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Twenty years of the European bison Lowland line *Bison bonasus bonasus* conservation in captivity

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Abstract: Twenty years of the Lowland European bison Lowland line Bison bonasus bonasus conservation in captivity. The aim of the work was to track back changes taking place in the Lowland European bison population kept in captivity in years 1995-2015. The material for the study was data from European Bison Pedigree Book, collected from the years 1924-2015. The parameters such as inbreeding coefficient, kinship coefficient, contribution of founder genes and completeness of pedigree information were analyzed as well as the demographic structure of the population. Over the past 20 years, a steady increase in the population size has been observed. The share of different countries in Lowland wisent breeding also changed. The study showed that the accuracy of pedigree information decreased significantly between 1995 and 2015. In 1995 169 from 342 animals living in captivity had full pedigree information. In 2005 it was 76 from 320 animals. Within the population being alive in 2015, only 62 form 577 (10%) of all animals from Lowland line have full pedigree information, that leads to the founders of the population. An increase in the average values of inbreeding coefficient in the population and mean kinship was also observed.

Key words: European bison, *Bison bonasus bonasus*, population genetics, captive breeding

INTRODUCTION

Efforts to rescue the European bison *Bison bonasus* from extinction began on 2 June 1923 with the speech of Jan

Sztolcman at the International Congress of Nature Conservation in Paris, and are continued to this day. Throughout all these years the work of many experts contributed to rebuilding the captive population and restoration of the European bison to the nature.

After the extinction in the wild at the begging of the 20th century, the European bison Bison bonasus population was saved from absolute extinction with only 54 individuals which survived in captivity. Later analyses have shown that only 17 actual founders of currently living population remained, representing 12 unique genotypes (Olech 2009). Only 7 from those 12 ancestors are the founders of the Lowland line. With so few animals in the breeding stock it was impossible to avoid mating related individuals. This caused the largest danger for the population – the loss of genetic diversity.

Maintaining genetic diversity is the biggest concern considering many endangered species. The loss of genetic diversity is directly associated with the mating of relatives. As many studies have already shown, the increase of inbreeding and subsequent probability of occurrence of inbreeding depression adversely affect the survival chances of the population. Inbreeding depression is manifested, i.a, by the decrease in reproductive success and the deterioration of the overall fitness of individuals. In the longer term, it also has a negative impact on the response of the population to environmental changes (Ralls et al. 1979, Frankham et al. 2002, Reed and Frankham 2003).

European bison population continuously increases its population size. In 2016, the world population, including representatives of both breeding lines Lowland (LB) and Lowland-Caucasian (LC) in captive, semi-free and free ranging herds, reached 6,573 individuals. Free ranging herds counted 4,472 individuals, of which 2,793 were representatives of the Lowland line. Among the animals living in captivity prevail representatives of LC. Among 1706 European bison there are 1,234 animals from Lowland--Caucasian line (Raczyński 2016). The conservation strategy for the European bison from 2007, formulated goals for further conservation of the species. One of those goals is the preservation of genetic variability within the Lowland line. Actions to be taken include: evaluating of the genetic value of the individuals and planning mattings based on this information, as well as international exchange of individuals between herds. The basis for the success of these plans is good cooperation between the breeders and the coordinator. All captive herds should be treated as one population.

The aim of the study was to investigate the demographic and genetic changes within the captive population of European bison *Bison bonasus bonasus* Lowland line, over the last 20 years.

MATERIAL AND METHODS

The basis for the analysis was the pedigree data on the Lowland line population. The data obtained from the European Bison Pedigree Book from the years 1924–2015, concerned 3,215 individuals. Genetic analysis of the population was done using the Endog program (Gutiérrez et al. 2010). The average inbreeding coefficient, percentage of completion pedigree and kinship coefficient were calculated. Inbreeding coefficient reflects the probability that an individual has two identical alleles by descent. It is computed according to Meuwissen and Luo (1992). The kinship of two individuals reveals the probability that two alleles taken at random, one from each, will be identical by descent. Kinship (coancestry) of two individuals indicates the inbreeding of their offspring. The mean kinship coefficient for an individual is the average of kinship values for that individual with every individual in the population, including itself. Mean kinship value for the whole population was calculated as an average of mean kinship coefficient for all individuals in the population (Frankham et al. 2002) and it informs how closely are related animals in the population. The percentage of completion pedigree was calculated as a sum of the share of founders genes in the pedigree of each individual. If such sum is equal to one, it means that the individual has full pedigree information. The share of founder genes is calculated on the basis of pedigree data. Each descendant obtains 50% of the founders alleles from sire and 50% from dam and such proportion continues

