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Parameters of a founder group and long term viability of a newly created European bison populations

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Abstract: Simulations of the European bison population development were carried out according to scenarios that included various characteristics of a founder group: size (N = 6; 10; 20; 30), age (calves versus sexually mature individuals), and females: males ratio (1:1, 2:1, 4:1). Introduction was simulated as a single event or a series of supplementations. Probability of population extinction, level of heterozygosity and the percentage of alleles retained in the extant populations, as well as the mean population growth rate were analysed at the end of 100-year period of population development. The results led to the following conclusions that may help to keep the level of genetic variability of created populations in the long term as high as possible:

1. The total number of founders should not be lower than 10 individuals; females : males ratio among founders is suggested to be 2:1 or higher. Founders should be selected on the basis of their pedigrees.
2. The new herds should be established in areas with possibly the highest carrying capacity. If the carrying capacity is low, the better solution would be to establish a new herd as a part of a meta-population or release bison in several stages with regular supplementations.
3. Supplementations with females or individuals of both sexes seem to be more favourable for population viability than supplementations with males only.

Key words: *Bison bonasus*, introduction, reintroduction, founder group, genetic variability

Introduction

At the beginning of the 20th century the European bison *Bison bonasus* was extirpated from the wild and only a few individuals survived in captivity. The contemporary world population was founded by only 12 ancestors (Slatis 1960), so the level of inbred is significant. At present, the world bison population is still not large (3810 individuals at the end of 2007, European Bison Pedigree Book 2007). Majority of bison (62%) live in the wild; however, most of free-ranging populations are small. At the end of 2007 half of 33 free and semi-free herds numbered less than 50 bison and only 4 exceeded 100 individuals (European Bison Pedigree Book 2007).

Population size is thought to be the main determinant of its extinction risk. It influences population viability and persistence as it is directly connected with the size of the gene pool. Species with low numbers are more vulnerable to extinction because they are more sensitive to stochastic fluctuations (demographic, genetic and environmental stochasticity). The smaller population, the greater probability that such fluctuations will lead to its extinction. Genetic variability of a population may be assessed as (1) the level of individual homozygosity because many harmful alleles are recessive and reveal only in homozygotes), or (2) the level of allelic polymorphism. Growing inbred may result in inbreeding depression and inability to adapt to changing environmental conditions.

How many individuals are needed to maintain a safe population in the long term? In literature there are some suggestions as to the size of the minimum viable population or effective population size. Minimum viable population is the smallest population size that guarantees its persistence in the wild in a long term. Effective population size means the average number of individuals in a population that actually contribute genes to succeeding generations through breeding (Allaby 2005); the real population size is several times larger. An effective population size of 500 individuals was proposed by Lehmkul (1984) for the long term compared with 50 breeding individuals as the minimum short-term size. Based on the analysis of data for numerous species, Traill et al. (2007) assessed the median of the minimum viable population size to 4169 individuals, and in the case of mammals to 3876. Similar value of 5816 was given by Reed et al. (2003). For the European bison a single population numbering $\geqslant$ 50 individuals was suggested as safe from a demographic point of view; however, while genetic variability is considered the population size should be much larger (Pucek *et al.* 1996).

It is rarely discussed in literature what size and age-sex structure of a founder group would allow to retain a viable population with largest possible genetic variability in the long term, at given population parameters including levels of breeding and mortality, sex ratio at birth, etc. Criteria for population viability and persistence are arbitrary, e.g. a 95% probability of a population persisting for at least 100 years (Boyce 1992) or retaining 95% of initial population heterozygosity for 100 years (Allendorf, Ryman 2002). To minimize the risk of the European bison population extinction caused by a natural catastrophe or a disease lethal for the species (e.g. foot-and-mouth disease – Hławiczka 2005; blue tongue disease – Glunz 2008), it is essential to keep them dispersed on the possibly largest. The aim of the study was to examine how viability of a newly created bison population and level of some genetic parameters were influenced by the size and age-sex structure of a founder group and method of its releasing, i.e. (1) the whole group was released at the same time, or (2) releasing of bison was carried out in several stages by supplementing the created population at regular intervals.

