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Pedigree Structure of American Bison (*Bison bison*) Population

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ABSTRACT

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An effective realization of breeding programs in zoos is strongly determined by completeness of animal pedigree information. The knowledge of pedigree structure allows to maintain optimal genetic variability of a given population. The aim of this study was to estimate the parameters describing the pedigree structure of American bison housed in zoos in the context of further management of the population. Finally, 4269 American bison were analysed (1883 males, 2217 females, and 169 with unknown sex). The registered animals were born between years 1874 and 2013. The following pedigree parameters were estimated: number of fully traced generations, number of complete generations equivalent, index of pedigree completeness, individual inbreeding coefficients, increase of inbreeding for each individual, effective population size, and genetic diversity. The maximum number of fully traced generations was 3 (the mean value is 0.693). The mean inbreeding coefficient for the population studied was 3.26%, whereas individual increase in inbreeding ranged from 0 to 25.12%. Although the pedigree parameters (including the inbreeding level) in the American bison obtained in the present study seem to be acceptable (from the perspective of other wild animal populations), they can be over/underestimated due to incomplete pedigree.

Keywords: relatedness coefficient; captive breeding; genetic diversity; inbreeding

In contrast to a majority of livestock species, wild captive animal populations are usually small. It is connected with an undesirable genetic structure of the populations and reduction of genetic diversity. Consequences of the gene pool reduction have been discussed by a number of authors (Sternicki et al. 2003; Graczyk et al. 2015a). One of the main consequences is an increase of homozygosity affecting inbreeding depression, mainly for fitness and related traits. Parameters describing the genetic structure are useful tools in conservative

breeding programs for both livestock and wild animal populations.

As already mentioned, knowledge on the genetic structure is especially important for species endangered by extinction when the pool of unrelated individuals is dramatically decreased. An inglorious example of how fast and rapidly this can happen is the history of the American bison.

Over the last centuries the size of the American bison population has been strongly reduced – from tens of millions to a few hundred by the mid-

1880s (Isenberg 2000). After this demographic crash, several small bison herds survived in North America and as a consequence of this fact – nearly all bison that exist today are the descendants of less than 100 individuals which were used to found 5 private herds and a remnant wild population in Yellowstone National Park (YNP) of approximately 30 bison (Heck 1968). Moreover, according to Heck (1968), at the end of the 19th century 256 bison were kept in zoos around the world.

Nowadays, American bison live in federal or commercial herds and the number of individuals exceeds half a million (Freese et al. 2007). Numerous efforts (Halbert 2003; Halbert et al. 2005; Ranglack et al. 2015) have been made to investigate the genetic structure of the population and its changes over time.

Over the last decades, zoos have been perceived as the main places for *ex-situ* conservation of wild animal species. It should be recalled that some populations (e.g. David's deer, Przewalski horse) were rebuilt due to breeding programs implemented in zoological gardens (Sternicki et al. 2003; Wolc et al. 2008).

The bison population housed in zoos is quite different compared to the wild one. The individuals kept in zoos played a very important role in restoring the American bison. According to Heck (1968), in October 1907, six male and nine female bison were transferred from Bronx Zoo

in New York to Wichita in Oklahoma for further breeding in their natural environment. The first American bison in European zoos appeared in the 16th century. Over hundreds of years, until the end of the First World War, the bison from European breeding were not crossed with individuals from North America (Heck 1968).

The demographic slump of the population can bring about some unfavourable effects in genetic structure parameters, for instance a reduction of genetic diversity and increase of inbreeding rate. Furthermore, considerable gaps in pedigree completeness were registered for wild animals. To our knowledge, in the literature there are no results of the complex pedigree analysis of American bison kept in zoological gardens.

The aim of this study was to estimate the parameters describing the pedigree structure of the American bison housed in zoos in the context of further management of the population.

