park; the site condition type is fresh, fairly fertile pine–oak site (B_2). The distribution of roe deer and fallow deer is confined to the poorest habitats—dry infertile pine site (A_2), dominated by pine-green moss-lichen associations with minimal development of undergrowth and ground cover. The specified lands are widespread on the periphery of the park, where roe deer occur, as well as in the centre of the estate, where fallow deer are localised. The European bison herd is primarily located in the north-eastern part of the Park, inhabiting mature pine stands with developed undergrowth; the forest site type is wet infertile pine site (B_3).

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Ратичні в Національному природному парку «Залісся»: стації існування та сезонні зміни поведінки

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Резюме. Досліджено поширення та сезонні зміни поведінки ратичних на території національного природного парку «Залісся». У 2025 р. найчисельнішими були два види — олень благородний (932 ос.) та олень плямистий (782 ос.); значно меншу чисельність мали лань (212 ос.) і сарна європейська (187 ос.), тоді як угруповання лося європейського (30 ос.) і зубра (14 ос.) перебували у депресивному стані. Локалізація окремих видів ратичних на території Парку пов'язана з видоспецифічними вимогами до кормозахисних властивостей угідь. В основу досліджень стацій існування тварин покладено лісівничі методики, зокрема тип умов місцезростання — трофотоп (рівень багатства ґрунту), гігротоп (режими вологості ґрунту), а також — домінуюча деревна порода, вік групи насаджень, щільність підліску та щільність надґрунтового покриву. Поширення оленя благородного охоплює центральну, південну та північно-східну частину Парку, де переважають стиглі та пристигаючі соснові насадження з бідним нижнім ярусом лісової рослинності, але пристойним трав'яним покривом; тип умов місцезростання — свіжий субір (B_2). Олень плямистий займає північно-західну частину Парку, де переважають чорновільхові заболочені насадження з густим підліском та багатим трав'яним покривом; тип умов місцезростання — сирий сугруд (C_4). Лось зустрічається епізодично у невеликих острівцях листяного лісу, або ж у густому підліску листяних порід під наметом сосни на північному сході та південному сході Парку; тип умов місцезростання — свіжий субір (B_2). Поширення сарни і лані приурочене до найбідніших угідь — сухих борів (A_2), де переважають сосново-зеленомохово-лишайникові асоціації з мінімальним розвитком підліску та надґрунтового покриву. В даному разі даються взнаки конкурентні стосунки з благородним оленем, який витісняє їх у стації з гіршими кормо-захисними характеристиками. Вказані угіддя поширені на периферії Парку, де трапляється сарна, а також в центрі господарства, де локалізується лань. Стадо зубрів дислокується, переважно, у північно-східній частині Парку — в стиглих соснових насадженнях з розвиненим підліском; тип умов місцезростання — вологий субір (B_3).

Ключові слова: ратичні, лісові насадження, поведінка, біотоп, сезон, НПП «Залісся».

Introduction

The greater part of the Zalissia National Nature Park (hereinafter referred to as the Park) is located within Brovary Raion, Kyiv Oblast, while a smaller part extends into the territory of Chernihiv (formerly Kozelets) Raion, Chernihiv Oblast. The predominant part of the Park's territory (12.5 thousand hectares) is enclosed by a wire mesh fence, which results in the semi-free keeping of wild animals in accordance with the Law of Ukraine 'On Hunting Economy and Hunting'. The lands are differentiated into four research and production departments that have retained the names of their predecessor forest departments: Desnianske, Litkivske, Rozhnianske, and Zalisske (Fig. 1).

