First Steps into the Wild – Exploration Behavior of European Bison after the First Reintroduction in Western Europe

Philip Schmitz[1]*, Stephanie Caspers[1], Paige Warren[2], Klaudia Witte[1]

1 Institute of Biology, Research Group of Ecology and Behavioral Biology, University of Siegen, Siegen, Germany, 2 Department of Environmental Conservation, University of Massachusetts, Amherst, Massachusetts, United States of America

* Schmitz.philip@gmail.com

Abstract

Biodiversity is rapidly declining globally. One strategy to help to conserve species is to breed species in captivity and release them into suitable habitats. The way that reintroduced animals explore new habitats and/or disperse from the release site is rarely studied in detail and represents key information for the success of reintroduction projects. The European bison (*Bison bonasus* L. 1758) was the largest surviving herbivore of the post-glacial mega-fauna in Europe before it became extinct in the wild, surviving only in captivity since 1919. We investigated the exploration behavior of a herd of European bison reintroduced into the Rothaargebirge, a commercial forest in low range mountain intensively used and densely populated by humans, in the first six months after release. We focused on three questions: (1) how did the European bison move and utilize the habitat on a daily basis, (2) how did the animals explore the new environment, and (3) did their habitat preferences change over time. The European bison dispersed away from their previous enclosure at an average rate of 539 m/month, with their areas of daily use ranging from 70 to 173 ha, their movement ranging from 3.6 km to 5.2 km per day, and their day-to-day use of areas ranged between 389 and 900 m. We could identify three major exploration bouts, when the animals entered and explored areas previously unknown to them. During the birthing phase, the European bison reduced daily walking distances, and the adult bull segregated from the herd for 58 days. Around rut, roaming behavior of the herd increased slightly. The animals preferred spruce forest, wind thrown areas and grassland, all of which are food abundant habitat types, and they avoided beech forest. Habitat preference differed slightly between phases of the study period, probably due to phenological cycles. After six months, the complete summer home range was 42.5 km². Our study shows that a small free-ranging herd of European bison can live in an area intensively used by humans and describes in detail the initial roaming behavior and habitat utilization of the animals.

Introduction

Biodiversity is rapidly declining globally. Out of the 61,898 taxa listed by the International Union for Conservation of Nature and Natural Resources (IUCN), 35.9% are either extinct in the wild (0.1%), critically endangered (7.4%), endangered (11.0%), or vulnerable (17.4%), and thus referred to as threatened species [1]. Of these threatened animals, 22.1% are mammals, including such large herbivorous species as the European bison (*Bison bonasus*, L. 1758). Most species became endangered due to overexploitation, habitat loss, invasive species and the synergistic effects of these factors [2], [3], [4], [5], [6], [7].

Commonly recommended strategies for preventing the loss of critically endangered species include *ex situ* approaches (protecting endangered species outside their natural habitats) and *in situ* approaches (protecting a species within its natural habitat), or a combination of both strategies by reintroducing captive bred animals to suitable habitats and to restore and connect populations [8], [9], [10]. Fragmented habitats can be connected by establishing (sub)-populations that work as corridors, thus increasing population size and gene flow, minimizing the risk of local extinction and promoting the species' survival [11], [12], [13]. Although reintroductions involve many logistical and financial challenges [14] they have been successfully carried out numerous times [6]. Examples include the Przewalski's horses (*Equus ferus przewalskii*) in Mongolia [15], the Arabian Oryx (*Oryx leucoryx*) in Saudi Arabia and Israel [16], [17], the European bison (*Bison bonasus*) in several eastern countries [11], [18], [19], the Alpine ibex (*Capra ibex ibex*) in the European Alps [20], the Black bear (*Ursus americanus*) in Arkansas [21], the River otter (*Lontra canadensis*) in Pennsylvania [22], the Bearded vulture (*Gypaetus barbatus*) in the European alps [23], the Yellow-Shouldered Amazon Parrots (*Amazona barbadensis*) in Venezuela [24], and the Baton Blue butterfly (*Pseudophilotes baton schiffermuelleri*) in Finland [25].

Because species considered for reintroduction may lack their original habitat types or lack unaltered habitat (e.g., due to human land use), it is essential for successful reintroductions to find suitable environments that can meet a species' habitat requirements [10]. Additionally, captive-bred animals must be able to develop natural behavior and acclimate to the new habitat. Therefore, reintroduction processes require a detailed knowledge of the animal's biology and behavior prior to and detailed monitoring after reintroduction [26]. In particular, knowledge of how animals explore the new habitat and whether they disperse from the release site are key pieces of information for evaluating the success of a reintroduction and for conflict management in human dimensions, especially in large animals [27], [28], [29]. Despite a rich publication record dealing with animal reintroductions, only a few detailed descriptions of newly reintroduced animals documenting the first dispersal from their release site are available [23], [24], [30]. Information about such processes and especially the exploration behavior of a reintroduced species are very important for further reintroduction programs and should carefully be investigated and documented.

The European bison is, aside from the now extinct Aurochs (*Bos primigenius* Bojanus, 1827), the largest surviving post-glacial megaherbivore in Western Europe. The species was extirpated in the wild in 1927 [11], but persisted due to a small captive breeding population [18]. Today, free roaming European bison live in 35 populations across seven countries. The world's population consists of 4,987 animals; 3,102 (62%) of these as free-ranging in eastern European countries [19], [31].

European bison were mainly reintroduced to forest ecosystems since their last appearance was in such areas (Białowieża primeval forest and Caucasus) and were commonly classified as forest specialists [11], [32]. In recent years, this classification has been revised according to the refugee species concept [33], [34], [35], [36]. Considerable evidence has emerged that

European bison are adapted to live in semi-open and mosaic-like habitats and were pushed into forest ecosystems by anthropogenic influences such as habitat loss and fragmentation, competition with livestock, diseases, hunting or poaching [11], [33], [34], [35], [36]. Today, there is almost no landscape without any anthropogenic influence left in Western Europe. Thus, the reintroduction of species faces the dual challenge of human imposed constraints and finding suitable areas for species whose original habitats are gone. As a result it is important to understand the animals' exploration behavior and ability to recolonize modified habitats as part of the reintroduction process [11], [29]. The first reintroduction of European bison into Western Europe has been carried out in a commercial forest in the Rothaargebirge in Germany.

We investigated the exploration behavior of the released herd for the first six months following reintroducing. We focused on three main questions to better understand the exploration behavior of a newly reintroduced large herbivore: (1) how did the European bison move and use habitat on a daily basis, (2) how did the animals explore the new environment, and (3) did their habitat preferences change over time.

Material and Methods

Study species

Since April 2010, a herd of European bison, obtained from different zoos in Germany and Belgium, were kept in an 89 ha enclosure within the Rothaargebirge (Gauss-Krueger coordinates: 3456254, 5663510) centrally located in the study area as described above. During a three-year period between 2010 and 2013 we intensively studied ethology and the habituation process of the animals and their impact on the area [37], [38], [39], [40], [41], [42], [43], [44]. A single herd of eight animals (1 bull, 6 cows, 1 calf, Table 1) was released into the commercial forest using a soft-release method by removing the fence on 11th April 2013. This was the first reintroduction of this species in Western Europe (Fig 1A and 1B) [45].

Study area

The area for the reintroduction was in the Rothaargebirge, Germany, in a low mountain range area located between 450 m and 750 m above sea level [45]. It was an intensively used commercial forest with a mosaic of open areas, meadows and mostly monoculture forest plantations, in the most densely populated federal state of Germany (North-Rhine Westphalia) with 523.4 inhabitants / km^2 and additional 1.5 million tourists visiting the area annually [29], [46], [47].

Table 1. European bison released into the wild on 11th April 2013. Pedigree numbers are listed in front of names. (*) Pedigree number not yet assigned.

Pedigree No, Name	Sex	Date of birth	Heritage	Father	Mother
11337 Abdia	f	17.09.2008	Bayerischer Wald	9737 Abkes	9701 Abdil
11336 Abtisa	f	09.10.2008	Bayerischer Wald	9737 Abkes	9186 Abtei
10661 Araneta	f	28.09.2006	Amsterdam	7642 Dudo	7636 Kreole
11303 Dareli	f	28.09.2008	Damerower Werder	8741 Eggedämon	10203 Dara
11347 Daviedi	f	08.12.2008	Damerower Werder	9570 Daaks	7064 Danica
10754 Egnar	m	22.09.2006	Hardehausen I	9583 Kuabo	9166 Eglaja
12044 Queen	f	17.08.2011	Bad Berleburg	11338 Horno	10661 Araneta
12272 Quandor	m	24.06.2012	Bad Berleburg	10754 Egnar	11303 Dareli
QU_05 *	m	05.05.2013	Bad Berleburg	10754 Egnar	10661 Araneta
QU_06 *	m	23.05.2013	Bad Berleburg	10754 Egnar	11337 Abdia

doi:10.1371/journal.pone.0143046.t001

a

b

c

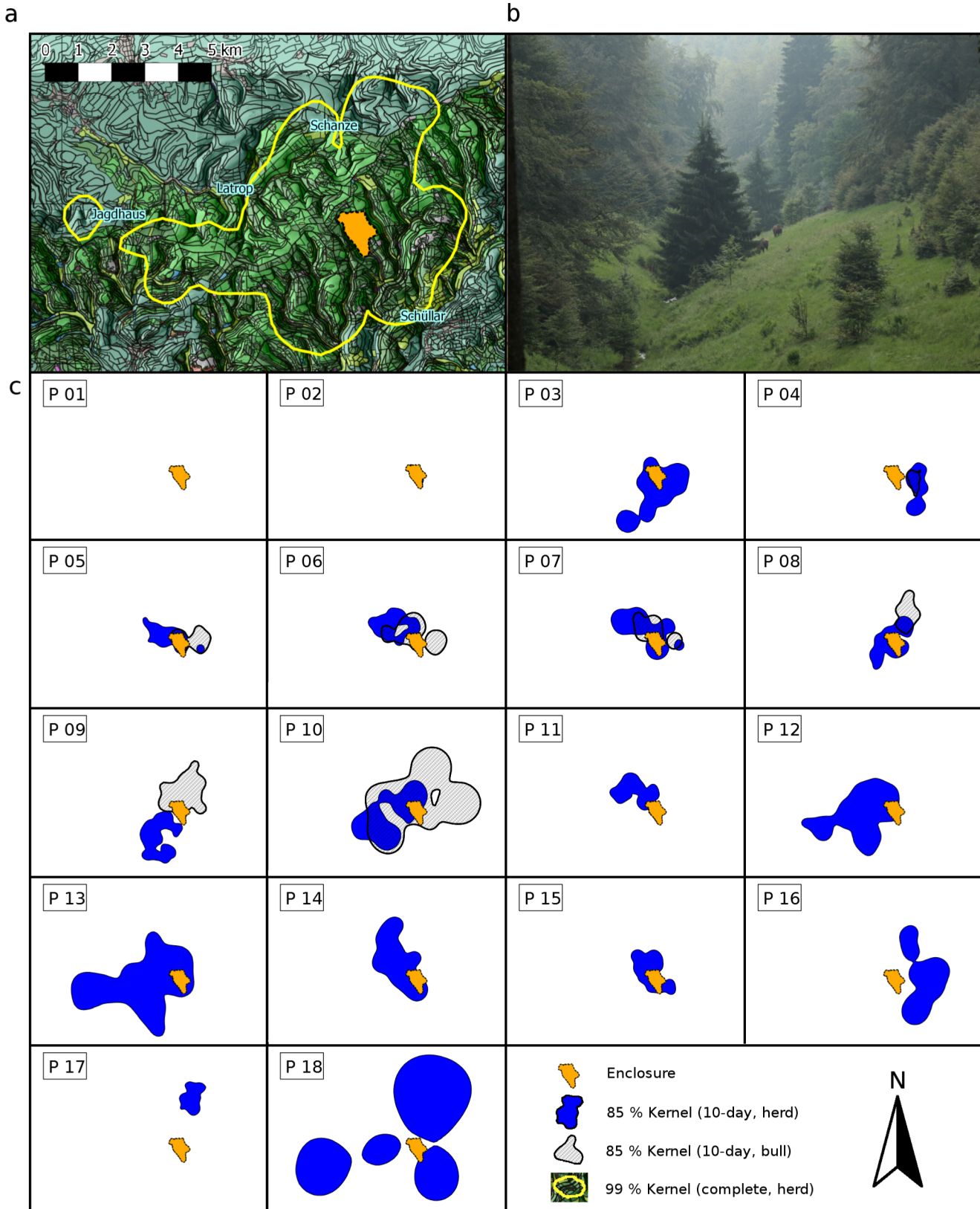| Enclosure |
| 85 % Kernel (10-day, herd) |
| 85 % Kernel (10-day, bull) |
| 99 % Kernel (complete, herd) |

