Sveriges lantbruksuniversitet
Swedish University of Agricultural Sciences

Faculty of Natural Resources
and Agricultural Sciences

GRIMSO WILDLIFE RESEARCH STATION

Habitat selection of the European bison

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Master's thesis
Grimsö 2015

Independent project/Degree project / SLU, Department of Ecology 2015:4

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Credits: 30 HEC
Level: A2E
Course title: Independent Project in Biology
Course code: EX0565
Programme/Education: Master in Ecology, Uppsala University
Place of publication: Grimsö
Year of publication: 2015
Picture cover: Ebba Hammarlund
Title of series: Independent project/Degree project / SLU, Department of Ecology
Part number: 2015:4
Online publication: http://stud.epsilon.slu.se

Keywords: European bison, Bison bonasus, habitat selection, refugee species, Resource Selection Function

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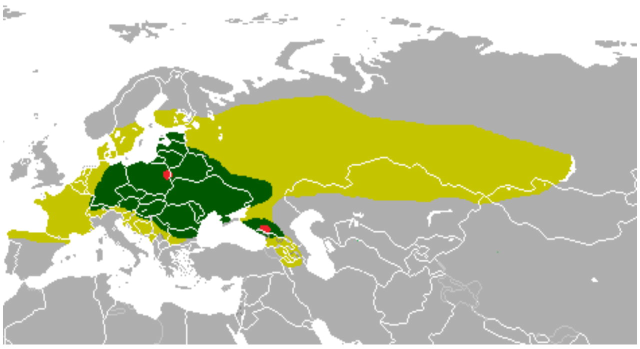
Skogens konung eller präriens prins: var hör visenten hemma egentligen?

Visenten är europas tyngsta nu levande landdjur. Då en vuxen tjur kan nå nästan två meter i mankhöjd och väga upp mot ett ton så är det sannerligen en uppseendeväckande best. Trots detta är den relativt okänd: många jag talat med har varit omedvetna om existensen av denna art. Av dom som känt till den har flera haft föreställningen om att den är utdöd, eller blandat ihop den med antingen uroxen eller myskoxen. Förklaringen kan ligga i att visenten idag är mycket ovanlig och endast undgick utrotning med ett nödrop.

Visenten (Bison bonasus) är det tyngsta landdjuret i europa, men är utrotningshotat. På bilden ses två tjurar i ett reservat i frankrike.

För ungefär 10 000 år sedan uppskattas visenten ha funnits från centrala asien i öster till västra europa. Men, när människopopulationen mångdubblades och jordbruket tog allt mer mark i anspråk samtidigt som jakttrycket ökade drevs arten mot utrotning. Den sista vilt levande individen sköts 1927: det som fanns kvar av arten var ett femtiotal individer i zoon och avelscenter runtom i europa. Nu påbörjades ett intensivt avelsprogram för att rädda arten och åter införa i det vilda, och även Sverige hjälpte till: avelsanläggningen Avesta visentpark startade 1939. Vid den här tiden ansåg vetenskapen att visenten var ett skogslevande djur: förknippad framförallt med centraleuropas lövskogar dominerade av ek, avenbok och lind. Sådana miljöer söktes nu ut när arten återinfördes på ett antal platser. Sedan starten av återintroduceringsprogrammet på 30-talet har arten mångdubblat i antal, och idag uppskattas 3000 djur leva i vilda populationer, med ungefär 1000 till i fångenskap. Programmet är ett exempel på lyckad naturvård; men trots detta anses visenten fortfarande vara ett utrotningshotat djur, bland annat då de vilda hjordar som finns är för små och isolerade för att undvika inavel.



Uppskattad utbredning av visenten i början av holocen 10000 år sedan (gult), mitten av medeltiden (grönt, kring år 1200) och början av 1900-talet i rött.

En fråga som uppkommit på senare år är dock om återintroduktionsprogrammet har varit delvis missriktat: Forskare har ifrågasatt huruvida visenten är anpassad till ett huvudsakligt liv i skogsmiljöer. De argumenterar för att arten egentligen utvecklats för ett liv ute i det öppna landskapet, liksom sin nära släkting den amerikanska bisonen. Att arten traditionellt ansetts vara ett skogslevande djur förklaras genom att visenten under människans historia allt mer trängts undan från de habitat där den själv valt att leva, och tvingats leva i miljöer där konflikter med människor minimerats: skogen. Under århundraden då den endast setts i skogsmiljöer har således bilden av visenten som ett skogsdjur växt fram. För att testa denna hypotes utrustades ett femtiotal visenter ur två hjordar i Polen med GPS-halsband, som varje timme gav en lokalisering av varje djur. Tillsammans med habitatkartor kunde jag nu jämföra vilka habitat som djuren valde gentemot vad som fanns tillgängligt. Resultatet var tydligt: öppna ytor med mycket gräsvegetation som hagmark, jordbruksmark och myrmark valdes i högre utsträckning än något annat habitat. I vissa fall var det 40 % troligare att återfinna en visent i ett sådant habitat än i en skogsmiljö. Dessa resultat ger tydligt stöd för hypotesen att visenten inte är anpassad till ett liv helt till skogs: om den själv får välja ser den sig gärna ute i öppna landskap.

Abstract

The European bison *Bison bonasus* was gradually driven to the brink of extinction during the last 10 000 years, most likely due to human hunting and habitat destruction. It survived in a few forests until finally being extirpated in the early 20th century. The species was saved through an extensive breeding and reintroduction program from individuals surviving in zoos and breeding centres. This effort is ongoing, with herds being reintroduced in forests throughout Europe. Recent research however has suggested that the European bison is not adapted to heavily forested habitats and is instead an example of a "refugee species": escaping to suboptimal habitats to minimize the effects of human conflict and persecution. Since the success of reintroductions relies on proper assessments of the fundamental niche of the species in question, research into which habitats fulfill the needs of the European bison is paramount for the recovery of the species. In this study I examine habitat selection of 50 GPS-collared bison across two study areas in Poland in a resource selection function (RSF) framework and try to determine which habitat types are selected for. I also look at the effect of supplementary winter feeding on habitat selection. I find strong effects of winter feeding in Białowieża forest on winter habitat selection. This effect diminishes when the feeding season is over and do not carry over to affect the habitat selection during summer. Further, there is a signficant pattern indicating that the European bison select open grass-rich areas and forested areas close to open areas in summer, irrespective of study area or gender. The results thus supports the idea of the current distributional range of European bison as a refugee, and gives reason for managers and conservationists to reassess potential areas for reintroduction of the species.

Introduction

The list of animal species that has been driven to extinction by humans is long and currently contains 765 species (The IUCN Red List of Threatened Species, 2008). A steadily increasing human population has over a few millenia changed the living conditions for a wide range of organisms worldwide, with major driving forces being habitat destruction and overexploitation of populations (Chapin *et al.*, 2000). A group of organisms for which the threat of humans has been especially dire is the large mammals. Due to their size and charisma they are often highly valued as game, and thus many populations and whole species have probably been hunted to extinction e.g. quagga (*Equus quagga*) and mammoth (*Mammuthus sp.*) (Sandom *et al.*, 2014). Carnivore species such as wolves (*Canis lupus*) are also often hunted and persecuted as they are viewed as a competitors to human interests (Cardillo *et al.*, 2004). Another important reason is that large mammals often need vast continuous habitats to thrive since their energetic demands force them to forage over large areas (Hendriks *et al.*, 2009). Habitat destruction by humans lead not only to loss of suitable habitat, it also fragments the remaining habitat degrading its value to the animals (Fahrig, 2003). It is thus not surprising that recent research suggests that humans were the primary cause of the loss of megafauna during the late quaternary (Sandom *et al.*, 2014).

One such large mammal that has seen a dramatic decline due to humans is the European bison (*Bison bonasus*), also known as the Wisent. Once widespread across Eurasia (Fig. 1) it suffered a continuous decline during holocene, and by the beginning of the 20^{th} century only two wild populations remained (Pucek *et al.*, 2004).

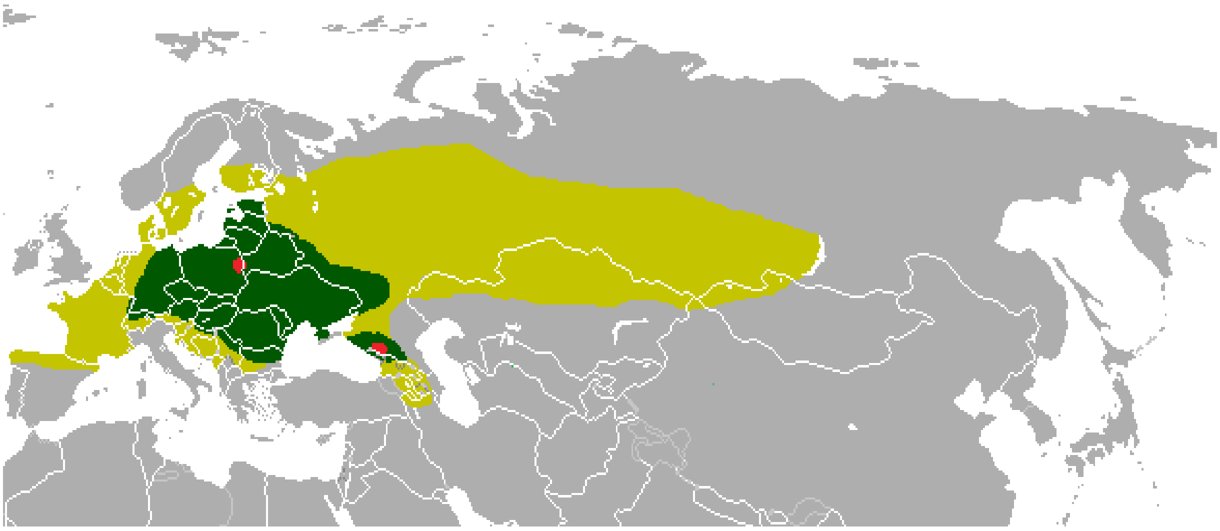


Figure 1. *Estimated range map of the European bison in holocene & historic times: Holocene in light green; high middle ages in dark green, beginning of 20th century in red. Image via Wikimedia Commons by user Altaileopard under creative commons license CC BY 3.0. Based on (Sipko (2009); Kerley* et al. *(2012).*

One of these two relict populations was in the Białowieża Forest (BF) in eastern Poland. From at least the 15th century and onwards the forest was a royal hunting ground, and as such under protection. Beginning with King Sigismund I a death penalty was instituted for poaching bison in 1538, and royal protection was continued by Russian Tsars when the area came under their jurisdiction from the 18th century until the beginning of World War I. During the war all the bison in the forest were killed, leaving only 54 known bison left in zoos and breeding centres around the world. In 1923 the International Society for the Protection of the European bison was established, with the aim of restoring the species across its former range (Pucek *et al.*, 2004). Today after numerous successful reintroductions in countries across Europe and intense conservation effort the world population numbers over 4500, with around 3000 of those free-ranging (Fig. 2) (European bison Network, 2014). The IUCN currently lists the species as vulnerable, citing among other factors the risk of inbreeding depression. The world population is severely fragmented with little genetic exchange between populations, which exacerbates the problem inherent with the genetic bottleneck the species has suffered (The IUCN Red List of Threatened Species, 2008). Many of the wild herds are also so small and isolated (less than 50 animals, Fig. 2) that they are at risk of extirpation due to demographic and environmental stochasticity (Traill *et al.*, 2010).

