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The Effect of European Bison (*Bison bonasus*) Translocations on the Persistence and Genetic Diversity of Ex Situ Herds—A Modelling Study

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Abstract: The conservation of the genetic diversity of the European bison population is carried out mainly in ex situ herds, constituting a functional metapopulation. The breeders have to balance between the available capacity of the reserves and the need to enrich the free and semi-free herds with appropriate individuals. If there are limitations (e.g., financial) in the transfer of individuals, breeders report a problem of surplus individuals. The aim of this study was to estimate the migration parameters in the wisent metapopulation ex situ to maintain genetic diversity in hypothetical herds. The analysis was a two-step process. The first part of this study was carried out between the years 1998 and 2017, based on information from the European Bison Pedigree Book about eight selected herds. The average annual share of exported and imported individuals in the chosen metapopulation were calculated (8.81% (SD: 11.51) and 0.75% (SD: 2.15), respectively). The proportion of males to females among the exported animals was close to 1:1. The sex ratio of imported animals was close to 2:1 (M:F). The majority of transports were exports of animals (92.1%). The share of individuals exported from different age–sex groups was calculated. On this basis, in the second part of the study, the proportion of exported surplus individuals in the smallest hypothetical herd was established as 5.89% of the adult females, or 8.98% of adult males, or 32.70% of females aged 1–3 years. In order to maintain the genetic sustainability of hypothetical herds it is crucial to import individuals (M/F: 1/1; interval: 10 years). The results of this study will provide necessary information to determine the tools of wisent population management in the enclosure.

Keywords: wisent; *Bison bonasus*; ex situ breeding; migrations; diversity; management

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1. Introduction

The European bison (*Bison bonasus*), also called wisent, population in Poland and in other European countries is increasing [1]. The number of European bison individuals in the world, as of 31 December 2021, amounted to 9558 [2]. This is of great interest for various specialists involved in research, application projects and pan-European cooperation [3]. Therefore, the status of this species in the Red List of the International Union for Conservation of Nature (IUCN) has also been changed. European bison are no longer classified as vulnerable (VU), but as near threatened (NT). This change was justified because in 2019 about 17% of the 47 free-living European bison herds were greater than the Minimum Viable Populations (MVP, 150 mature animals) [4]. Despite this achievement in European bison restoration, there are still several threats raising doubts about the future of this species [5]. In the face of Russia's aggression against Ukraine, herds located in Russia, Ukraine and Belarus were affected by this military conflict [6]. Those herds constitute over half of the world European bison population (50.4%), and almost two-thirds of free-ranging populations (61.8%) [1]. For this reason, the protection of European bison should be intensified. The most important reservoir for the establishment and improvement of current or future free-living European bison populations have been captive herds. The need to manage captive herds, as part of European bison ex situ conservation, is enhanced with the constant loss of genetic variability as a result of genetic drift, which is highly effective in small isolated herds [7].

In the context of the European bison, the basic question is how to preserve genetic diversity and persistence of herds ex situ. In herds smaller than 50 individuals, the probability of extinction is associated with demographic and environmental factors [8]. Small- and medium-size herds that meet the basic behavioral requirements maintain genetic variability if they are combined into a metapopulation. Building structures, combining and mating appropriate individuals (avoiding high-kinship mating and promoting reproduction between individuals with unique genes in the population) serve to safeguard genetic diversity of the species [9]. The process of active exchanging of individuals among a metapopulation is one of the main directions of European bison adaptive management [5]. So-called over-number (surplus) individuals participate in this exchange. Their presence in each European bison herd results from biology. Concerning demography, the persistence of a herd is described as the function of its size. The population grows if reproduction is greater than mortality. The natural mortality of the European bison is low and is not significant for regulating the size of a herd [10]. In the years 1960–2004, the mean natural mortality of the population in Białowieska Forest was 2.8 $\pm$ 1.3% [11]. The average growth rate amounts to 12–15%, which causes the size of the herd to double in 5–6 years [3,12,13]. As a consequence, a certain challenge for breeders is fitting the herd size to the capacity of breeding enclosures. The managers of free-roaming herds have also reported conflicts with agriculture, forestry and transport, resulting from herds' uncontrolled increase in number [1,3,5,13,14]. Regarding captive herds, the presence of over-number is a result of their different roles in the conservation strategy. Breeding centers focused on reproduction have different parameters to determine the over-number of European bison individuals than small exhibition enclosures. The common features are connected with behavior (outstanding aggression) and health (infertility, permanent trauma). We consider additionally the uniqueness of genotypes for the population and the kinship level among the herd (e.g., two cows being daughters of the same pair of individuals, father of sexually mature daughters, sexually mature males staying in the enclosure with mothers). In exhibition enclosures and zoos, the available space will be a limitation, but exterior features will be an important criterion for staying in the herd. Hence, it is possible that a cow of reproductive age with a unique genotype will be considered as an over-number in the herd of origin, but she and her offspring will perfectly fit in the breeding plan of another center. Further growth of the European bison population is desirable, but it is very important to have the acceptance of local society for in situ herds [5,15] and any threat for the animal welfare ex situ. Over-number individuals are managed by export because of the need to provide the selected individuals to create new herds and enrich the genetic diversity of existing ones. Simultaneously, the requirement to preserve the sustainability of herds exporting individuals is raised.