through all generations. In the study compared were the above-mentioned parameters in populations of years 1995, 2005 and 2015. Only individuals with full pedigree information (leading to the founders) were included in the estimation of the chosen parameters. In 1995 there were 169 animals, in 2005, 76 and in 2015 only 62 such animals. The demographic analysis concerned all individuals living in years: 1995 (342 individuals), 2005 (320 individuals) and 2015 (581 individuals), according to the European Bison Pedigree Book. Changes in the structure of captive herds and the participation of different countries in wisents breeding were also analysed.

RESULTS AND DISCUSSION

Demography

The length of animal's life depends on many factors, usually in captivity it is longer than in the wild. Female bison only exceptionally live longer than 25 years, and males longer than 20 (Krasińska and Krasiński 2004). Period of reproductive activity of females usually starts at age of three years, so the first calf is born in the fourth year of life. Females often give birth until the old age. Males reach maturity around the third year of life. However in the wild, because of competition with dominant bulls, they become reproductively active later, when they are about 7 years old. In captivity, the beginning of mating depends on the breeder decision. Spermatogenesis usually disappears after 12th year of life (Krasińska and Krasiński 2004, Olech 2008, Olech and Perzanowski 2014).

The percentage of males (between 3 and 12 years old) and females (older than 3 years) being in reproductive age, was similar in populations living in years 2005, and 2015. Higher proportion of animals that could reproduce was observed in the year 1995. There were 68.8% of such females in 1995, 63.72% in 2005 and 65.92% in 2015. For males, there were 57.25, 46.55 and 47% of all males in 1995, 2005, and 2015 respectively.

Sex ratio (number of females to number of males, in reproductive age) were 2.23 : 1 in 1995, 2.60 : 1 in 2005 and 2.50 : 1 in 2015. The proportion of the young (animals younger than three years) in the population was: 31.00% in 1995, 38.44% in 2005 and 38.05% in 2015. Sex ratio in this group of animals was: 1.5 : 1 in 1995; 1.3 : 1 in 2005, and 1.1 : 1 in 2015 (Fig. 1).

Over the whole analysed period of 20 years, from 1995 to 2015, observed was a general increase in the size of captive European bison population. However initially, between the years 1995-2005 there was a slight decrease of this population. In 1995 registered were 342 animals, in 2005 - 320, and in 2015 the population reached 578 individuals. Unfortunately during that time, there was a decrease of the pedigree information accuracy. This is an effect of introduction of individuals from the wild, with unknown pedigree, into the captive herds. This resulted in reduction of the proportion of individuals with a well-known pedigree. Moreover, only full pedigree information (from founders to the individual) allows for sufficiently accurate estimation of the inbreeding coefficient and coancestry between individuals in the population.





In analysed years the percentage of individuals with full-known pedigree was respectively equal to: 49.42, 29.79 and 10.55% (Fig. 2).

The proportion of individuals in freeranging herds and in the captive herds kept changing over the years. Some of the animals remained in the captive herds only for some time and then they were transferred to semi-free or free-ranging herds in various countries. In 1995, from the free-ranging herd of Białowieska Primeval Forest, introduced into captive breeding were only 19 individuals. In 2005, 22 animals were transferred to the captive population, and in 2015 - 38 animals. The largest number, 53 individuals from free-ranging herds, were introduced to the captive population in 2007. Descendants of these animals have either none or very incomplete pedigree information. That causes the overall decrease in the accuracy of the pedigree data.

We know exactly which animals were the founders of the free-ranging herd of Białowieska Primeval Forest: 20 females and 10 males (Grzegrzółka et al. 2004). Basing upon this information, we can supplement with a certain degree of probability the pedigree data for individuals transferred to the captive population. This may significantly improve the level of pedigree knowledge on captive individuals, but since it still would be only a simulation, chosen parameters calculated in this way may be not precise.

