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ORIGINAL PAPER

Habitat use by wisents *Bison bonasus* of the Białowieska Primeval Forest

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ABSTRACT

Spatial distribution and habitat preferences of wisents (European bison) *Bison bonasus* (Linnaeus 1758), were studied in Białowieska Primeval Forest (north-eastern Poland) composed of 94% broadleaved and mixed tree stands, on the basis of telemetric data obtained from 11 individuals (4 males and 7 females). Data was collected between 2012-2015 within the area of over 98 thousand ha. A majority of records for both sexes' presence was from the forested area, regardless of the season, compared to open areas (forest meadows, openings and agriculture neighbouring the forest). Outside of the forest in vegetative seasons, 36% of presence records of males and 26% of females were registered, and respectively about 39% and 41% in winter. This confirms the importance of an access to open areas for this species. Considering the availability of both types of habitats within home ranges occupied by wisents, the non-forest category was generally preferred over the forest; however, those differences were the highest regarding the data on MCP area (the value of Ivlev's index 0.64), but were the lowest for the area representing concentrated use (kernel 50%) of a habitat. Regarding forest habitats, wisents selected against broadleaved stands but selected towards riparian vegetation. Although this species is not territorial, the degree of overlap between home ranges of particular mixed groups (consisting of cows, youngsters and calves) was very low. Data obtained in this study reveals patterns of the spatial structure of this wisent population, the oldest in the world, and therefore truly well established in its environment, free ranging population of this species. Hence, the data for this population on trends in habitat selection may be a credible basis for the evaluation of habitat suitability of sites either already inhabited by this species or being considered for its future reintroductions and be useful in further management of its free ranging populations.

KEY WORDS

European bison, habitat preferences, home ranges, Ivlev's index, kernel, spatial distribution

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Introduction

Terrestrial animal species are either gregarious, living in groups and inhabiting ranges without obvious boundaries, or territorial, and occupying well defined fragments of available space. Very often, habitat patches used by males are different from females' ranges in both size and quality. Sometimes, like in the case of roe deer *Capreolus capreolus* L. males, individuals are strictly solitary and territorial in summer, then join larger groups in winter and move all over the available area. All these differences in spatial distribution result from a variety of factors including foraging requirements, seasonal changes in habitat quality, mating patterns, maternal care, anti-predation strategies, *etc*. (Putman, 1988; Andersen *et al*., 1998; Schneider *et al*. 2013).

In the case of wisents (or European bison), their breeding season lasts from August to October, and calves are born between May and July. Lactation usually ends in spring before the next calf is born. The reproduction cycle also influences the spatial patterns of these animals. For this species, it is characteristic to form mixed groups composed of females with calves and youngsters, while males either form separate bachelor groups or remain solitary. In the Białowieska Forest the only natural predator for this species is the wolf *Canis lupus* L.; however, wolves occur in very low numbers. Therefore, predators' pressure upon this population of wisents can be estimated as marginal (Krasińska and Krasiński, 2007; Meletti and Burton, 2014).

Generally, habitat selection by large mammals is mostly driven by two factors: availability of food and cover conditions. Białowieska Forest is a mosaic of numerous habitat patches differing in species composition and age of tree stands, hydrological conditions, proportion of open grounds etc., as well as in distance from human settlements and agriculture. The wisent, a native species there, was extirpated by 1919, but reintroduced again to the wild in 1952. Since then its numbers grew to reach over 700 in 2020. During that time, this population remained unrestricted regarding the selection of the most preferred parts of about 630 km^2 of the Polish part of the Forest. The only intentional, human related influence was the provision of supplemental food in winter, causing seasonal concentrations of animals in the vicinity of main feeders. At the moment, this is the oldest, largest and well established European population of the species (Krasińska and Krasiński, 2007; Okołów *et al*., 2009; Krasińska *et al*., 2014).