MATERIAL AND METHODS

The pedigree data were extracted from Species360 base (<https://www.species360.org>). Prior to main analysis, the data were edited for detailed verification. Incomplete and repeated records were removed. Finally, 4269 American bison were analysed (1883 males, 2217 females, and 169 with

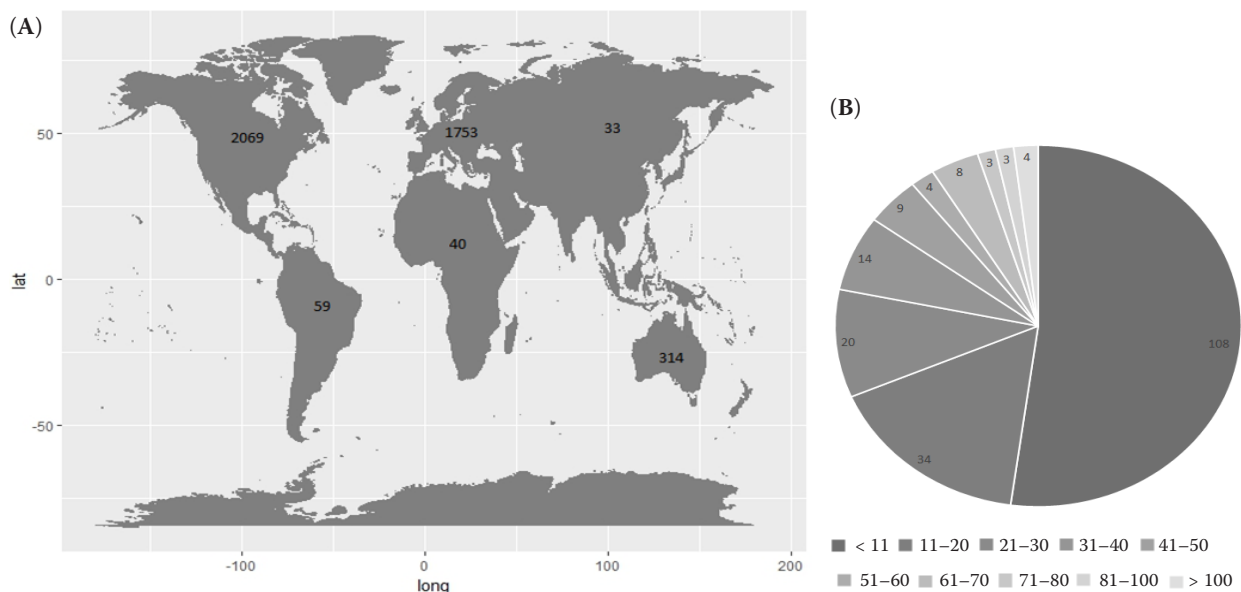


Figure 1. (A) Number of bison recorded in the database via world's regions, (B) distribution of the numbers of zoological gardens depending on the number of bison recorded

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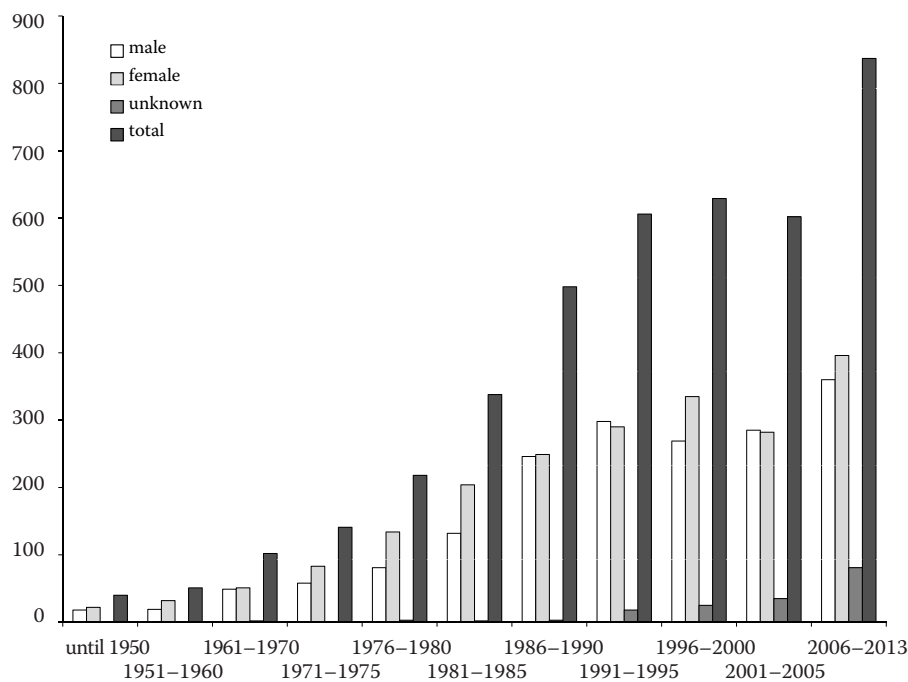


Figure 2. Numbers of recorded bison born in consecutive years

unknown sex). The registered animals were born between years 1874 and 2013 and information about birth year was available for 4062 bison. 3946 individuals were born in captivity, 24 were wild born, and for others the birth type was unknown. The recorded animals were housed in 207 zoos around the world. The numbers of recorded individuals depending on six continents are presented in Figure 1A. For one individual the name of zoo was impossible to establish, so the sum of the numbers printed on the map is 4268. The distribution of number of zoos depending on the number of bison housed is presented in Figure 1B. In more than half of the recorded zoos the number of bison did not exceed 10 and only 22 gardens bred more than 50 bison during the analysed time period. The distribution of the number of individuals in consecutive years of birth is presented in Figure 2.