For this reason, the attempt to determine the number of individuals for import and export purposes is important. To determine the increase in herds, the number of births and deaths during the year, as well as the level of migration are used [16]. One of the tools for population viability analysis (PVA) is the VORTEX software [17], which can be used to assess demographic, environmental and genetic factors [18]. VORTEX analysis has been conducted in many European bison studies [19–21]. For management purposes it was important to determine the development of the population with different levels of mortality [22,23].

The aim of this study is to estimate the appropriate translocation pattern to maximize diversity and reduce the probability of extinction in model ex situ herds based on diversified translocation parameters calculated in the eight selected herds existing in 1998–2017. The results of the analysis will provide useful data for the management of European bison herds.

2. Materials and Methods

The material used for analysis was data from the European Bison Pedigree Book (EBPB) volumes published in the years 1999–2018 about individuals from 8 herds from three European countries, Poland, Germany and Sweden, as these herds have generally comparable numbers to the average captive European bison herds (Table 1).

Table 1. Herds included in analysis with average size in years 1998–2017.

	Herd Name	Herd Name Shortcut	Coury	Average Herd Size (SD)
1	Avesta	A	Sweden	29.1 (3.0)
2	Damerower Werder	D	Germany	32.4 (3.1)
3	Eriksberg	E	Sweden	29.9 (17.0)
4	Gołuchów	G	Poland	8.8 (2.5)
5	Hardehausen I	H	Germany	17.6 (2.2)
6	Pszczyna	P	Poland	36.2 (6.9)
7	Sababurg	Sa	Germany	16.3 (2.5)
8	Springe	Sp	Germany	26.8 (6.0)

Each transport (both to ex situ herds and to the wild) of an individual from one of the selected herds was considered as export. Each transport of an individual to the herd was considered as import and the premigrations were not taken into account.

In a 20-year observation, the shares of females and males within the total number of analyzed exports (N = 351) and imports (N = 30) were calculated. The annual level of export and import at the metapopulation level (8 herds in total) was calculated as a weighted average. The numbers of individuals in individual herds in particular years were used as weights.

The export coefficient within the age–sex group was calculated, i.e., the proportion of the number of individuals exported to the size of the age–sex group in each year; then, the 20-year average for every herd and metapopulation was calculated. Based on Krasińska and Krasiński [11], the division into 5 age classes was applied (calves (0–12 months), adolescents (13–36 months), adults under 10 years of age (37–120 months), adults above 10 years of age (121–180 months) and old (181 months and more)).

Due to the small number of imports, 3 age classes (calves (0–12 months), adolescents (13–36 months) and adults (37 months and more)) were applied. Based on 20 years of observation, the total number of females and males imported to the age–sex groups in individual herds and the percentage share of transported animals in the metapopulation were calculated.

The effect of the herd size and translocation pattern on herd sustainability was estimated with the use of the software VORTEX (version 10.3.6.0) [24]. Stochastic modeling was used, i.e., assuming the variability of demographic parameters over time, as well as influence of inbreeding, which is particularly important in the case of European bison [25,26]. Reproduction rates were based on Kaczmarek-Okrój and Olech [27]. Mortality rates from free-roaming populations in Białowieska Forest in the years 1984–1993 were used (Table 2) [25]. The lethal equivalent was applied as 6.29 [28]. The VORTEX input variables are presented in Table S1 in the Supplement.