A typical feature of the Park is the prevalence of forest landscapes (10.2 thousand hectares), which are primarily composed of pine (*Pinus sylvestris*) and pine–oak (*Quercus robur*) forests. Smaller areas are occupied by oak and oak–hornbeam (*Carpinus betulus*) (850 ha) forests, birch (*Betula pendula*) (250 ha) forests, and black alder (*Alnus glutinosa*) (600 ha) forests. In small areas, there are formations of aspen (*Populus tremula*), ash (*Fraxinus excelsior*), sharp-leaf willow (*Salix acutifolia*), etc. The understorey consists of European rowan (*Sorbus aucuparia*), red redberry elder (*Sambucus racemosa*), black cherry (*Prunus serotina*), and common hazel (*Corylus avellana*).

The distribution of vegetation within the Park is characterised by pronounced heterogeneity. Dry infertile pine site (A_2)—open-canopy woodlands with low stand density and sparse undergrowth—are distributed in the central part and, in places, also on the periphery. Overcrowded pine stands occur locally on the peripheral areas, and their high density negatively impacts both the forest understorey and herbaceous vegetation. The most common forest type in the southern and northeastern parts is fresh fairly fertile pine–oak site (B_2); wet infertile pine site (B_3) occurs sporadically.

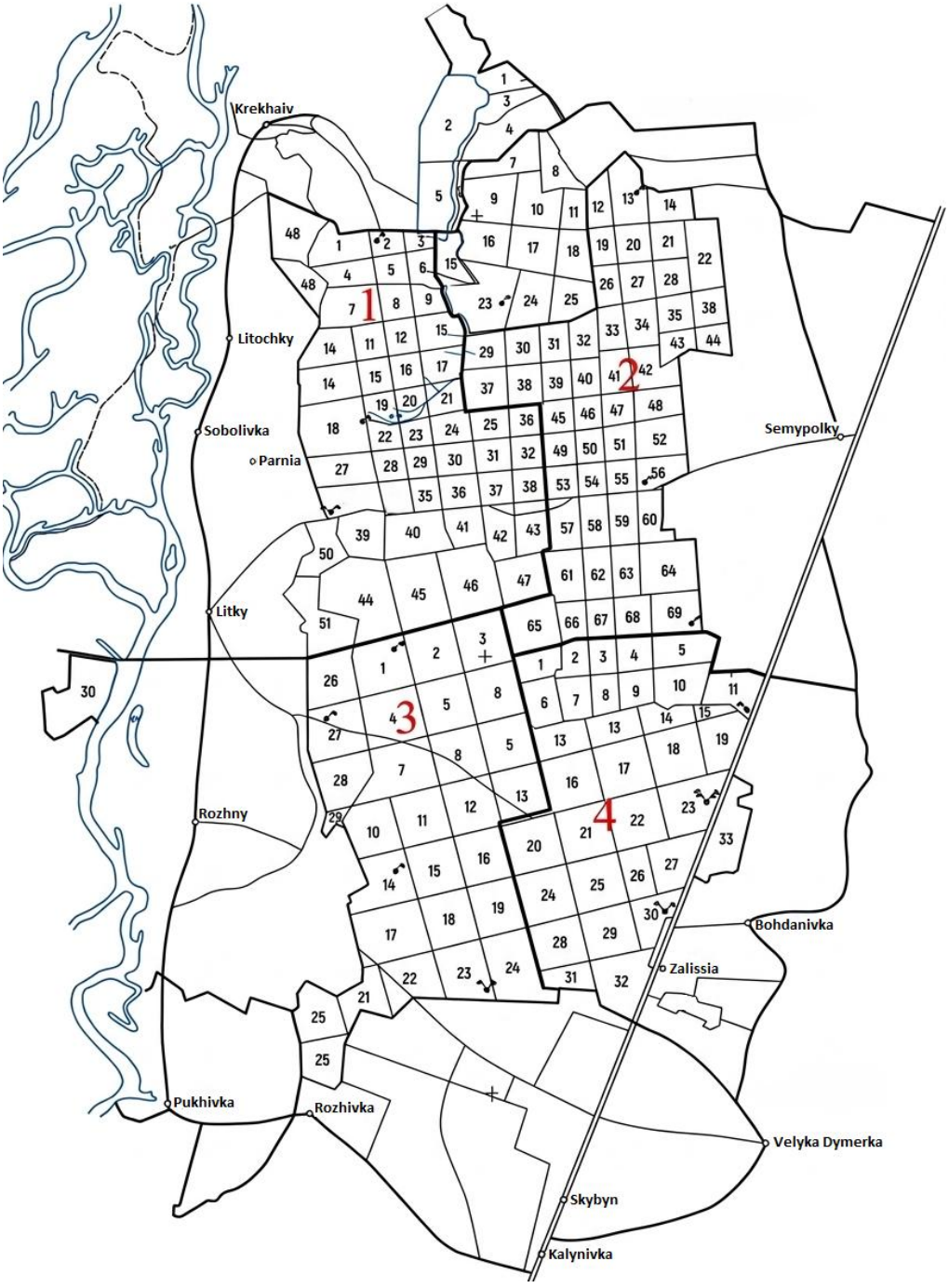

Fig. 1. Subdivision of the Zalissia National Nature Park into structural units: (*1*) Desnianske; (*2*) Litkivske, (*3*) Rozhnianske; and (*4*) Zalisske departments.

Рис. 1. Поділ національного природного парку «Залісся» на структурні одиниці: (*1*) Деснянське; (*2*) Літківське, (*3*) Рожнянське; та (*4*) Заліське відділення.

The most common forest type in the southern and northeastern parts of the park is fresh fairly fertile pine–oak site (B_2); wet infertile pine site (B_3) occurs sporadically. The northwestern part of the Park is characterised by excessive moisture, which leads to the distribution of wet fertile oak–hornbeam site (C_4).

Effective management of ungulate populations requires a detailed analysis of their habitat preferences, as habitat selection directly affects species survival and reproductive success. Contemporary research indicates significant species-specificity in habitat use, which is determined by the balance between food availability, cover properties of the grounds, and anthropogenic pressure.