Pedigree completeness. The following parameters were calculated (according to Gutierrez and Goyache 2005): number of fully traced generations, maximum number of generations traced, and equivalent complete generations. The number of fully traced generations is defined as the number of generations separating an individual from the generation with both known ancestors of this individual. Ancestors with unknown parents are considered as founders and the founders are assumed to be unrelated. The maximum number of generations traced is defined as the number

of generations separating an individual from its furthest ancestor. The equivalent complete generations (t) is computed as the sum over all known ancestors of the terms computed as the sum of $(1/2)^n$, where n is the number of generations separating the individual from each known ancestor (Maignel et al. 1996).

Moreover, MacCluer et al.'s (1983) index of pedigree completeness (PCI) was computed, which describes the frequency of the contribution of a given ancestor in the pedigree to the 5th parental generation. This index is given by the formula:

$$id = \frac{2id_{sire}id_{dam}}{id_{sire} + id_{dam}}$$

where:

id_{sire} = index for paternal contributions

id_{dam} = index for maternal contributions

and:

$$id_* = \frac{1}{d} \sum_{i=1}^d a_i$$

where:

* = sire or dam

a_i = percentage of ancestors known in generation i

d = number of generations traced back in the pedigree.

Pedigree analysis. The individual inbreeding coefficient (F_i) was computed using the modified algorithm developed by Colleau (2002). The

increase of inbreeding for each individual (ΔF_i) was estimated following the approach proposed by Gonzalez-Recio et al. (2007) as:

$$\Delta F_i = 1 - \sqrt[t_i]{1 - F_i}$$

where:

F_i = inbreeding coefficient

t_i = equivalent complete generations for i^{th} individual

As suggested by Gonzalez-Recio et al. (2007), ΔF_i can be treated as an alternative measure of inbreeding adjusted for the pedigree depth, distinguishing between animals with the same F_i but a different number of known generations in the pedigree. Moreover, replacing t by $(t - 1)$ in formula for ΔF_i , the average of the ΔF_i s of N individuals included in a given population was applied to estimate the realised effective population size \bar{N}_e (Gutierrez et al. 2009).

According to Cervantes et al. (2011) the effective population size N_e can be estimated from increase in coancestry instead of increase in inbreeding and this method is recommended especially for structured populations. Increase in coancestry between individuals j and k is computed as:

$$\Delta c_{jk} = 1 - \sqrt[\frac{t_j+t_k}{2}]{1 - c_{jk}}$$

where:

c_{jk} = inbreeding value corresponding to an offspring from individuals j and k

t_j, t_k = discrete equivalent generation of individuals j and k

Despite inbreeding, also the average relatedness coefficient (AR) was estimated. It is defined for each individual as the probability that an allele randomly selected from the whole pedigree belongs to the given animal. According to Gutierrez et al. (2003) and Goyache et al. (2003), the AR coefficient can be interpreted as a representation of the individual in the whole pedigree regardless of the knowledge of its own pedigree.

The following probabilities of gene origin were computed: effective number of founders (f_e), effective number of ancestors (f_a), and founder genome equivalent (f_{ge}). The effective number of founders is defined as the number of equally contributing founders, which would give the same amount of genetic diversity that is present in the current population. The effective number of ancestors (Boichard et al. 1997) is the minimum number

of ancestors explaining the genetic diversity in a population. Founder genome equivalent (Caballero and Toro 2000) is taken as the number of equally contributing founders with no loss of founder alleles that would give the same amount of genetic diversity as is given in the reference population. This parameter shows the loss of genetic diversity in the population occurring due to genetic drift and bottlenecks. It should be stressed that f_a differs from f_e in the extent of the existence of bottlenecks in the pedigree.

The computations were performed using the CFC (Sargolzaei et al. 2006) and the ENDOG v4.8 (Gutierrez and Goyache 2005) software packages.