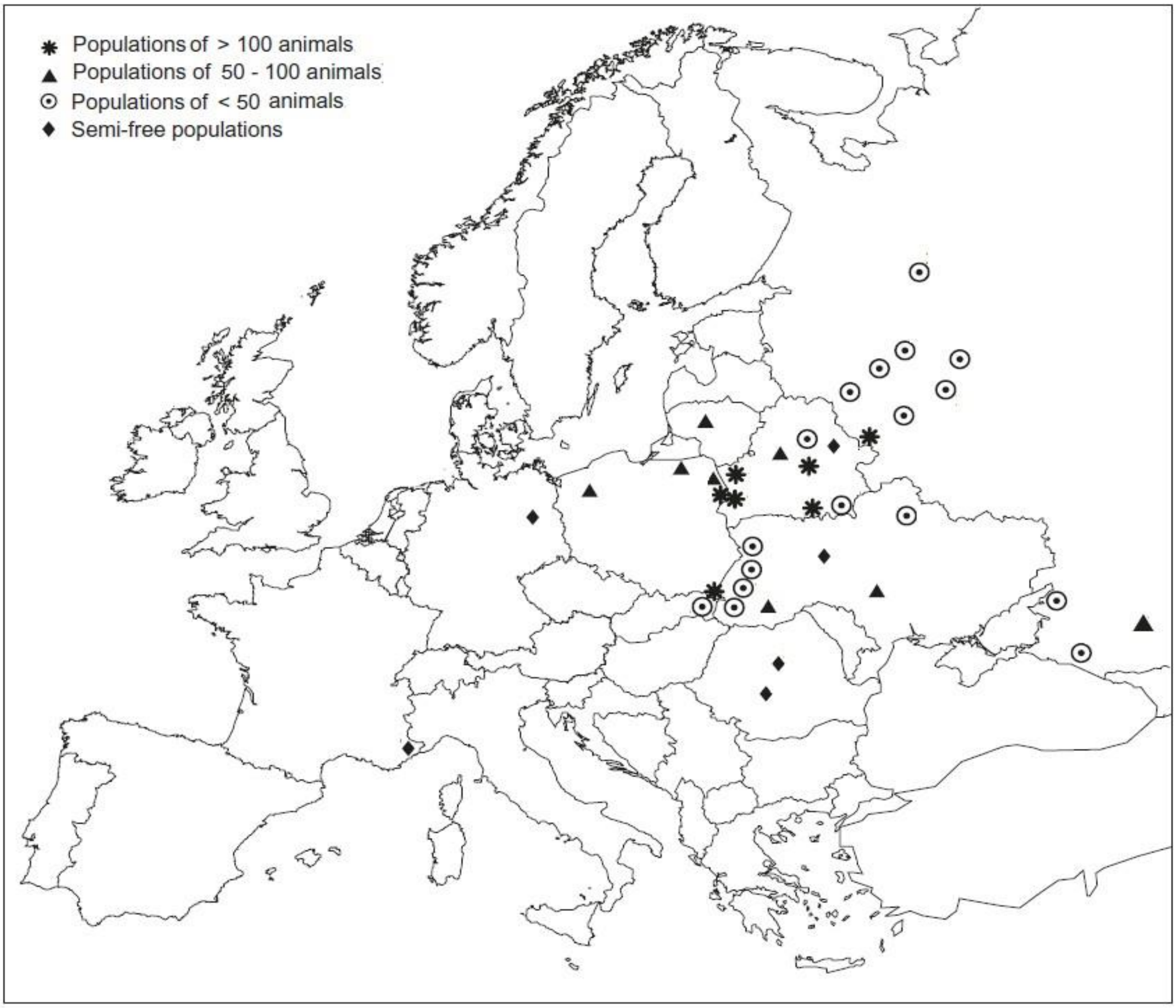


Figure 2. *A map of all free-ranging and semi-free populations of European bison (Bison bonasus) in 2010. Since then a few more populations have been introduced. Modified from (Krasiński & Krasińska 2013).*

One of the main tools of the conservation programs have been captive breeding coupled with reintroductions in areas which have been identified as suitable habitat. This has been recognized as the most cost-effective method of increasing bison numbers; however the method relies on proper identification of what constitutes suitable habitat (Kuemmerle *et al.*, 2011). The traditional view of the European bison is that of a forest-dwelling species, needing large areas of mainly deciduous forest for its survival and occasionally feeding in more open, grass-rich areas (e.g. Pucek 2004; Krasińska & Krasiński 2013). With this view in mind managers have searched for suitable forests for reintroduction (Parnikoza & Kaluzhna, 2009; Kuemmerle *et al.*, 2010). However, in more recent years this idea has been challenged with researchers (Kerley *et al.*, 2012) suggesting that the European bison is an example of a refugee species, which has been forced into its current habitat by human encroachment. Kerley *et al.* (2012) argue that forest-dominated areas do not represent optimal habitat, but is simply the few places where the species has managed to evade persecution. They point to a multitude of factors that indicate that the species is more adapted to open grass-rich habitats: Comparing it to its closest living relative, the American bison (*Bison bison*, which is typically associated with grasslands) the likeness in morphology and their ease of hybridisation indicates a very large degree of genetic similarity. Further, the mother - offspring follower strategy (Lent, 1974) is suggested to be atypical in a forest-dwelling species, instead of a hiding strategy (Krasiński & Krasińska, 2013). Additionally, their cranio-dental morphology display clear adaptations for a grazing diet instead of a browsing diet (Mendoza & Palmqvist, 2008). For a more detailed review of the argument against the European bison being a species adapted for a predominantly forest-dominated landscapes see Kerley *et al.* (2012).

Studies on habitat selection of the European bison are scarce, and conclusions have been consistently muddled by the fact that the individuals under study have been supplementarily fed hay during winter, possibly affecting their behaviour (e.g Krasińska & Krasiński 1995; Daleszczyk 2007). For example, it has been shown that fed bison exhibit different resting site selection in comparison to non-fed bison, where the non-fed bison select resting sites closer to open areas rich in forage (Schneider *et al.*, 2013). The reason for supplementary feeding is to increase winter survival and also to decrease the risk of human-bison conflicts by keeping bison from foraging in neighboring arable land (Krasiński & Krasińska 2013). Still, the studies that have been carried out have shown that bison do utilize open areas such as meadows within the forest for grazing, despite these types of habitat constituting a small percentage of the total available habitat (Daleszczyk *et al.* 2007).

In this thesis I present and analyse the largest dataset ever based on GPS-collared wild European bison. The data that is collected in three different bison herds in Poland is analysed with the pronounced aim to investigate general habitat selection patterns in the European bison. Particularly, I investigate the effects of study area, season and gender on habitat selection. The result is discussed in terms of potential contrasting patterns in habitat selection between open grass-rich environments and closed forested environments. As previously stated, the outcome might have important ramifications for current and future management and conservation efforts: to ensure long-term survival of the species more populations need to be reintroduced, and the global population to increase. The species has also garnered interest for its potential as a tool in fauna restoration: reintroducing it not only to conserve the species but also because of the species' impact on the ecosystem. Suggested gains are for example restoring historical levels of grazing pressure in areas where the abandonment of traditional agriculture have led to overgrowth and loss of biodiversity (e.g. Metera et al. 2010), or the role of the species as a seed disperser (Jaroszewicz *et al.*, 2011).

To avoid re-introductions in environments where survival might depend on continuous supply of artificial feeding, a proper assessment of what constitutes suitable habitat is needed. To accomplish this a resource selection function (RSF) framework will be used. Resource selection functions are models created by generalized linear regression that produce values that correspond to probability of use of a certain resource, such as habitat type (Manly *et al.*, 2002).

Study species

With an average weight of 634 kg for bulls and 424 kg for females the European bison is the heaviest extant land animal in Europe. 2.1 to 3.5 m in length and 1.6 to 1.95 m in height it is an imposing beast (Fig. 3). Rutting period is between August and October with bulls sexually mature from 4 years of age, however older bulls (6-12 years old) account for the majority of reproduction. Gestation period is on average 267 days in length, resulting in a small calf weighing between 15 and 35 kg (Krasiński & Krasińska 2013). It is a gregarious animal occuring in mixed herds of 10-40 individuals, with older bulls however mostly traveling alone or in smaller groups outside of the rut. Herds are not fixed, with individuals at times switching herds (Krasiński & Krasińska 2013). It is a ruminant, with studies of extant bison revealing a diet mainly consisting of soft herbaceous vegetation of the forest floor, grasses in meadows and the shrub layer. To some degree it consumes woody material: shoots and the bark of trees, mainly oak (*Quercus robur*), hornbeam (*Carpinus betulus*), ash (*Fraxinus excelsior*) and Norway spruce (*Picea abies*) (Krasiński & Krasińska, 2013). However, isotope analysis comparing the diet of fossil bison to extant bison show that prehistoric bison had a significantly higher degree of grass in their diet, suggesting that the results of recent studies of bison diet might be the results of the species currently residing in suboptimal landscapes (Bocherens *et al.*, 2015).