The European bison (*Bison bonasus*) was originally an inhabitant of open landscapes but was forced into forested areas under anthropogenic pressure [Bocherens *et al.* 2015; Llamas *et al.* 2025]. Telemetry studies revealed that within the forest interior, European bison prefer habitats with low canopy cover, clearings, and disturbed areas with well-developed herbaceous cover [Klich *et al.* 2023].

Optimal habitats for the Eurasian elk (*Alces alces*) include areas with wetlands, alder groves, and natural shrubby meadows [Cederlund & Okarma 1989; Smagol *et al.* 2012]. A critical factor in habitat selection during the summer period is the presence of a dense forest canopy, which is used as a thermal shelter to prevent heat stress. Winter distribution shifts toward young pine stands and early-successional clearcuts that provide maximum availability of woody browse [Courtois *et al.* 2002; Nikula *et al.* 2004]. The sika deer (*Cervus nippon*) is also characterised by its affinity for dense, often humid forest habitats with a well-developed shrub layer [Carden *et al.* 2010; Saggiomo *et al.* 2020]. The authors point to the aggressiveness of the species, which allows it to compete effectively for habitats with native cervids.

Unlike the previous species, the European roe deer (*Capreolus capreolus*) selects forest edges, sparse shrubs, and young stands [Hofmann 1989; Zorzi *et al*. 2022]. Habitats with high biodiversity of the understorey and ground cover determine its optimal biotopes. An important aspect of the habitat distribution of roe deer is competitive exclusion: at high densities of red deer (*Cervus elaphus*), roe deer are forced to shift to suboptimal habitats with poorer foraging characteristics [Torres *et al.* 2012; Mysłajek *et al.* 2024]. The fallow deer (*Dama dama*) also prefers open deciduous forests with rich ground vegetation and open pastures [Nugent 1990; Focardi *et al.* 2006], making its ecological niche similar to that of the roe deer, which often leads to the spatial displacement of the latter.

