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ORIGINAL ARTICLE

Habitat characteristics of European bison (*Bison bonasus*) in Ukraine

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Abstract
Beginning in the 1960s, restoration of the European bison (*Bison bonasus*) in Ukraine has resulted in seven herds with approximately 350 total individuals currently. For the first time, we describe characteristics of habitats used by these seven European bison herds located in forest, forest-steppe, and mountain zones of Ukraine. During the growing season across all ecological zones and herds, we observed variation in bison use of woodland and open habitats associated with temporal variation in landscape scale habitat characteristics. During winter across all ecological zones and herds, variation in habitat use declined dramatically with supplementary feeding that incentivized sedentary association with woodlands. Our descriptive field observations are intended to improve understanding of European bison landscape ecology and serve as a basis for additional quantitative investigations.

Keywords European bison · Restoration · Forest · Forest-steppe · Carpathian Mountains · Supplemental feeding

Introduction

With a wide muzzle, hypsodont teeth, and strong anterior jaw, the European bison (*Bison bonasus*) is adapted to consumption of a wide array of herbaceous and woody species (Mendoza and Palmqvist 2008), and is thus capable of a dynamic foraging ecology among mixed- and open-habitat types (Kowalczyk and Plumb 2020). Early investigations on European bison habitat ecology in mosaic-type forest and mountain landscapes have indicated that the species preferred broad-leaved or mixed forests (Perzanowski et al. 2008, Krasińska and Krasiński 2013). Kuemmerle et al. (2011) developed a range-wide framework of predictive broad scale factors characterizing European bison habitat suitability, and found that habitat conditions used by bison were much broader than previously reported. There is emerging evidence that the European bison is not a strict forest species, but rather, a generalist species that uses a variety of habitat types, including open natural areas and abondoned fields; and may exhibit selective preference for these areas depending on seasonal characteristics and availability at the landscape scale (Kuemmerle et al. 2018). Indeed, we actually know little about the characteristics of habitats used by the European bison across forest, forest steppe, and mountains zone outside Poland. Monitoring of bison restoration in Ukraine has heretofore focused on protection, health, conflict management, and initial home range mapping (Smagol 2019). Our objective is to provide the first detailed description of habitat characteristics for seven herds in order to address the extent that European bison utilize open and forested habitat across ecological zones in Ukraine.

Methodology

The forest landscapes for all seven bison herds in Ukraine are divided into square management units (usually 1 km^2) that are each bound by clear cut fire-breaks (3 to 5 m wide) that served as transects to access seasonal bison habitats for each herd (Smagol 2019). During 2019, we re-visited the seasonal home ranges for each herd described by Smagol (2019) to conduct field surveys for typological evaluation of forest habitats and geobotanical surveys of open habitats according to Guirs et al. (2004) and State Committee for Forestry of Ukraine (2002). We also utilized existing forest

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cover maps, along with field verification of forest condition and orographic peculiarities. It should be noted that seasonal habitat patterns for each herd have become well established with little inter-annual variation, and so we used Smagol (2019) as our initial starting reference from which we surveyed habitats along the network of fire-break transects to visually locate a herd that remained in the same general area during subsequent visits. In order to minimize disturbance to bison, we rarely left the fire-break transects. We thus consistently visually field-characterized main forest type, understory woody species, herbacious species, and soil surface vegetation cover (Pogrebniak 1959) at one randomly located site on the interior side of each of four fire-break transects bounding the 1-km^2 square management unit(s) being utilized by bison.