Table 2. European bison mortality in Białowieska Forest in 1984–1993 [25].

Age [Years]	Females	Males
0–1	10.32 (5.98)	9.40 (6.70)
1–2	3.53 (3.00)	7.04 (6.84)
2–3	6.55 (5.53)	3.29 (3.72)
3–4	3.87 (2.68)	3.66 (5.42)
4–...	3.74 (1.68)	5.19 (2.03)

Simulations were performed according to three models. Model I included a variable enclosure capacity (K = 20, K = 30 and K = 50). In Model II, a regular enrichment with import of a single or pair of animals in 10-year intervals was added. Model III was expanded with the export of individuals from one of 3 different age and sex groups: sexually mature females, sexually mature males or females aged 1–3 years. The share of exported individuals that does not cause a threat to the sustainability of the analyzed herds has been defined as an over-number. The multipliers (0.5, 1.0, 1.5, 2.0) of mean export coefficients for adult females (4–10 years old), adult males (4–10 years old) and females aged 1–3 years based on Tables 4 and 5 were applied.

In all simulation results, the assessment criterion was the positive stochastic growth rate (stoch-R), the probability of a herd extinction (PE) less than 5.00% [26] and the level of preserved genetic diversity (GeneDiv) not lower than 80.0%. An additional factor assessed in export simulations was the number of individuals in the herds that survived (N-extant).

3. Results

3.1. Imports and Exports

Exports of 351 individuals (181 females and 170 males) and imports of 30 individuals (11 females and 19 males) were analyzed. The level of export in the metapopulation was 8.81% (SD: 11.51). Average import of animals to the metapopulation amounted to 0.75% (SD: 2.15). Most of the transports were exports of animals (92.1%) (Table 3). The proportion of males and females among the exported animals was close to 1:1 (females: 51.57%). A different sex proportion was found in the case of imports (females: 36.67%). The ratio of imported males to females was equal to 1.72.

Table 3. The distribution of transports (N = 381) of females and males at the metapopulation level.

	Export (92.1%)		Import (7.9%)	
	Males	Females	Males	Females
Total	48.43	51.57	63.33	36.67

The mean export coefficients for individual herds and for the metapopulation in age and sex classes are presented in Tables 4 and 5. The high values of the standard deviation reflect the uneven level of exports across years and are a consequence of the low size of individual age classes, analyzed by year and by herd.

Mainly young animals aged 1–3 years were exported (females: 21.80%, males: 17.26%). The share of exported calves was similar for both sexes (females: 4.26%, males: 4.01%). Animals at the age of 4–10 years were also often exported: 5.89% females and 17.96% males from the metapopulation. The export of adult females (5.89%) was almost four times lower than of adolescent females (21.80%). No individuals over the age of 15 were exported.

Table 4. The share (%) of exported females in age groups in analyzed herds and metapopulation with s.d in parentheses.

Age Class	A	D	E	G	H	P	Sa.	Sp.	Average
Calves	1.25 (5.45)	6.56 (21.98)	0	5.00 (21.79)	0	0	20.00 (42.36)	1.25 (5.45)	**4.26 (6.38)**
Adolescents	9.24 (24.16)	29.25 (47.99)	17.50 (65.72)	15.00 (65.38)	16.00 (38.91)	27.00 (37.80)	22.50 (51.17)	37.88 (52.40)	**21.80 (8.15)**
Adults under 10 years	2.25 (6.80)	2.95 (10.97)	4.88 (15.05)	5.00 (21.79)	1.04 (3.19)	21.16 (29.57)	3.33 (14.53)	6.50 (18.45)	**5.89 (5.99)**
Adults at least 10 years	0	0	0	5.00 (21.79)	0	2.67 (8.27)	0	2.29 (7.62)	**1.24 (1.77)**

Table 5. The share (%) of exported males in age groups in analyzed herds and metapopulation.