Since wisents are very attractive game, they have been subject to special management that included supplementary feeding in winter since medieval ages (Rokosz, 1995; Dzieduszycki *et al*., 2010). The current population reintroduced from the 1950s is also managed with supplementary feeding during winter. This undoubtedly exerted a significant influence upon their behaviour and changed their patterns on the use of space. With the onset of winter, the majority of the population used to gather around one or two main feeding points situated in the central part of the forest, and remained there in high density for a couple of months, waiting for regular provision of the forage (Krasińska and Krasiński, 2007).

Only in the last few years has there been attempts to change this unnatural behaviour by dispersing winter feeding to various parts of the forest and to make it less intensive (Krasińska *et al*., 2014). Nevertheless, changes in spatial distribution of this population are already noticeable, and continuation of this trend may bring promising results in re-naturalisation of wisents' behaviour. At the same time this raises questions about whether weakening the bond of a wisent herd to the centre of the forest would not result in increased penetration of animals towards surrounding farmlands, which already creates some conflict (Hoffman-Kamińska and Kowalczyk, 2012).

The aim of this paper is an attempt to identify predominant factors that determine habitat preferences of wisents in wegetative and winter seasons on the basis of data collected over a three year period concerning habitat use and movement patterns of 11 individuals (4 males and 7 females) fitted with GPS collars between 2012-2015 at Białowieska Forest. Results of this analysis may also supply additional arguments to recent discussion whether wisents are truly a forest dwelling species or if they use the forest just as refuge after being pushed there by anthropogenic habitat alterations (Cromsigt *et al*., 2012; Kerley *et al*., 2012, 2020; Kowalczyk *et al*., 2013; Perzanowski *et al*., 2019; Kuemmerle *et al*., 2020). This has direct implications for planning conservation measures for this species, including the evaluation of presently inhabited ranges and selection of optimal sites for its reintroductions.

Study area, materials and methods

Data were collected in the Białowieska Primeval Forest (north-eastern Poland), situated on both sides of the Polish-Belarussian border (52°30'-52°54' N, 23°26'-23°56' E) (Fig. 1).

This lowland forest (144-176 m above sea level) is composed of 94% broadleaved [dominated by oak *Quercus robur* L., lime *Tilia cordata* Mill., hornbeam *Carpinus betulus* L. and alder *Alnus glutinosa* (L.) Gaertn.], and mixed [with spruce *Picea abies* (L.) H. Karst and Scots pine *Pinus sylvestris* L.] tree stands. The remaining part consists of open habitats including glades with meadows, riparian valleys, and marshes (Więcko 1984; Sokołowski 2004). The Polish part of the Forest is inhabited by over 700 wisents, separated since 1981 by a border fence from their Belarussian counterparts (Krasińska and Krasiński, 2007); an additional fence on the Polish side of the border was constructed in 2022. From the west, southwest and north, the forest borders an agricultural landscape consisting of pastures and meadows (24%) and cultivated fields (48%) with an admixture of woodlands (25%). The dominant land use is an extensive type of agriculture with small-sized farms and relatively low human density (30 inhabitants/km^2). The main crops there are rye *Secale cereale* L. (51%) and potatoes *Solanum tuberosum* L. (5% of arable area). Between autumn and spring, some 25% of tilled area is used for cultivation of winter cereals (*S. cereale*, *Triticum aestivum* L.) and winter rape *Brassica napus* L. (Statistics Poland, 2014a, b).