We characterized forest habitat soil richness by available phosphorus (P_2O_5) and potassium (K_2O) according to Migunova (2009): A (poor): P_2O_5 < 0.02%, K_2O < 0.03%; B (relatively poor): P_2O_5, 0.02–0.04%, K_2O, 0.03–0.06%; C (relatively rich): P_2O_5, 0.04–0.06%, K_2O, 0.06–0.2%; and D (rich): P_2O_5 > 0.06%, K_2O > 0.2%. We collected mixed soil samples by drill or shovel at 0–40 cm depth at 20 random points in a randomly selected area of at least 0.25 hectare in size and with at least 200 trees of the main forest species. We utilized a random sub-sample of the mixed soil sample to determine phosphorus on a photoelectric colorimeter KFK-2, and potassium on a ICAR 500-metering device. Soil moisture was characterized by available moisture (mm) according to Migunova (2009): 0 (very dry, < 200 mm); 1 (dry, 200–300 mm); 2 (fresh, 300–400 mm); 3 (moist, 400–500 mm); 4 (damp, 500–1000 mm); 5 (wet, > 1000 mm). At the same location used for phosphorus and potassium sampling described above, we used a hand-operated soil core drill to collect samples every 10 cm to a depth of 1.5 m. Soil samples were immediately transferred into aluminum containers with airtight lids and weighed on a laboratory electronic scale to 0.1 g accuracy. Soil containers were then left open to dry at 100–105 °C until stable weight was achieved, with soil moisture then calculated as a percentage of the weight of the dry sample. We field-classified forest maturity according to Soudiev et al. (1989) as "young" < 40 years, "middle-age" 40–60 years, "maturing" 60–80, and "matured" 80–100 years. While some old growth forests remain in Ukraine in the Carpathian Mountains, all forests currently inhabited by bison in Ukraine were planted by humans. We thus consulted detailed age-specific forest management maps where each bison herd is located. We field-characterized primary seasonal open habitat and meadow dominant species, and generic and species composition according to Afanasiev (1968) and Grygora and Solomakha (2000) in 3 to 10 100-m^2 plots (proportional to the total area) by visually identifying dominant families, e.g., Poáceae, Fabáceae, and Apiáceae; and individual species that clearly dominated sites. Soil richness and moisture for open habitats were determined as described above according to Migunova (2009).

Results

Tsumanska herd

This population of 19 individuals (EBPB 2020) is free-ranging on approximately 7000 ha at the State Enterprise "Kivertsi Forestry" (Smagol and Sharapa 2009) with distribution among the forest zone in the Volyn region (Marynych et al. 2003) (Fig. 1). During March–July, bison utilized mixed and maturing (C_3-B_3) oak (*Quercus* sp.) forests that also included birch (*Betula* sp.), alder (*Alnus* sp.), aspen (*Populus* sp.), and maple (*Acer* sp.) species. The understory was composed mainly of hazel (*Corylus* sp.), buckthorn(*Ramnus* sp.), and rowan (*Sorbus* sp.) (Table 1). During July–October, bison shifted to middle-aged and maturing ($C_{3\text{-}4}$) woodlands comprised primarily of alder and birch that also include mixed oak, aspen, hornbeam (*Carpinus* sp.) and ash (*Fraxinus* sp.), and closed ($D_{2\text{-}4}$) pine (*Pinus* sp.) and hornbeam-oak forests with sparse understory of buckthorn and hazel. Understory was dense hazel, buckthorn, blackberry (*Rubus* sp.), and various species of willows (*Salix* sp.) predominated with rare surface vegetation. Throughout the growing season, bison foraged primarily in patchily distributed and fragmented open areas, including peat meadows, oligotrophic rough meadows, and swamp meadows dominated by sedges (*Cyperaceae* sp.). During November–February, bison shifted from using native meadow habitats to concentrate near supplementary feeding stations (Table 1).

Zaliska herd

This population of 22 individuals (EBPB 2020) is semi-free ranging on approximately 3500 ha at the National Nature Park "Zalissja" (Sagaydak et al. 2006) in the forest zone in the north of the Kyiv region (Marynych et al. 2003) (Fig. 1). With the onset of spring during March–May, bison used peaty meadows characterized by low-middle quality grasses, and also reed (*Phragmites* sp.) and sedge associations in wet lowland bogs; and some use of relatively rare true and rough meadows found on drier sites (Table 1). Also during March–May, alder forests ($D_{4)}$ with mixed birch, aspen, and willow provided protective resting cover during non-foraging activities. During June–November, bison shifted to pine-oak (B_2-C_2) woodlands and foraged exclusively in extensive forest glades. During December–February, bison exclusively located near supplementary feeding stations until the onset of spring meadow phenology.