Age Class	A	D	E	G	H	P	Sa.	Sp.	Average
Calves	1.25 (5.45)	0	0	1.25 (5.45)	0	3.33 (14.53)	21.67 (87.10)	4.58 (11.02)	**4.01 (6.86)**
Adolescents	14.63 (43.62)	20.42 (65.54)	9.13 (23.20)	5.00 (21.79)	24.17 (45.79)	37.67 (67.01)	6.67 (22.61)	20.42 (51.27)	**17.26 (10.12)**
Adults under 10 years	2.67 (8.27)	0	2.50 (10.90)	5.00 (15.00)	19.17 (65.67)	31.42 (39.30)	5.00 (21.79)	31.96 (75.40)	**17.96 (24.66)**
Adults at least 10 years	0	5.00 (21.79)	0		0	0	0	0	**0.63 (1.65)**

The highest percentages of exported females were found for Springe, Damerower and Pszczyna (37.88%, 29.25% and 27.00%, respectively). In case of males, the highest values were in Pszczyna (37.67%) and German herds (Hardehausen: 24.17%, Damerower and Springe 20.42%). In the case of three herds (Eriksberg, Hardehausen and Pszczyna), there was no export of female calves, and in the case of three herds (Eriksberg, Hardehausen and Damerower), there was no export of the youngest males. The largest percentage of exported calves was in Sababurg (20.00% and 21.67% for females and males, respectively). In other herds the largest value of female exports up to a year was in Damerower (6.56%) and in the case of males in Springe (4.58%).

The highest values of adult male exports were in Springe (31.96%), Pszczyna (31.42%) and Hardehausen (19.17%). The Damerower herd did not export any bull from this age group but was the only herd that exported bulls aged 11–15 years (5.00%). Adult cows (4 years and more) were exported most intensively from Pszczyna (21.16%) and later from Springe 6.50%). Females aged 4–10 years were exported from all herds, while females aged 11–15 years only from Gołuchów (5.00%), Pszczyna (2.67%) and Springe (2.29%).

The average number of individuals brought to the single herd over 20 years was 3.75 ± 2.17 (1.38 ± 1.73 for females and 2.38 ± 0.99 for males), i.e., on average one female and two males were imported to every herd. The number of imported animals is presented in Table 6. At the metapopulation level, the most frequent import concerns adolescents (males: 33.33%, females: 20.00%) and adults (males: 26.67%, females: 10.00%). Among the calves, the share of females (6.67%) was twice as high as that of males (3.33%).

Table 6. The number and share (%) of imported males (M) and females (F).

Age Class	**Number of Imported Animals**																**%**	
	A		**D**		**E**		**G**		**H**		**P**		**Sa.**		**Sp.**		**Metapopulation**	
	M	**F**	**M**	**F**	**M**	**F**	**M**	**F**	**M**	**F**	**M**	**F**	**M**	**F**	**M**	**F**	**M**	**F**
Calves	-	-	-	1	-	-	-	-	-	-	-	-	1	-	-	1	3.33	6.67
Adolescents	3	-	-	1	-	1	1	1	1	-	-	-	-	-	2	3	33.33	20.00
Adults	-	-	3	1	1	-	1	1	3	-	2	-	-	-	1	1	26.67	10.00
Total	3	0	3	3	1	1	2	2	4	0	2	0	1	0	3	5	63.30	36.7
TOTAL	3		6		2		4		4		2		1		8		100.00	

At the level of a single herd, the most intensive was the import of adult males (75% of herds), and next were adolescent males (50% of herds). Every second herd imported adolescent females, three herds imported adult cows and two herds imported a female calf. Only two herds (Damerower and Springe) imported females of all age groups, and every herd brought males of all age groups. No female was imported to four herds in a period of 20 years. One herd (Sababurg) imported a male calf (10042 FAVORIT).This male became the father of numerous calves. At least one male was imported to each herd within 20 years for blood refreshment.

3.2. Model I

The probability of extinction of an isolated herd of K = 20 in the model without imports (0/0) was high (19.00%), while the genetic diversity after a hundred years was low (54.15%) (Table 7). In the case of the herd of K = 30, there was a risk of extinction, but less than 5.0%. In the herd of K = 50, such a risk did not occur at all (PE = 0.00%). The rate of herd development ranged from 4.08% for the smallest herd to 7.08% for the largest one. Our model assumed a limited herd capacity. In VORTEX, the default setting under this assumption is that once the allowable capacity is exceeded, individuals are removed (equally from each age and sex group). It was concluded that for small herds without regular import, it is not recommended to designate over-number individuals.

Table 7. Effect of herd size (baseline model, M/F: imports of males and females).