Figure 3. *Two bison in Réserve biologique des Monts d'Azur, Haut-Thorenc, France. Image via Wikimedia Commons by Valène Aure under Creative Commons license CC BY-SA 3.0.*

Study areas

Movement data on bison were collected from three areas in Poland: Białowieża forest (BF), Knyszyn Forest (KF) and Western Pomerania (WP).

Białowieża forest

BF is situated in the border region between Poland (650 km^2) and Belarus (875 km^2). The area is delineated by the coordinates 23 31' – 24 21' °E and 52 29' – 52 47' °N. The landscape is flat and dominated by old stands of hemiboreal forest, mainly consisting of oak, lime and hornbeam with some coniferous forest (Scots pine) and mixed stands. The interior of the forest is interspersed with a small amount of meadows and other open grass-rich environments such as river valleys. There are currently around 900 bison in the forest, split in two herds, one in each country. They are fully separated by a fence.

Knyszyn forest

Situated 50 km north of BF lies this 1,235 km^2 protected area containing 20 nature reserves. The habitat composition differs to BF (Fig. 4) with a smaller amount of deciduous and mixed forest: up to 80 % of the forest complex is composed of coniferous forest. As of 31 December 2010 there were 94 bison in the park (Krasiński & Krasińska 2013).

Western Pomerania

Similar in habitat composition to KF (Fig. 4) the study area in WP however lies between 15 45' – 16 48' °E and 53 02' – 53 62' °N and is thus situated in the nemoral zone. The bisons are separated in two herds, a western in the Drawsko forest and an eastern in the Mirosławiec forest. Both forests are cut across by river valleys and ribbon lakes. As of 31st December 2010 there were 81 bison, divided into two herds (Krasiński & Krasińska 2013).

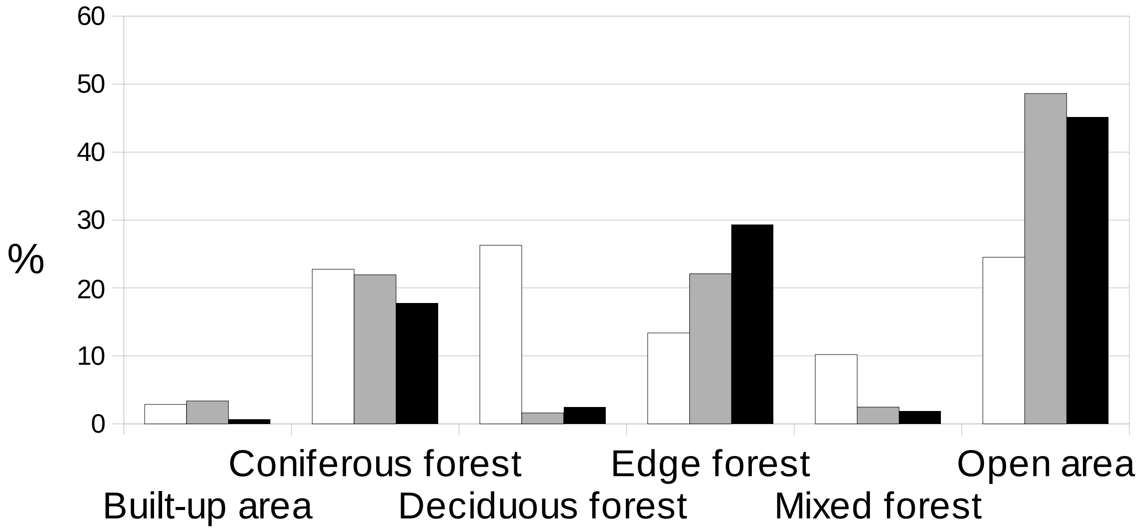


Figure 4. *Habitat composition, divided in 6 different habitats, in the three study areas in Poland. Białowieża forest in white, Knyszyn forest in grey and Western Pomerania in black.*

Materials & methods

GPS data

GPS fixes of 52 collared bison (32 female, 20 male) during 2005-2013 from the three study areas was supplied by the Mammal Research Institute of the Polish Academy of Sciences (MRI PAS) in Białowieża. GPS collars were set to attempt to acquire a fix ever hour. All animals were adult and judged to be ≥2 years old at first marking. Raw data contained 306,256 GPS locations and was screened for low quality fixes according to the methods of Bjørneraas et al. (2010). Individuals with very little data (less than one month continuous monitoring) or which had been subject to interference during the study period, e.g. relocation by park rangers, were excluded from analysis. As habitat selection was expected to differ between summer and winter (Daleszczyk 2007), GPS fixes were divided into summer and winter seasons, with summer defined as April until end of October and winter as November until end of March. This definition of winter rougly coincides with the timing of when supplementarily fed individuals move to (November) or from (April) the vicinity of feeding sites. Using this definition of two main seasons generates 150 bison-seasons in this data set. Since the dataset contained gaps e.g. due to collar failures and mortality, the quality of each bison-season was ranked depending on how complete the coverage was for that season: bison-seasons containing full continuous coverage (defined as having gaps no longer than one week) during a season were graded "Good", bison-seasons with continuous coverage for at least two months during a season were graded "Average" and bison-seasons with coverage between 1-2 months were graded "Poor" (Tab. 1).

Table 1. *The number and subjective quality of coverage of bison-seasons in the study for each study area. The bison-seasons originated from 52 individuals, 32 female and 20 male.*

	Summer			Winter		
	Good	Average	Poor	Good	Average	Poor
Białowieża forest	28	4	6	14	4	12
Knyszyn forest	2				2	
WesternPomerania	35	1	0	25	1	16

The study period differed between areas, with BF being studied between 2005-2011, KF between 2009-2011 and WP between 2010-2013.

Cartography

Habitat maps were constructed in a GIS (ArcMap 10.2® by Esri). The base map layer used was CORINE 2006 supplied by the European Environment Agency, combined with Polish state databases for road networks supplied by the MRI PAS. Since all study areas were affected to some extent by forestry during the study period, the Global Forest Watch database for yearly forest loss was used to create habitat maps for each year in the study period (Hansen *et al.*, 2013). Areas where forest loss had occured were classified as habitat class "Clearcut". Distance to the nearest trafficked road and distance to the nearest open habitat was calculated for each relocation, where open habitat was classified as any arable land, meadow or clearcut with a size of at least 1 hectare. All forests within 200 meters of an open area were classified as "Edge forest". The distance 200 meters was determined to be a reasonable estimate of how far a bison ventures into a forest to find shelter (Rafał Kowalczyk personal communication). CORINE habitat classes were reclassified from 34 classes to 7 (Appendix 1). Rare habitats (less than 0.1 % of GPS fixes) were excluded from analysis.

Since the fence that limits bison movement between Poland and Belarus not exactly overlaps with the official border 73 GPS fixes in Białowieża were inside Belarusian territory where CORINE has no coverage. For these fixes habitat was classified according to local map layers supplied by the MRI PAS.

Statistical analysis

Research has shown that the method of acquiring the availability sample for the study species is of high importance in order to obtain a good RSF (Boyce *et al.* 2002). Following the advice set out in Northrup et al. (2013) habitat availability for each individual bison-season was assessed in two ways: by a minimum convex polygon (MCP) and a kernel density estimate isopleth 95 % (KDE, generated using h_{ref} as suggested by Worton (1989), Fig. 5). Within each polygon or isopleth an equal amount of randomly located points to the number of GPS fixes were placed. For each subsequent RSF model the sensitivity of the regression coefficients to the different availability samples was analysed to see if the choice of availability sample affected the results. The MCPs were also used to estimate seasonal homeranges. Bison-seasons of "Poor" quality were excluded from statistical analysis.