Materials and methods

Simulations of bison population development during 100 years period were carried out using various variants of the size and age-sex structure of a founder group. Population viability analysis (PVA) was conducted with the use of

VORTEX 9.61 programme (Lacy *et al.* 2006). VORTEX is an individual-based simulation model for PVA that helps to understand the influence of various demographic, environmental, and genetic parameters on the dynamics of wildlife populations. Parameters used in simulations are given in table 1. Mortality and reproduction parameters were adopted as mean values of parameters calculated for free-ranging European bison populations from the Polish and Belarusian parts of the Białowieża Forest based on long-term data collected in the years 1970–2005 for the Polish population and in 1981–2005 for the Belarusian one (Daleszczyk, Bunevich, in print). Coefficient of fecundity was the percentage of adult females ($\geqslant$ 4 years old) calving annually. Coefficient of fecundity used in the simulations was similar to those obtained from analyses of development of small bison herds performed by Suchecka (2008). The European bison is a polygynous species and although males become sexually mature at 4 years of age, only males $\geqslant$ 6 years old are assumed to be physically, psychologically and socially capable of breeding (Krasińska, Krasiński 2007). Accordingly, the percentage of adult males participating in breeding was calculated as participation of males $\geqslant$ 6 years old among adult ($\geqslant$4 years old) males based on mortality rates. Inbreeding is supposed to significantly influence the persistence of small bison populations (Pucek *et al.* 1996) so it was included in the models as the number of lethal equivalents. Number of lethal equivalents was taken after Ralls *et al.* (1988) (the median value for 40 species of captive mammals); it was consistent with the number of lethal equivalents assessed for fecundity in free-ranging bison compared to captive ones (2.46; Daleszczyk, Bunevich in print). Parameters used by Pucek *et al.* (1996) in the simulation of the development of European bison population in the Białowieża Forest, based on a period of 10 years (1984–1993), differ from the ones used in the presented study; mortality rates in various age-sex classes and fecundity coefficient were higher in the earlier work (Table 1).

Variants of the founder group size were N = 6, 10, 20, and 30. Variants of the sex ratio among founders (females to males) were 1:1, 2:1, and 4:1, to analyse the importance of the sex of released animals. Variants of the age of founders were calves (individuals one year old) versus adults (sexually mature individuals, i.e. females 3 years old and males 4 years old). In the analyses with supplementations only adults were added to population under analysis to reflect exchange of bison in nature (Bunevich 2004).

The following variants of bison releasing were analysed:

(1) releasing of the whole founder group as a single event;

(2) releasing of a part of a founder group followed by supplementations with one male or female every 5 years or with 3 individuals (3 males, 3 females, or 2 females +1 male = sex ratio of 2:1) every 10 years.

The variants were chosen to compare the effects of more frequent releasing of a smaller number of animals with less frequent releasing of a larger number of individuals. A population was assumed to become extinct when individuals

Table 1. Parameters used in the simulation of bison population development during 100 years conducted with the use of VORTEX software. Standard deviations (SD) are given in parentheses

Parameter	Value used in simulation
Sex ratio at birth [in % of males]	50
Coefficient of fecundity (SD)	39 (8.8)
Mortality of females 0–1 year old [%] (SD)	3.8 (6.9)
Mortality of females 2–3 years old [%] (SD)	2.1 (3.2)
Mortality of females $\geqslant$ 4 years old [%] (SD)	3.2 (1.5)
Mortality of males 0–1 year old [%] (SD)	3.8 (5.3)
Mortality of males 2–3 years old [%] (SD)	3.2 (3.4)
Mortality of males $\geqslant$ 4 years old [%] (SD)	4.4 (3.2)
% of adult males participating in breeding	46
Level of inbreeding depression expressed as a number of lethal equivalents	3.14

of only one sex remained alive. If not stated otherwise, carrying capacity was assumed to 1000 bison not to limit the development of the population under analysis. All stochastic simulations were replicated 500 times to ensure statistical reliability (Brook *et al.* 2000).

Results

The following statistics of simulated populations after 100-year development were analysed: the probability of population extinction (PE), expected heterozygosity remaining in the extant populations, percentage of alleles retained in the extant populations from an original number equal to twice the number of all founders, and mean population growth rate.