K	**M/F**	**Stoch-r**	**PE**	**GeneDiv**
20	0/0	4.08	19.00	54.15
30	0/0	5.82	0.60	67.36
50	0/0	7.08	0.00	78.96

3.3. Model II

Import of at least one individual to the smallest herd led to retaining 74.94% of the genetic diversity (Table 8).

In a herd of 50 individuals, 78.96% of genetic diversity was retained without import and 83.24% was retained with imports. Importing at least one male into the herd of K = 20 in a 10-year interval reduced the risk of extinction to the level of PE = 6.40%, i.e., three times compared to the model without import; however, the PE was still over 5.0%. Import of one female in the same interval reduced PE to 0.60%. In the herd of K = 20, a two-fold increase in imports resulted in a reduction in the risk of extinction to the expected level below 5.0%. The highest risk of extinction was associated with the import of one male to the smallest herd (PE = 6.40%). In the herd of K = 30, the probability of extinction occurred (one male and two males) at a level below 1.0% (0.2%). In the herd of K = 50, where the risk of extinction did not occur, even without enrichment, it is worth assessing the genetic diversity retention effect. In the herd of K = 50, the level of genetic diversity in the base model (78.9%) was lower than that obtained in any case of import (from one individual—83.24% to two individuals—86.49%). Import of individuals to medium and large herds increased the retention of genetic diversity. In K = 20 and K = 30 herds, the lowest risk of extinction is associated with the import of at least two animals. Taking into account the level of genetic diversity, the most favorable was the import of one female and one male every 10 years. Such an import scheme has been implemented in all export simulations as a necessary element for sustainable herd management.

Table 8. The effect of herd size and import in 10-year intervals.

K	(M/F)	Stoch-r	PE	GeneDiv
20	1/0	5.86	6.40	74.94
	0/1	6.77	0.60	75.49
	1/1	7.58	0.00	81.49
	2/0	6.52	4.60	81.46
	0/2	8.15	0.20	80.39
30	1/0	6.75	0.20	79.28
	0/1	7.37	0.00	77.89
	1/1	7.89	0.00	84.07
	2/0	7.18	0.20	83.51
	0/2	8.44	0.00	83.02
50	1/0	7.56	0.00	83.57
	0/1	7.88	0.00	83.24
	1/1	8.25	0.00	86.28
	2/0	7.85	0.00	86.49
	0/2	8.63	0.00	85.55

3.3.1. Model III (Adult Cows)

For herds of K = 20 the annual export of adult cows to the level of 5.89% did not threaten herd sustainability (PE = 0.6%). In the K = 30 herd, a level of 8.84%, and for K = 50, a level 11.78% for the export of adult females did not pose such a threat (Table 9). Taking into consideration the retention of genetic diversity, it was assumed that the export of 8.84% adult cows did not pose a threat to the sustainability of herds of more than 30 individuals.

Table 9. The impact of a variable level of adult females exported on stabilized herds.

			%		
K	Export Level	Stoch-r	PE	GeneDiv	N-Extant
20	2.95	6.03	0.00	81.57	18.10
	5.89	4.55	0.60	81.81	17.14
	8.84	3.12	5.20	82.09	15.62
	11.78	1.72	12.20	81.02	13.26
30	2.95	6.19	0.00	84.14	28.13
	5.89	4.68	0.60	84.60	26.67
	8.84	3.12	1.60	84.25	24.15
	11.78	1.65	5.20	83.86	20.71
50	2.95	6.63	0.00	86.23	48.11
	5.89	4.95	0.00	86.81	46.83
	8.84	3.26	0.20	86.71	42.95
	11.78	1.60	2.00	86.03	35.29

3.3.2. Model III (Adult Males)

Only in herds of K = 20 was there a risk of extinction (PE > 5.00 %) with annual exports of over 35.92% of adult bulls. In larger herds (K = 30), the risk was less than 1.00% (Table 10).

Table 10. The impact of variable levels of adult male exports on stabilized herds.