N

Fig 1. Exploration of the new habitat in the European bison during the first six month after release into the wild. (a) The overall used area (99% kernel h_{ref} of the herd after six months). (b) Typical habitat frequently used by the European bison in the Rothaargebirge. (c) Used areas (85% kernel h_{ref}) of the herd and the solitary roaming bull of each 10-days period (P1-P18). The former enclosure is indicated by the orange area. Three major exploration bouts were observed in P3, P13 and P18, when the animals entered new areas.

The area covered over 4,500 ha of private commercial forest, consisting of spruce forest (*Picea abies*, 44.4%), beech forest (*Fagus sylvatica*, 33.7%, e.g. *Luzulo-Fagetum*), oak forest (*Quercus robur*, 0.4%), douglas fir forest (*Pseudotsuga menziesii*, 0.4%), larch forest (*Larix sp.*, 0.2%), other deciduous forest (0.6%), storm damaged areas (succession zones, e.g. *Digitalis purpurea-Epilobium angustifolium*-association, 4.4%), grasslands (8.7%), roads (6.9%), many creeks, and other land use (settlements and pine forests, 0.3%, Fig 1B). The herbaceous biomass and available nutritional energy per hectare in the study area was unevenly distributed among the forest types [48]. Ungulate game species occurring in this area included wild boar (*Sus scrofa*), mouflon sheep (*Ovis orientalis musimon*), roe deer (*Capreolus capreolus*) and red deer (*Cervus elaphus*). Sightings of single European lynx (*Lynx lynx*) and wolves (*Canis lupus*) were reported, but these animals did not regularly occur in the Rothaargebirge [49]. The study area was demarcated in the south by a game fence, built some 25 years ago (Gauss-Krueger coordinates: southernmost point: 3452862, 5657882). The western border was the street K42 (westernmost point: 3448397, 5662446) and the eastern border the street B480 (easternmost point: 3460432, 5662412). To the north it was demarcated by the ridge of the Rothaargebirge and the hiking trail "Rothaarsteig" (northernmost point: 3459880, 5667353). There was no physical border aside from the game fence in the south part of the reintroduction area. Centrally located in this study area was an enclosure (now removed) of 89 ha in which the herd lived for three years (2010–2013) before release with a feeding site. Concentrated feed (corn, wheat, dried beet slices) was given in small amounts (ca. 2.5 to 5.0 kg) several times per week at irregular intervals.

Data analyses

General procedure. We divided the six month observation period (2nd April–30th September) into 18 periods of 10 days each (P1—P18, Fig 1C, Fig 2) starting with 10 days prior to release (P1).

Based on the release date and the behavior of European bison we assigned the 10-day-periods to six different phases: pre-release, post release, birthing, pre-rut, rut, and post-rut and the separation and reunion of the adult bull to the herd (Table 2, Fig 2, S1A–S1E Table) and calculated medians, and the first and third quartiles, for each phase to give a general overview of the changes in behavior. All geographical analyses were carried out using Quantum GIS 1.8 [50]. Statistical analyses were calculated using PAST 3.0 [51]. We used a significance level of $P < 0.05$ for each test.

GPS data. Before release, the leading cow, the adult bull, and another adult cow were tagged with GPS-telemetry collars (GPS Plus, Vectronic Aerospace, Germany). GPS-positions of the animals were recorded individually at intervals of 60 minutes (pre-release), 30 and 20 minutes for different collars (post release) to acquire a higher resolution data set in this important phase after release. The accuracy of the GPS positions was 7.62 ± 19.44 m (average ± SD) [43]. Additionally, direct observations were made and the animals' GPS-positions were calculated trigonometrically using a handhold GPS (Garmin Etrex Venture CX), a laser distance scanner (Bushnell, Yardage Pro Sport 450), and a compass. These observations were made to check whether all non-collared animals were within the herd, to further enlarge the location data set and to observe the behavior of the animals, births, etc. All calculations were made on daily sub-samples of the data set.
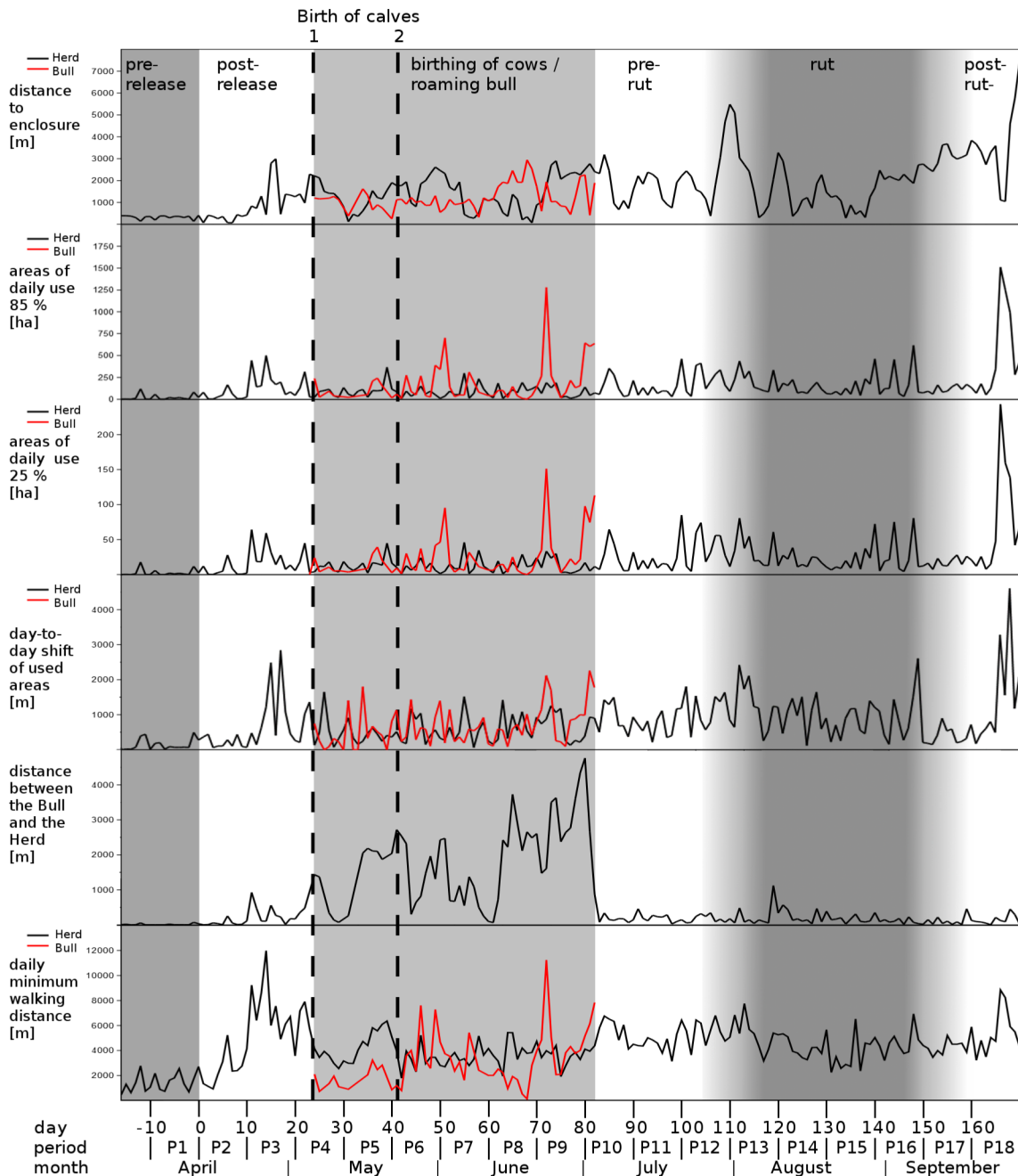
Fig 2. Overview of our measurements during the eighteen 10-days-periods assigned to six different phases (pre-/ post-release, birthing / roaming bull, pre-rut, rut, post-rut). Distinct phases are indicated by underlying grey bars. The births of the calves are indicated by dotted lines. We distinguished between the bull (red line) and herd (black line) for most measurements between day 24 and 82 (P4-P10).

doi:10.1371/journal.pone.0143046.g002

We pooled all GPS-positions and direct observations when the animals did not separate from each other [40], [43], [52], [53] and regarded these data as positions of the entire herd. We controlled for separation of herd members by direct observations and by calculating the distance between the centroids of individual daily data sub-samples. If an individual was > 500 m away from the others it was defined as being apart and its positions during that period were analyzed separately.

Table 2. Description of phases.

Phase	Days	Date	Description
Pre-release	-10 to 0	02.04.2013 to 11.04.2013	Animals were kept inside the enclosure (management).
Post-release	1 to 23	12.04.2013 to 05.05.2013	Animals were released into the Rothaargebirge (management).
Birthing of cows / solitary roaming bull	24 to 82	06.05.2013 to 03.07.2013	The bull was mainly separated from the herd. Two calves were delivered.
Pre-rut	83 to 108	04.07.2013 to 29.07.2013	Period between the adult bull's return to the herd and the rutting season.
Rut	109 to 155	30.7.2013 to 14.09.2013	The rutting season was determined following [18], [54], [71], [73] [77], [78]. Additional direct observation revealed the occurrence of rutting behavior in the herd.
Post-rut	156 to 171	15.09.2013 to 30.09.2013	Period after rutting season till end of observation period.

doi:10.1371/journal.pone.0143046.t002

We removed redundant data from the data set if temporal proximity between pooled GPS positions were too close ($\leq$ 15 min). Average interval between GPS fixes was 24 ± 13.8 min (mean ± SD) with minimal/maximal intervals of 0:17 h/16:40 h. Data were subdivided into single days, counting from midnight to midnight, as European bison usually do not move during the night [39], [54]. Between ten days prior to and the first 171 days after release (2nd April to 30th September 2013) we sampled 18,471 locations (120 observations and 18,351 GPS-fixes). After removal of redundancies 12,256 data points remained.