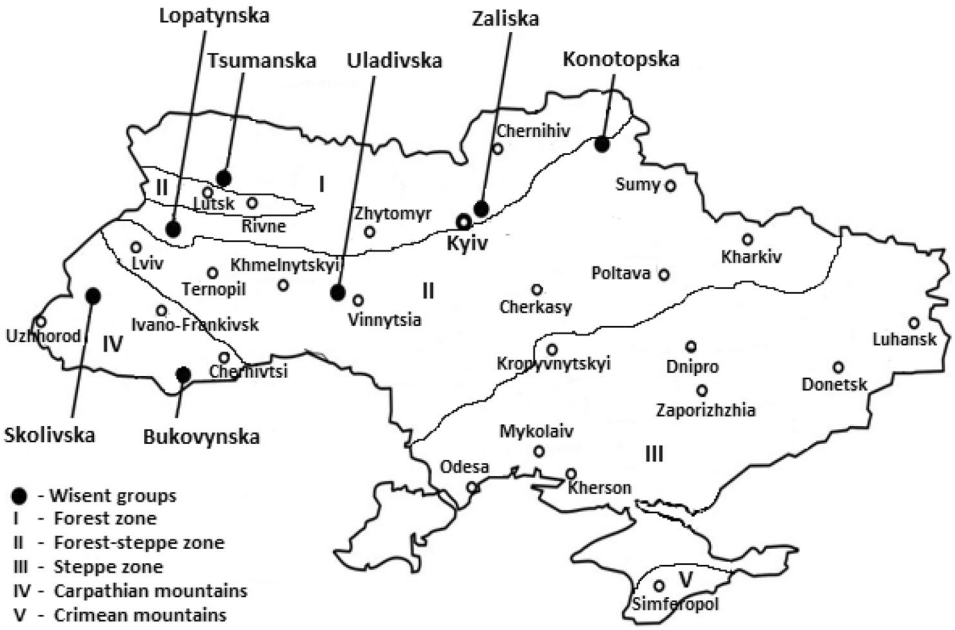

Fig. 1 Location of seven free and semi-free ranging European bison (*Bison bonasus*) herds in Ukraine

Lopatynska herd

This population of 84 individuals (EBPB 2020) is free-ranging across approximately 18,000 ha at the State Enterprise "Brody Forestry" (Sharapa 2010) (Fig. 1) in the forest zone in the north of the Lviv region (Marynych et al. 2003). During March–September, bison foraged almost exclusively among vast fields of agricultural crops, initially focusing on oat (*Avena* sp.) and rapeseed (*Brassica* sp.), and shifting to soy in mid-summer. Bison only occupied middle-aged ($C_{3\text{-}4}$) hornbeam-oak-pine woodlands with mixed birch, aspen, linden (*Tilia* sp.), and oak adjacent to agriculture fields, for protective resting cover during non-foraging activities (Table 1). By October–November, as agricultural fields were being harvested, bison began to utilize sparse woodland understory of hazel, rowan, linden, birch, wild rose (*Rosa* sp.), bilberry (*Vaccinium* sp.), and blackberry; including foraging on mast year oak acorns. During December–February, bison localized exclusively around supplementary feeding stations.

Uladivska herd

This population of 107 individuals (EBPB 2020) is free-ranging on approximately 36,000 ha at the State Enterprise "Khmilnyk Forestry" (Smagol 2019) in the Vinnytsia region in the north-west part of the Forest-Steppe zone (Marynych et al. 2003) (Fig. 1). During March–May, bison utilized hornbeam stands, and by late May shifted to middle-aged ($D_{2\text{-}3}$) hornbeam-oak forests with admixture of maple, ash, linden, and birch in order to reduce exposure to blood-sucking insects (Table 1). There is little understory in these woodlands, and bison moved to forest fringes and glades each morning and evening to forage. During June–August, bison transitioned to foraging in agricultural fields of oat, corn (*Zea* sp.), and beet (*Beta* sp.) that are located farther away from forested habitats. During September–February, bison utilized agricultural fields of rapeseed and winter cereal crops, periodically foraging on willow and aspen along forest margins, and entirely avoided moving deeper into woodlands.