RESULTS

The number of individuals recorded in the analysed database in subsequent years increased from 40 animals born before year 1950 to 837 individuals born between years 2006 and 2013. Beginning from the 1970s, the number of bison recorded grew by circa one hundred every five years except the period between 1995 and 2005 (about 600 individuals per period). Generally, the distributions of numbers across both sexes were similar (Figure 2).

From 4269 individuals entering the pedigree, 762 were the founders and both parents were known for 2579 individuals. For 204 founders the birth year was not recorded and from the founders with known birth year, 394 individuals were born before the year 1990.

Furthermore, 430 non-founders were the parents whereas 3077 individuals did not have offspring. In the group of 3507 non-founders there were 96 sires with 920 progeny and 334 dams with 1256 progeny. The disproportion in number of progeny for sires and dams was determined by completeness of parental information. So, the average size of full sib group was 4.05 (ranging from 2 to 35).

The maximum number of traced generations was 7, but the average number of traced generations was low and equal to 1.49 with standard deviation (SD) 1.19. The maximum number of fully traced generations was equal to 3 with the average less than one and equal to 0.693 (SD = 0.627). The maximum value was reached by seven female bison. The mean of equivalent complete generations was also low and equal to 1.01 (SD = 0.701) so the

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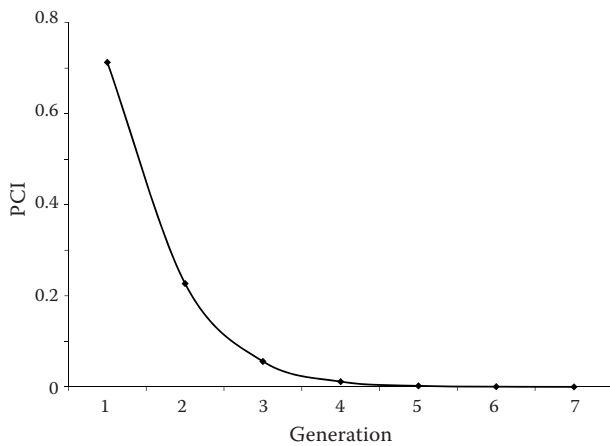


Figure 3. Pedigree completeness index

depth of analysed pedigree is strongly scarce. The minimum values of the number of generations traced, the number of fully traced generations, and the numbers of equivalent complete generations traced were zero. The completeness of the pedigree for each extant parental generation in the pedigree is given in Figure 3 (where generation 1 denotes sires, generation 2 grandsires, etc.). The PCI was equal to 0.7 for the first generation and it was near zero for the third generation.

From the set of 4269 animals, 616 individuals (14.43%) were characterised by non-zero inbreeding coefficient, namely 281 bulls, 320 cows, and 15 individuals with unknown sex. The number of inbred animals systematically increased and this

process seems to have accelerated with the beginning of the current century when the number of inbred individuals doubled during last thirteen years (Figure 4). It should be stressed that the computed increase of inbreeding level is determined by more complete pedigree information in consecutive years.

The average inbreeding coefficient in whole population was 3.26%. The inbreeding level was similar for both sexes and equal to 3.35% in the group of males and 3.27% in females, respectively. The maximum inbreeding coefficient was 37.5% for males (26 individuals) and 46.9% for females (3 individuals). Taking into account only the inbred individuals, the average inbreeding coefficient for the whole group was equal to 22.61%, 22.45% for males, and 22.64% for females, respectively. There were 41 (0.96%) full-sib matings, 186 (4.36%) matings of half-sibs, and 368 (8.62%) parent-offspring matings. The average inbreeding levels in consecutive years of birth for all recorded animals and for the inbred animals indirectly fluctuated as presented in Figures 5 and 6, respectively.

The highest inbreeding coefficient 46.87% for this population was estimated for three female bison (full-sib) from Zoological Garden in Zurich (years: 1987–1992). For 837 individuals born in the last analysed time period (2006–2013), 169 (20.2%) were inbred (including 85 males, 80 females, and 4 with unknown sex). While twenty years earlier, i.e. between years 1986 and 1990, out of the 498 animals born then, 49 were inbred