Among all ungulates, the red deer exhibits the highest habitat plasticity. However, the distribution of these animals is differentiated by the time of day: during the day they select sheltered habitats with dense forest cover, whereas at night they move to open meadows and agricultural lands [Donini *et al.* 2025]. Human activity is the primary driver forcing deer to avoid potentially rich foraging sites during the day.

The aim of this study was to analyse the specifics of habitat use by ungulates within the Park, where the fenced area and high animal density provide a unique background for investigating interspecific competition and the transformation of behavioural strategies.

Materials and Methods

When studying the habitats of ungulates, the forest-growing conditions of the animals' localities were assessed, and the silvicultural and inventory descriptions of individual forest stands were analysed, among other factors. The grouping of forest lands was carried out taking into account the forest typology adopted by forest management in Ukraine. The forest site type (FST) was determined according to the Alekseev–Pogrebnyak forest typological classification [Pohrebniak 1959]. Against this background, the seasonal biotopic distribution of individual species was studied, taking into account the sex and age structure of their populations.

An ecological and silvicultural assessment of animal concentration sites was performed based on the analysis of forest management data, followed by itinerary-reconnaissance surveys of the areas using generally accepted field techniques in accordance with the 'Guidelines for Management of Hunting Grounds' (2002). A comparative analysis of ungulate concentration sites was conducted.

Studied habitats were characterised by six indicators: (1) parameters of the forest site type (FST)—trophotope (A...D soil fertility tiers: infertile, fairly fertile, fertile, and very fertile), (2) hygrotope (0...5 soil moisture regimes: dry, fresh, moist, wet, damp, swampy), (3) the dominant tree species, (4) stand age group, (5) understorey density, and (6) ground cover density.

In this study, the terms *biotopes* (relatively homogeneous landscape areas with characteristic abiotic conditions such as soil, water, and climate, occupied by a specific community of living organisms, or biocoenosis), *stations of existence* (specific environmental areas providing the necessary set of conditions, including climate, topography, food, and shelter for the existence of a particular animal species), and *habitats* (land or water areas permanently or temporarily occupied by populations of a specific species of plants, animals, or other organisms) are used interchangeably, as the authors see no significant difference between them in the given context.

Results

The distribution of certain ungulate species within the Park is linked to their species-specific requirements for the foraging and shelter characteristics of the habitats, which leads to the differentiation of their communities even within a relatively small area.

Status of ungulate communities

Currently, the ungulate fauna of the Park comprises six species, four of which are native— European roe deer, Eurasian elk, red deer, and European bison (the latter two re-introduced)—and two are acclimatised: fallow deer and sika deer.

The most numerous species (based on 2025 data) are the red deer (932 individuals) and the sika deer (782 individuals), which have taken a dominant position in the Park's faunal complex. The numbers of the European roe deer (187 individuals) and the Eurasian elk (30 individuals) have significantly decreased during the enterprise's existence as a result of changes in the structure of natural habitats [Smagol *et al.* 2005]. The populations of fallow deer (212 heads) and the European bison (14 heads) on the Park's grounds have never reached high numbers.

Until 2015, the wild boar (*Sus scrofa*) was a typical representative of the local faunal complex; however, an outbreak of African swine fever (*Pestis africana suum*) drastically reduced the species' population, and radical measures to control the epizootic put an end to its existence within the Park.

The distribution of ungulates during the spring–summer season

During the most favourable season, the seasonal distribution of the red deer covers the central, southern, and north-eastern parts of the Park, which correspond to the territories of the Zalisske, Rozhnianske, and Litkivske departments. Thus, during the spring and summer seasons, the red deer is widespread throughout most of the Park's territory. At the same time, the highest concentration of the species was observed in the central and south-eastern quarters.