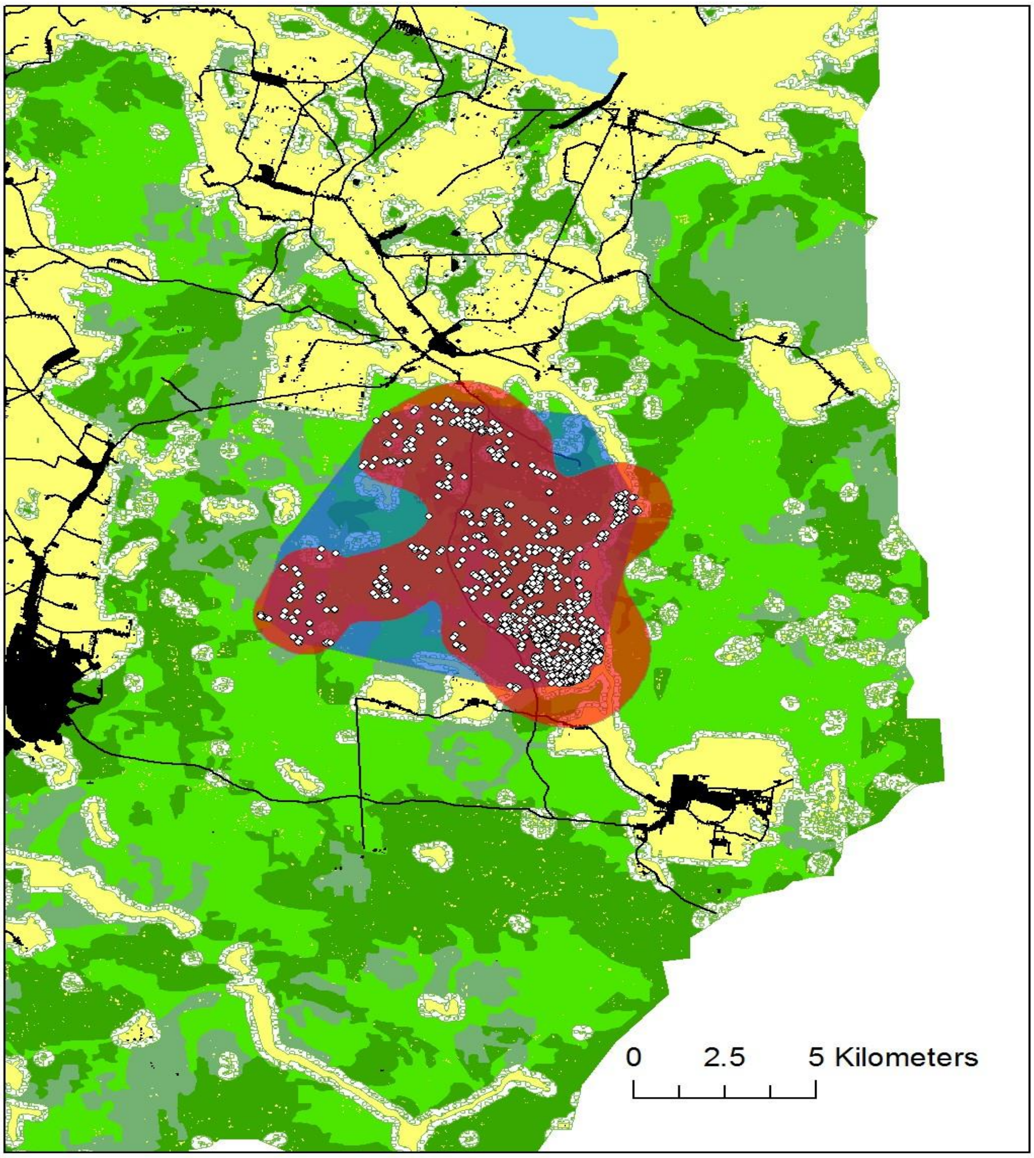


Figure 5. *A part of Białowieża forest (BF) with GPS fixes of one summer season of bison #32. Minimum convex polygon (MCP) in blue, Kernel density estimate (95%) in red. Light green indicates deciduous forest, dark green coniferous forest, grey-green mixed forest and light yellow is open areas such as meadows, marshlands and arable land. A buffer zone of 200m along all forest edges is indicated in speckled white-green.*

Analysis by Generalized Linear Models (GLM) with logistic regressions was created in R statistical software using the package 'lme4' (Bates *et al.*, 2014). To produce RSF models the regression coefficients were transformed according to equation 1 (Manly *et al.*, 2002).

$$RSF\ score = e^{B_0 + B_1 X_1 + \dots B_i X_i} \tag{1}$$

Where B_i is the i_{th} coefficient of the GLM and X_i is the corresponding factor, with B_0 the intercept.

Two models were constructed: the first with data from the BF only, examining the effect of different levels of supplementary feeding on habitat selection in summer and winter. Bison in Białowieża have access to 40 feeding stations, where supplementary fodder (typically hay) is made available in winter. Some of the main feeding stations are continuously supplied *ad libitum* with hay throughout the winter, while others are more peripheral that are only stocked once per season. This makes it possible to divide the bison into groups according to how much they utilize feeding in winter: ”unfed bison”, ”partly fed bison” and ”intensively fed bison”. Since the number of unfed bison were few, they were later grouped with the partly fed bison into a new "less intensively fed" group. This group was then compared to the "intensively fed" group. Bison in WP are also fed, but the feeding intensity was not known on an individual level and could not be used for this analysis.

The second model compared habitat selection in BF and WP in summer. KF was excluded from this analysis due to small sample sizes (n = 2).

For each model a number of candidate models were produced with all relevant factors and interactions investigated. As recommended by Burnham & Anderson (2010), model selection was based on the second-order Akaike Information Criterion (AICc) as a result of the number of parameters in the models in relation to sample size. The model with the lowest AICc was chosen.

Results

Using the MCPs to estimate seasonal home ranges showed that there was differences between study areas. Home ranges were larger in KF and WP (Fig. 6). The sample size of KF is unfortunately very low, and the variation in both BF and WP is large. One individual in WP who performed a partial migration was removed due to the home range estimate being deemed unreasonably large (900 km^2). There were no significant differences in home range sizes between ”intensively fed” bison and ”less intensively fed” bison in winter ($p > 0.8074$, $t = 0.2492$, $df = 12$) or in summer ($p > 0.6447$, $t = 0.4666$, $df = 26$). The choice to use the MCPs to estimate home ranges was made in order to facilitate comparison with previously reported home range sizes in the literature.

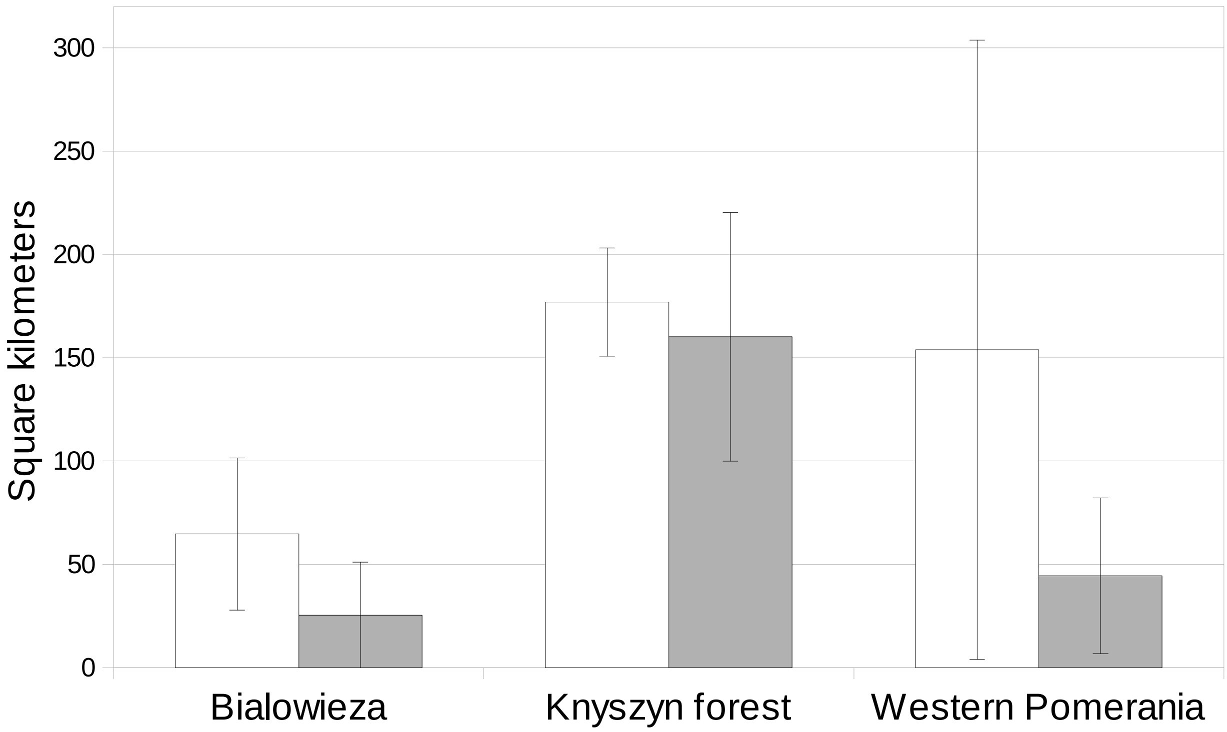


Figure 6. *Mean seasonal home range size of European bison in three locations in Poland estimated by Minimum Convex Polygon around all GPS fixes collected between 2005 – 2013. Summer (white) and winter (grey) seasons. Sample sizes in each area are respectively (summer, winter): Białowieża forest (28, 14), Knyszyn forest (2, 2), Western Pomerania (35, 25). Error bars represent one standard deviation.*

For the RSF analysis the choice of availability sample (MCP vs KDE 95 %) did not significantly affect estimates of model parameters. In the pursuit of brevity and clarity only models using KDE 95 % as availability sample are presented below.

Effect of feeding in Białowieża

Constructing the model including different factors and interactions between factors revealed that the model including interactions between habitat and sex, habitat and season and a three-way interaction between habitat, season and feeding intensity had the lowest AICc score (Tab. 2).

***Table 2**. Second-order AICc selection summary of five models examining the contribution of the following independent variables to the binary factor "Use": habitat class (habitat), season (summer or winter), sex (male or female) and feeding intensity (less intensively fed or intensively fed). (1|bisonseason) denotes including random effects of bison-seasons. K refers to the total number of estimable parameters plus 1. Total sample size (n) in each model = 24. Models are ordered in terms of Δ_{AIC} where Δ_{AIC} = AICc - AICc of best model. Interaction effects denoted by semicolon. Selected model is marked by bold text.*

Model	K	AIC	AICc	Δ_{AIC}
habitat + habitat:sex + habitat:season + habitat:feeding:season +(1|bisonseason)	**30**	**267212**	**266946**	**0**
habitat + habitat:sex + habitat:season + habitat:feeding + habitat:feeding:sex:season + (1|bisonseason)	42	267258	267068	122
habitat + habitat:sex + habitat:season + (1|bisonseason)	18	266966	267103	157
habitat + habitat:season + (1|bisonseason)	12	267155	267183	237
habitat+(1|bisonseason)	6	267517	267522	576

Using estimated regression coefficents (Appendix 2) the RSF was constructed using equation 1, comparing habitat selection in summer and winter for both sexes in regards to intensity of feeding. Significant differences in habitat selection was found between intensively fed and less intensively fed bison in winter regardless of sex, with four of six habitat classes exhibiting significant differences between feeding groups for female bison and five for male bison (Fig. 7-8). For the summer season differences in habitat selection were much less apparent, with only "Coniferous forest" exhibiting significant differences between feeding groups for both sexes (Fig. 9 and 10).