Releasing bison with no further supplementation

PE reached almost 20% for founder groups of N = 6, was much lower for N = 10, and for bigger founder groups PE = 0 (Fig. 1). Females : males ratio of 1:1 was the least favourable for the population survival (Fig. 1) as well as for the level of heterozygosity and the percentage of alleles retained within the extant populations (Fig. 2). Mean expected heterozygosity remaining in the extant populations grew with increasing founder group size, while the percentage of alleles retained within the extant populations did not differ among founder groups of various sizes (Fig. 2A, B). There were slight differences in PE, mean population growth rate and genetic parameters

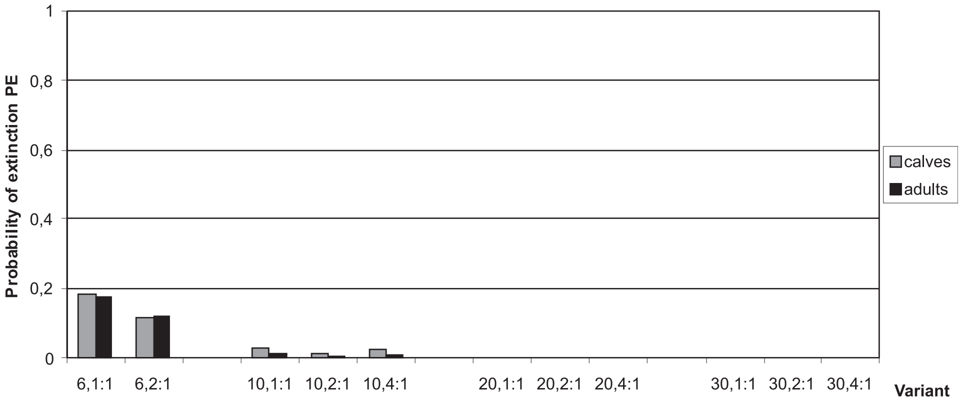


Figure 1. Simulated values of probability of population extinction PE during 100 years in relation to various size and age-sex structure of a founder group. Variants of size: N = 6, 10, 20, 30. Variants of sex ratio (females : males): 1:1, 2:1, 4:1. Variants of age: calves – individuals one year old; adults – sexually mature individuals (females 3 years old and males 4 years old). In the figure variants are described as 'N, sex ratio'

between populations founded by groups consisted of calves versus adults (Fig. 1, 2; Table 2). The mean population growth rate was higher when females: males ratio in a founder group rose (Table 2).

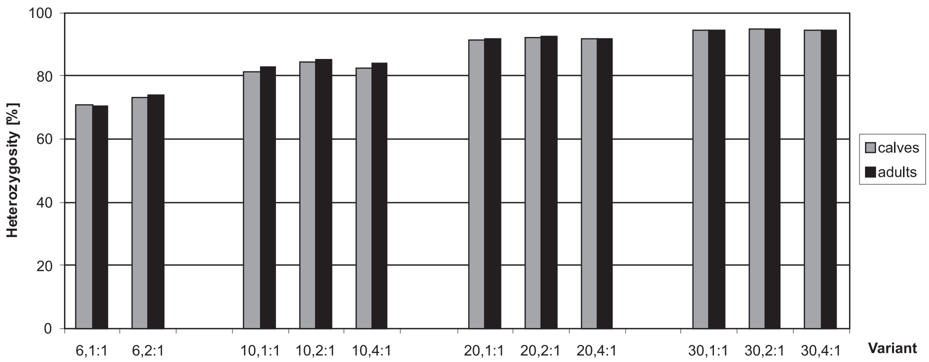
Gradual supplementation of newly created population

More frequent supplementations with fewer individuals and releasing females or females + males seemed to be more favourable variants to retain the highest possible percentage of alleles in the created population during 100 years period (Fig. 3). The relations among studied variants were similar independently of values of fecundity coefficient and percentage of males in the breeding pool used in the simulations (Fig. 3: black bars). PE ranged from 0 to 0.006. The mean population growth rate equalled 0.56 when only males were added and 0.61–0.64 in the case of supplementing populations with females or females + males.

Table 2. Values of the mean population growth rate for various variants of age-sex structure and size of founder groups.

Age	Calves			Adults		
Sex ratio	1:1	2:1	4:1	1:1	2:1	4:1
Size N=6	.037	.040	–	.037	.042	–
N=10	.045	.052	.051	.049	.054	.053
N=20	.055	.059	.061	.056	.061	.062
N=30	.058	.061	.066	.060	.063	.065

(A)



(B)