The spring–summer habitat of the sika deer also covers a considerable area of the Park, but it is more localised compared to that of the red deer occurring only in the north-west (Desnianske department). During the aforementioned season, the distribution patterns of both species are primarily determined by female behaviour, specifically by calving and nursing. During this period, practically all ungulate species show the least tendency to form large groups. Females lead a solitary lifestyle, moving only short distances, and their home ranges have the smallest area [Smagol 2001]. The vast majority of pregnant and lactating females stay in local pockets with the highest concentration of conspecifics. The location of these foci is repeated year after year. Such local biotopes are limited in area, yet they possess a complete set of 'key' characteristics specific to each species: the protective properties of the habitats, a significant abundance and appropriate species composition of forage, the availability of watering places, and a low abundance of blood-sucking insects, among others.

The concentration centres of red deer are located primarily in mature and premature pine stands with thinned undergrowth (Fig. 2 *a*), which have a high site index for this animal species. Thus, within the forest-covered area, these indicators depend entirely on the silvicultural and mensuration characteristics of the biotopes (Table 1).

In areas where the biotopes of red and sika deer overlap, a phenomenon of contiguous allopatry is observed [Dajoz 1990], where the ranges and ecological niches of closely related species do not overlap, but are not completely isolated either.

Table 1. Ecological and silvicultural characteristics of ungulate habitats in the Park during the spring–summer period
Таблиця 1. Еколого-лісівничі характеристики середовищ існування копитних в Парку у весняно-літній період

Species	FSC		Dominant tree species	Age group	Understory density	Density of grass cover
	Trophotope	Hygrotope				
Cervus elaphus	B	2	*Pinus sylvestris*	Maturing	Sparse	Medium
Alces alces	B	2	*Pinus sylvestris*	Mature	Dense	Sparce
Cervus nippon	C	4	*Alnus glutinosa*	Middle-aged	Dense	Dense
Capreolus capreolus	A	2	*Pinus sylvestris*	Middle-aged	Sparse	Sparse
Dama dama	A	2	*Pinus sylvestris*	Middle-aged	Sparse	Sparse
Bison bonasus	B	3	*Pinus sylvestris*	Mature	Medium	Medium