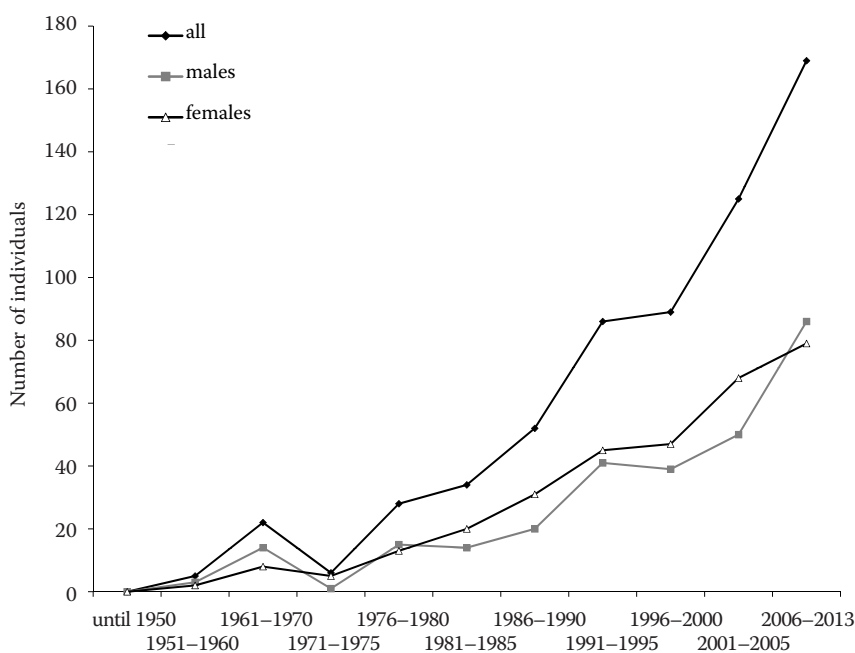


Figure 4. Number of inbred animals born in subsequent years



Figure 5. Average inbreeding coefficient for subsequent birth years of all recorded animals

(9.84%): 20 males, 28 cows, and 1 with unknown sex. However, this high increase of the proportion of the inbred individuals in the analysed population is evidently affected by the increase of the pedigree knowledge.

The individual increase in inbreeding ΔF_i ranged from 0% (3653 individuals) to 25.12% (10 individuals), and the average of this parameter was equal to 1.91% for all animals, 3.16% in group of animals with both parents known, and 6.42% for the animals with the equivalent complete generations equal to 2 or more. Ten animals reached the maximum value, all with the inbreeding coefficient equal to

37.5% and equivalent complete generations equal to 1.625. The realised effective population size was estimated as $\bar{N}_e = 11.64$. The average relatedness coefficient (AR) for the analysed population was low and equal to 0.31% (median 0.23%), 0.327% for males (median 0.27%) and 0.287% for females (median 0.21%). The minimum level of this coefficient was 0.035% while the maximum was 1.5%.

Changes of AR s over time are shown in Figure 7. After several years of an upward trend some discrepancy between sexes can be observed. In this century, the AR value for males is still on the rise whereas for females a decreasing tendency is observed.

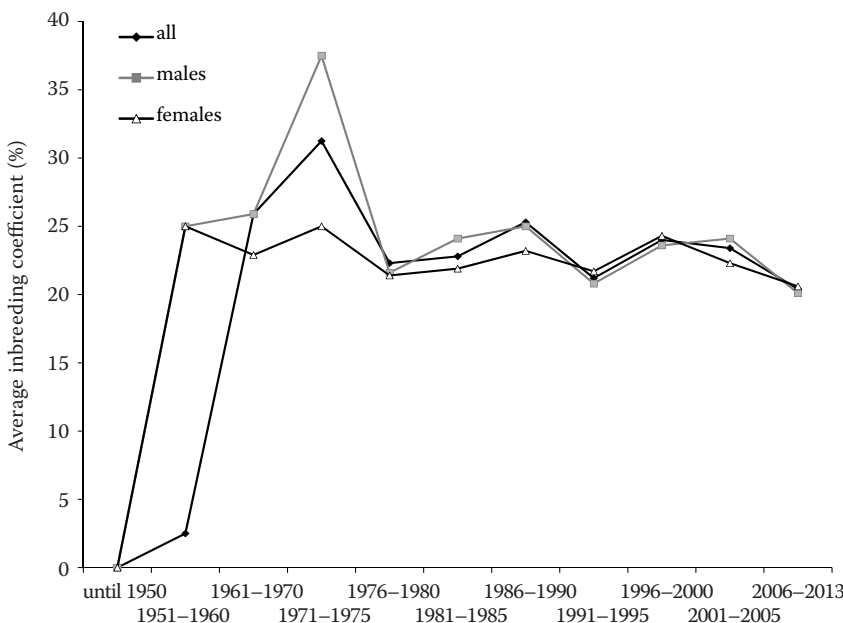


Figure 6. Average inbreeding coefficient for subsequent years of birth of inbred animals