According to Olech and Perzanowski (2016) between 2000 and 2015, the number of herds (both Lowland and Lowland-Caucasian line) increased by 50%. The number of semi-free herds grew up, and the number of herds where both genetic lines were kept simultaneously, was reduced. Such trend is positive because it helps to avoid introducing the genetic material of the Lowland line



FIGURE 2. The number of all individuals belonging to the Lowland line (including Pszczyna line) of the captive part of European bison population, and individuals with full pedigree information in the years from 1995 to 2015

to the Lowland-Caucasian line. It is also optimistic that during these years the percentage of the smallest herds (up to 5 individuals) decreased, and the percentage of large herds - over 20 individuals, increased. Our analysis shown that animals belonging to Lowland line are a minority among all captive wisents - only 27.67% by the end of 2016. Currently the Polish population represents a significant part of all LB bison, and is undoubtedly the largest population of this line living in one country. Over the years, the number of countries other than Poland, which took part in Lowland line breeding, has grown steadily (Fig. 3). In 1995 (Raczyński 1995–2016) the animals of the Lowland line were kept in 11 countries apart from Poland, but only 9 out of 29 (31%) of foreign herds kept only wisents of LB line. Most of the foreign herds consisted of LC animals with only single LC individuals. In time those proportions have changed. For example, the German herd in Nürnberg in 1995 had 6 wisents, of which only 2 were representatives of the Lowland line. In 2005, there were 4 wisents, all from Lowland line. In 2015 there were already 8 animals also only from the Lowland line. Also, the herd in Springe (Germany) in 1995 consisted of 6 animals from Lowland line and 24 animals from Lowland-Caucasian line. In 2005 there were 29 LC animals, and in 2015 two separate herds with both LB (13 animals) and LC (19 animals) lines. In 1995 Polish population was 53% of all animals living in captivity. There were 18 captive herds in Poland. In 2005, 16 countries besides Poland bred Lowland line. Only 13 out



FIGURE 3. Distribution of captive European bison of Lowland line in 1995 and 2015 among European countries

of 35 (37%) breeding centers maintained only the LB animals. In Poland, there were 17 herds which members accounted to 53% of all LB wisents kept in captivity. In 2015, wisents of the Lowland line were maintained in 15 countries, including Poland. Foreign herds with only Lowland line wisents represented 75% of all herds. The Polish population in 2015 accounted for 36% of all captive LB animals. We can observe a positive change in the development of foreign breeding places, and a decrease of herds where both breeding lines remain mixed. Some of the herds has changed their status from captive to free or semi-free ranging. For example, the herd in Cherga (Russia) in 1995 was regarded as a captive one but in 2015 it became a semi-free herd, because it was not possible to obtain the pedigree data for such large group of animals with uncontrolled mating.

Pedigree analysis

There is a significant difference in the inbreeding coefficient between individuals living in 1995, 2005 and 2015. Over the 20 years of this population history, there is a significant increase in the average value of inbreeding coefficient among the individuals with full pedigree information living in subsequent years. Significant increase of coancestry among individuals in the population are also observed (Table 1) and decrease in completeness of pedigree data (Table 2). In 1995 average inbreeding coefficient equalled to 0.4299 (computed for 169 individuals with full pedigree information, including 26 from Pszczyna line). In 10 years it has grown to 0.4869 (computed for 76 individuals with full pedigree information, including 15 from Pszczyna line). Between years 2005–2015 this was