Konotopska herd

This population of 64 individuals (EBPB 2020) is free-ranging on approximately 17,000 ha at the State Enterprise "Konotop Forestry" in the Sumy region (Smagol and Gavris 2013) primarily in the north-east part of the Forest-Steppe zone (Marynych et al. 2003) (Figure 1). From March–November, bison were closely associated with B_2-C_2 middle-aged, maturing and matured pine-oak forest with admixture of maple, linden, and spruce. During April–May, bison sought out early successional growth in recently harvested slashes with open canopy, and returned to rest in the protective cover of forests with a sparse understory of buckthorn, elder (*Sambucus* sp.), spindle tree (*Euonymus* sp.), rowan, hazel, and brambleberry (*Rubus* sp.). During June–August, bison moved nocturnally to forage in open meadows of *Poaceae* sp. and *Fabaceae* sp., and returned diurnally to protective cover of oak-pine forests. During September–November, bison again concentrate in the pine-oak forest, foraging in recent open canopy slashes. During December–March, bison localize exclusively around supplementary feeding stations.

Table 1 Habitat characteristics for seven herds of European bison (*Bison bonasus*) in Ukraine

Herd name	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Tsumanska (Forest zone)	Supplemental feeding places		B_3-C_3; oak forest with admixture of birch, alder, aspen, maple; maturing age. Peaty meadows				C_{3-4}; alder-birch forest with admixture of oak, aspen, hornbeam, ash; middle and maturing age. Peaty meadows			D_{2-4}; pine forest and hornbeam-oak one; middle age. Peaty meadows		Supplemental feeding places
Zaliska (Forest zone)	Supplemental feeding places		Peaty meadow. D_4; alder forest with admixture of birch, aspen and willow; middle and maturing age			B_2; pine forest with admixture of oak; maturing and matured age						Supplemental feeding places
Lopatynska (Forest zone)	Supplemental feeding places		Fields of agricultural crops (oat, rapeseed, soya)								C_{3-4}; pine forest with admixture of hornbeam, linden, common oak, red oak; maturing and matured age	Supplemental feeding places
Uladivska (Forest-Steppe zone)	Fields of agricultural crops (oat, corn, beet, rapeseed, winter cereal crops)		D_{2-3}; hornbeam forest; matured age			D_{2-3}; hornbeam forest with admixture of oak, maple, ash, linden, birch; youngsters and middle-aged			Fields of agricultural crops (oat, corn, beet, rapeseed, winter cereal crops)			
Konotopska (Forest-Steppe zone)	Supplemental feeding places		B_2-C_2; pine-oak forest with admixture of maple, linden, spruce; middle-aged, maturing and matured age. Meadows with rich species diversity									Supplemental feeding places
Bukovynska (Carpathian Mountain)	Thickets of blackberries on the southern slopes			Meadows in the foothills		D_2; beech-spruce forest with admixture of sycamore maple, birch, larch; middle-aged					Thickets of blackberries on the southern slopes	
Skolivska (Carpathian Mountain)	Supplemental feeding places in the foothills			C_3-D_3; spruce forest with admixture beech and fir; beech forest; middle-aged. Mountain meadows						Supplemental feeding places in the foothills		

Bukovinska herd

This population of 47 individuals is free-ranging on approximately 32,000 ha at the State Enterprise "Storozhynets Forestry" and State Enterprise "Beregomet Forestry and Game Husbandry" in the Chernivtsi region (Smagol and Cherevatov 2014) in the Ukrainian part of the Carpathian Mountains (Marynych et al. 2003) (Fig. 1). In the process of adaptation to conditions of the mountainous region, bison have developed dynamic habitat use along the elevation gradient. For the main part of year, bison select for the middle belt of the mountains (from 600 to 1000 m) (Khoyetskyy 2009). During April–May, bison moved down the elevation gradient to foothills, where they were attracted by early phenology of meadow plants (Table 1). During June–October, when lower elevation meadows senesced, bison moved upslope to occupy mixed middle-aged (D_2) beech (*Fagus* sp.) and spruce forests with mixed maple, birch and larch; and a sparse understory of individual hornbeam, maple, birch, hazel, and elder trees. During this time, bison foraged in a variety of open habitats (slashes, glades, hayfields) that were characterized by blackberry, wild rose, bilberry, and strawberry *(Fragaria* sp.). During November to March, bison remained at mid-elevations to forage primarily on blackberry on south facing slopes.