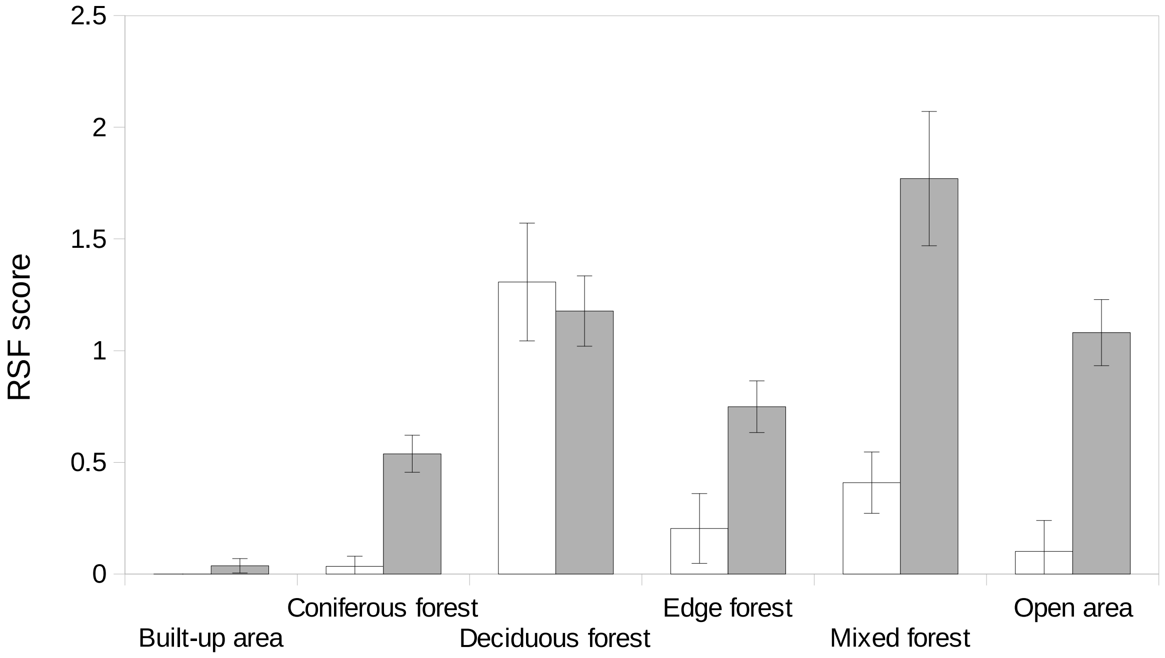


Figure 7. *Effect of supplementary feeding on the relative probability of usage of 6 main winter habitats by female bison in Białowieża forest, Poland, based on 8 females: 2 intensively fed (white) and 6 less intensively fed (grey). Error bars represent ±2 standard deviations.*

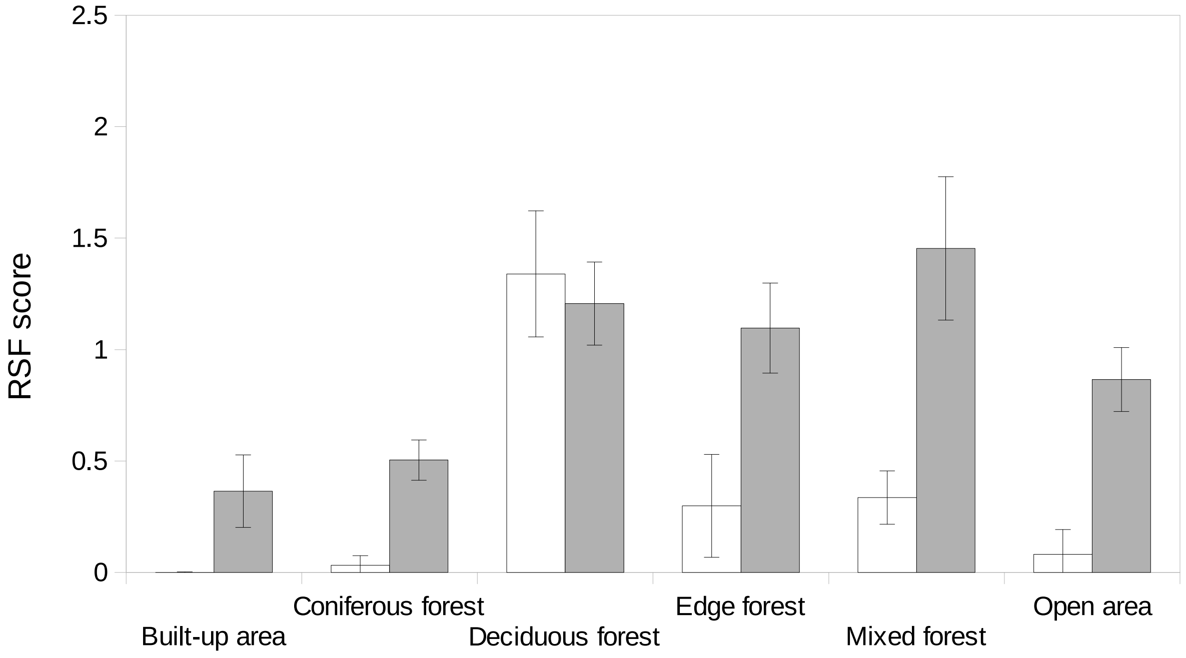


Figure 8. *Effect of supplementary feeding on the relative probability of usage of 6 main winter habitats by male bison in Białowieża forest, Poland, based on 6 bison: 2 intensively fed (white) and 4 less intensively fed (grey). Error bars represent ±2 standard deviations.*

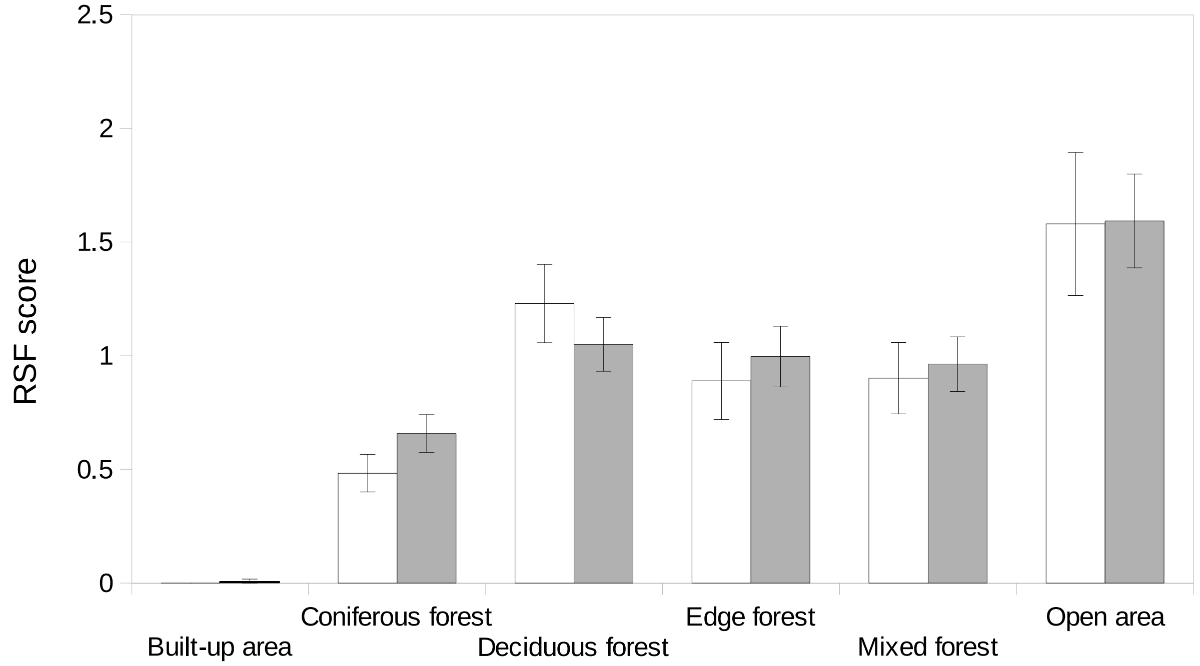


Figure 9. *Effect of supplementary feeding on the relative probability of usage of 6 main summer habitats by female bison in Białowieża forest, Poland, based on 12 females: 4 intensively fed (white) and 8 less intensively fed (grey). Error bars represent ±2 standard deviations.*

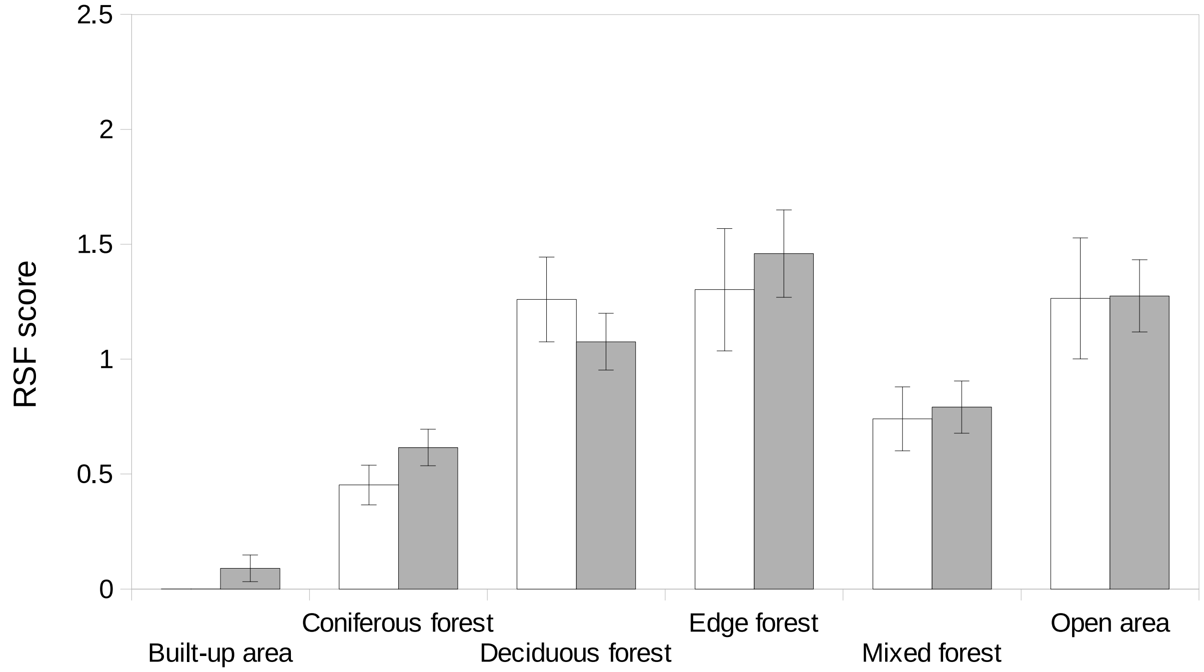


Figure 10*. Effect of supplementary feeding on the relative probability of usage of 6 main summer habitats by male bison in Białowieża forest, Poland, based on 13 bison: 4 intensively fed (white) and 9 less intensively fed (grey). Error bars represent ±2 standard deviations.*

Comparing Białowieża forest to Western Pomerania

Since there was no remaining delayed effect of supplementary winter feeding on summer habitat selection, habitat selection in summer could be analyzed, comparing selection in WP and BF regardless of individual differences in winter feeding. The model selection procedure revealed that a model including interactions between habitat and sex in addition to habitat and location had the lowest AICc score (Tab. 3).