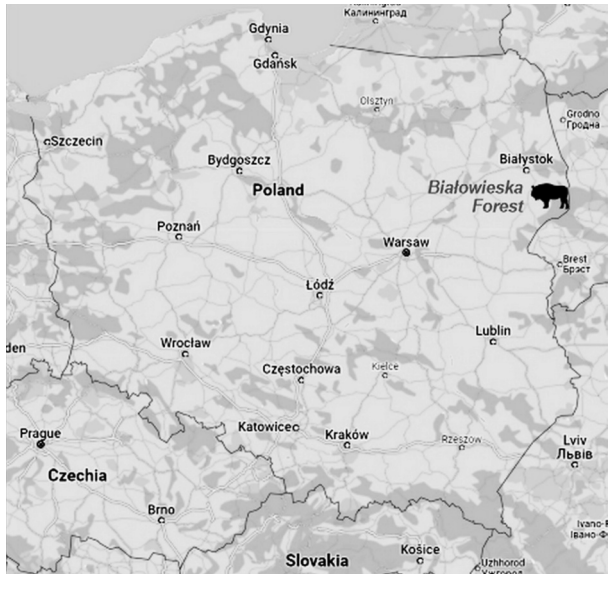

Fig. 1.
The location of Białowieska Forest at the border of Poland and Belarus

The climate of the area is a sub-continental transitional type. The average amount of annual precipitation is 606 mm. Average monthly temperatures range between –3.0°C (January) and 18.3°C (July) with annual mean: 7.1°C, and annual absolute amplitude of 69.2°C. Growing season lasts on average 206 days. Snow cover occurs between 45 and 97 days, with maximal recorded depth of 95 cm (Okołów *et al*., 2009).

Since 2012, 11 wisents (4 males and 7 females) have been fitted with GPS collars under the framework of a monitoring program in Białowieski N.P. Their locations n=12026 and 22 742 for males in growing (April-October) and winter (November-March) seasons respectively; *n*=51618 and 48 613 for females, respectively were recorded until the end of 2015. An example of obtained records of wisents' presence is given at Figure 2. Total analysed area was 98139,97 ha, including Białowieski National Park and forest districts of: Browsk, Hajnówka and Białowieża.

Data for this study was collected with GPS collars (ML 931 XL) manufactured by Agricolis (Szczecin). Hosting of data was provided by Inventia (Warsaw). Records of wisents' presence were taken in 1 hour intervals. Data transmission through GPRS to a nearest mobile phone station (Plus) was performed every 6 hrs. Collars were equipped with 2 types of antennas: internal and external, and a VHF transmitter which allowed for additional use of ground telemetry.

The dataset for every record included the date and hour, the location of an animal in WGS84 projection, horizontal precision (error), the number of active satellites, momentary speed of animal's movement, and the source of data (transmitter No.). Acquired data were filtered by selection of a time interval (as file *.csv from the server), and included rejection of records obtained with less than 3 satellites, records with an accuracy of over 10 m, or doubled records.

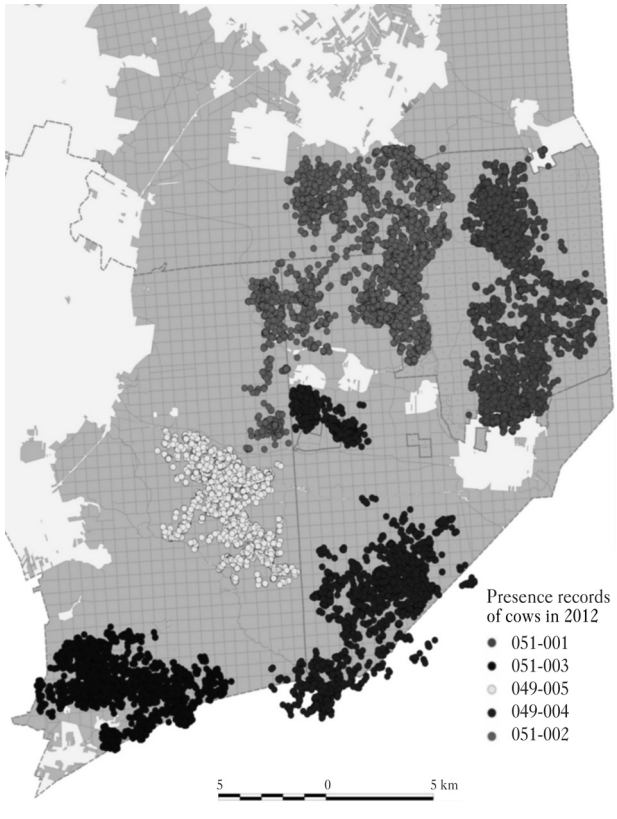

Fig. 2.
An example of distribution of records of radio-collared wisent females (cows) within Białowieska Forest in 2012