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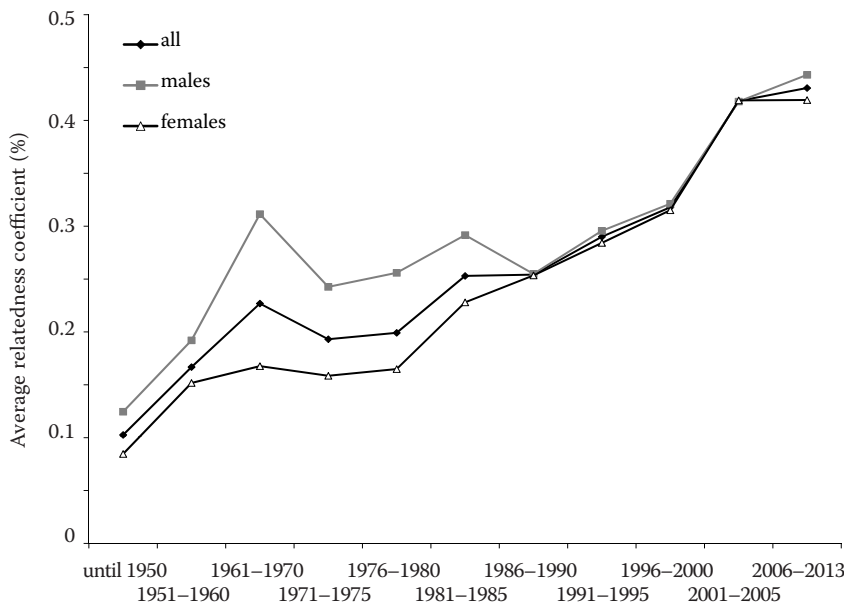


Figure 7. Average relatedness coefficient across birth years

Table 1. Parameters of gene origin

Parameters	
Number of animals	4269
Number of founders	762
Number of animals with one or two unknown parents	1690
Number of animals in reference population (born in 2006–2013)	837
Founder equivalent for reference population	130
Founder genome equivalent for reference population	95
Effective number of ancestors for reference population	108
Number of ancestors contributing to reference population	539
Number of ancestors explaining 50% of genetic variability	48

Gene origin parameters are listed in Table 1. Taking into account as the reference population the individuals born in the last analysed time period (i.e. 837 bison born in years 2006–2013), the cal-

culated values of founder equivalent and founder genome equivalent were 130 and 95, respectively, the effective number of ancestors was 108, the number of ancestors contributing was 539, and 48 ancestors explain 50% of population genetic variability (Table 1). So, a great part of founders' alleles could be lost by non-random mating and bottleneck. On the other hand, the obtained results are also a consequence of the fact that for the analysed population of bison no common breeding program was applied.

The inbreeding and coancestry information expressed as the number of full generations traced or by the maximum number of generations traced is presented in Tables 2 and 3, respectively. As it was already mentioned, the mean of equivalent complete generations for all individuals was 1.01. The average inbreeding coefficient for total population was 3.26% although for individuals with maximum number of generations traced exceeding 2 the average inbreeding level oscillates from 8.34 to 10.84% (Table 3). However, the inbreeding level of inbred individuals corresponds with the

Table 2. Coancestry information given by the number of full generations traced

J_GenCom	<i>n</i>	<i>F</i> (%)	Inbred individuals (%)	Average inbreeding for inbred animals (%)	<i>AR</i> (%)	<i>N_e</i>
0	1690	0			0.17	
1	2208	3.59	14.63	24.52	0.33	13.9
2	364	15.82	78.85	20.06	0.74	3.9
3	7	36.16	85.71	42.19	0.83	2

J_GenCom = number of full generations traced, *n* = number of individuals, *F* = average inbreeding coefficient, *AR* = mean average relatedness, *N_e* = effective population size (for *i*th generation when *F_i* > *F_{i-1}*)

Table 3. Coancestry information given by maximum number of generations traced

J_GenMax	<i>n</i>	<i>F</i> (%)	Inbred animals (%)	Average inbreeding for inbred animals (%)	Mean <i>AR</i> (%)	<i>N_e</i>
0	762	0			0.11	
1	1812	0			0.23	
2	950	6.74	31.79	21.19	0.40	7.4
3	461	10.84	43.81	24.74	0.57	11.3
4	195	8.34	38.97	21.40	0.55	
5	57	10.31	43.86	23.50	0.55	
6	28	10.04	35.71	28.12	0.41	
7	4	9.37	25.00	37.50	0.37	