Item		1995			2005			2015			
Number of individuals		169			76			62			
Statistics		\overline{x}	SD	domi- nant	\overline{x}	SD	domi- nant	\overline{x}	SD	domi- nant	
Mean kinship		0.3816	0.098	0.3225	0.4201	0.0568	0.486	0.5318	0.0923	0.5849	
Inbreeding coefficient		0.4299	0.1024	0.5209	0.4869	0.1139	0.3517	0.5704	0.103	0.6034	
Contri- bution of founders genes	45	0.5707	0.0979	0.6953	0.5826	0.1087	0.6836	0.6478	0.0902	0.6948	
	42	0.3007	0.0261	0.3047	0.2919	0.0192	0.3047	0.2997	0.0136	0.3047	
	87	0.0278	0.0242	0	0.0205	0.0211	0	0.0084	0.0163	0	
	89	0.0278	0.0242	0	0.0205	0.0211	0	0.0084	0.0163	0	
	15	0.0182	0.0205	0	0.0211	0.0216	0	0.0089	0.0176	0	
	16	0.0365	0.0409	0	0.0422	0.0431	0	0.0178	0.0353	0	
	147	0.0182	0.0205	0	0.0211	0.0216	0	0.0089	0.0176	0	

TABLE 1. Changes of analysed parameters in years 1995, 2005 and 2015 in Lowland line of captive *E. bison* population, determined for animals with full pedigree information, including Pszczyna line

Parameters were calculated for individuals being alive in analysed years.

Item	1995	2005	2015
Number of individuals (M, F)	342 (124, 218)	320 (116, 204)	577 (215, 362)
Average percentage of known pedigree	67.43	61.65	57.31
Number of individuals with known 100% of pedigree (% of the population)	169 (49.42)	76 (23.75)	62 (10.75)

TABLE 2. Changes in population size and completeness of pedigree data in years 1995, 2005 and 2015 in the captive part of the Lowland line of European bison

an increase of 0.0835, from 0.4869 in 2005 to 0.5704 in 2015 (only 62 animals with full pedigree information, including 32 from Pszczyna line). Therefore, in the past 20 years (1995–2015), the average value of inbreeding coefficient increased by 0.1405 (32.68%). Data given in Table 1 represent relatively high standard deviation. Although these values apply to individuals with full pedigree information from Lowland line (including Pszczyna line), living in analysed years, some of those animals could be included in the analyses more than once.

Contribution of the seven founders to the contemporary genetic pool of European bison was never equal. The most represented in the population are genes of the male 45 PLEBEJER and female 42 PLANTA. This dominance has been already proved in many papers (Olech 2003, Krasińska and Krasiński 2004, Tokarska 2010). Equally represented in the population are genes of the founders 15 BEGRÜNDER and 147 BIS-MARCK. The 87 BILL and 89 BILMA have the same, the lowest representation in the gene pool. Over the years 1995-2015 the share of male 45 PLEBE-JER increased while the share of genes 42 PLANTA, 87 BILL and 89 BILMA decreased. The representation of individuals 15 BEGRÜNDER, 16 PLAVIA and 147 BISMARCK increased by year 2005, but decreased again in 2015 (Table 1). Genes of these three founders were transferred only by female 524 BESTE (Krasiński 1994), which inherited 25% genes from male 15, 50% from female 16 and 25% from male 147. That is why males 15 and 147 have always the same representation in the population and female 16 is represented twice stronger.

All individuals living in analysed years were included in Table 2.

A large part of individuals with full pedigree information in the 2015 population (51.61%), were representatives of the Pszczyna line. It is a highly inbred line separate within the Lowland line. It derives only from two founders, male 45 PLEBEJER and female 42 PLANTA. For many years, the herd in Pszczyna was isolated and today it becomes an interesting research object (Krasińska and Krasiński 2004, Pigan and Wójtowicz 2015). Such high proportion of representatives of this herd among a captive part of the Lowland line could result in a serious bias in the calculation of the level of inbreeding coefficient. Estimation of average inbreeding performed for the entire Lowland line, including wisents from Pszczyna, does not reflect the true increase of inbreeding in the remaining part of the population, that is managed to minimize the rate of inbreeding.