Daily movements and habitat utilization

We calculated the size of the areas of daily use by using a conservative measurement of 85-%-isopleths for fixed kernel (kernel h_{ref}) to determine the total area and 25-%-isopleths to determine the core area of areas of daily use. Börger et al. [55] found that ten locations per month are sufficient to calculate accurate kernel home ranges, while other authors state that at least 30–50 fixes are required (simulated data) [56]. Since animals do not develop a home range over the course of a single day, we called the calculated isopleths "areas of daily use" instead of "home ranges". Exclusive use of independent observations is not necessary when range size is estimated using kernel methods, but the whole sampling regime has to be standardized to acquire statistically reliable results. Once the sampling regime is standardized, inferences are robust to sampling variation in the number of fixes, which is especially important for ecological data [55], [56], [57].

We measured the day-to-day shift of the areas of daily use by calculating the distance between consecutive days' centroids of the daily used core areas. We measured the minimal daily walking routes of the animals by calculating a straight line between subsequent daily accumulated GPS fixes. We measured the distance between the adult bull and the herd by calculating the distance between the centroids of daily GPS fixes of the adult bull and those of the herd.

Exploration behavior

To determine exploration rate (m/month) of the European bison, we measured the distances between the centroids of the areas of daily use of the herd and the centroid of the former enclosure. To test whether the exploration behavior was linked to specific phases (Table 2) we compared the exploration rate and the distances to areas of daily use, obtained for the periods P1-P18. We used the Friedman test [51], [58] to test for behavioral changes over time, using

pairwise Wilcoxon comparison with sequential Bonferroni correction as post-hoc tests. The Friedman test is a non-parametric test for equality of medians in several repeated-measures univariate groups [51].

We calculated the 99% isopleth of the complete fixed kernel (kernel h_{ref}) summer home range. To obtain an overview of the habitat used each day, we calculated in a precautionary approach the 85% isopleth for the total and the 25% isopleth for the core area to receive higher accuracy in calculating the summer home range according to [55], [59], [60], [61], [62].

Habitat preferences

We used the location data (GPS data combined with observational data) to calculate the animals' habitat preferences within the complete summer home range. The habitat preferencee was calculated by counts of location data on a habitat type [63], [64], [65], [66], [67]. Habitat types were derived from the forestry map of the land owner. Areas not labeled with a habitat type were removed from the map. Habitat preference was tested for significant differences from a random distribution using the Chi-square test comparing numbers of locations with the area of the habitat type. We used the Jacobs' modified electivity index [68], to identify the predominately used areas. This electivity index ranges from -1 (strong avoidance) over 0 (random use) to +1 (strong preference). We calculated Bailey's confidence intervals [69] to decide whether a habitat type was significantly preferred or avoided. To test whether habitat preferences changed over time we calculated electivity indices and confidence intervals for each subset of location data within each phase and the overall values for the complete observation period.

Ethics statement

The animals were housed in an 89 ha enclosure under semi-natural conditions prior to reintroduction, and were under control of the local district veterinarian. The animals were owned by the NGO "Wisent-Welt Wittgenstein e.V.". The enclosure and project area were in private ownership of Richard, Prince of Sayn-Wittgenstein-Berleburg. No protected animals were sampled. Animal handling were conducted by the NGO "Wisent-Welt Wittgenstein", under supervision of the district veterinarian. The permit for handling and releasing the animals was granted by a contract between the NGO "Wisent-Welt Wittgenstein e.V.", the county government of North-Rhine Westphalia, the Bezirksregierung Arnsberg, the Landesbetrieb Wald und Holz NRW and the Wittgenstein-Berleburg'sche Rentkammer.

Results

Daily movements and habitat utilization

The herd significantly altered the size of the areas of daily use during the observation period (core area: $\chi^2 = 58.13$, df = 17, p < 0.001; total area: $\chi^2 = 58.19$, df = 17, p < 0.001, Fig 1C). The average core areas of daily use ranged between 10 and 26 ha. The median size of total areas covered 70 to 173 ha. Areas of daily use were largest during pre- and post-rut (Table 3). One day previous to the birth of calves on days 24 and 41 the herd increased the size of the area of daily use first and then decreased it for 10 to 20 days afterwards. The areas of daily use during the birthing phase of cows between P4 and P10 were significantly smaller than in other phases (Fig 1C, Fig 2, S1A and S1B Table). Shortly before and during the rutting season in August/September the animals increased their areas of daily use. The largest area of daily use was observed in P18 (Fig 1C, Fig 2). The size of areas of daily use in phases P12, P15 and P18 were accompanied by short excursions into new areas.

Table 3. Overview of measurements during the six phases. The median is shown, 1st and 3rd quartiles are given in brackets.

	Pre-release	Post-release	Birthing of cows, herd	Solitary roaming bull	Pre-rut	Rut	Post-rut
Distance to previous enclosure [m]	361 (270–376)	454 (364–1.326)	1.420 (808–2.121)	1.131 (861–1.646)	1.814 (1.054–2.293)	2.011 (1.073–2.714)	3.236 (2.921–3.708)
Areas of daily use 85% [ha]	10 (1–29)	70 (25–167)	74 (36–115)	92 (38–241)	125 (54–280)	119 (73–194)	173 (120–505)
Areas of daily use 25% [ha]	1 (0–3)	10 (2–26)	10 (5–16)	10 (6–17)	20 (8–47)	19 (11–28)	26 (15–70)
Day-to-day shift of areas used [m]	73 (55–190)	389 (18–927)	481 (269–872)	563 (231–930)	836 (531–1.314)	900 (458–1.243)	596 (298–1.273)
Distance between bull and herd [m]	4 (2–9)	108 (16–269)		2,002 (712–2.553)	168 (93–250)	119 (72–207)	90 (40–232)
Minimal daily walking routes [m]	1.487 (855–1.905)	5.072 (2.475–7.052)	3.638 (3.168–4.200)	2.514 (1.926–4.006)	5.171 (4.396–6.228)	4.349 (3.653–5.207)	4.780 (4.348–5.902)

doi:10.1371/journal.pone.0143046.t003

The day-to-day shift of areas of daily use differed significantly between the 10-days-periods (χ^2 = 61.66, df = 17, p < 0.001, S1D Table). The day-to-day shift of areas of daily use during the birthing phase (P4—P10) differed significantly from those during the pre-rut (P10—P12) and the post-rut (P17–P18, Fig 2, S1A–S1E Table). After the first exploration in P3, the day-to-day shift of areas of daily use was at median 481 m (269–872 m) during the phase of birthing (P4–P10, Fig 2, Table 3). After that phase the day-to-day shift of areas of daily use increased to 900 m (458–1,243 m) during the rut in August/September. The largest day-to-day shift of 4,609 m was recorded in P18 with highest values for the size of areas of daily use and the largest distance to the former enclosure. In general, the areas of daily use were typically not more than 1,500 m apart from that of the previous day. In general, animals showed an alternation of longer and shorter day-to-day shifts of areas of daily use every two or three days.

The length of minimal daily walking routes differed significantly between the 10-days-periods (χ^2 = 88.13, df = 17, p < 0.001, (Fig 2, Table 3, S1E Table) and were highest during the post-release phase with a median distance of 5,072 m, and one of 5,171 m in the pre-rut phase. The longest covered route was 8,843 m on day 166. The herd's minimal daily walking distance was especially low in the first days after the two birth events with the minimum of 1,790 m occurring on day 42. The highest values of more than 11 km were shown by the herd during the first exploration phase on day 14.

The adult bull separated from the herd between day 24 and 82 in the phases P4—P10 (May—July) and was analyzed separately. He left the herd at the day of the birth of the first calf on day 24 and successively increased his distance from the herd to a median of 2,002 m (712–2,553 m, max. 4,764 m at P9, Fig 2, Table 3). The solitary adult bull's areas of daily use were only slightly larger than those of the herd (Table 3). Cows never separated from the herd. The lone roaming adult bull covered lower daily walking routes than the herd, with the exception of a few larger displacements. The minimal daily routes of the adult bull were 2,514 m in median (1,926–4,006 m). His areas of daily use were comparable in size to those of the herd with the exception of three events lasting one to three days in P7, P9 and during P10, when his areas of daily use increased up to 300% (core areas: 95 ha, 151 ha, 113 ha).

Although distances between the herd and the adult bull were large (in detail 2,211 and 2,717 m one day prior to birth), at the days of the two births the adult bull entered the herd (by reducing the distance to less than 500 m) immediately after each birth and then left the herd for a few days again. During his entire roaming phase of 58 days he reduced the distances to the herd three times for short events, and finally returned to the herd on day 82. The highest

values of more than 11 km were shown by the adult bull when he searched for the herd on day 72. The herd did not show an increase in roaming activity (Fig 1C, Fig 2).

Exploration behavior

The animals (total herd) started to explore the new habitat around day 10 (21st April) after removal of the fence on 11th April 2013. The exploration rate during the first six months was 539 m/month, calculated from average values (Table 3). The distances to the enclosure differed significantly between the 10-days-periods (χ^2 = 101.18, df = 17, p < 0.001, Table 3, S1A–S1E Table). The first increase in the distance to the former enclosure on day 11 was 837 m, and rose further to 1,290 m on day 13 in P3 (Fig 2). A second major increase in distance to the former enclosure occurred on day 110 in P13 with an increase to 5,486 m and a third one on day 171 in P18 to 7,969 m. These maximal distances were accompanied by increases in the size of areas of daily use, increases in the day-to-day shift of used areas, and by explorations of previously unused areas (Fig 1C). The median distances between the former enclosure and the areas of daily use increased gradually and were highest with 3,236 m (2,921–3,708 m) after the rut in September 2013 (Table 3), six months after release. The animals returned to the former enclosure with the feeding site only occasionally during the six months period. All measurements mentioned above differed between the periods P1 to P18, and subsequently between the six different phases (S1A–S1E Table). Strongest differences in the rate of habitat exploration were found during pre and post release (P1—P2), at the end of the birthing phase (P8—P9) and at the end of the rut and the post-rut (P15—P18, S1A Table). The size of the overall area the herd used, the summer home range, on 30th September, 171 days after release, was 45.2 km^2, the core area covered 1.85 km^2 (99% and 25% kernel h$_{ref}$, Fig 1A). We note that by the end of our observation period, the herd's core area had grown to twice the size of the original enclosure.

Habitat preferences

Within the complete summer home range of 45.2 km^2, 10,468 location data were obtained (Table 4). The distribution of the animals' locations within each habitat type differed significantly from a random distribution (χ^2 = 1,308.2, df = 10, p < 0.001). In general the animals showed preferences for spruce forest, storm damaged areas and grasslands. They avoided

Table 4. Habitat preferences in each phase and overall. Jacobs preference indices and Bailey's confidence intervals were calculated [68], [69]. Habitat types were: (+) preferred; (-) avoided; (=) used according to their size.

Habitat type	Pre-release	Post-release	Birthing / roaming bull	Pre-rut	Rut	Post-rut	Overall
Beech	-	-	-	=	-	-	-
Spruce	-	=	+	=	+	+	+
Oak	=	=	=	=	=	=	=
Douglas fir	=	=	=	=	=	=	=
Larch	=	=	=	=	=	=	=
Other deciduous forest	=	=	+	=	-	=	=
Storm damaged area	=	+	+	=	=	=	+
Grassland	+	+	+	=	+	+	+
Road	+	+	=	=	=	=	=
Creek	=	+	=	=	=	=	=
Other	=	=	=	=	=	=	-
Location data (n)	352	1.350	4.130	1.868	2.408	360	10.468

doi:10.1371/journal.pone.0143046.t004

beech forest and other structures like settlements, functional forestry areas and pine planta-tions. Other forest types were frequented in relation to their size (Table 4, S2A–S2G Table).