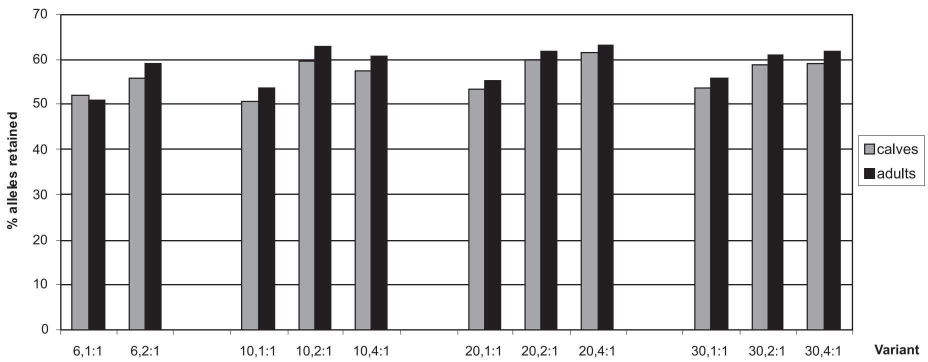


Figure 2. Simulated values of heterozygosity (A) and the percentage of alleles (B) retained in the population for 100 years in relation to various size and age-sex structure of a founder group. Variants as in the caption to figure 1

In the last analysis each population was created from a total of 30 founders with females to males ratio = 2:1 and supplementation was conducted by adding two females and one male every 10 years. The difference was in the size of a group released at the beginning and the duration of supplementation. While comparing the percentage of alleles retained within the extant populations, results differ because of various carrying capacity K used in simulations (Fig. 4). For K = 1000 the percentage of alleles retained grew with the size of the group released at the beginning of population creation, while for K = 200 the trend was opposite and a longer gradual supplementation was more favourable for the percentage of alleles retained (Fig. 4). So carrying capacity was a limiting factor even when the starting group consisted of only 6 bison. For all variants in this analysis PE ranged from 0 to 0.002.

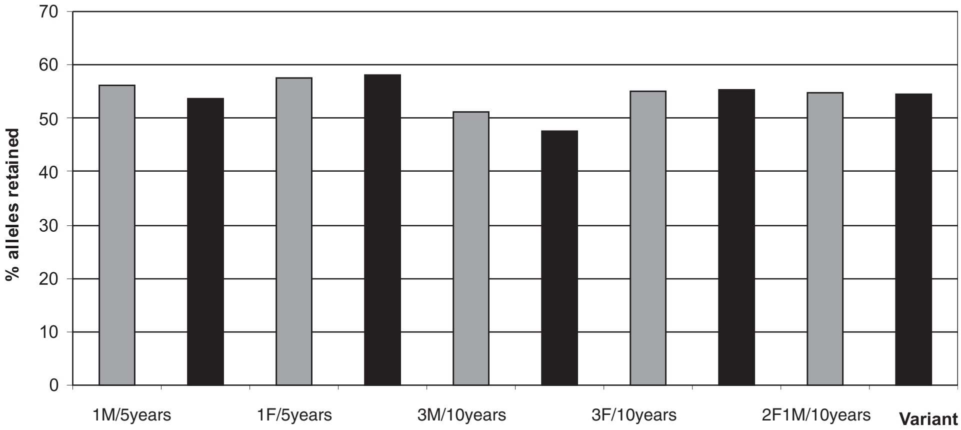


Figure 3. Simulated values of the percentage of alleles retained in the population for 100 years in relation to different variants of supplementation. A group released at the beginning consisted of 10 individuals with females to males ratio = 2:1 and was supplemented with 1 individual – a male (1M) or a female (1F) every 5 years; or with 3 individuals – all males (3M), all females (3F), or two females and a male (2F1M) every 10 years until the total number of founders reached 30. Grey bars represent the analysis with parameters given in table 1. Black bars represent the analysis with changed parameters of reproduction (coefficient of fecundity = 35%; 100% of adult males participating in breeding)

Discussion

In presented study the smallest founder group (N = 6) had a quite considerable probability of extinction. In Poland, in the case of European bison herds originating from small founder groups (in the Knyszyńska Forest the founder group consisted of 3 males and 3 females, and in Zachodniopomorskie province of 4 males and 4 females), their development was much slower than predicted due to high mortality caused by poaching and car accidents (Suchecka, Olech 2004; Suchecka 2008). Such incidents are especially harmful for small populations where loss of every singe individual may impede their development. This confirms that very small founder groups may be often unsuccessful in establishing viable populations if they are not supplemented with new individuals. In the presented simulation with a starting group of 6 bison, supplementations with 3 individuals per 10 years decreased PE to 0.