Table 3. *Second-order AICc selection summary of four models examining the contribution of the following independent variables to the binary factor "Use": habitat class (habitat), location (study area: Białowieża forest or Western Pomerania) and sex (male or female). (1|bisonseason) denotes including random effects of bison-seasons. K refers to the total number of estimable parameters plus 1. Total sample size (n) in each model = 50. Models are ordered in terms of* Δ_{AIC} *where* Δ_{AIC} *= AICc - AICc of best model. Interaction effects denoted by semicolon. Selected model is marked by bold text.*

Model	K	AIC	AICc	Δ_{AIC}
habitat + habitat:sex + habitat:location + (1|bisonseason)	**20**	**567510**	**567539**	**0**
habitat + habitat:sex + habitat:location + habitat:sex:location + (1|bisonseason)	27	567710	567779	240
habitat + habitat:sex + (1|bisonseason)	14	567990	568002	463
habitat+(1|bisonseason)	7	568720	568723	1184

Using estimated regression coefficents (Appendix 3) the RSF was constructed using equation 1. I found "Open area" to be significantly more probable to be chosen than any other habitat class for female bison (Fig. 11) in both study areas ($p < 0.0001$, df = 22 and 34, $t \geq 17.2665$ in all cases). For male bison selection for ”Open area” was significantly more likely than all other habitat classes ($p < 0.0001$, df = 6 and 24, $t \geq 23.605$ in all cases) with the exception of “Open area” vs “Edge forest” in BF and WP ($p \geq 0.13$, df = 6 and 24 , $t \leq 1.5$, in both cases; Fig. 11-12).

Between-sex variation in habitat selection exhibited similar trends for both study areas, with males more probable to select ”Edge forest” and females ”Deciduous forest” (Fig. 11-12). Both study areas showed similar patterns in habitat selection, with significant differences in the probability of usage of ”Deciduous forest” and ”Coniferous forest” (Fig. 11-12).

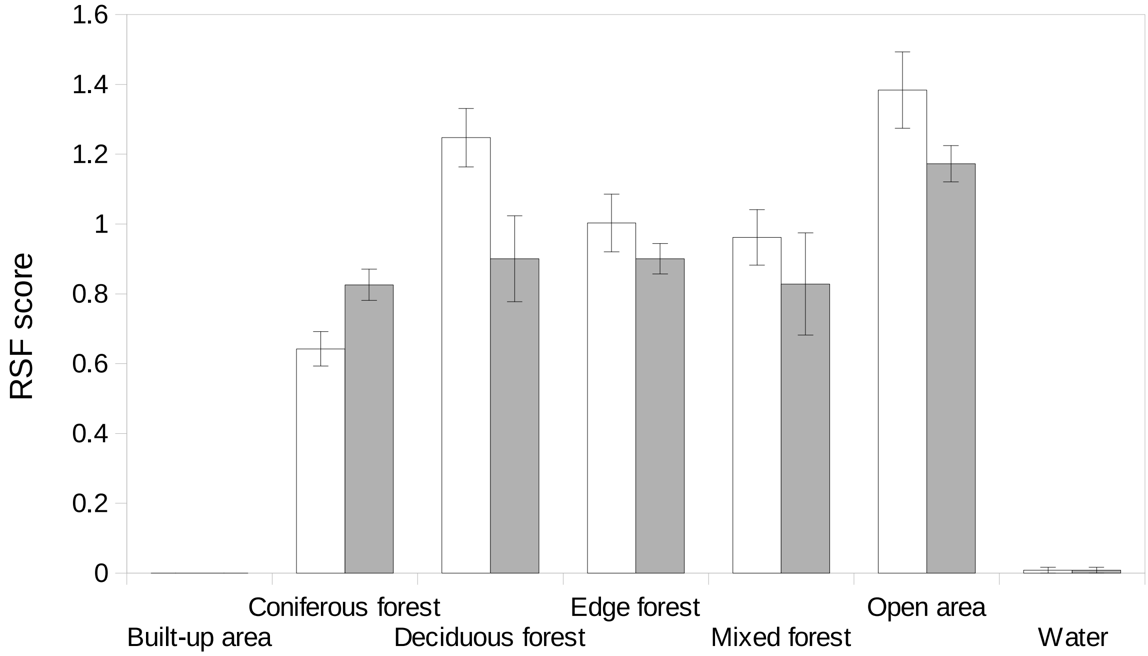


***Figure 11**. Relative probability of selection of 7 main summer habitats by female bison in Białowieża forest (white) and Western Pomerania (grey), Poland. Based on 30 bison: 12 in Białowieża and 18 in Western Pomerania. Error bars represent ±2 standard deviations.*

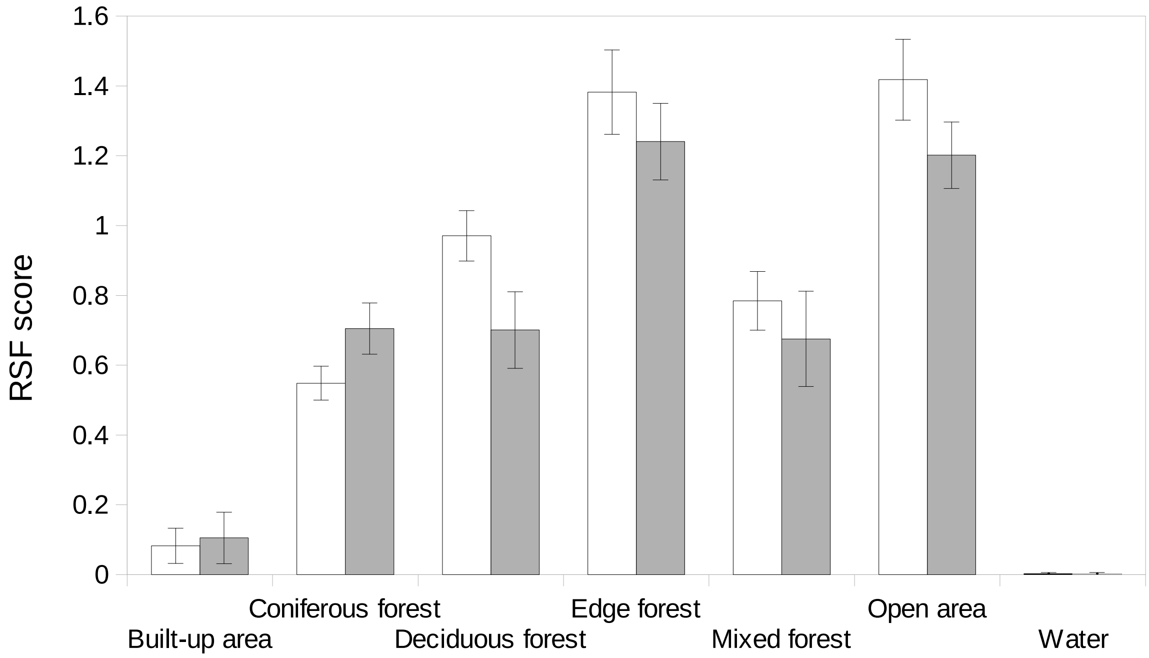


***Figure 12**. Relative probability of selection of 7 main summer habitats by male bison in Białowieża forest (white) and Western Pomerania (grey), Poland. Based on 17 bison: 13 in Białowieża and 4 in Western Pomerania. Error bars represent ±2 standard deviations.*

Discussion

Comparing bison in the Białowieża forest (BF) to Western Pomerania (WP) shows that open grass-rich areas and areas associated with them ("Edge forest") are consistently among the two highest ranked habitats in summer (Fig. 11-12). In the perspective of the repeatedly debated question of whether the European bison is adapted to forested landscape or not, my results indicate that open grass-rich areas are clearly selected regardless of study area or sex (Fig. 11-12). This is further evidence that support the idea of the European bison as a refugee species, utilizing suboptimal forest-dominated landscapes to minimize human conflict (Kerley *et al.* 2010). Managers and conservationists should with this in mind reevaluate possible locations for reintroductions. It is obvious that the European bison can persist and thrive in heavily forested areas, with a continuously positive population trend since reintroductions began (European bison Network, 2014). However, long-term conservation needs of the species call for larger, more connected herds (The IUCN Red List of Threatened Species, 2008). Finding suitable areas to reintroduce will be more productive if conservationists do not unnecessarily constrain their search to habitats which might be suboptimal habitats.

This study clearly indicates that the intensity of artificial feeding affects habitat selection of the European bison in Białowieża during winter, but that the ”feeding effect” does not carry over into the selection of habitats during summer (Fig. 7-10). As previously mentioned, one of the reasons for supplementary feeding is to avoid human-bison conflicts by minimizing damage to agricultural lands bordering to the BF and keeping the bison within the borders of the BF. Our results show that less intensively fed bison are significantly more likely to select habitats of class "Open area" than more intensively fed bison (Fig. 7-8). Since this habitat class includes all habitats that lack a canopy cover such as meadows, marshlands and arable land this could be indicative of less intensively fed bison being more likely to intrude and cause damage to arable land. To properly assess this, an analysis where "arable land" is distinguished as its own habitat class would need to be carried out. Due to time-constraints this was not investigated in this project.

A caveat to the differences found in the habitat selection between intensively fed animals and less intensively fed animals in winter (Fig. 7-8) is that this might not truly reflect habitat selection *per se*. A possible interpretation is that the RSF simply reflects the habitat composition surrounding the feeding stations, since the feed animals most likely spend a lot of time there resting and ruminating

(Krasiński & Krasińska, 2013; Schneider *et al.*, 2013). Regardless of whether this is the case or not, I have shown that the intensity of feeding in winter does not affect the animals behaviour in the summer season (Fig. 9-10). This result is the basis to allow the comparison between the two study areas in summer. However, to further elucidate the effect of feeding stations in Białowieża, a future analysis could include the factor "distance to nearest feeding station".