Data for each animal, separately for growing and winter seasons, were transformed into thematic layers with the software QGIS ver. 1.8., and recorded as raster files *.jpg. The following were calculated using software ArcMap (ESRI): the size of individual home ranges in both seasons as MCP (minimal convex polygon) and kernel 95%, area of concentration sites (kernel 50%) following Worton (1989), overlap between male and female home ranges, and habitat preferences calculated according to electivity index by Ivlev. The index ranges from –1 (total avoidance of a food item) to +1 (maximum selection of a food item). Values close to 0 indicate consumption of a food item proportional to its availability (Ivlev, 1961).

The assessment of habitat use was based on two habitat categories: forest and non-forest (forest openings, meadows, glades, agriculture), and within the forest: coniferous forest (dominated by spruce *P. abies* or pine *P. sylvestris*), broadleaved forest (dominated by oak *Q. robur*, hornbeam *C. betulus* L. and linden *T. cordata*), and riparian forest (dominated by alder *A. glutinosa*) (Keczyński, 2017; Stereńczak, 2022).

Results

Areas of MCP, kernel 95%, and kernel 50%, for both males and females were significantly larger in the vegetative season. In all cases, areas penetrated by males considerably exceeded those of females. Especially high (by 88 times in vegetative seasons and 65 times in winter) were differences between the area of concentrated use (kernel 50%) estimated for both sexes. High values of SD indicate great variability of home ranges occupied by particular individuals (Table 1).

Forested areas were much more frequently used by both sexes regardless of the season. This was particularly apparent regarding the percentage of MCP area within the forest (over 90% in case of males and almost 85% in case of females in growing season, and almost 85% for both sexes in autumn/winter season). Also, the percentage of locations recorded within the forest exceeded 60% in both seasons, and was as high as 77% in the case of females in the vegetative season. Those values were slightly lower for areas estimated as kernels 95% and 50%. The highest percentage of MCP area of both sexes was situated within coniferous stands, followed by broadleaved and riparian habitats. However, a comparison of data for the area of concentrated use (kernel 50%) shows that those values were the highest for broadleaved stands in all seasons, as well as for females in riparian habitats during the growing season. Stands along watercourses or bogs dominated by alder displayed the highest difference of intensity in use between both sexes (Table 2, 3).

The degree of overlap among ranges occupied by particular animals was very low. In the whole set of data, there were only 10 such cases: five of them between males and females and five among females. Nine of these cases occurred in the vegetative season, and only one in winter. The degree of overlap of MCPs varied between 2.28% and 33.66% (the highest value in a vegetative season between two cows), in case of kernel 95% it was 1.11-24.37%, while areas of kernel 50% overlapped only in one case (in 10.12%) between a male and a female in the vegetative season.

Table 1.

Average values (±SD) of home ranges (MCP), truly used area (kernel 95%), and areas of concentrated use (kernel 50%) of wisents at Białowieska Forest, in vegetative and winter seasons between 2012-2015

Sex/season	MCP [ha]	Kernel 95% [ha]	Kernel 50% [ha]
Males/vegetative	9517.0 ±3624.3	2671.5 ±1804.9	318.2 ±236.4
Males/winter	3831.3 ±2051.6	219.9 ±76.6	26.0 ±8.0
Females/vegetative	6225.1 ±3263.0	296.6 ±180.2	3.6 ±1.5
Females/winter	3684.5 ±2896.0	40.1 ±29.4	0.4 ±0.3

Table 2.