The next important factor is sex ratio in a founder group. In the simulated development of a bison population based on the given parameters of mortality and reproduction, females to males ratio greater than 1:1 was more favourable for population development and the level of genetic parameters retained. Repeating the analysis with 100% of males participating in breeding did not change the results. In the study on viability of European bison populations from the Polish and Belarusian parts of the Białowieża Forest, the probability of population survival decreased rapidly when the coefficient of fecundity

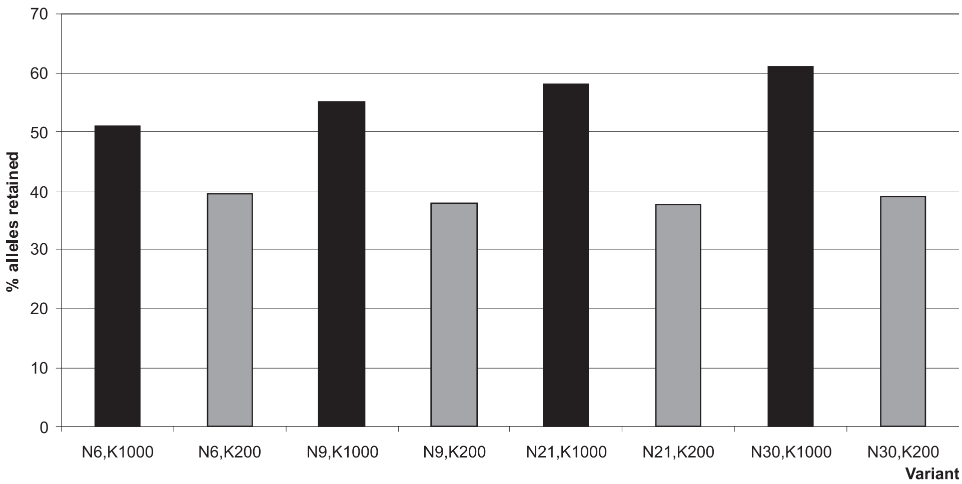


Figure 4. Simulated values of the percentage of alleles retained in the population for 100 years in relation to different variants of supplementation and two sizes of carrying capacity (K = 1000 – black bars, and K = 200 – grey bars). A group released at the beginning consisted of N = 6; 9; 21 individuals and was supplemented with 3 individuals every 10 years until the total number of founders reached 30. The last two bars present results for releasing of 30 individuals as a single event with no further supplementation. In all groups and among supplemented individuals females to males ratio = 2:1. In the figure variants are described as 'N released at the beginning, K carrying capacity'

declined below 30%, but was little affected by decrease in the percentage of males participating in breeding (Daleszczyk, Bunevich in print). Species of larger body size seem to be more vulnerable to extinction risk than smaller species. When body size and phylogeny were controlled for, litter size was found to be a significant predictor of extinction risk probably because larger litters contribute to fast population growth (Cardillo 2003). In the European bison giving birth to one calf is a rule so it is just the level of females' fecundity that forms an important factor influencing population survival. More females in a founder group ensure a faster population growth which is especially important in the earliest period of population development (Pucek *et al.* 1996). Moreover, when a greater number of males is included in a founder group, not all of them will participate in breeding and contribute their genes to next generations because of polygynic system of bison reproduction and competition among males during the rutting season which allows only the most dominant males to take part in breeding (Krasińska, Krasiński 2007). So in a founder group sex ratio 1:1 does not seem to be the optimal solution.

To prevent the loss of genetic variability in the meta-population of bison in Ukraine, Perzanowski *et al.* (2004) suggested an exchange of 1–3 individuals per 6–8 years between herds. There were no suggestions as to the sex of those animals. In a polygynic species a single male may sire a considerable number of offspring but he may also not sire any offspring at all, and then the expected aim of supplementation is not achieved. Females have only one calf per parturition but their participation in reproduction is more certain than that of males. Paszkiewicz (2007) analysed supplementation of the European bison population in the Bieszczady Mountains with 7 (4, 3) individuals. He underlines that bison females integrated into the existing population faster than males and that for some males such integration may be impossible which will result in no genes left. The best solution may be to add individuals of both sexes.

Pucek *et al.* (1996) found that releasing younger, not sexually mature individuals had only a slightly negative effect compared to adults; in the presented study results were similar. Younger animals may adapt to new conditions more easily than older ones but their mortality rates before achieving sexual maturity should be taken into consideration. Furthermore, in a social species like the European bison, presence of one or two adult females in a founder group consisted of calves or subadults would help to establish a natural hierarchy and provide the group with a leader.