Generally in subsequent years, the number of wisents with 100% known pedigree declines (Table 3). Average value of inbreeding coefficient among the individuals from Pszczyna line is higher than for the whole Lowland line (Fig. 4). However among animals from Pszczyna line, changes in the inbreeding coefficient over the last 20 years are lower and remain within the range from 0.55 to 0.63. During the same time, the average value of inbreeding coefficient,

TABLE 3. Individuals with full pedigree information for which the average inbreeding coefficient was calculated in 1995-2015

Line	1995	1997	1999	2001	2003	2005	2007	2009	2011	2013	2015
Lowland	143	107	102	95	77	61	52	47	47	40	30
Pszczyna	26	24	16	8	12	15	17	24	24	27	32



FIGURE 4. A comparison of average values of inbreeding coefficient among wisents belonging to Lowland line living between 1995 and 2016

among the individuals from Lowland line, ranged between 0.41 and 0.51. The highest and constant increase of inbreeding was observed between the years 2007–2013. The value of inbreeding coefficient has grown then from 0.45 in 2007 to 0.5 in 2013. All individuals from Lowland line born in this period of time, with full pedigree information, were offspring of the male 9368 PLISZAJ (Pszczyna line) and five females from Lowland line. Coancestry between these animals is high (from 0.6016 with female 8714 PODPINIA: to 0.6628 with female 9148 POTOWA), and that is why the average inbreeding coefficient was growing so quickly. In these years, the male 9997 PLAWAN born in Pszczyna in 2003, with full pedigree information, could be used for reproduction. Coancestry coefficients between him and five, already mentioned, females were lower (0.5864 with female 8714 PODPINIA; 0.6231 with female 9367 POLUCJA) than between these females and male 9368 PLISZAJ. However the male 9997 PLAWAN, died in 2012 in Karolew, leaving no offspring. Six individuals born between 2013--2015 (five born in Pszczyna and one in Jabłonowo) are the offspring of the male 11053 PLUDAR and five other females. Coancestry between these animals is lower than in previously described matings. It is coefficient takes values from 0.5669 (with female 8714 PODPINIA) to 0.5948 (with female 11771 POTYNKA).

CONCLUSIONS

An increase of inbreeding in a small population that has gone through a very radical reduction in numbers is unavoidable. An importance of preservation of genetic variability is raised almost in every study on European bison conservation (Strategy 2007, Olech 2008, Perzanowski 2016). Therefore every European bison herd should actively participate in the exchange of individuals. In the years 1995–2015, there is a positive change in the structure of *E. bison* herds of the Lowland line. There are more of large herds (more than 5 individuals). Also the number of such herds outside of Poland has increased. Exchange of animals among breeding centers in various countries can be observed. Individuals suitable for further breeding should be selected on the basis of their inbreeding coefficient, and more importantly - the mean kinship value. However the correct estimation of these parameters is possible only on the basis of complete pedigree information leading to founders of contemporary population (Olech 2008). The observed decrease in pedigree completeness may be an impediment to the use of these criteria for the selection of genetically valuable individuals. If individuals with gaps in pedigree information are considered for further breeding, it should be remembered that the parameters calculated on the basis of incomplete pedigree are underestimated. Therefore the only solution in such cases remain methods based on molecular genetics.

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Streszczenie: Dwadzieścia lat ochrony linii nizinnej żubra Bison bonasus bonasus w niewoli. Celem pracy było prześledzenie zmian zachodzących w populacji żubrów linii nizinnej utrzymywanych w niewoli w latach 1995-2015. Materiał do badania stanowiły dane z ksiegi rodowodowej żubrów zebrane z lat 1924-2015. Analizie podlegały takie parametry, jak: współczynnik pokrewieństwa, współczynnik kinship, udział genów założycieli oraz kompletność informacji rodowodowej. Analizie podlegała także struktura demograficzna populacji. W ciągu ostatnich 20 lat obserwowany jest stały wzrost liczebności populacji. Zmienił się także udział poszczególnych krajów w hodowli żubrów linii nizinnej. Wykazano, że w latach 1995-2015 znacząco spadła dokładność informacji rodowodowej. W 1995 roku 169 z 342 zwierząt utrzymywanych w niewoli miało pełną informację rodowodową. W 2005 roku było to już jedynie 76 z 320 zwierząt. W populacji żyjącej w 2015 roku jedynie 62 z 577 (10%) zwierzat miało pełna informację rodowodową, taką która prowadzi do założycieli populacji. Obserwowany jest także wzrost średniego współczynnika inbredu i średniej pokrewieństwa w populacji.

Slowa kluczowe: żubr, Bison bonasus bonasus, genetyka populacji, hodowla w niewoli

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