			%		
K	**Export Level**	**Stoch-r**	**PE**	**GeneDiv**	**N-Extant**
20	8.98	7.25	0.20	80.03	18.3
	17.96	6.79	1.00	79.47	18.02
	26.94	6.43	3.40	78.79	17.67
	35.92	5.88	5.60	79.94	17.30
30	8.98	7.67	0.00	82.41	28.48
	17.96	7.43	0.00	81.59	28.25
	26.94	7.35	0.00	81.09	28.21
	35.92	6.99	0.40	81.20	27.88
50	8.98	8.09	0.00	85.32	48.41
	17.96	7.91	0.00	84.70	48.31
	26.94	7.83	0.00	84.12	48.16
	35.92	7.75	0.00	83.64	47.87

The most favorable level of export in terms of the probability of survival and the genetic diversity retention (min. 80.0%) with a satisfactory size of surviving herds was up to 8.98 % for the K = 20 herd and up to 26.94% for the K = 30 and K = 50 herds.

3.3.3. Model III (Adolescent Females)

Regarding K = 20 and K = 30 herds, the annual export of over-number females aged 2–3 years to the level of 32.70% did not threaten sustainability (PE < 5.0%) (Table 11). In herds of K = 50, doubling the coefficient of export of adolescent females to the level of 43.60% also did not pose such a threat. It could be assumed that the export of females aged 2–3 years to the level of 32.70% does not pose a threat to the persistence of larger herds.

Table 11. The impact of variable levels of adolescent female exports on stabilized herds.

			%		
K	**Export Level**	**Stoch-r**	**PE**	**GeneDiv**	**N-Extant**
20	10.90	6.12	0.20	81.89	18.22
	21.80	4.76	2.20	82.27	17.37
	32.70	3.11	4.80	81.53	15.32
	43.60	1.46	14.60	80.21	12.48
30	10.90	6.41	0.00	83.61	28.23
	21.80	4.86	0.00	84.08	27.15
	32.70	3.05	1.20	83.55	24.45
	43.60	1.13	8.80	82.22	18.25
50	10.90	6.76	0.00	86.70	11.76
	21.80	5.13	0.00	86.56	48.34
	32.70	3.29	0.20	86.17	47.43
	43.60	1.31	4.80	85.00	43.48

4. Discussion

The effective population size of a European bison herd minimizing extinction risk was determined as 50 animals [8]. To preserve genetic diversity in free-living herds, it is recommended to import one to three individuals in the range of 6–8 years of age [29]. This corresponds to the principle of bringing in one migrant per generation. The studied ex situ metapopulation was managed by importing an average of three (3.75) individuals during 20 years, so it can be concluded that it guarantees its durability over 100 years. Similarly in Belarus, the translocation of males between free-living micropopulations at least one to two times per generation was conducted [30]. Therefore, each herd should import a minimum of three individuals in a period of 20 years. The Eriksberg and Pszczyna herds (two imported individuals each) and Sababurg (one imported individual) did not meet this criterion. In other herds, the number of imported animals was at least three. For other species from the Bovidae family, in ex situ conditions the breeding male was replaced every two years, and females every three years [31,32].

The average annual export from the studied ex situ metapopulation was 8.81% ± 11.51 and could be analyzed in relation to described free-living populations from Białowieska Forest. In the years 1971–2002 this free-living population was managed with the elimination of 11.0% of individuals per year. In the 1970s this free population export was at 9.6% with a low share of culling (1.1%). Later the share of culling was much higher than export as a result of a new disease (*posthitis*) that impacted the export of males [11]. The proportion of males and females removed from the free-living population as well as ex situ herds did not differ from the 1:1 ratio. Most often, adolescents were eliminated from both populations, but the export of adolescents from the ex situ metapopulation (51.57%) was much higher than from the free-roaming herd (29%). Calves and adult bulls were removed from the free herd with the same intensity (25% each). Adult bulls (19.08%) were intensively exported from the ex situ metapopulation, and calves, unlike in the free herd, were the least frequently exported (11.96%). On the other hand, the export and culling of adult females was the lowest in the free herd (21%). In the ex situ metapopulation, the share of adult cow exports amounted to 17.38%. Karpachev and Prigoryanu [14] calculated the acceptable level of export in the Orłowskie Polesie National Park (Russia) as 11.0%, which is similar to the ex situ population and the free population in Białowieska Forest.