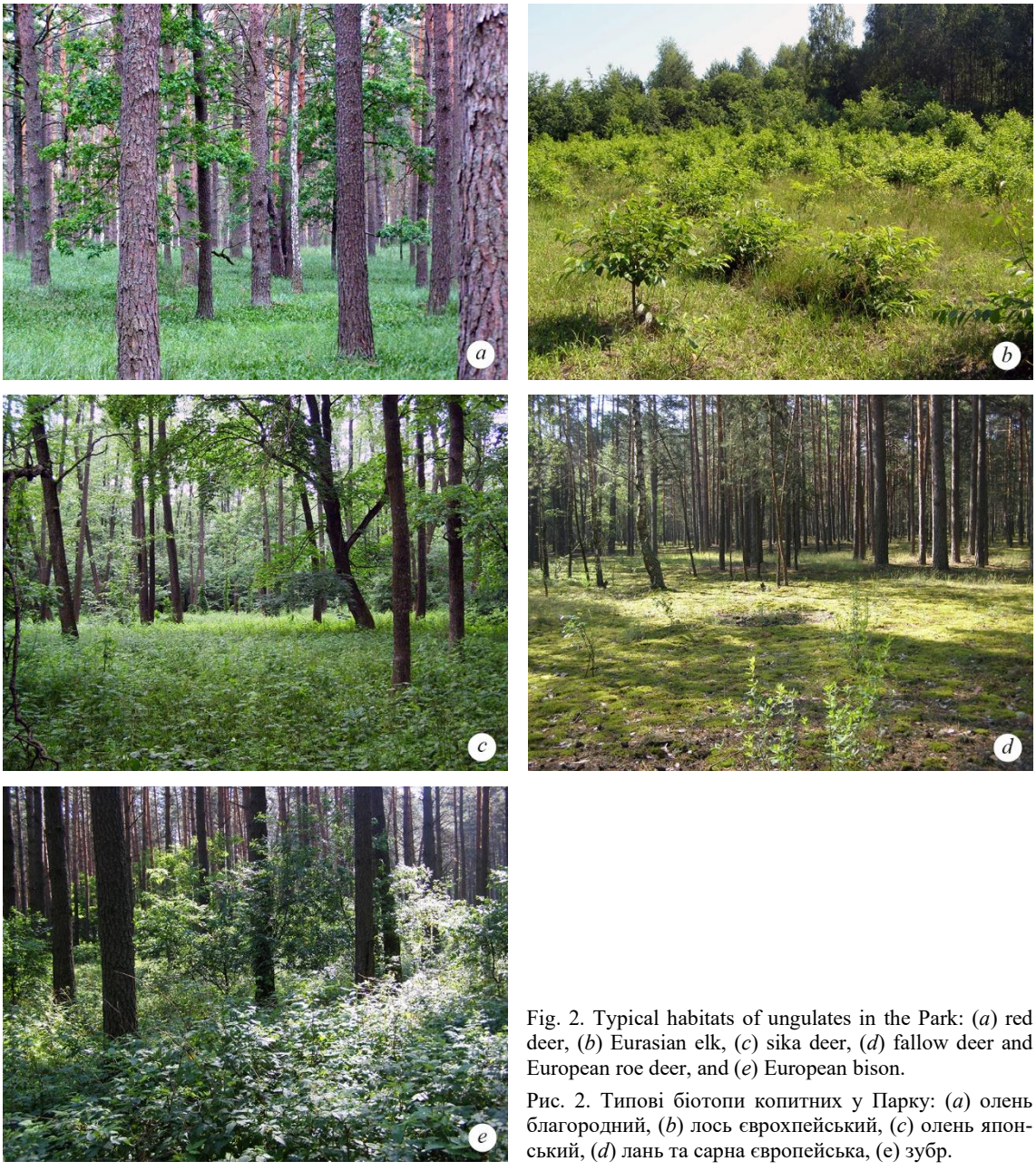

Fig. 2. Typical habitats of ungulates in the Park: (*a*) red deer, (*b*) Eurasian elk, (*c*) sika deer, (*d*) fallow deer and European roe deer, and (*e*) European bison.

Рис. 2. Типові біотопи копитних у Парку: (*a*) олень благородний, (*b*) лось єврохпейський, (*c*) олень японський, (*d*) лань та сарна європейська, (е) зубр.

In this case, habitat sharing occurs only between the males of both species. Females are rarely recorded in zones of species intergradation. This phenomenon can be explained by the fact that male deer have home ranges three times larger than those of females [Kamler *et al.* 2008]. Furthermore, males are less attached to 'key' habitats than females with offspring.

Determining the ranges of Eurasian elk within the Park is quite difficult, given their low numbers and lack of tendency to form groups. It is only possible to speak of certain trends related to the dispersed distribution of pine stands, small islands of deciduous forest (birch, aspen) (Fig. 2 *b*), or a dense understorey of broadleaved species (hazel, black cherry) under the pine canopy. Consequently, Eurasian elk are most frequently encountered in the south-eastern compartments of the Zalisske department, and less commonly in the northern compartments of the Litkivske department. Characteristically, the association of the elk with the aforementioned habitats shows virtually no seasonal variations.

Under natural conditions, the Eurasian elk prefers riparian willow stands, deciduous forests with well-developed undergrowth and tall herbs, as well as wetlands overgrown with willows and stunted pine [Smagol *et al.* 2012]. However, the corresponding ecological niche with wet biotopes within the Park is occupied by the sika deer, which gravitates toward black alder wetlands with dense undergrowth and rich herbaceous cover (Fig. 2 *c*).

The distribution of roe deer within the Park is confined to the poorest habitats in terms of foraging and shelter properties—fresh and dry pine forests dominated by pine–green moss–lichen associations (Fig. 2 *d*). The aforementioned lands are located along almost the entire periphery of the Park; however, the locations where roe deer are most frequently encountered during the spring–summer period are situated in the far south, north, and north-east. In this case, competitive relationships with larger species are taking a toll, primarily with the red deer, which displaces the roe deer into inferior foraging habitats [Smagol & Yarysh 2017].