Minimum viable population size should be assessed while considering characteristics of a given population and its environment; there is not one 'golden' value which guarantees persistence of different animal populations (Thomas 1990). The size of a founder group alone does not ensure the success of a new population (Lehmkuhl 1984) because the level of genetic variability retained in the population is connected with possibilities of its growth and development which are limited by the carrying capacity in the given area. Based on the analysis of polymorphic microsatellite markers, the effective population size of the bison population living in the Polish part of the Białowieża Forest in 1955–2005 was assessed to range from 7.9 to 28.4 what made less than 1/3 of the total numbers of the population (Tokarska *et al.* 2009). Because of genetic similarity of all European bison due to a small number of the founders (only seven individuals founded the Lowland line that lives in the Białowieża Forest) this value could be underestimated. According to analysis conducted by Frankham (1995) based on 192 estimates from 102 species, a comprehensive ratio of effective to actual population size (Ne/N) is of the order of 0.1. For the American bison the Ne/N ratio was assessed to about 0.07–0.3 (review in Frankham 1995). Effective population size of a demographically safe European bison population proposed by Pucek *et al.* (1996) was 50 individuals, so a total population size should be about 500 bison. However, free-ranging European bison live in populations which are usually much smaller and in addition isolated from each other. This forms a significant threat for the persistence of such herds and of the contemporary bison population in general. One of the solutions is creating meta-populations consisted of spatially separated populations which exchange individuals. Thanks to exchange of genes even smaller herds may be demographically safe.

Such a meta-population is being created for example in the Carpathian region (Olech, Perzanowski 2002). Establishing meta-populations seems to be the most valuable and most realistic management option to preserve maximum genetic variability in free-living bison. So it would be desirable that newly formed herds were located in areas providing contact with the already existing bison populations.

European bison are highly inbred (inbreeding coefficient = 0.48 for Lowland bison of known pedigrees, Olech 2003) and inbreeding may significantly affect viability of the population. To ensure the lowest possible inbreeding level among founders, it is essential to choose bison for releasing based on their pedigrees. Olech (2003) found that inbreeding did not influence calves' survival in the Lowland line of European bison while in the Lowland-Caucasian line the influence was significantly negative. In presented simulations founders were not related so the results do not fully reflect the development of bison population and may be overoptimistic. However, it was recommended to use relative and not absolute values of the PVA estimates to choose the best management option for a given population (McCarthy *et al.* 2003).

Conclusions

To keep the level of genetic variability of newly created populations as high as possible, the following rules are proposed:

1. The total number of founders should not be less than 10 individuals, and females : males ratio in the founder group is suggested to be 2:1 or higher. Founders should be chosen based on their pedigrees.
2. The new herds should be established in areas with the possibly highest carrying capacity. If the carrying capacity is small, the better solution would be to establish a new herd as a part of a meta-population or release bison in several stages with regular supplementations.
3. Supplementations with females or individuals of both sexes seem to be more favourable for population viability than supplementations with males only.

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Parametry grupy założycielskiej a żywotność tworzonej populacji żubra w długim okresie

Streszczenie: Symulowano rozwój populacji żubra w oparciu o scenariusze różniące się takimi parametrami grupy założycieli jak wielkość (N = 6; 10; 20; 30), wiek osobników w grupie (cielęta lub osobniki dojrzałe płciowo), oraz stosunek liczby samic do liczby samców (1:1, 2:1, 4:1). Żubry albo były wypuszczane jednorazowo, bez dalszych uzupełnień, albo tworzona populacja była regularnie uzupełniana kolejnymi osobnikami. Po 100 latach rozwoju populacji analizowano ryzyko jej wymarcia, poziom heteryzygotyczności i procent alleli pozostałych w populacji, a także średnie tempo wzrostu populacji. W oparciu o uzyskane wyniki zaproponowano następujące zasady, które mogą pomóc w utrzymaniu możliwie wysokiego poziomu zmienności genetycznej tworzonych populacji w długim okresie:

1. Całkowita liczba założycieli nie powinna być niższa od 10. Sugerowany stosunek samic do samców w grupie założycielskiej to 2:1 lub wyższy. Założyciele powinni być dobieraniu w oparciu o ich rodowody.

2. Nowe populacje winny być tworzone na obszarach o możliwie wysokiej pojemności środowiska. Gdy jest to niemożliwe, lepszym rozwiązaniem byłoby utworzenie nowego stada jako części metapopulacji lub też wypuszczanie żubrów nie jednorazowo, a z uzupełnieniami.

3. Uzupełnianie populacji samicami lub osobnikami obu płci wydaje się być bardziej korzystne dla żywotności populacji niż uzupełnianie stada samymi samcami.