The distribution of the animals' locations within each habitat type was significantly different from a random distribution in all six phases (pre-release: $\chi^2 = 179.69$, df = 10, p < 0.001; post-release: $\chi^2 = 1{,}237.3$, df = 10, p < 0.001; birthing: $\chi^2 = 474.82$, df = 10, p < 0.001; pre-rut: $\chi^2 = 55.052$, df = 10, p < 0.001; rut: $\chi^2 = 245.74$, df = 10, p < 0.001; post-rut: $\chi^2 = 113.05$, df = 10, p < 0.001).

The animals showed clear preferences for different habitat types, except during the pre-rut phase, when no preference or avoidance could be found. These preferences, however, changed slightly during the observation period (Table 4, S2A–S2G Table). Storm damaged areas and other deciduous forest types were preferred only in spring. Spruce forests were avoided in spring, but preferred later in the year. Roads and creeks were preferred during the initial phase around release. Grasslands were continuously preferred and beech forests continuously avoided.

Discussion

Daily movements and habitat utilization

During the first 6 months after reintroduction of the herd, the sizes of areas of daily use found in our study were comparable to home ranges of free ranging herds in Poland [70], [71]. Home range sizes are probably most related to the availability of food [71], [72]. Monthly home range sizes in Białowieża are significantly larger during the rut than during pre-rut in mixed herds [73]. Similarly, the sizes of areas of daily use of the herd in our observation were largest before, during, and especially after the rut. During the pre- and post-rut phases the animals conducted two explorations into unknown areas. The movement of a herd, especially the start of walking, is usually determined by the leading cow. If this animal is engaged in rutting behavior it may shift its behavior to more short-term locomotion and reduced foraging [54] or resting, thereby increasing the herd's areas of daily use.

The sizes of the areas of daily use in the Rothaargebirge herd differed among phases and appeared to be strongly affected by birthing of calves. Prior to and during the birthing phase the areas of daily use of the herd were comparably small but increased just before parturition and decreased afterwards for a several days. An European bison cow may leave the herd to give birth [18], [74]. Calves remain stationary close to the place of birth for the first 1 to 20 hours of their life. Afterwards, they follow when the herd is moving [75]. In the Rothaargebirge, the first calf was born by the leading cow, which was spotted with the herd one day prior and after parturition. The second calf was born by another cow within the herd. European bison calves usually stay especially close to their mother during the first week [74], [75], [76]. Our observations suggest that the entire herd adjusted their exploration behavior to the locomotion ability of the newborn calves for about two weeks and, thus, decreased areas of daily use, the day-to-day shift and walking distances (Fig 2) [18], [74].

In the Rothaargebirge the European bison did not shift the location of daily use areas more than 1,500 m from day to day (Fig 2, Table 3). The distances fluctuated every two or three days between several hundred and more than one thousand meters. Such behavior is known for other mixed herds as well [18], [77]. Longer shifts of the areas of daily use occurred only occas-sionally. We could identify only four dislocations of more than 2 km, namely at the very begin-ning of the exploration (P3), at the beginning and end of rut (P13, P16) and at the start of the third exploration event (P18).

The animals in the Rothaargebirge roamed less than animals in other populations. The daily walking distances were, with few exceptions, more or less constant during the observation period after release. The highest values of more than 11 km were found during the first

exploration phase of the herd in P3. In the calving season, the herd covered lower distances after the births, and larger distances previous to the rut. Walking distances of mixed herds are described as highly variable. They range between 2 and 17 km, changing between months and depending on phenological cycles [54], [71]. The situation of the herd in the Rothaargebirge differs from most other free roaming populations, in that no bachelor bulls or other herds were around. Nevertheless, the adult bull showed a roaming behavior that was similar to bulls of other populations. In our study the adult bull separated from the herd, immediately after the first birth for 58 days (Fig 1, Fig 2). He returned to the herd several times for only short periods during that time. After this period of absence he suddenly caught up and remained with the herd. Bulls of free ranging European bison may leave herds with the start of the calving season [71], [73], [77]. They live either alone or in bachelor groups and enter herds previous to or at the beginning of the rut in July or August [18], [73]. This behavior seems to be age dependent [18], [78]. Young European bison bulls may visit herds with estrous cows to mate even before the rutting season when older bulls are not staying with the herds [18], [79]. Adult bulls show increased roaming activity during the rut under natural population conditions and visit several herds [18], [78]. Similar behavioral patterns occur in the American bison [80], [81].

The adult bull's areas of daily use during the roaming phase were similar to those of the herd except on three occasions in P7, P9 and P10, when the adult bull contacted the herd. The lone adult bull covered lower walking distances than the herd. Similar behavior is reported from other populations: home ranges and daily searched areas of lone bulls vary between the periods of the growing seasons and from year to year, most probably related to habitat quality in terms of food [71]. The movement of the animals might be further influenced and stimulated by the movement of conspecifics, and therefore the walking routes are higher for a herd than for a lone bull.

Exploration behavior

The reintroduced European bison continuously increased their distance from their former enclosure, by an average value of 539 m/month. The explored habitat was enlarged three times to a complete summer home range size of 45 km^2. An animals' exploration rate is affected by several factors, including the environmental barriers, the movement pace, feeding frequency or site fidelity [70]. The main reason for exploration behavior is searching for preferred feeding habitats. Under free-ranging conditions European bison switch to patches with high herbaceous vegetation cover [71]. They leave these places after a few days, thus avoiding overgrazing of the vegetation. The use of small preferred patches in the forest, covering 100–200 ha, takes at most 7–10 days [71]. We observed a similar behavioral pattern in our European bison herd on a smaller temporal scale (Fig 2). The observed speed and pattern of exploration of the herd in the Rothaargebirge lies within the range of the exploration rate of reintroduced European bison in the Bieszczady Mountains [18], [52]. These exploration rates varied between 0.7 and 5.3 km / year [70]. The animals in our study preferred foraging sites in adjacent valleys, clear cuts and light forest with dense herbal vegetation (Fig 1B). Occasionally, the herd entered the former enclosure and the feeding site, but these events were infrequent and rare.

The exploration behavior of the Wood bison (*Bison bison athabascae*) is described as "a series of [population] increases in local areas followed by pulses of dispersal and range expansion" [82]. Our results showed that a similar behavioral pattern occurs on the level of a single herd as it explores new areas as well. In our study, the European bison explored the new habitat in three different exploration events: in the post-release, pre-rut and post-rut phase. These events were accompanied by larger areas of daily use, larger day-to-day shifts of these areas and longer walking distances. In all occasions, the animals left a previously used area and entered

an area that was previously unknown to them. The distances to the former enclosure increased gradually to a maximum of almost 8 km by the third exploration event. In the first two exploratory phases (pre-rut and during rut), the animals showed higher levels of exploratory activities (daily use, day-to-day shifts, and walking distances). This difference might be a function of generally higher levels of movement associated with the rut (in terms of searching for other herds or solitary bulls) or might be due to the increased activity of the leading cow engaged in rutting behavior (see above). Within the post-rut phase the exploration activity of the herd was slightly reduced, but the distance to the former enclosure remained large. At the end of the observation period the animals showed the third and largest exploration event.

Home ranges are generally dependent on the habitat quality, group size, behavioral strategies, competitors or predators. These features are unique for every habitat and shape the species specific home range [83], [84], [85], [86], [87]. In the case of European bison in the Rothaargebirge, the complete summer home range covered 45.2 km^2 by the end of the six months' observation period. This home range size was comparable to other free roaming herds [11], [71], [72]. Maximum home ranges of herds in other settings cover approximately 100 km^2 [11]. Home ranges for other herds also differed seasonally, with the largest home ranges in May and smallest in April and October [11], [71].

Habitat preferences

We observed a shift from strong habitat preferences during the spring to a lack of habitat preference during the pre-rut. We cannot rule out whether the lack of habitat preference exhibited during the pre-rut was due to its coincidence with the second exploration event, or a feature of rutting behavior. However, the rut is a period with increased roaming activity [18], [71], [73]. Food-rich grasslands (meadows and pastures) were preferred throughout the observation period, indicating their importance as a reliable food source. The preferences for roads and creeks in the initial post-release phase might have been related to the first exploration event. When walking, animals tend to use routes easy to use like roads, frozen rivers or creeks [88], [89], [90], [91], [92].

Overall, the animals in the Rothaargebirge showed clear preferences for spruce forest, storm damaged areas and grasslands, all of which are areas with high food availability. They avoided beech forests and other areas (settlements, pine plantations, area close to settlement, maintenance and operations areas like parking spaces or storage and loading zones). The herbal biomass and available nutritional energy per hectare in the study area was unevenly distributed among the forest types. It was especially low in stands of beech and young spruce, highest values were found on storm damaged areas and grasslands [48], [71], [72], [93]. An adult European bison requires up to 19.5 kg of dry plant matter per day and feeds mostly on grasses and herbs [94], [95]. The avoidance of beech forest was congruent with findings of Kuemmerle et al. [96]. The herd also avoided pine plantations, areas close to settlements, and maintenance and operations areas.

Other studies find widely different patterns of habitat preferences for the European bison, each of which differs slightly from the patterns found in our study: European bison in Białowieża prefer deciduous forest types and avoid coniferous forests [97]. In the Carpathian mountains, they show no clear preference for any particular forest type but a strong preference for managed grasslands or select forest-dominated habitats and show preferences for mosaics of forest and grasslands [96]. In the Ukraine they prefer large, open canopied forest structures dominated by fir, spruce or mixed coniferous trees [98], [99] or prefer generally broadleaved or mixed forests [11]. Some authors suggest that the European bison is actually an open grazing specialist and, as a refuge species inhabits forests only due to a lack of naturally preferred

habitats [13], [34]. In general, literature suggests that European bison shows a high variability in habitat use [13], [18], [100] and to be mostly dependent on food availability [18], [73]. Our observations appear to support this generalization. One potential implication is that European bison may be relatively flexible in their habitat use and, given sufficiently high quality forage, may be reintroduced in managed landscapes like the commercial forest in the Rothaargebirge.

In recent decades many reintroductions of European bison were conducted in Eastern Europe and Asia. In 2012, 35 populations in seven countries were introduced [11], [18], [19], but the roaming and exploration behavior after release was not recorded in as much detail as in this study. The project in the Rothaargebirge is the first one in Western Europe in a densely populated area, where the animals were released into a commercial forest with several mostly monoculture forest plantations [29]. This project is attracting considerable interest by managers of other planned reintroductions [101], [102], [103], but recently serious problems arose as the animals damaged trees of a private landlord [104], [105], [106], [107]. Our studies, however, showed the animals' ability to live in an intensively used commercial forest [45], [108]. It remains to be seen whether acceptance of the presence of the European bison will grow in this area and in Western Germany in general. It may require support on the political level to be successful.

Although we described in detail the exploration behavior of the herd after release, this study can only put a spotlight on a single herd. Therefore our findings should be interpreted cautiously, since the behavior of other populations under different conditions might differ. Nevertheless, our study gives detailed insight into the exploration behavior of this large herbivore in a human-dominated landscape back into the wild.