The habitats of fallow deer in the territory of the Park, according to their ecological and silvicultural characteristics, are similar to those of roe deer, but the location of the fallow deer is limited to a small area in the central management unit. During the spring and summer periods, the European bison herd is located mainly in the north-eastern part of the Park (Litkivske department). In the second half of summer, European bison are also occasionally recorded in the southern quarters. At the same time, despite extensive movements, the forest inventory characteristics of the species habitats remain unchanged, being mature pine stands with a well-developed understorey (Fig. 2 *e*).

Analysis of the spring–summer distribution of ungulates within the Park demonstrates that:

- under conditions of excessive population density, most species maintain territorial segregation due to the intensive occupation of only their characteristic biotopes;
- the overlap of habitats of taxonomically close species (red deer and sika deer) in uncharacteristic biotopes occurs solely due to adult males; accordingly, females with offspring remain in the most optimal habitats.

The distribution of ungulates during the autumn season

The dispersal of most artiodactyl species during the mentioned period was driven by the intensification of reproductive processes, accompanied by corresponding behaviour: mating of males and females occurs; antagonistic relationships, characterised by ritualised combat, are observed among males [Smagol & Stekleniov 2003; Stekleniov 2006].

Males of fallow deer, sika deer, and red deer are distinctly polygamous, meaning that each of them mates with several females during the rutting season. As a rule, male deer form a common mating territory (so-called 'lek'), placing their individual areas next to each other, where they try to keep the females for as long as possible [Apollonio 1989; Carranza 1992]. The population density of a given species drives the concentration of males in such limited areas.

The association of such mating territories with the rutting season largely corresponds to the areas of spring–summer female concentration, where they give birth and nurse their offspring. It can be confidently stated that throughout the autumn period, only the distribution of males changes, with

the majority of them also concentrating in the aforementioned pockets during the rutting season. During the rut, the vast majority of males of both species gather in their mating territories regardless of age or potential reproductive success. Therefore, it is in the autumn that the highest level of population differentiation is observed, exhibiting a classic case of species allopatry. The locomotor activity of males reflects only their sexual behaviour (courtship displays, tournament fighting, etc.); other motor acts, and in particular movement in search of food, are minimised.

Thus, over a significant area of the Park, particularly in those habitats shared by male red deer and sika deer in summer, they are practically not recorded in autumn. This points to a temporary (seasonal) emptying of the respective ecological niche. However, according to the rule of mandatory occupation of ecological niches [Dedyu 1990], this phenomenon is temporary. The vacated functional niche of a species in a biocoenosis is immediately filled by another ecologically close species, the roe deer.

Unlike true deer (genus *Cervus*), the roe deer's sexual activity spans the summer months; therefore, areas of spring concentration where females give birth (i.e., the peripheral areas of the Park) become the arena for the rut of this ungulate species in summer. With the onset of autumn (the deer rutting season), roe deer begin to occur across the entire central area of the estate, overlapping the summer intergradation zone of sika and red deer.

As previously mentioned, in spring and summer, roe deer and fallow deer occupy habitats with similar silvicultural characteristics (see Table 1). The difference lies in their location. Fresh and dry pine forests occupy the peripheral areas of the estate (where roe deer stay) and its small central part (which is a concentration site for fallow deer).

Interestingly, roe deer sporadically appear in the autumn within the fallow deer's range, a phenomenon likely driven by changes in the latter's movement behaviour. During the rut, fallow deer males (like other deer species) eat virtually nothing and lose up to a third of their body weight [Apollonio *et al.* 1994]. This phenomenon can be explained by the significant energy expenditure required for finding females, complex mating rituals, and antagonistic interactions with competitors. Thus, a significant portion of forage resources in the fallow deer's range becomes available to the roe deer.

The European bison herd undergoes certain habitat shifts, moving north-west in autumn (Desnianske department) [Smagol & Gavris 2013], where they can be found in meadows and birch woodlands.