Skolivska herd

This population of 37 individuals is free-ranging on approximately 6000 ha at the National Nature Park "Skoly Beskids" of the Lviv region (Sharapa et al. 2010) in the Ukrainian Carpathian Mountains (Marynych et al. 2003). This herd utilizes 1 year-round home range, that is a 6000-ha mountainous "pot hole" that is a valley of a mountainous river with slopes rising in both the directions. During April–September, bison utilize eastern facing foothill slopes of true meadows with rich species composition of miscellaneous herbs and high quality *Poaceae* sp., *Fabaceae* sp., and *Apiaceae* sp. throughout the growing season (Table 1). Upslope from these meadows is primarily characterized by middle-aged (C_3-D_3) spruce forests with mixed beech and fir (*Abies* sp.); with an understory of maple, birch, and aspen in the lower beech forests (Deineka et al. 2006; Kramarets et al. 2019). From October to March, bison move downslope to foothills of beech-spruce-fir woodlands to localize exclusively near supplemental feeding stations, with some mature males venturing into village gardens.

Discussion

Following upon restoration as free-ranging wildlife, the European bison has exhibited plasticity and variation in habitat use and preference in response to landscape patterns and processes of forest and non-forested habitats (Kowalczyk and Plumb 2020). Within a landscape matrix of natural mixed forest-meadow habitats and high quality agricultural fields, bison commonly carry out foraging bouts in open meadows and agricultural fields followed by movements to forest edges for protection, resting, and rumination (Korochkina 1958; Tereshkin 1966; Kozlo et al. 2004; Krasińska and Krasiński 2013; Shakun 2011; Solonina 2017; Hofman-Kaminska et al. 2018; Marszałek and Perzanowski 2018).

Our descriptive observations for seven herds across three ecological zones evidences support of the overarching importance of open lands for foraging and forests for protection, with limited exceptions of early successional renewal in recently harvested forest areas, oak acorn mast years, and blackberry undergrowth. For newly established and relatively small bison populations, the importance of access to both foraging and protection habitats should not be understated. In the forest zone, bison spent the summer diurnal period deep in the forest to avoid blood-sucking insects, and emerged nocturnally to forage in forest margin glades and adjacent open habitats. In the forest zone, absence of meadow complexes resulted in bison foraging in open agricultural fields in combination with sparse woodland glades. In forest-steppe landscapes without native meadows, bison were influenced by the rotation of agricultural crops, shifting from succulent crops in autumn to cereal crops in winter. In the Carpathian Mountains, bison utilized lower and mid-elevation valley meadow complexes rather than higher elevation wooded hillsides, and as temperature declined and snow cover increased, bison shifted to southern exposure wooded slopes dominated by blackberry undergrowth. During winter across ecological zones and herds, variation in habitat use declined dramatically under supplementary feeding that incentivized sedentary association with woodlands.

While our research was limited to descriptive methodologies and data, we attempted to apply consistent field surveys across multiple sites across three ecological zones. Despite these limitations, our findings suggest further research investigation of bison in Ukraine are warranted to test specific habitat use hypotheses through detailed habitat mapping, GPS collar, and foraging ecology data. Of key interest is to generate resource selection functions (Boyce et al. 2002) that will help us better understand the landscape-scale ecology of bison across ecological zones; including optimal landscape patterns and processes for long-term herd viability, and implications of winter supplemental feeding for European bison landscape ecology and population viability. Our findings also support that European bison are variable in their habitat use and can be highly responsive to seasonally dynamic habitat patterns and process, without defaulting to a dichotomy of forest vs. open-land species (see Kerley et al. 2011, Kummerle et al. 2012, Kummerle et al. 2018,

Pezanowski et al. 2019, Kerley et al. 2020, Kummerle et al. 2020). Looking to a dynamic future of bison restoration in Ukraine, we adhere with Redford et al. (2016) to "reach further, dig deeper, confront our limits and those of nature, and work harder," and recognize that we are just beginning to understand the full complexity of the species and it potential for restoration as a dynamic ecological actor in wildland and human-dominated landscape systems.

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