A comparison of an intensity of use of particular habitat categories at Białowieska Forest by wisent bulls and cows in vegetative season

Habitat category	Sex	% of MCP area	% of kernel 95 area	% of kernel 50 area	% localisations in a habitat
Forest	Males	91.6	72.1	60.9	64.4
	Females	84.9	86.8	72.87	77.2
Non-forest	Males	8.5	27.9	39.1	35.6
	Females	19.4	18.0	27.2	26.3
Coniferous forest	Males	52.7	43.7	25.0	32.8
	Females	38.4	36.8	21.7	26.8
Broadleaved forest	Males	23.6	18.8	28.0	27.3
	Females	25.7	26.6	23.0	25.7
Riparian forest	Males	15.3	9.7	7.9	4.3
	Females	20.9	23.5	28.1	24.8

Table 3.

A comparison of an intensity of use of particular habitat categories at Białowieska Forest by wisent males and females in autumn/winter season

Habitat category	Sex	% of MCP area	% of kernel 95 area	% of kernel 50 area	% localisations in a habitat
Forest	Males	83.1	64.4	78.6	60.4
	Females	84.9	64.0	59.0	60.8
Non-forest	Males	16.9	35.6	21.5	39.3
	Females	20.1	36.7	41.0	41.2
Coniferous forest	Males	41.3	20.7	26.8	15.3
	Females	36.0	23.1	19.6	20.7
Broadleaved forest	Males	24.5	32.0	47.3	40.7
	Females	21.8	22.9	28.5	24.5
Riparian forest forest	Males	17.3	11.7	4.4	4.6
	Females	27.0	18.0	10.8	15.6

Preference towards available habitats was measured with Ivlev's index. Generally, the non-forest category was preferred over the forest; however, those differences were the highest when comparing the percentage of MCP area (the value of Ivlev's index 0.64), but the lowest when comparing the area of concentrated use, *i.e.*, kernel 50% (–0.01). Negative values of Ivlev's index were obtained in all cases for broadleaved stands (even as low as –0.51, in the case of males in winter). Most positive were index values for riparian stands, especially for the areas of concentrated use by males in winter (up to 0.51). Positive, however much lower (0.12-0.24), were values of that index for coniferous stands (Table 4, 5).

Discussion

Papers concerning habitat selection by wisents provide quite different results. Classic data collected in Białowieska Forest suggest strong associacion of wisents with forest stands, although openings and grassland patches are important as grazing grounds (Krasińska and Krasiński, 2007). Similarly, the occurrence of wisents from Bieszczady Mountains was in about 80% of cases recorded within the forest (Marszałek and Perzanowski, 2018). Data for a wisent populations from north-western Poland (so called West-Pomeranian herd) and Lithuania, both living in highly mosaic landscapes show, that those animals most willingly graze within open grasslands or at cultivated fields with

Table 4.

Values of Ivlev's index reflecting preferences of wisent males and females towards considered habitat categories in analysed parts of their home ranges in vegetative seasons. Values in bold indicate avoidance (<-0.2) and those in italics the preference (>0.2)

Habitat category	% in area	Sex	% of MCP area	% of kernel 95 area	% of kernel 50 area	% localisations in a habitat
Forest	60.87	Males	**–0.20**	–0.08	0.00	–0.03
		Females	–0.16	–0.18	–0.09	–0.12
Non-forest	38.75	Males	*0.64*	0.16	–0.01	0.04
		Females	0.33	0.37	0.08	0.19
Coniferous forest	31.99	Males	**–0.24**	–0.15	0.12	–0.01
		Females	–0.09	*–0.07*	0.19	0.09
Broadleaved forest	15.49	Males	**–0.21**	–0.10	**–0.29**	**–0.28**
		Females	**–0.25**	–0.26	–0.19	**–0.25**
Riparian forest	13.76	Males	–0.05	0.17	*0.27*	*0.52*
		Females	**–0.21**	**–0.26**	–0.34	**–0.29**

Table 5.

Values of Ivlev's index reflecting preferences of wisent males and females towards considered habitat categories in analysed parts of their home ranges in winter seasons. Values in bold indicate avoidance (<–0.2) and in italics the preference (>0.2).