J_GenMax = maximum number of generations traced, *n* = number of individuals, *F* = average inbreeding, *AR* = average relatedness, *N_e* = effective size (for *i*th generation when $F_i > F_{i-1}$)

value estimated for total population (22.61%). The percentage of the number of inbred individuals in whole analysed population was 14.43% and this value arises to approximately 40% for individuals with known ancestors in the third, fourth or fifth generation (Table 3). Naturally, mean *AR* for those individuals also exceeds the mean for all population.

DISCUSSION

Wild animal populations tend to be affected by a number of both genetic and environmental factors such as lethal and semi-lethal mutations, sudden climatic changes, industrial pressure etc. The usual consequences are a reduction of population size as well as unfavourable demographic and genetic structure. Hence, it seems necessary that complex efforts should be undertaken by zoological gardens and the academia to develop breeding conservation programs.

In the early 1870s, the population of the American bison was decimated from millions to several hundred (Gates et al. 2010). Plains bison were saved from extinction by five private herds and one herd at the New York Zoological Park (Meagher 1973). These six groups were established with less than 100 wild born animals which became the founders for the reconstructed herds. In addition, a small group of bison consisting of 25 individuals in 1902 survived in the area of Yellowstone National Park (Meagher 1973).

The number of bison kept in zoos at that time is difficult to estimate exactly, but Heck (1968) assessed this number as 256. The database analysed in our paper included only 16 individuals born

before 1920 (8 males and 8 females). Only one of them was wild born, whereas 11 animals were captive born and for the others 4 the type of birth was not known. Eight of them were the parents of 14 individuals. For all bison from this oldest group the inbreeding coefficient was 0 and the equivalent complete generations did not exceed 1 and was equal to 0 for eight animals, 0.5 for two and 1 for six individuals. The average relatedness coefficient for this group was low and equal to 0.053%. So, by contrast to European bison, the earliest American bison recorded in zoos' studbooks were not the founders for the next generations included in the analysed database. During the next decades the number of bison recorded in the analysed database grew systematically but in many cases information on the origin of the new registered individuals was not available. In consequence, in our data, the number of non-founders being the parents as well as the average family size still remained low, while the coefficient of equivalent complete generations equalled to 1.01 for the whole population analysed. This is also confirmed by the PCI index which quickly tends to zero. However, for endangered species similar values were listed in the literature for example by Armstrong et al. (2011) and Graczyk et al. (2015b).

However, the recorded data enabled us to compute the non-zero inbreeding coefficients for 616 individuals. For inbred individuals, the average inbreeding coefficient was also similar for both sexes and equal to 22.45% for males and 22.64% for females. This corresponds with results obtained for captive David's deer population (Sternicki et al. 2003) and some population of Przewalski horse (Wolc et al. 2008). On the other hand, the computed

<https://doi.org/10.17221/120/2017-CJAS>

average inbreeding level was lower compared to the one of European bison reported in the late 1990s which equalled 43.98% for the Lowland line and 26.28% for the Lowland-Caucasian line (Olech 1998). However, in the population analysed in the present study, the number of inbred animals increases over subsequent years (Figure 4), but the level of the average inbreeding coefficient seems to decrease (Figure 5 and 6). It should be recalled that inbreeding coefficients (obtained via pedigree data) are determined both by matings of relatives and pedigree completeness.

The bison housed in public herds in the USA are also assumed to be inbred, as a result of their history, bottleneck and low numbers of individuals used to create those herds. Nevertheless, some authors (Halbert 2003; Hedric 2009) claim that the surviving bison do not suffer from the inbreeding as much as expected. Observed heterozygosity for nine federal bison herds was estimated from 55.4% for Henry Mountains herd to 64.3% for Wind Cave NP herd (Ranglack et al. 2015).

As it is well known, inbreeding may negatively impact animal fitness traits. The detrimental effect of inbreeding was reported also for bison. For instance, Halbert (2003) pointed out that several demographic features of the current Texas State Bison Herd population concur with documented examples of inbreeding depression and/or loss of genetic variation through drift, such as low natality rates, probable male infertility, and high calf mortality rates. This is obviously the influence of the dramatic history of the bison and the maintenance of extant individuals in small populations. In consequence, the bison population tends to have less genetic variation and lower heterozygosity compared to cattle (Halbert 2003). Some authors (see e.g. Halbert 2003) found that the reduction of genetic diversity of bison caused by the bottleneck in the late 1800s may not have been so great as expected.