As previously mentioned, the method for assessing available habitats affects the subsequent RSF's. Still, we found no difference between using MCP or KDE, which makes intuitive sense since these two estimates for the most part gave similar geometries (Fig. 6). In current literature a wide variety of methods apart from the MCP and KDE are used in similar studies, for example buffers around GPS fixes, with a fixed width based on average step-length between fixes or a variable width where buffer size depends on distance to the next fix (Selonen *et al.*, 2010). More exotic estimates are for example the Localized Convex Hull method (LoCoH, Getz et al. 2007) or the Brownian Bridge Movement Model (BBMM, Horne et al. 2007). There is no clear consensus on which method that is the most appropriate for high-resolution GPS data such as the dataset in this study (Kie *et al.*, 2010). Analyzing the dataset with other availability samples might exhibit different results, and could be a worthwhile endeavour.

Since the bison roam over large areas (Fig. 6) the question of scale arises. In this study we have attempted to look at individual bison selecting habitats within their home ranges, the 3rd order selection according to the classification scheme of Meyer & Thuiller (2006). For reintroduction purposes it would also be of interest to study larger scales of habitat selection and suitability, e.g. looking at selection of individual home ranges within population range (2nd order selection) and selection of population home range on a regional scale (1st order selection). The latter is however a doubtful enterprise simply by the fact that the current wild populations of bison have not selected their habitats themselves on the regional level, since they've been deliberately reintroduced (Krasiński & Krasińska, 2013).

Built-up areas consistently recieved low RSF scores (Fig. 7-12), suggesting the presence of humans may be selected against by the bison. In this study we have not investigated anthropogenic effects on habitat selection in detail. Still, some exploratory analysis of the effects of human disturbance was performed, showing that the bison seemed to avoid highly trafficked roads (unpublished data).

Other important and in this study overlooked ecological factors could be effects of large predators such as wolves (Fortin *et al.*, 2010), effects of water availability in summer (Goulart *et al.*, 2009) and effects of population density (Krasiński & Krasińska, 2013) on habitat selection.

In summer, bison exhibit regular patterns to their 24-hour cycle with four main feeding periods during the day (Krasiński & Krasińska 2013). These correspond to dawn, two periods during the day and the approach of sunset. Analysing the dataset and including time of day as a factor might thus disentangle which habitats that are the most important for feeding, and also for other behaviours such as ruminating.

A clear weakness of this study, is that no effort has been made to mitigate the problem of a habitat dependent GPS fix success rate. A lower fix-rate in closed-canopy environments is to be expected and could severely skew the resulting analysis (Lewis *et al.*, 2007). It has even been suggested that a loss of more than 10 % of fixes (a 90 % successful fix rate) is enough to skew inferences about habitat selection (D'Eon, 2003). I did not calculate the fix rate success, however, the use of short fix intervals as in this study (1 hour) have been shown to improve total fix rate success (Cain *et al.*, 2005). The fix rate success in our study also probably varies during the study period, with earlier years suffering a worse fix rate success than later years due to more developed and reliable collars being deployed for every year.

The estimates of Białowieża mean home range size (Fig. 6) correspond well to what has been previously reported in literature: 69-70 km^2 in summer and 8-11 km^2 in winter (Krasiński & Krasińska 2013). Although the variance is large due to small sample size, there seems to be a trend of smaller home ranges in Białowieża compared to the other two study areas. Previous research has suggested that fed bison utilize a smaller home range (Krasiński & Krasińska 2013), a result which I could not confirm in this study.

My study has contributed to our understanding of the habitat selection of a globally threatened charismatic species. This new knowledge may be used in steering restoration efforts towards efficient decisions that put together ecological knowledge on the fundamental niche of the species and current status and characteristics of European landscapes.

Acknowledgments

I would like to thank my supervisors Petter Kjellander, Rafał Kowalczyk, Grzegorz Mikusiński and Andreas Zetterberg for their guiding presence, without which this work would not have been possible. I would also like to thank the Mammal Research Institute of the Polish Academy of Sciences in Białowieża and its Director for their hospitality during my stay, Marcin Górny for his willingness to share his GIS expertise and Andrew Lewis for comments and critique. Lastly I would like to give thanks to Ebba Hammarlund, forever my lantern on dark moors.

References

Bates, D., Mächler, M., Bolker, B. M. & Walker, S. C. (2014). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*,.

Bjørneraas, K., Van Moorter, B., Rolandsen, C. M. & Herfindal, I. (2010). Screening global positioning system location data for errors using animal movement characteristics. *Journal of Wildlife Management*, 74(6), pp 1361–1366.

Bocherens, H., Hofman-Kamińska, E., Drucker, D. G., Schmölcke, U. & Kowalczyk, R. (2015). European bison as a refugee species? Evidence from isotopic data on early holocene bison and other large herbivores in northern europe. *PloS one*, 10(2), p e0115090.

Burnham, K. P. & Anderson, D. R. (2010). *Model Selection and Multimodel Inference*. 4th. ed New York: Springer.

Cain, J. W., Krausman, P. R., Jansen, B. D. & Morgart, J. R. (2005). Influence of topography and GPS fix interval on GPS collar performance. *Wildlife Society Bulletin*, 33(3), pp 926–934.

Cardillo, M., Purvis, A., Sechrest, W., Gittleman, J. L., Bielby, J. & Mace, G. M. (2004). Human Population Density and Extinction Risk in the World's Carnivores. *PLoS Biol*, 2(7), p e197.

Chapin, F. S., Zavaleta, E. S., Eviner, V. T., Naylor, R. L., Vitousek, P. M., Reynolds, H. L., Hooper, D. U., Lavorel, S., Sala, O. E., Hobbie, S. E., Mack, M. C. & Díaz, S. (2000). Consequences of changing biodiversity. *Nature*, 405(6783), pp 234–42 Macmillan Magazines Ltd.

D'Eon, R. G. (2003). Effects of a Stationary GPS Fix-Rate Bias on Habitat-Selection Analyses. *The Journal of Wildlife Management*, 67(4), pp 858–863.

Daleszczyk, K. (2007). Habitat structure, climatic factors, and habitat use by European bison (Bison bonasus) in Polish and Belarusian parts of the Bialowieza Forest, Poland. *Canadian journal of …*, 85(2), pp 261–272.

European Bison Network. *Bison herds*. [online] (2014). Available from: http://www.bison-ebcc.eu/. [Accessed 2015-01-01].

Fahrig, L. (2003). Effects of Habitat Fragmentation on Biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, 34, pp 487–515.

Fortin, D., Beyer, H. L., Boyce, M. S., Smith, D. W., Mao, J. S., Ecology, S. & May, N. (2010). Wolves Influence Elk Movements : Behavior Shapes a Trophic Cascade in Yellowstone National Published by : Ecological Society of America WOLVES INFLUENCE ELK MOVEMENTS : BEHAVIOR SHAPES A TROPHIC CASCADE IN YELLOWSTONE NATIONAL PARK. 86(5), pp 1320–1330.

Getz, W. M., Fortmann-Roe, S., Cross, P. C., Lyons, A. J., Ryan, S. J. & Wilmers, C. C. (2007). LoCoH: nonparameteric kernel methods for constructing home ranges and utilization distributions. *PloS one*, 2(2), p e207.

Goulart, F. V. B., Cáceres, N. C., Graipel, M. E., Tortato, M. A., Ghizoni, I. R. & Oliveira-Santos, L. G. R. (2009). Habitat selection by large mammals in a southern Brazilian Atlantic Forest. *Mammalian Biology - Zeitschrift für Säugetierkunde*, 74(3), pp 182–190.

Hansen, M. C., Potapov, P. V., Moore, R., Hancher, M., Turubanova, S. A., Tyukavina, A., Thau, D., Stehman, S. V., Goetz, S. J., Loveland, T. R., Kommareddy, A., Egorov, A., Chini, L., Justice, C. O. & Townshend, J. R. G. (2013). High-Resolution Global Maps of 21st-Century Forest Cover Change. *Science*, 342(6160), pp 850–853.

Hendriks, a. J., Willers, B. J. C., Lenders, H. J. R. & Leuven, R. S. E. W. (2009). Towards a coherent allometric framework for individual home ranges, key population patches and geographic ranges. *Ecography*, 32(6), pp 929–942.

Horne, J. S., Garton, E. O., Krone, S. M. & Lewis, J. S. (2007). Analyzing Animal Movements Using Brownian Bridges. *Ecology*, 88(9), pp 2354–2363.

Jaroszewicz, B., Sondej, I. & Stebel, A. (2011). Biodiversity of Bryophytes Growing on the Faeces of Ungulates-a Case Study from north-eastern Poland. *Cryptogamie*, *Bryologie*, 32(3), pp 221–231.

Kerley, G., Kowalczyk, R. & Cromsigt, J. (2012). Conservation implications of the refugee species concept and the European bison: king of the forest or refugee in a marginal habitat? *Ecography*, 35(6), pp 519–529.

Kie, J. G., Matthiopoulos, J., Fieberg, J., Powell, R. a, Cagnacci, F., Mitchell, M. S., Gaillard, J.-M. & Moorcroft, P. R. (2010). The home-range concept: are traditional estimators still relevant with modern telemetry technology? *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, 365(1550), pp 2221–2231.

Krasińska, M. & Krasiński, Z. A. (1995). Composition, group size, and spatial distribution of European bison bulls in Białowieża Forest. *Acta theriologica*, 40(1), pp 1–21.

Krasiński, Z. A. & Krasińska, M. (2013). *European Bison*. ISBN 2831707625.

Kuemmerle, T., Perzanowski, K., Akçakaya, H. R., Beaudry, F., Van Deelen, T. R., Parnikoza, I., Khoyetskyy, P., Waller, D. M. & Radeloff, V. C. (2011). Cost-effectiveness of strategies to establish a European bison metapopulation in the Carpathians. *Journal of Applied Ecology*, 48(2), pp 317–329.

Kuemmerle, T., Perzanowski, K., Chaskovskyy, O., Ostapowicz, K., Halada, L., Bashta, A. T., Kruhlov, I., Hostert, P., Waller, D. M. & Radeloff, V. C. (2010). European Bison habitat in the Carpathian Mountains. *Biological Conservation*, 143(4), pp 908–916 Elsevier Ltd.