Habitat category	% in area	Sex	% of MCP area	% of kernel 95 area	% of kernel 50 area	% localisations in a habitat
Forest	60.87	Males	–0.15	–0.03	–0.13	0.00
		Females	–0.16	–0.02	0.01	0.00
Non-forest	38.75	Males	*0.39*	0.04	0.29	–0.01
		Females	*0.32*	0.03	–0.08	–0.03
Coniferous forest	31.99	Males	–0.13	0.21	0.09	0.35
		Females	–0.06	0.16	*0.24*	*0.21*
Broadleaved forest	15.49	Males	**–0.22**	**–0.35**	**–0.51**	**–0.45**
		Females	–0.17	–0.19	**–0.30**	**–0.22**
Riparian forest	13.76	Males	–0.11	0.08	*0.51*	*0.50*
		Females	**–0.33**	–0.13	0.12	–0.06

corn or rape (Tracz and Tracz, 2010; Marozas *et al*., 2019). According to a review of the use of various sites in the Europe occupied by wisents done by Kuemmerle *et al*. (2018), 65% on average of wisents' occurrences were recorded in the forest, but that assessment performed across multiple herds revealed a more generalist habitat use pattern than when studying individual herds only. Results of studies done for semi free herds indicated high preference of wisents towards managed open areas but this data are difficult to compare because of limited choice of habitats in such conditions (Červený *et al*., 2014; Zikmund *et al*., 2021).

Our data were collected during the period when supplementary feeding applied in Białowieska Forest became more dispersed, so the effect of seasonal concentration was much less pronounced. GPS collared females belonged to different mixed groups characteristic for the species (adult females, youngsters and calves) (Fig. 2), while adult males were solitary and penetrated much larger home ranges (Table 1). Therefore, data for females obtained through radio tracking represented movements of groups of animals between several to over 20 individuals. This may explain large differences in the size of particular home ranges. The wisent is not a territorial species; however, home ranges of separate groups usually do not overlap (Krasińska and Krasiński, 2007).

Within Białowieska Forest boundaries, some 6% of the area belongs to an 'open habitat' category; however, since there is no fencing or other physical obstacles within its Polish part, animals have unrestricted access to various types of agriculture just outside of the forest (Okołów *et al*., 2009). In vegetative seasons, some 28% and 18% (for males and females respectively) of open habitats were within the kernel 95% area, which was assumed as an area actually penetrated by those animals. In winter, this proportion was about 36% and 37%. Even higher values are for the area of kernel 50%, which represents parts of the home range highly preferred by animals. When we compared data on intensity of use, *i.e*., the percentage of wisent locations recorded outside of the forest, we obtained the following figures: about 36% and 26% for males and females in the vegetative season, and about 39% and 41% in winter (Table 2, 3). This clearly proves that open areas are of key importance for the normal functioning of the species, especially after the end of the vegetative season when they may graze upon winter crops. This aspect was also stressed by other authors (Kerley *et al*., 2012, 2020; Kowalczyk *et al*., 2013).

Among types of forest stands, the highest coefficients of preference were found for riparian habitats, especially for females in the vegetative season, which can be explained by an abundance of plant biomass there and difficult accessibility for people, which is important for females with young. Apparently, broadleaved stands were of low preference. However, the percentage of animals' presence there was the highest in winter, and comparable to those observed in coniferous stands in the vegetative season. Similarly, the percentage of the kernel 50% area, *i.e*., the parts of the forest where wisents tend to concentrate, was higher for broadleaved stands compared to coniferous (Table 2, 3).

Obtained data confirms the dependency of this species on the access to open areas allowing grazing; however, a cover provided by dense, poorly accessible forest stands is important for females with calves. Wisents of Białowieska Forest were able to use almost all habitats available there, which proves their flexibility and high ability for adaptation to existing habitat conditions (Kowalczyk *et al*., 2019). This data confirms a strong association of wisents with forest habitats, albeit as bulk grazers, they require easy access to open pastures (Kuemmerle *et al*., 2020). Hence, wisents can be classified as opportunistic species adapted to mosaic landscapes predominantly forested, but with a considerable proportion of grazing grounds. This information indicates much higher ability of wisents to adapt for various habitat types than traditionally assumed. Therefore it can be useful in a suitability assessment of ranges already inhabited by wisents as well as in optimal selection of sites appropriate for future reintroductions of the species.