Supporting Information

S1 Table. Tables of Post-hoc test results. Pairwise Wilcoxon comparison with sequential Bonferroni correction. Measurements of the different 10-day periods are compared. Significant results are indicated by light gray background. Calculations are given for (a) expansion rate; (b) areas of daily use of the herd, complete area (kernel h_{ref} 85%); (c) areas of daily use of the herd, complete area (kernel h_{ref} 25%); (d) day-to-day shift of daily used areas; (e) minimal daily walking routes.
(PDF)

S2 Table. Habitat preferences. For each period of higher ranking behaviour Jacobs' preference indicies for each habitat type and Bailey's confidence intervals were calculated. The area of each habitat type is given. According to the number of location counts the expected and observed location data (Expected, Observed) and the respective proportions (p(exp), p(obs)) are given. Bailey's confidence intervals (Bailey -, Bailey +) are calculated and Jacobs preference index (Jacobs). The preferences are calculated according to these borders; p(obs) lies between Bailey–and Bailey +: (=) p(exp) lies within the range of the confidence intervals, the habitat type is used according to its size. (-) p(exp) lies above the range of the confidence intervals, the habitat type is avoided. (+) p(exp) lies below the range of the confidence intervals, the habitat type is preferred.
(PDF)

S3 Table. Raw location data. For each record the timestamp (UTC), Gauss-Krueger coordinates (EPSG 31467), the animal ID, the dilution and the day after release is given.
(CSV)

Acknowledgments

Author Contributions

Conceived and designed the experiments: PS. Performed the experiments: PS SC. Analyzed the data: PS SC. Contributed reagents/materials/analysis tools: PS SC KW. Wrote the paper: PS SC KW PW. Supervision of the work: KW.

References

1. IUCN (2014) The IUCN Red List of Threatened Species. Version 2013.1. Available: www.iucnredlist.org. Assessed 30 June 2014.

2. Brook BW, Sodhi NS, Bradshaw CJ (2008) Synergies among extinction drivers under global change. Trends Ecol Evol 23: 453–460. doi: 10.1016/j.tree.2008.03.011 PMID: 18582986

3. Caughley G (1994) Directions in conservation biology. J Animal Ecol 63: 215–244.

4. Diamond JM (1984) 'Normal' extinction of isolated populations. In: Nitecki MH, editor. Extinctions. Chicago University Press, Chicago. pp. 191–246.

5. Diamond JM (1989) Overview of recent extinctions. In: Western D, Pearl M, editors. Conservation for the Twenty-First Century. Oxford University Press, New York. pp. 37–41.

6. Seddon PJ (2010) From reintroduction to assisted colonization: moving along the conservation translocation spectrum. Restoration Ecology 18: 796–802.

7. Sodhi NS, Bickford D, Diesmos AC, Lee TM, Koh LP, Brook BW, et al. (2008) Measuring the meltdown: drivers of global amphibian extinction and decline. PloS ONE 3: e1636. doi: 10.1371/journal.pone.0001636 PMID: 18286193

8. Bowkett AE (2009) Recent captive-breeding proposals and the return of the ark concept to global species conservation. Conserv Biol 23: 773–776. doi: 10.1111/j.1523-1739.2008.01157.x PMID: 19220367

9. Ebenhard T (1995) Conservation breeding as a tool for saving animal species from extinction. Trends Ecol Evol 10: 438–443. PMID: 21237098

10. Osborne PE, Seddon PJ (2012) Selecting suitable habitats for reintroductions: variation, change and the role of species distribution modelling. In: Ewen JG, Armstrong DP, Parker KA, Seddon PJ, editors. Reintroduction Biology. Integrating Science and Management. Wiley-Blackwell. pp. 73–104.

11. Pucek Z, Belousova I, Krasińska M, Krasiński Z, Olech W (2004) Status survey and conservation action plan. European bison. In: Pucek Z, editor. IUCN/SSC Bison Specialist Group (IUCN, Gland, Switzerland and Cambridge, UK. 54 p.

12. Perzanowski K, Olech W, Kozak I (2004) Constraints for re-establishing a meta-population of the European bison in Ukraine. Biol Conserv 120: 345–353.

13. Kuemmerle T, Perzanowski K, Akcakaya H, Beaudry F, Van Deelen T, Parnikoza I, et al. (2011) Cost-effectiveness of strategies to establish a European bison metapopulation in the Carpathians. J Appl Ecol 48: 317–329.

14. Kareiva PM, Marvier M (2011) Conservation science: balancing the needs of people and nature. Roberts and Company Greenwood Village, Colorado, USA. 576 p.

15. Wakefield S, Knowles J, Zimmermann W, Van Dierendonck M (2002) Status and action plan for the Przewalski's horse (*Equus ferus przewalskii*). In: Moehlman PD, editor. Equids: Zebras, Asses and Horses: Status survey and conservation action plan. IUCN/SSC Equid Specialist Group. pp. 82–92.

16. Ostrowski S, Bedin E, Lenain DM, Abuzinada AH (1998) Ten years of Arabian oryx conservation breeding in Saudi Arabia-achievements and regional perspectives. Oryx 32: 209–222.

17. Saltz D (1998) A long-term systematic approach to planning reintroductions: the Persian fallow deer and the Arabian oryx in Israel. Anim Conserv 1(04): 245–252.

18. Krasińska M, Krasiński Z (2007) European bison. The nature monograph. Mammal Research Institute, Polish Academy of Science. 317 p.

19. Raczynski J (2013) European bison pedigree book 2012. Białowieza National Park. 77 p.

20. Stüwe M, Nievergelt B (1991) Recovery of alpine ibex from near extinction: the result of effective protection, captive breeding, and reintroductions. Appl Anim Behav Sci 29(1): 379–387.

21. Smith KG, Clark J, Gipson P (1991) History of black bears in Arkansas: over-exploitation, near elimination, and successful reintroduction. Eastern Workshop on Black Bear Research and Management 10: 5–13.

22. Hubbard B, Serfass T (2004) Assessing the distribution of reintroduced populations of River Otters in Pennsylvania (USA); Development of a landscape-level approach. IUCN Otter Specialist Group Bulletin 21: 60–65.

23. Hirzel AH, Posse B, Oggier P- A, Crettenand Y, Glenz C, Arlettaz R (2004) Ecological requirements of reintroduced species and the implications for release policy: the case of the Bearded vulture. J Appl Ecol 41(6): 1103–1116.

24. Sanz V, Grajal A (1998) Successful reintroduction of captive-raised Yellow-shouldered Amazon Parrots on Margarita Island, Venezuela. Conserv Biol 12(2): 430–441.

25. Marttila O, Saarinen K, Jantunen J (1997) Habitat restoration and a successful reintroduction of the endangered Baton Blue butter-fly (*Pseudophilotes baton schiffermuelleri*) in SE Finland. Ann Zool Fennici. 34(3): 177–185.

26. Curio E (1996) Conservation needs ethology. Trends Ecol Evol 11: 260–263. PMID: 21237835

27. Etienne R, Wertheim B, Hemerik L, Schneider P, Powell J (2002) The interaction between dispersal, the Allee effect and scramble competition affects population dynamics. Ecol Modell 148: 153–168.

28. Yott A, Rosatte R, Schaefer JA, Hamr J, Fryxell J (2011) Movement and spread of a founding population of reintroduced elk (*Cervus elaphus*) in Ontario, Canada. Restoration Ecology 19: 70–77.

29. Lindner U, Bunzel-Drüke M, Reisinger E (2006) Vorstudie zum E+E-Vorhaben „Wiederansiedlung von Wisenten im Rothaargebirge". Taurus Naturentwicklung e.V. 172 p.

30. Hayward MW, Adendorff J, Moolman L, Hayward GJ, Kerley G (2007) The successful reintroduction of leopard *Panthera pardus* to the Addo Elephant National Park. Afr J Ecol 45(1): 103.

31. Perzanowski KA, Wołoszyn-Gałęza A, Januszczak M (2013) Efektywność restytucji żubra w Karpatach. Studia i Materiały CEPL w Rogowie 36: 11–16.

32. Mohr E (1952) Der Wisent. Akademische Verlagsgesellschaft Geest & Portig. 75 p.

33. Cromsigt JP, Kerley GI, Kowalczyk R (2012) The difficulty of using species distribution modeling for the conservation of refugee species-the example of European bison. Divers Distrib 18: 1253–1257.

34. Kerley GIH, Kowalczyk R, Cromsigt JPGM (2012) Conservation implications of the refugee species concept and the European bison: king of the forest or refugee in a marginal habitat? Ecography 35: 519–529.

35. Kuemmerle T, Hickler T, Olofsson J, Schurgers G, Radeloff VC (2012) Refugee species: which historic baseline should inform conservation planning? Divers Distrib 18: 1258–1261.

36. Kuemmerle T, Hickler T, Olofsson J, Schurgers G, Radeloff VC (2012a) Reconstructing range dynamics and range fragmentation of European bison for the last 8000 years. Divers Distrib 18: 47–59.

37. Tillmann J, Bunzel-Drüke M, Finck P, Reisinger E, Riecken U (2012) Etablierung einer freilebenden Wisentherde im Rothaargebirge. Naturschutz und Landschaftsplanung 44: 267–272.

38. Kalden N, Caspers S, Schmitz P, Witte K (2013) Ethologische Untersuchungen im E+E-Vorhaben „Wisente im Rothaargebirge"—Nahrungsanalyse. Chapter 3.5. In: Tillmann J, Finck P, Riecken U, editors. Wisente im Rothaargebirge. Ergebnisse und Erfahrungen aus dem gleichnamigen Erprobungs- und Entwicklungsvorhaben (E+E) des Bundesamtes für Naturschutz. BfN Schriftenreihe „Naturschutz und Biologische Vielfalt"133. pp. 56–65.

39. Schmitz P, Caspers S, Witte K (2013) Ethologische Untersuchungen im E+E-Vorhaben „Wisente im Rothaargebirge"—Aktivitätsbudget. Chapter 3.3. In: Tillmann J, Finck P, Riecken U, editors. Wisente im Rothaargebirge. Ergebnisse und Erfahrungen aus dem gleichnamigen Erprobungs- und Entwicklungsvorhaben (E+E) des Bundesamtes für Naturschutz. BfN Schriftenreihe „Naturschutz und Biologische Vielfalt"133. pp.44-50.

40. Schmitz P, Witte K (2013a) Ethologische Untersuchungen im E+E-Vorhaben „Wisente im Rothaargebirge"—Sozialverhalten. Chapter 3.1. In: Tillmann J, Finck P, Riecken U, editors. Wisente im Rothaargebirge. Ergebnisse und Erfahrungen aus dem gleichnamigen Erprobungs- und Entwicklungsvorhaben (E+E) des Bundesamtes für Naturschutz. BfN Schriftenreihe „Naturschutz und Biologische Vielfalt"133. pp. 29–36.

41. Schmitz P, Witte K (2013b) Ethologische Untersuchungen im E+E-Vorhaben „Wisente im Rothaargebirge"—Verhalten gegenüber Menschen. Chapter 3.2. In: Tillmann J, Finck P, Riecken U, editors. Wisente im Rothaargebirge. Ergebnisse und Erfahrungen aus dem gleichnamigen Erprobungs- und Entwicklungsvorhaben (E+E) des Bundesamtes für Naturschutz. BfN Schriftenreihe „Naturschutz und Biologische Vielfalt"133. pp. 37–43.

42. Schmitz P, Witte K (2013c) Ethologische Untersuchungen im E+E-Vorhaben „Wisente im Rothaargebirge"—Zauntest. Chapter 3.4. In: Tillmann J, Finck P, Riecken U, editors. Wisente im Rothaargebirge. Ergebnisse und Erfahrungen aus dem gleichnamigen Erprobungs- und Entwicklungsvorhaben (E+E) des Bundesamtes für Naturschutz. BfN Schriftenreihe „Naturschutz und Biologische Vielfalt"133. pp. 51–55.