Lent, P. C. (1974). The behavior of ungulates and its relation to management.(Geist, V. & Walther, F., Eds) *The behavior of ungulates and its relation to management*, 1(24), pp 14–55 IUCN Publications new series.

Lewis, J. S., Rachlow, J. L., Garton, E. O. & Vierling, L. A. (2007). Effects of habitat on GPS collar performance: using data screening to reduce location error. *Journal of Applied Ecology*, 44(3), pp 663–671.

Manly, B. F. J., McDonald, L. L. & Thomas, D. L. (2002). *Resource Selection by Animals: Statistical Design and Analysis for Field Studies*. Kluwer Academic Publishers. ISBN 9781402006777.

Mendoza, M. & Palmqvist, P. (2008). Hypsodonty in ungulates: an adaptation for grass consumption or for foraging in open habitat? *Journal of Zoology*, 274(2), pp 134–142.

Metera, E., Sakowski, T., Krzysztof, S. & Romanowicz, B. (2010). Grazing as a tool to maintain biodiversity of grassland - a review. *Animal Science Papers and Reports*, 28(4), pp 315–334.

Meyer, C. B. & Thuiller, W. (2006). Accuracy of resource selection functions across spatial scales. *Diversity and Distributions*, 12(3), pp 288–297.

Northrup, J. M., Hooten, M. B., Anderson, C. R. & Wittemyer, G. (2013). Practical guidance on characterizing availability in resource selection functions under a use-availability design. *Ecology*, 94(7), pp 1456–1463.

Parnikoza, I. & Kaluzhna, M. (2009). Primary search of woodlands suitable for free ranging Bison bonasus populations in Ukraine. *European Bison Conservation Newsletter*, 2, pp 47–53.

Pucek, Z., Belousova, I., Krasińska, M., Krasiński, Z. A. & Olech, W. (2004). *European bison: status survey and conservation action plan*.(Pucek, Z., Ed) 1st. ed Gland, Switzerland ; Cambridge: IUCN/SSC Bison Specialist Group. ISBN 2831707625.

Sandom, C., Faurby, S., Sandel, B. & Svenning, J.-C. (2014). Global late Quaternary megafauna extinctions linked to humans, not climate change. *Proceedings of the Royal Society of London B: Biological Sciences*, 281(1787), p 20133254.

Schneider, T. C., Kowalczyk, R. & Köhler, M. (2013). Resting site selection by large herbivores - The case of European bison (Bison bonasus) in Białowieża Primeval Forest. *Mammalian Biology*, 78(6), pp 438–445 Elsevier GmbH.

Selonen, V., Hanski, I. K. & Desrochers, a. (2010). Measuring habitat availability for dispersing animals. *Landscape Ecology*, 25(3), pp 331–335.

The IUCN Red List of Threatened Species. *European Bison IUCN status*. [online] (2008). Available from: http://www.iucnredlist.org/details/2814/0. [Accessed 2015-02-02].

Traill, L. W., Brook, B. W., Frankham, R. R. & Bradshaw, C. J. a (2010). Pragmatic population viability targets in a rapidly changing world. *Biological Conservation*, 143(1), pp 28–34 Elsevier Ltd.

Worton, B. (1989). Kernel Methods for Estimating the Utilization Distribution in Home-Range Studies. *Ecology*, 70(1), pp 164–168.

Appendix 1. *Reclassification of CORINE. Habitat types that made up less than 0.1 % of GPS fixes were defined as "Other" and excluded from analysis.*

CORINE code	Code translation	Reclassified habitat
111	Continuous urban fabric	Built-up area
112	Discontinuous urban fabric	Built-up area
121	Industrial or commercial units	Built-up area
122	Road and rail networks and associated land	Built-up area
123	Port areas	Built-up area
124	Airports	Built-up area
131	Mineral extraction sites	Built-up area
132	Dump sites	Built-up area
133	Construction sites	Built-up area
141	Green urban areas	Built-up area
142	Sport and leisure facilities	Built-up area
211	Non-irrigated arable land	Open area
222	Fruit trees and berry plantations	Open area
231	Pastures	Open area
242	Complex cultivation patterns	Open area
243	Agriculture, significant natural areas	Open area
311	Broad-leaved forest	Deciduous forest
312	Coniferous forest	Coniferous forest
313	Mixed forest	Mixed forest
321	Natural grasslands	Open area
322	Moors and heathland	Open area
324	Transitional woodland-shrub	Open area
331	Beaches, dunes, sands	Other
332	Bare rocks	Other
333	Sparsely vegetated areas	Open area
411	Inland marshes	Open area
412	Peat bogs	Open area
511	Water courses	Water
512	Water bodies	Water
521	Coastal lagoons	Water
523	Sea and ocean	Water

Appendix 2. *Estimates of regression coefficients from generalized linear model of habitat selection in Białowieża with standard errors and Wald statistics. Reference categories are Built-up area, Summer, Białowieża, F and Intensively fed for habitat, location, sex and feeding intensity respectively. Semicolons denotes interaction effects. Statisticial significance: *** p<0.001 ** p<0.01 * p<0.05.*

Fixed effect	Estimate	Std. Error	Z value	Pr(>|z|)	
(Intercept)	-13.670182	0.164188	-83.26	< 2e-16	***
habConiferous forest	12.942716	0.171896	75.29	< 2e-16	***
habDeciduous forest	13.877098	0.169116	82.06	< 2e-16	***
habEdge forest	13.552816	0.173731	78.01	< 2e-16	***
habMixed forest	13.56646	0.169298	80.13	< 2e-16	***
habOpen area	14.127278	0.170935	82.65	< 2e-16	***
habBuilt-up area:sexM	2.302796	0.21251	10.84	< 2e-16	***
habConiferous forest:sexM	-0.065817	0.037402	-1.76	0.07845	
habDeciduous forest:sexM	0.024216	0.031491	0.77	0.44189	
habEdge forest:sexM	0.381521	0.038814	9.83	< 2e-16	***
habMixed forest:sexM	-0.196686	0.040605	-4.84	< 2e-16	***
habOpen area:sexM	-0.222243	0.036605	-6.07	1.27e-9	***
habBuilt-up area:feedLess intensively	8.95413	0.262801	34.07	< 2e-16	***
habConiferous forest:feedLess intensively	0.3082	0.048318	6.38	1.79e-10	***
habDeciduous forest:feedLess intensively	-0.158078	0.039749	-3.98	0.0000698	***
habEdge forest:feedLess intensively	0.113536	0.052663	2.16	0.03109	*
habMixed forest:feedLess intensively	0.066015	0.047726	1.38	0.1666	
habOpen area:feedLess intensively	0.008353	0.053819	0.16	0.87666	
habBuilt-up area:feedIntensively:seasonWinter	-0.207906	2.785402	-0.07	0.9405	
habConiferous forest:feedIntensively:seasonWinter	-2.642379	0.309867	-8.53	< 2e-16	***
habDeciduous forest:feedIntensively:seasonWinter	0.061002	0.058459	1.04	0.29672	
habEdge forest:feedIntensively:seasonWinter	-1.471491	0.192278	-7.65	1.96e-14	***
habMixed forest:feedIntensively:seasonWinter	-0.791107	0.092396	-8.56	< 2e-16	***
habOpen area:feedIntensively:seasonWinter	-2.748263	0.322666	-8.52	< 2e-16	***
habBuilt-up area:feedLess intensively:seasonWinter	1.404239	0.186826	7.52	5.63e-14	***
habConiferous forest:feedLess intensively:seasonWinter	-0.199844	0.045073	-4.43	0.00000926	***
habDeciduous forest:feedLess intensively:seasonWinter	0.1145	0.039914	2.87	0.00412	**
habEdge forest:feedLess intensively:seasonWinter	-0.285432	0.046293	-6.17	7.01e-10	***
habMixed forest:feedLess intensively:seasonWinter	0.608674	0.050264	12.11	< 2e-16	***
habOpen area:feedLess intensively:seasonWinter	-0.387658	0.042163	-9.19	< 2e-16	***

Appendix 3. *Estimates of regression coefficients from generalized linear model of habitat selection in Białowieża and Western Pomerania with standard errors and Wald statistics. Reference categories are Built-up area, Białowieża and F; for habitat, location and sex respectively. Semicolons denote interaction effects. Statistical significance: *** p<0.001 ** p<0.01 * p<0.05.*

Fixed effect	Estimate	Std. error	Z value	Pr(>|z|)	
(Intercept)	-12.65635	0.14865	-85.14	< 2e-16	***
habConiferous forest	12.2138	0.14926	81.83	< 2e-16	***
habDeciduous forest	12.87736	0.15023	85.72	< 2e-16	***
habEdge forest	12.65926	0.14963	84.6	< 2e-16	***
habMixed forest	12.61754	0.1517	83.18	< 2e-16	***
habOpen area	12.98123	0.15035	86.34	< 2e-16	***
habWater	7.88604	0.2753	28.64	< 2e-16	***
habBuilt-up area:sexM	10.16056	0.20747	48.97	< 2e-16	***
habConiferous forest:sexM	-0.15848	0.02549	-6.22	5.08e-10	***
habDeciduous forest:sexM	-0.25095	0.02436	-10.3	< 2e-16	***
habEdge forest:sexM	0.32062	0.02312	13.87	< 2e-16	***
habMixed forest:sexM	-0.20404	0.03235	-6.31	2.85e-010	***
habOpen area:sexM	0.02417	0.02116	1.14	0.253393	
habWater:sexM	-1.18081	0.3069	-3.85	0.000119	***
habBuilt-up area:locationWestern Pomerania	0.24314	0.16396	1.48	0.138103	
habConiferous forest:locationWestern Pomerania	0.25122	0.0221	11.37	< 2e-16	***
habDeciduous forest:locationWestern Pomerania	-0.32586	0.03679	-8.86	< 2e-16	***
habEdge forest:locationWestern Pomerania	-0.10795	0.02206	-4.89	0.0000009	***
habMixed forest:locationWestern Pomerania	-0.14992	0.04757	-3.15	0.001624	**
habOpen area:locationWestern Pomerania	-0.16565	0.02073	-7.99	1.35e-15	***