Conclusions

Wisents of Białowieska Forest show very high potential for habitat adaptation, nevertheless, open areas providing good pasture conditions are very important to them. This is proven by a frequent presence of animals outside the forest within cultivated grasslands and agriculture. Dense tree stands securing necessary cover, like riparian habitats with abundant plant biomass, that are hardly accessible for people, are especially important for females with young calves.

Nonetheless, forested areas were much more frequently used by both sexes regardless of the season, which indicates high affinity of this species to forest habitats even if open spaces are easily available. Therefore, the selection of optimal sites for the introduction of wisents should consider the accessibility of open areas suitable for grazing (preferably forest meadows and openings rather than agriculture), but at the same time the ease of access to tree stands securing appropriate cover in all seasons.

Authors' contributions

KP and WO conceived the ideas and designed methodology; AB collected the data; MJ, KP and WO analysed the data; KP and WO led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Conflict of interest

The authors declare no conflict of interest.

Ethical approval

All applicable institutional and/or national guidelines for the care and use of animals were followed.

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STRESZCZENIE

Użytkowanie siedlisk Puszczy Białowieskiej przez żubry *Bison bonasus*

Badania nad rozmieszczeniem przestrzennym i preferencjami siedliskowymi żubrów *Bison bonasus* Linnaeus, 1758 przeprowadzono w Puszczy Białowieskiej (północno-wschodnia Polska) (ryc. 1; tab. 1), przy użyciu obroży telemetrycznych założonych 11 osobnikom (4 samce i 7 samic). Dane zbierano w latach 2012-2015. Większość stwierdzeń obecności żubrów, niezależnie od płci i sezonu, uzyskano z terenów leśnych. Z obszarów otwartych (łąki leśne, polany oraz tereny rolnicze w sąsiedztwie lasu) w sezonach wegetacyjnych pochodziło 36% stwierdzeń obecności samców i 26% stwierdzeń obecności samic, natomiast w sezonach zimowych około 39% stwierdzeń dotyczących samców i 41% stwierdzeń obecności samic (tab. 2 i 3). Dane te potwierdzają znaczenie dla tego

gatunku dostępności terenów otwartych. Biorąc pod uwagę dostępność obu głównych typów siedlisk (obszary zalesione i tereny otwarte) w obrębie areałów bytowania żubrów, stwierdzono, że tereny otwarte były generalnie wyżej preferowane niż obszary pokryte lasem. Różnica ta była największa w odniesieniu do areału określanego jako MCP (minimal convex polygon), gdzie wartość wskaźnika Ivleva wynosiła 0,64, natomiast najniższa w obrębie areału kernel 50%, a więc obszaru najintensywniej użytkowanego przez te zwierzęta (tab. 4 i 5). Białowieskie żubry preferowały siedliska położone wzdłuż cieków lub zbiorników wodnych, natomiast unikały siedlisk typowych dla drzewostanów liściastych. Jakkolwiek gatunek ten nie jest terytorialny, to stopień nakładania się areałów poszczególnych ugrupowań mieszanych (składających się z dorosłych samic, młodzieży i cieląt) był bardzo niski (ryc. 2).

Uzyskane dane pozwoliły na wskazanie wzorców struktury przestrzennej najstarszej na świecie wolno żyjącej populacji żubra – więc bardzo dobrze przystosowanej do warunków środowiskowych w obrębie swego areału bytowania. Dlatego też uzyskane tu dane dotyczące trendów preferencji siedliskowych żubrów mogą być uważane za wiarygodną podstawę dla oceny przydatności siedlisk zarówno obecnie zamieszkiwanych przez ten gatunek, jak i tych, które są rozważane jako potencjalne miejsca dla jego reintrodukcji w przyszłości.