43. Schmitz P, Witte K (2013d) Ethologische Untersuchungen im E+E-Vorhaben „Wisente im Rothaargebirge"—Raumnutzung. Chapter 3.6. In: Tillmann J, Finck P, Riecken U, editors. Wisente im Rothaargebirge. Ergebnisse und Erfahrungen aus dem gleichnamigen Erprobungs- und

Entwicklungsvorhaben (E+E) des Bundesamtes für Naturschutz. BfN Schriftenreihe „Naturschutz und Biologische Vielfalt"133. pp 66–78.

44. Schmitz P, Witte K (2013e) Ein Wildtier aus Menschenhand—Entwicklung des natürlichen Scheuver-haltens bei zur Auswilderung vorbereiteten Wisenten. In: Feit U, Korn H, editors. Treffpunkt Biolo-gische Vielfalt XIII. Interdisziplinäres Expertentreffen im Rahmen des Übereinkommens über die biologische Vielfalt. BfN-Skriptenreihe 370. pp. 89–94.

45. Tillmann J, Finck P, Riecken U (2013) Wisente im Rothaargebirge. Ergebnisse und Erfahrungen aus dem gleichnamigen Erprobungs- und Entwicklungsvorhaben (E+E) des Bundesamtes für Nat-urschutz. Naturschutz und Biologische Vielfalt 133. Bundesamt für Naturschutz. 234 p.

46. Federal statistical office and the statistical offices of the Länder. Accessed 16.04.2014

47. Harrer B (2006) Wirtschaftliche Effekte durch den Tourismus am Rothaarsteig. dwif-Consulting GmbH. no pag.

48. Caspers S (2013) Vegetationsökologische Untersuchungen zur Habitatqualität im E+E-Vorhaben "Wisente im Rothaargebirge". Diploma thesis. Rheinische Friedrich-Wilhelms Universität Bonn, Zool-ogisches Forschungsmuseum Alexander König. 166p.

49. Hucht-Ciorga I (2012) Luchsmonitoring (*Lynx lynx*) in Nordrhein-Westfalen—Hinweise aus den Jah-ren 1985 bis 2011. Monitoring in Lynx (*Lynx lynx*) in North Rhine-Westphalia–records from the years 1985 to 2011. Säugetierkundliche Informationen. Symposiumsband: Europäische Wildkatze und Luchs. 8(45): 463–481.

50. Quantum_GIS_Development_Team (2012) Quantum GIS Geographic Information System. Open Source Geospatial Foundation Project. Available: http://qgis.osgeo.org. Assessed 02 April 2012.

51. Hammer Ø, Harper D, Ryan PD (2001) PAST: Paleontological Statistics Software Package for Educa-tion and Data Analysis. Palaeontol Electronica 4: 1–9.

52. Schmitz P, Witte K (2012) E+E-Vorhaben „Wisente im Rothaargebirge". In: Feit U, Korn H, editors. Treffpunkt Biologische Vielfalt 11. BfN-Skriptenreihe 309. pp. 107–111.

53. Schmitz P, Caspers S, Witte K (2014) "Make the first move!" Habitat use and exploration behaviour of free roaming European bison in a commercial forest. 19th Graduate Meeting of the Evolutionary Biol-ogy Group of the DZG. March 19th–21st, Universität Bremen. 15 p.

54. Caboń-Raczyńska K, Krasińska M, Krasiński ZA, Wojcik JM (1987) Rhythm of daily activity and behavior of European bison in the Białowieza forest in the period without snow cover. Acta Theriol 32: 335–372.

55. Börger L, Franconi N, De Michele G, Gantz A, Meschi F, Manica A, et al. (2006) Effects of sampling regime on the mean and variance of home range size estimates. J Anim Ecol 75: 1393–1405. PMID: 17032372

56. Seaman DE, Millspaugh JJ, Kernohan BJ, Brundige GC, Raedeke KJ, Gitzen RA (1999) Effects of sample size on kernel home range estimates. J Wildl Manage 63: 739–74.

57. De Solla SR, Bonduriansky R, Brooks RJ (1999) Eliminating autocorrelation reduces biological rele-vance of home range estimates. J Anim Ecol 68: 221–234.

58. Bortz J, Lienert G, Bohenke K (2008) Verteilungsfreie Methoden in der Biostatistik. Springer; Heidel-berg. no. pag.

59. Eggermann J (2009) The impact of habitat fragmentation by anthropogenic infrastructure on wolves (*Canis lupus*). PhD-Thesis. Ruhr-University Bochum. 115 p.

60. Kenward R (2001) A manual for wildlife radio tagging. Academic Press. San Diego, San Francisco, New York, Boston. 301 p.

61. Swihart RK, Slade NA (1997) On testing for independence of animal movements. J Agric Biol Environ Stat 2: 48–63.

62. Krone O, Berger A, Schulte R (2009) Recording movement and activity pattern of a White-tailed Sea Eagle (*Haliaeetus albicilla*) by a GPS datalogger. J Ornithol 150: 273–280.

63. Brandtberg NH, Dabelsteen T (2013) Habitat selection of two European bison (*Bison bonasus*) on the Danish island Bornholm. European Bison Conservation Newsletter 6: 73–80.

64. Cristescu B; Bernard RT, Krause J (2013) Partitioning of space, habitat, and timing of activity by large felids in an enclosed South African system. J Ethol 31: 285–298.

65. Hayward MW (2006) Prey preferences of the spotted hyaena (*Crocuta crocuta*) and degree of dietary overlap with the lion (*Panthera leo*). J Zool 270: 606–614.

66. Rduch V (2013) Ecology and population status of the puku antelope (*Kobus vardonii* LIVINGSTONE, 1857) in Zambia. PhD thesis. Rheinische Friedrich-Wilhelms-Universität of Bonn, Faculty of Mathe-matics and Natural Sciences. 287 p.

67. Schneider C, Kowalczyk R, Köhler M (2013) Resting site selection by large herbivores–The case of European bison (*Bison bonasus*) in Białowieza Primeval Forest. Mamm Biol 78: 438–445.

68. Jacobs J (1974) Quantitative measurement of food selection. Oecologia 14(4): 413–417.

69. Bailey BJR (1980) Large sample simultaneous confidence intervals for the multinomial probabilities based on transformations of the cell frequencies. Technometrics 22(4): 583–589.

70. Perzanowski K, Januszczak M (2010) A dispersal rate in a wisent population of Bieszczady Mountains. European Bison Conservation Newsletter 3: 45–52.

71. Krasińska M, Caboń-Raczynska K, Krasiński ZA (1987) Strategy of habitat utilization by European bison in the Białowieza Forest. Acta Theriol 32: 147–202.

72. Krasińska M, Krasiński Z, Bunevich AN (2000) Factors affecting the variability in home range size and distribution in European bison in the Polish and Belarussian parts of the Bialowieza Forest. Acta Theriol 45: 321–334.

73. Krasińska M, Krasiński Z (1995) Composition, group size, and spatial distribution of European bison bulls in Białowieza Forest. Acta Theriol 40: 1–21.

74. Daleszczyk K, Krasiński Z (2001) Parturition behaviour of European bison *Bison bonasus* living in reserves. Folia Zool 50: 75–78.

75. Daleszczyk K (2004) Mother-calf relationships and maternal investment in European bison *Bison bonasus*. Acta Theriol 49: 555–566.

76. Daleszczyk K (2005) Activity pattern of calf and its integration into herd in European bison, *Bison bonasus*. Folia Zool 54: 359–363.

77. Krasiński ZA (1978) Dynamics and structure of the European bison population in the Bialowieza Primeval Forest. Acta Theriol 23: 3–48.

78. Daleszczyk K, Czykier E (2010) Do European bison bulls in Białowieza Forest differ in their rutting behaviour depending on age? European Bison Conservation Newsletter 3: 5–16.

79. Daleszczyk K (2002) Behawior rozrodczy *Bison bonasus* (L.). PhD-Thesis. Mammal Research Institute PAS in Bialowieza. 109 p.

80. Fuller W (1960) Behaviour and social organization of the wild Bison of Wood Buffalo National Park, Canada. Arctic 13: 1–19.

81. Komers PE, Messier F, Gates CC (1992) Search or relax: the case of bachelor Wood bison. Behav Ecol Sociobiol 31: 192–203.

82. Larter NC, Sinclair ARE, Ellsworth T, Nishi J, Gates CC (2000) Dynamics of reintroduction in an indigenous large ungulate: the Wood bison of northern Canada. Anim Conserv 3: 299–309.

83. Fryxell J, Sinclair A (1988) Causes and consequences of migration by large herbivores. Trends Ecol Evol 3: 237–241. doi: 10.1016/0169-5347(88)90166-8 PMID: 21227239

84. Hebblewhite M, Merrill E, McDermid G (2008) A multi-scale test of the forage maturation hypothesis in a partially migratory ungulate population. Ecol Monogr 78(2): 141–166.

85. Hebblewhite M, Merrill EH (2009) Trade-offs between predation risk and forage differ between migrant strategies in a migratory ungulate. Ecology 90(12): 3445–3454 PMID: 20120812

86. Kamler JF, Jędrzejewska B, Jędrzejewski W (2007) Factors affecting daily ranges of Red deer *Cervus elaphus* in Białowieza Primeval Forest, Poland. Acta Theriol 52(2): 113–118.

87. Mysterud A, Larsen PK, Ims RA, Østbye E (1999) Habitat selection by Roe deer and sheep: does habitat ranking reflect resource availability? Can J Zool 77(5): 776–783.

88. Clevenger AP, Wierzchowski J, Chruszcz B, Gunson K (2002) GIS-generated, expert-based models for identifying wildlife habitat linkages and planning mitigation passages: Modelos generados con GIS y basados en expertos para la identificación de conexiones del hábitat para vida silvestre y la planeación de pasajes de Mitigación. Conserv Biol 16(2): 503–514.

89. Schippers P, Verboom J, Knaapen J, Apeldoorn Rv (1996) Dispersal and habitat connectivity in complex heterogeneous landscapes: an analysis with a GIS-based random walk model. Ecography 19 (2): 97–106.

90. Wu H-I, Li B-L, Springer TA,& Neill WH (2000) Modelling animal movement as a persistent random walk in two dimensions: expected magnitude of net displacement. Ecol Modell 132(1): 115–124.

91. Petrak M (1999) Raumnutzung und Wildwechsel—Schlüssel zur Überlebensstrategie des Rothirsches (*Cervus elaphus*) und zu den Wechselbeziehungen zwischen Lebensraum und Wildbestand. Natur-und Kulturlandschaft 3: 289–297.

92. Musiani M, Okarma H, Jędrzejewski W (1998) Speed and actual distances traveled by radiocollared wolves in Białowieza Primeval Forest (Poland). Acta Theriol 43(4): 409–416.

93. Hofmann G, Jenssen M, Pommer U (2008) Wildökologische Lebensraumbewertung für die Bewirtschaftung des wiederkäuenden Schalenwildes im nordostdeutschen Tiefland. In: Engel J, editor. Eberswalder Forstliche Schriftenreihe. Ministerium für Ländliche Entwicklung, Umwelt und Verbraucherschutz des Landes Brandenburg XXXIX. 205 p.

94. Borowski S, Krasiński Z, Miłkowski L (1967) Food and role of the European bison in forest ecosystems. Acta Theriol 12: 367–376.

95. Jaroszewicz B, Piroznikow E (2008) Diversity of plant species eaten and dispersed by the European bison *Bison bonasus* in Białowieza Forest. European Bison Conservation Newsletter 1: 14–29.