The natural mortality in free-roaming herds in Białowieska Forest in the years 1960–2004 was equal to 2.8% ± 1.3 [11]. Krasińska and Krasiński [11] noticed that the 11.00% reduction level was not sufficient to maintain the population at a constant level in Białowieska Forest. If the above-mentioned mortality rate and the average annual export from the studied ex situ metapopulation (8.81% ± 11.51) are added, the result is of similar value (11.61%). The direct effect of such an export/reduction level is the presence of supernumerary individuals both in some free-living and ex situ herds. Miller et al. [8] calculated that only a fourfold increase in the adult cows' mortality in a K = 250 herd causes a significant decrease in the population size, with the risk of extinction remaining at 0.00%. In 2021, there were 47 free herds of European bison. More than half of them (26 herds) were herds of less than 50 individuals [1]. Only six free-living herds would be numerous enough ($K > 250$) to be managed in the manner proposed by Miller et al. [8]. In our study, the average captive herd size was nearly 25 individuals, which requires an individual management approach with connectivity to other herds. In our study, although export dominated over import, it has been shown that import is crucial for maintaining the sustainability of small herds. Without the imports of individuals, the sustainability of the least-numerous herds (K = 20) is endangered (PE_{20} = 19.00%). Import of two individuals (M/F: 1/1) at 10-year intervals is necessary to maintain at least 80.0% of the initial genetic diversity (GD_{20} = 80.39%, GD_{30} = 83.02%, GD_{50} = 85.55%). In the default settings of VORTEX all imported individuals are unrelated to each other, as well as to animals from the destination herd. In the case of the European bison, this leads to caution in interpreting the results of imports, which is why the simulations included the import of only two individuals (although the average import to the modern herd was calculated as 3.75).

The definition of a surplus individual in an ex situ herd was confirmed as an individual that can be removed from the herd with probability of herd extinction less than 5.0%, and the retention of the genetic diversity above 80.0%. In the smallest herds with regular enrichment, export (adult females: 5.89%, adult males: 8.98%, adolescent females: 32.70%) does not pose a threat to their persistence and the level of retained genetic diversity, and may be temporarily justified in terms of the available capacity of the centers. The mortality rate used in above simulations is based on free-roaming populations Białowieska Forest in the years 1984–1993. It is advisable to analyze the level of export in relation to the mortality observed in captive herds [33].

For adaptive management, various scenarios for solving the problem of overcrowded herds are analyzed [12]. In the IUCN action plans for the European and American bison, one of the methods of solving the problem of over-number animals is culling, under the condition of ensuring the sustainability of populations [10,34]. The American bison conservation strategy includes specific recommendations for this regulation. It was recommended to maintain a balanced proportion of both sexes, with a slight predominance of females because of the higher natural mortality of males. The culling of dominating bulls has been recommended to counteract the loss of valuable alleles of less-represented males [33]. In European countries there are different strategies for managing over-number European bison individuals. According to the strategy for the conservation of the European bison (*Bison bonasus* L.) in Poland, some of the surplus individuals from ex situ herds were exported to the Borecka Forest where decisions were made regarding management (including culling) [35]. In Germany and Sweden, it is possible to eliminate the over-number of European bison in the enclosure. In Poland, this species is protected and permission is required for culling [36,37]. Culling of individuals, even sick ones, is criticized by public opinion in Poland, where the European bison is considered a monumental species [15]. In Belarus, micropopulations have been established for which management strategies including culling have been developed and adaptively changed [30].The search for new sites seems to be a strategy acceptable to all parties involved [1]. Reintroductions and translocations of European bison in recent years serve to expand and connect the currently occupied areas and to create new populations [1], but they are also an example of a rational use of over-number animals from ex situ populations [38]. Considering the complex problem of European bison conservation and identifying new threats, such as the war in Ukraine, the conservation strategy should develop actions at the EU level [6].

5. Conclusions

The import of individuals into European bison herds is crucial to minimize the likelihood of extinction, especially for herds with low numbers. Within herds with capacities of K = 20, K = 30 and K = 50, it is possible to annually designate surplus individuals from one selected age–sex group. In order to maintain the sustainability of the herd, the level of export of surplus individuals should be modified depending on the level and schedule of the import of individuals, as well as the fertility rate of females and mortality rates in the age–sex groups. In the smallest herds with regular enrichment, the export of individuals (adult females: 5.89%; adult males: 8.98%; adolescent females: 32.70%) does not pose a threat to their persistence and the level of retained genetic diversity, and may be temporarily justified in terms of the available capacity of the centers. In the absence of regular imports, it is not advisable to nominate surplus individuals from herds with fewer than 30 individuals.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d15020129/s1, Table S1: Parameters used in simulations in VORTEX 10 software.

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