A minimum effective population size (N_e) of 50 individuals is commonly used as a population management goal to minimise inbreeding for short-term population survival (Franklin 1980). Halbert (2003) estimated the effective population size of the current Texas State Bison Herd population as 13.3. The ratio of effective population size to the census population size has most commonly been estimated to be between 0.16 and 0.42 (Shull and Tipton 1987; Berger and Cunningham 1994).

However, Shull and Tipton (1987) suggested that the ratio could be as low as 0.084 in some managed populations. For the population analysed here, effective population size (estimated on the basis of the number of full generations traced) was equal to 13.9 for the first generation and only 3.9 for the second generation (Table 2). When the maximum number of generations traced was considered, the N_e was even lower and equalled 11.3 in the third generation (Table 3). The higher value of effective population size equal to 26 was obtained taking into account the individual increase in coancestry instead of the individual increase in inbreeding. However, because of a weakness of pedigree information, those values must be treated very watchfully. The small effective population sizes were also reported for other endangered species living in zoos. Armstrong et al. (2011) estimated it as 3.13 for the African antelope (*Addax nasomaculatus*) with the equivalent generations equal to 1.78.

The estimated mean AR (0.3%) is very low. For instance, Malhado et al. (2013) obtained mean AR equal to 12.5% for Jaffarabadi buffaloes with the equivalent complete generations estimated as 1.76 and average inbreeding coefficient 4.22%.

The obtained low values of founder equivalent (130) and founder genome equivalent (95) show a substantial loss of the genetic variability from unequal founder contribution and genetic drift. The ratio of founder genome equivalent to the total number of founders was for analysed data 0.17 and it is similar to that of some herds of European bison (Olech and Perzanowski 2002). According to Lacy (1995), the founder equivalent and the founder genome equivalent can be used to display the loss of genetic diversity due to unbalanced contributions of the founders. If all founders contributed equally to the descendant population, the founder equivalent would be equal to the actual number of founders. However, it should be stressed that the number of bison with unknown parents recorded in the database analysed here was relatively large. With the beginning of the 21st century, this number decreased significantly.

According to Boichard et al. (1997) the effective number of founders, the effective number of ancestors, and the founder genome equivalent are affected by the completeness of pedigree but with different magnitude. A high value of ratio of the effective number of founders and the effective number of ancestors indicates a stronger

bottleneck effect and the equality of these parameters is desirable. For analysed data this ratio is 1.2 when as the reference population were taken the individuals born between 2006–2013. However, because of the very strong incompleteness of analysed pedigree, this value should be treated informative only.

By contrast to livestock, the structure of animal populations kept in zoos is quite different. It is directly connected with magnitudes of estimated pedigree parameters. Over last years a number of reports on livestock pedigree parameters have been available. Krupa et al. (2015) obtained the parameters of gene origin for five pig breeds, where the ratio of effective number of founders to total number of founders ranged from 0.11 to 0.17. Oliveira et al. (2016) investigated the parameters describing the probability of gene origin in the Spanish Murciano-Granadina goat breed and estimated effective numbers of founders as 967 (with total numbers of founders equal to 10 810 individuals) and the contribution of the founders ranged between 0.1–0.2%. Hazuchova et al. (2012) obtained for Slovak Spotted bulls the effective number of founders equal to 150 whereas the effective number of ancestors equal to 85 with total number of founders 308 and total number of individuals equal to 752.

Regarding of the presented results for analysed bison population, it seems to be clear that this population is relatively high inbred despite of the low values of parameters measuring the relationships between animals. Two basic ways could be recommended to overcome this issue. The first approach is the more interchanging individuals between zoos. In the analysed population only 10% bison had parents coming from another zoos than the progeny. The second one is the support by information on historic records of genetic sources for individuals building the pedigree. Precise information obtained from studbooks kept by managements of zoological gardens is necessary if advanced pedigree analysis procedures are to be used to protect the genetic potential of endangered species.

CONCLUSION

An effective realization of breeding programs requires more complete pedigree information. Although the pedigree parameters (including the inbreeding level) in the American bison population

received in the present study seem to be acceptable (from the perspective of other wild animal populations), they can be over/underestimated due to incomplete pedigree.

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