Summarising the observations throughout the autumn period, we conclude that the most abundant ungulate species exhibit a pronounced differentiation of their stations of existence, which is primarily driven by male behaviour and associated with the activation of their reproductive processes. Instead, the stand characteristics of the habitats of red deer, sika deer, and fallow deer do not differ during the spring–summer and autumn seasons. Probably, the same could be said about the Eurasian elk, if encounters with it were not so sporadic in the same territory throughout the year.

The study of the autumn distribution of ungulates leads to the following conclusions:

- as a result of increased sexual activity, male red and sika deer become more attached to key habitats, leading to the complete separation of their ranges;
- in autumn, the roe deer becomes more widespread, occupying the spring–summer intergradation zone of the red deer, and sika deer;
- the silvicultural characteristics of the habitats of Eurasian elk, fallow deer, red deer, and sika deer remain almost unchanged in autumn, as well as in spring and summer;
- the pressure on plant communities within these sites does not increase because during the rutting season, male deer consume virtually no food for nearly 1.5 months.

Winter season

With the establishment of snow cover, most ungulate species lose connection with their characteristic biotopes and inhabit areas only around feeding stations. Indicators such as protective traits, sexual activity, or care for offspring lose their significance. The sole priority factor for locomotor

activity is foraging. At the same time, it is necessary to note the territorial attachment of certain species to the sites of their spring–summer–autumn stay. That is, animals concentrate near feeding stations without leaving their key habitats, which lack distinct forest inventory characteristics in winter.

The Eurasian elk is the only ungulate species that does not exhibit seasonal movements related to seasonal changes in food resources. This species is a typical dendrophage, so its association with young pine stands is most justified precisely during the winter period.

Discussion

The results of our research confirm that the localisation of individual ungulate species within the Park is associated with species-specific requirements for the foraging and sheltering properties of the habitats. The red deer demonstrates the highest habitat plasticity, encompassing most of the territory; however, its affinity for fresh relatively fertile fresh fairly fertile pine–oak site (B_2) with mature pine stands indicates a selection of the most energetically profitable biotopes. Under such conditions, animals strike a balance between the availability of grass cover and the protective properties of thinned undergrowth.

The sika deer is localised in moist wet fertile oak–hornbeam site (C_4) in the north-western part of the Park, which correlates with data on its biology within its natural range. Instead, the high competitive ability of the sika deer allows it to effectively maintain these specific habitats, displacing potential competitors, such as the elk, into less favourable conditions.

The biotopes of roe deer and fallow deer are confined to the poorest lands—dry infertile pine site (A_2). As noted above, at high densities of red deer, both species are displaced into suboptimal habitats with poorer foraging characteristics. Within the Park's territory, we observe an identical pattern: the roe deer is forced to exist on the periphery, while the fallow deer occupies the central part, where extremely poor plant communities predominate, providing minimal forage resources but reducing the frequency of contact with larger competitors.

Within the Park, European bison are primarily located in moist wet infertile pine site (B_3) with dense undergrowth, which somewhat contradicts their natural preference for semi-open habitats. Therefore, the low abundance and limited reproductive capacity of the local population may result from the species residing in suboptimal conditions. The forest canopy limits the development of herbaceous cover, which is the basis of the European bison's diet.

The low population density of Eurasian elk correlates with data on their vulnerability to heat stress. In particular, elk experience discomfort at temperatures higher than 14–17°C [Moen *et al.* 1997; Romportl *et al.* 2017]. That is, in summer, the presence of a dense forest canopy as a thermal shelter is vital. Within the Park's grounds, the situation is further complicated by the fact that the habitats most suitable for cooling (alder groves, wetlands) are intensively utilised by sika deer. Thus, the Eurasian elk finds itself in a situation of dual pressure—climatic and competitive. Its occasional sightings indicate that the species is constantly searching for a suitable habitat.

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Declarations

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