96. Kuemmerle T, Perzanowski K, Chaskovskyy O, Ostapowicz K, Halada L, Bashta A-T, et al. (2010) European bison habitat in the Carpathian Mountains. Biol Conserv 143: 908–916.

97. Daleszczyk K, Krasińska M, Krasiński, Bunevich A (2007) Habitat structure, climatic factors, and habitat use by European bison (*Bison bonasus*) in Polish and Belarusian parts of the Białowieza Forest, Poland. Can J Zool 85: 261–272.

98. Perzanowski KA, Woloszyn-Galeza A, Januszczak M (2008) Indicative factors for European bison refuges in the Bieszczady Mountains. Ann Zool Fennici 45(4): 347–352.

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

100. Chistopolova M, Hernandez-Blanco J, Litvinova E (2009) The using of new areas for free-ranging group of European bison (*Bison bonasus*) in European Russia. European Bison Conservation Newsletter 2: 40–46.

101. van de Vlasakker J (2014) Rewilding Europe 2014–2024. Rewilding Europe's contribution to the comeback of the European bison. Rewilding Europe, Nijmegen, The Netherlands. 64 p.

102. dlv Deutscher Landwirtschaftsverlag GmbH (2013) Wildlebende Wisente für die Schweiz. Available: http://www.jagderleben.de/wisente-fuer-die-schweiz. Accessed 20 October 2014.

103. Didriksen U (no date) Bisons auf Bornholm. Available: http://www.bornholm.info/de/bisons. Accessed 20 October 2014.

104. dlv Deutscher Landwirtschaftsverlag GmbH (2014a) Versicherer steigt aus. Available: http://www.jagderleben.de/versicherung-kuendigt-wisent-verein. Accessed 20 October 2014.

105. dlv Deutscher Landwirtschaftsverlag GmbH (2014b) "Betretungsverbot" für Wildrinder ausgesprochen. Available: http://www.jagderleben.de/schwarzer-tag-fuer-wisentprojekt. Accessed 20 October 2014.

106. dlv Deutscher Landwirtschaftsverlag GmbH (2014c) Wisente jetzt "herrenlos". Available: http://www.jagderleben.de/wisente-jetzt-herrenlos. Accessed 20 October 2014.

107. dlv Deutscher Landwirtschaftsverlag GmbH (2014d) Wisente doch (noch) nicht herrenlos. Available: http://www.jagderleben.de/wisente-doch-noch-nicht-herrenlos. Accessed 20 October 2014.

108. Schmitz P (2015) Back home! The first reintroduction of the European bison into Germany. Ethological and ethological investigations on the European bison (*Bison bonasus* Linnaeus, 1758) within the E+E-Project "Wisente im Rothaargebirge". PhD-Thesis. Institute of Biology, University of Siegen. 147 p.

Supporting information 1:

Tables of Post-hoc test results: pairwise Wilcoxon comparison with sequential Bonferroni correction. Measurements of the different 10-day periods are compared. Significant results are indicated by light gray background.

Calculations are given for

a)   expansion rate,
b)   daily used areas of the herd, complete area (kernel h_{ref} 85%),
c)   daily used areas of the herd, core area (kernel h_{ref} 25%),
d)   day-to-day shift of daily used areas,
e)   minimal daily walking routes.

a) expansion rate

		P1	P2	P3	P4	P5	P6	P7	P8	P9	P10	P11	P12	P13	P14	P15	P16	P17	P18
pre-release	P1																		
post-release	P2	0.625																	
	P3	0.003	0.003																
birthing of cows, roaming bull	P4	0.003	0.003	0.276															
	P5	0.011	0.003	0.276	0.020														
	P6	0.003	0.003	0.276	0.376	0.005													
	P7	0.011	0.003	0.922	0.376	0.276	0.233												
	P8	0.038	0.028	0.132	0.005	0.770	0.005	0.065											
	P9	0.003	0.003	0.038	0.028	0.003	0.432	0.106	0.011										
pre-rut	P10	0.003	0.003	0.323	0.323	0.085	0.922	0.011	0.005	0.865									
	P11	0.003	0.003	0.276	0.432	0.050	0.846	0.085	0.003	0.323	0.276								
	P12	0.003	0.003	0.233	0.323	0.015	0.194	0.065	0.011	1.000	0.846	0.696							
rut	P13	0.005	0.003	0.194	0.493	0.085	0.625	0.005	0.015	0.846	0.557	0.376	0.625						
	P14	0.005	0.003	0.432	0.922	0.106	0.432	0.323	0.028	0.493	0.846	1.000	0.194	0.132					
	P15	0.011	0.007	0.493	0.050	1.000	0.005	0.161	0.493	0.015	0.011	0.003	0.005	0.011	0.020				
	P16	0.003	0.003	0.020	0.028	0.003	0.085	0.020	0.003	0.922	0.696	0.050	0.770	1.000	0.132	0.003			
post-rut	P17	0.003	0.003	0.003	0.003	0.003	0.003	0.003	0.003	0.003	0.007	0.003	0.038	0.432	0.011	0.003	0.003		
	P18	0.003	0.003	0.015	0.011	0.011	0.015	0.003	0.005	0.038	0.003	0.005	0.007	0.194	0.005	0.003	0.020	0.696	

b) areas of daily use of the herd (complete area)

		pre-release	post-release		birthing of cows, roaming bull						pre-rut			rut				post-rut	
		P1	P2	P3	P4	P5	P6	P7	P8	P9	P10	P11	P12	P13	P14	P15	P16	P17	P18
pre-release	P1	■																	
post-release	P2	0.065	■																
	P3	0.003	0.003	■															
birthing of cows, roaming bull	P4	0.020	0.085	0.085	■														
	P5	0.003	0.050	0.233	0.625	■													
	P6	0.015	0.028	0.050	0.696	0.432	■												
	P7	0.020	0.194	0.194	1.000	0.625	0.625	■											
	P8	0.015	0.132	0.194	0.846	0.770	0.846	1.000	■										
	P9	0.028	0.323	0.065	1.000	0.770	0.922	0.922	1.000	■									
pre-rut	P10	0.015	0.011	0.557	0.276	0.625	0.194	0.376	0.432	0.770	■								
	P11	0.005	0.085	0.106	1.000	0.922	0.432	0.493	1.000	0.432	0.625	■							
	P12	0.003	0.003	0.770	0.050	0.038	0.003	0.050	0.028	0.015	0.106	0.015	■						
rut	P13	0.003	0.007	1.000	0.005	0.106	0.028	0.065	0.028	0.005	0.276	0.020	0.557	■					
	P14	0.003	0.020	0.432	0.161	0.376	0.050	0.194	0.432	0.161	0.922	0.493	0.038	0.085	■				
	P15	0.003	0.020	0.233	0.625	0.922	0.233	0.557	0.557	0.696	0.625	1.000	0.038	0.065	0.557	■			
	P16	0.011	0.065	0.432	0.323	0.161	0.106	0.106	0.376	0.132	0.194	0.161	0.493	0.846	0.922	0.161	■		
post-rut	P17	0.003	0.007	0.323	0.161	0.432	0.028	0.493	0.194	0.432	0.770	0.557	0.028	0.106	0.432	0.922	0.696	■	
	P18	0.003	0.005	0.233	0.038	0.085	0.015	0.005	0.005	0.194	0.106	0.038	0.432	0.557	0.085	0.007	0.276	0.028	■

c) areas of daily use of the herd (core area)

		pre-release	post-release		birthing of cows, roaming bull						pre-rut			rut				post-rut	
		P1	P2	P3	P4	P5	P6	P7	P8	P9	P10	P11	P12	P13	P14	P15	P16	P17	P18
pre-release	P1	■																	
post-release	P2	0.065	■																
	P3	0.003	0.020	■															
birthing of cows, roaming bull	P4	0.020	0.065	0.106	■														
	P5	0.003	0.065	0.323	0.557	■													
	P6	0.015	0.065	0.132	0.493	0.625	■												
	P7	0.020	0.233	0.194	1.000	0.696	0.696	■											
	P8	0.011	0.132	0.194	0.770	0.770	1.000	0.846	■										
	P9	0.028	0.276	0.161	0.922	1.000	0.770	0.922	0.696	■									
pre-rut	P10	0.015	0.011	0.625	0.276	0.625	0.194	0.376	0.323	0.922	■								
	P11	0.003	0.065	0.233	0.557	1.000	0.323	0.376	0.376	0.696	0.922	■							
	P12	0.003	0.005	0.161	0.050	0.028	0.003	0.038	0.015	0.020	0.132	0.015	■						
rut	P13	0.003	0.007	0.493	0.005	0.038	0.028	0.065	0.020	0.011	0.233	0.028	0.557	■					
	P14	0.003	0.028	0.922	0.085	0.233	0.050	0.233	0.038	0.276	0.846	0.493	0.038	0.276	■				
	P15	0.003	0.020	0.432	0.493	0.922	0.233	0.323	0.323	0.770	0.625	0.696	0.020	0.065	0.557	■			
	P16	0.011	0.065	0.922	0.323	0.194	0.085	0.065	0.376	0.132	0.233	0.323	0.161	0.770	1.000	0.194	■		
post-rut	P17	0.003	0.007	0.625	0.132	0.432	0.065	0.557	0.132	0.557	1.000	0.696	0.020	0.132	0.432	0.922	0.696	■	
	P18	0.003	0.005	0.233	0.038	0.085	0.011	0.005	0.003	0.194	0.085	0.085	0.376	0.696	0.085	0.011	0.323	0.028	■

d) day-to-day shift of daily used areas

Column group headers: P1 = pre-release; P2–P3 = post-release; P4–P9 = birthing of cows, roaming bull; P10–P12 = pre-rut; P13–P16 = rut; P17–P18 = post-rut

	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10	P11	P12	P13	P14	P15	P16	P17	P18
P1 (pre-release)																		
P2 (post-release)	0.085																	
P3	0.011	0.038																
P4 (birthing of cows, roaming bull)	0.015	0.065	0.432															
P5	0.005	0.028	0.233	0.846														
P6	0.003	0.038	0.493	0.770	0.557													
P7	0.005	0.015	0.276	0.922	0.493	0.922												
P8	0.015	0.050	0.276	0.696	0.557	1.000	0.493											
P9	0.015	0.028	0.696	0.557	0.233	0.557	0.557	0.696										
P10 (pre-rut)	0.005	0.003	1.000	0.276	0.020	0.007	0.085	0.161	0.276									
P11	0.003	0.005	0.770	0.625	0.038	0.161	0.276	0.625	1.000	0.493								
P12	0.003	0.005	0.625	0.050	0.003	0.065	0.065	0.020	0.106	0.132	0.050							
P13 (rut)	0.003	0.003	0.493	0.020	0.011	0.003	0.015	0.050	0.020	0.233	0.106	1.000						
P14	0.003	0.007	0.922	0.065	0.020	0.132	0.085	0.020	0.050	0.557	0.194	0.696	0.557					
P15	0.003	0.007	0.846	0.376	0.065	0.065	0.132	0.323	0.922	0.323	0.376	0.276	0.161	0.233				
P16	0.003	0.011	0.770	0.323	0.028	0.085	0.106	0.376	0.323	0.922	0.276	0.846	0.625	0.696	0.376			
P17 (post-rut)	0.038	0.194	0.038	0.233	0.432	0.028	0.194	0.194	0.085	0.003	0.050	0.007	0.003	0.015	0.015	0.020		
P18	0.005	0.007	0.696	0.132	0.028	0.106	0.085	0.161	0.557	0.376	0.493	0.770	0.846	1.000	0.625	0.846	0.028	

e) daily minimum walking routes

Column group headers: P1 = pre-release; P2–P3 = post-release; P4–P9 = birthing of cows, roaming bull; P10–P12 = pre-rut; P13–P16 = rut; P17–P18 = post-rut

	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10	P11	P12	P13	P14	P15	P16	P17	P18
P1 (pre-release)																		
P2 (post-release)	0.015																	
P3	0.003	0.003																
P4 (birthing of cows, roaming bull)	0.003	0.038	0.011															
P5	0.003	0.003	0.011	0.770														
P6	0.003	0.028	0.005	0.376	0.065													
P7	0.003	0.050	0.003	0.161	0.015	1.000												
P8	0.003	0.028	0.005	0.846	0.233	0.557	0.323											
P9	0.003	0.085	0.005	0.233	0.132	0.922	0.770	0.625										
P10 (pre-rut)	0.003	0.003	0.015	0.432	0.194	0.015	0.003	0.005	0.011									
P11	0.003	0.007	0.011	0.770	1.000	0.065	0.085	0.194	0.020	0.233								
P12	0.003	0.003	0.085	0.161	0.161	0.003	0.003	0.015	0.005	0.696	0.028							
P13 (rut)	0.003	0.007	0.011	0.161	0.493	0.020	0.011	0.028	0.011	0.846	0.050	0.770						
P14	0.003	0.028	0.007	0.557	0.557	0.085	0.028	0.493	0.028	0.132	0.493	0.028	0.038					
P15	0.003	0.007	0.011	0.625	0.132	0.770	0.922	0.922	1.000	0.050	0.323	0.015	0.065	0.323				
P16	0.003	0.007	0.011	0.770	0.922	0.050	0.005	0.161	0.015	0.085	0.557	0.065	0.194	0.376	0.194			
P17 (post-rut)	0.003	0.005	0.005	1.000	0.376	0.106	0.020	0.106	0.132	0.015	0.432	0.007	0.085	0.846	0.432	0.376		
P18	0.003	0.003	0.323	0.376	0.132	0.011	0.005	0.028	0.011	0.696	0.132	0.846	0.770	0.106	0.003	0.432	0.028	

Supporting information 2:

For each period of higher ranking behaviour Jacobs' preference indicies for each habitat type and Bailey's confidence intervals were calculated.
The area of each habitat type is given.
According to the number of location counts the expected and observed location data (Expected, Observed)
and the respective proportions (p(exp), p(obs)) are given.
Bailey's confidence intervals (Bailey -, Bailey +) are calculated and Jacobs preference index (Jacobs).

The preferences are calculated according to these borders; p(obs) lies between Bailey – and Bailey +:

(=)	p(exp) lies within the range of the confidence intervals, the habitat type is used according to its size.
(-)	p(exp) lies above the range of the confidence intervals, the habitat type is avoided.
(+)	p(exp) lies below the range of the confidence intervals, the habitat type is preferred.

a) pre-release

Habitat type	Area m²	Expected	Observed	p(exp)	p(obs)	Bailey -	Bailey +	Jacobs	Preference
Beech	16805779	147	72	0.4164	0.2045	0.1459	0.2699	-0.4702	-
Spruce	16577187	145	110	0.4108	0.3125	0.2428	0.3849	-0.2106	-
Oak	8118	0	0	0.0002	0.0000	0.0000	0.0156	-1.0000	=
Douglas fir	95643	1	0	0.0024	0.0000	0.0000	0.0156	-1.0000	=
Larch	44433	0	0	0.0011	0.0000	0.0000	0.0156	-1.0000	=
Other deciduous forest	220585	2	0	0.0055	0.0000	0.0000	0.0156	-1.0000	=
Wind thrown areas	1097805	10	5	0.0272	0.0142	0.0018	0.0413	-0.3199	=
Greenland	2659188	23	103	0.0659	0.2926	0.2246	0.3641	0.7086	+
Road	2696086	24	62	0.0668	0.1761	0.1213	0.2387	0.4983	+
Creek	34391	0	0	0.0009	0.0000	0.0000	0.0156	-1.0000	=
Other	118950	1	0	0.0029	0.0000	0.0000	0.0156	-1.0000	=

b) post-release

Habitat type	Area m²	Expected	Observed	p(exp)	p(obs)	Bailey -	Bailey +	Jacobs	Preference
Beech	16805779	562	170	0.4164	0.1259	0.1012	0.1531	-0.6640	-
Spruce	16577187	555	504	0.4108	0.3733	0.3357	0.4111	-0.0784	=
Oak	8118	0	0	0.0002	0.0000	0.0000	0.0041	-1.0000	=
Douglas fir	95643	3	7	0.0024	0.0052	0.0011	0.0132	0.3739	=
Larch	44433	1	0	0.0011	0.0000	0.0000	0.0041	-1.0000	=
Other deciduous forest	220585	7	16	0.0055	0.0119	0.0049	0.0225	0.3715	=
Wind thrown areas	1097805	37	76	0.0272	0.0563	0.0397	0.0760	0.3617	+
Greenland	2659188	89	424	0.0659	0.3141	0.2783	0.3506	0.7330	+
Road	2696086	90	142	0.0668	0.1052	0.0825	0.1305	0.2430	+
Creek	34391	1	10	0.0009	0.0074	0.0022	0.0164	0.7949	+
Other	118950	4	1	0.0029	0.0007	0.0000	0.0057	-0.5990	=

c) birth giving

Habitat type	Area m²	Expected	Observed	p(exp)	p(obs)	Bailey -	Bailey +	Jacobs	Preference
Beech	16805779	1720	1205	0.4164	0.2918	0.2717	0.3121	-0.2680	-
Spruce	16577187	1696	1803	0.4108	0.4366	0.4145	0.4585	0.0528	+
Oak	8118	1	0	0.0002	0.0000	0.0000	0.0013	-1.0000	=
Douglas fir	95643	10	5	0.0024	0.0012	0.0002	0.0036	-0.3243	=
Larch	44433	5	3	0.0011	0.0007	0.0000	0.0028	-0.2052	=
Other deciduous forest	220585	23	40	0.0055	0.0097	0.0058	0.0147	0.2805	+
Wind thrown areas	1097805	112	205	0.0272	0.0496	0.0404	0.0599	0.3026	+
Greenland	2659188	272	612	0.0659	0.1482	0.1327	0.1643	0.4230	+
Road	2696086	276	255	0.0668	0.0617	0.0515	0.0730	-0.0421	=
Creek	34391	4	2	0.0009	0.0005	0.0000	0.0023	-0.2755	=
Other	118950	12	0	0.0029	0.0000	0.0000	0.0013	-1.0000	-

d) pre-rut

Habitat type	Area m²	Expected	Observed	p(exp)	p(obs)	Bailey -	Bailey +	Jacobs	Preference
Beech	16805779	778	761	0.4164	0.4074	0.3748	0.4398	-0.0186	=
Spruce	16577187	767	800	0.4108	0.4283	0.3954	0.4609	0.0359	=
Oak	8118	0	0	0.0002	0.0000	0.0000	0.0030	-1.0000	=
Douglas fir	95643	4	12	0.0024	0.0064	0.0022	0.0134	0.4626	=
Larch	44433	2	2	0.0011	0.0011	0.0000	0.0052	-0.0140	=
Other deciduous forest	220585	10	4	0.0055	0.0021	0.0002	0.0070	-0.4384	=
Wind thrown areas	1097805	51	36	0.0272	0.0193	0.0112	0.0299	-0.1746	=
Greenland	2659188	123	147	0.0659	0.0787	0.0618	0.0977	0.0954	=
Road	2696086	125	105	0.0668	0.0562	0.0419	0.0727	-0.0917	=
Creek	34391	2	0	0.0009	0.0000	0.0000	0.0030	-1.0000	=
Other	118950	6	1	0.0029	0.0005	0.0000	0.0042	-0.6932	=

e) rut

Habitat type	Area m²	Expected	Observed	p(exp)	p(obs)	Bailey -	Bailey +	Jacobs	Preference
Beech	16805779	1003	709	0.4164	0.2944	0.2681	0.3212	-0.2620	-
Spruce	16577187	989	1171	0.4108	0.4863	0.4570	0.5151	0.1518	+
Oak	8118	0	4	0.0002	0.0017	0.0001	0.0055	0.7843	=
Douglas fir	95643	6	9	0.0024	0.0037	0.0010	0.0086	0.2246	=
Larch	44433	3	0	0.0011	0.0000	0.0000	0.0023	-1.0000	=
Other deciduous forest	220585	13	3	0.0055	0.0012	0.0000	0.0048	-0.6300	-
Wind thrown areas	1097805	66	56	0.0272	0.0233	0.0153	0.0332	-0.0802	=
Greenland	2659188	159	283	0.0659	0.1175	0.0994	0.1370	0.3075	+
Road	2696086	161	168	0.0668	0.0698	0.0557	0.0855	0.0233	=
Creek	34391	2	0	0.0009	0.0000	0.0000	0.0023	-1.0000	=
Other	118950	7	5	0.0029	0.0021	0.0003	0.0061	-0.1738	=

f) post-rut

Habitat type	Area m²	Expected	Observed	p(exp)	p(obs)	Bailey -	Bailey +	Jacobs	Preference
Beech	16805779	150	72	0.4164	0.2000	0.1425	0.2642	-0.4811	-
Spruce	16577187	148	196	0.4108	0.5444	0.4663	0.6172	0.2632	+
Oak	8118	0	0	0.0002	0.0000	0.0000	0.0153	-1.0000	=
Douglas fir	95643	1	1	0.0024	0.0028	0.0000	0.0214	0.0794	=
Larch	44433	0	0	0.0011	0.0000	0.0000	0.0153	-1.0000	=
Other deciduous forest	220585	2	0	0.0055	0.0000	0.0000	0.0153	-1.0000	=
Wind thrown areas	1097805	10	8	0.0272	0.0222	0.0054	0.0528	-0.1033	=
Greenland	2659188	24	51	0.0659	0.1417	0.0928	0.1993	0.4012	+
Road	2696086	24	32	0.0668	0.0889	0.0505	0.1381	0.1536	=
Creek	34391	0	0	0.0009	0.0000	0.0000	0.0153	-1.0000	=
Other	118950	1	0	0.0029	0.0000	0.0000	0.0153	-1.0000	=

g) Sum

Habitat type	Area m²	Expected	Observed	p(exp)	p(obs)	Bailey -	Bailey +	Jacobs	Preference
Beech	16805779	4359	2989	0.4164	0.2855	0.2730	0.2982	-0.2820	-
Spruce	16577187	4300	4584	0.4108	0.4379	0.4241	0.4517	0.0555	+
Oak	8118	2	4	0.0002	0.0004	0.0000	0.0013	0.3103	=
Douglas fir	95643	25	34	0.0024	0.0032	0.0019	0.0051	0.1567	=
Larch	44433	12	5	0.0011	0.0005	0.0001	0.0014	-0.3951	=
Other deciduous forest	220585	57	63	0.0055	0.0060	0.0041	0.0084	0.0484	=
Wind thrown areas	1097805	285	386	0.0272	0.0369	0.0318	0.0424	0.1558	+
Greenland	2659188	690	1620	0.0659	0.1548	0.1448	0.1650	0.4438	+
Road	2696086	699	764	0.0668	0.0730	0.0659	0.0804	0.0475	=
Creek	34391	9	12	0.0009	0.0011	0.0004	0.0024	0.1474	=
Other	118950	31	7	0.0029	0.0007	0.0001	0.0017	-0.6308	-