The Participation of Ancestral Genes in the Existing Population of European Bison

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Olech W., 1989: The participation of ancestral genes in the existing population of European bison. Acta theriol., 34, 29: 397—407 [With 6 Tables & 3 Figs]

The genetic pool of the present population of European bison, *Bison bonasus* Linnaeus, 1758, contains genotypes of 12 individuals. The aim of this paper was the determination of the participation of those ancestors in the existing population of European bison. The variability in the population of European bison was not lost. The proportions of 12 ancestral genotypes did not change significantly for 30 years in a genetic pool of the entire species, which indicates that genetic variability has been maintained. The different numbers of ancestors in two lines (Białowieża line — LB, and lowland-Caucasus line — LC) and the systems of mating used in both lines had significant influence on the level of inbreeding in each of them. The level of inbreeding in the open LC line was lower (0.193) than in the LB line (0.324). In line LC, one can notice a disturbing decrease in ancestral participation typical for this line (mainly male Kaukasus 100). The inbreeding depression in LC line was higher while the level of inbreeding was lower. In order to maintain the present level of variability and even increase it in the future the method of breeding of European bison should in each line, attempt equalize the participation of all ancestors. From the selected centers of closed breeding, the best equality of participation of all ancestors was in Hardehausen, Springe and Duisburg.

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1. INTRODUCTION

The breeding of endangered species of wild animals with the aim of conserving their genotypes is completely different than breeding farm animals or only maintaning wild animals in captivity such as in ZOOs. The basis purpose of this kind of breeding should be the reintroduction of a species into a natural environment, which requries viable animals genetically different and not adapted to conditions of captivity.

Frankel (1983) concentrated on the necessity of variability in populations of wild animals which diffuses plasticity in a changing environment and makes survival possible under environmental pressures for it. The main goal of breeding wild species is the conservation of its genetic variability. Variability can be calculated on two levels: for individuals (heterozygosity of individual) and for populations (genes frequency).

The level of variability depends on the initial gene pool of a popula-

tion (Ralls & Ballou, 1986). This includes the number of its ancestors and proper methods of conserving the whole spectrum of this pool in the future (Bouman & Bouman, 1979).

Many species of animals are or were endangered because of considerable bottleneck. Okapi (*Ocapia johnstoni*) has genes of only 24 ancestors (Foose & Foose, 1983), and the Siberian tiger (*Panthera tigris altaica*) of 25 (Foose *et al.*, 1986). Bouman & Bouman (1979) stated that the number of ancestors of presently alive Przewalski horses is limited to 13. The existing European bison population has only 12 ancestors (Slatis, 1960). Foose et al. (1986) feel that 5 to 10 pairs of ancestors are enough to cause an insignificant decrease of variability in relation to the initial one. Senner (1980) adds that the size of a founding herd has significant influence on the viability of a population.

The effective population size was determinated using formula (Falconer, 1974):

$$N_e = \frac{4 \times M \times S}{M + S}$$

where:
Ne — effective population size;
M — number of males in founding herd;
S — number of females in founding herd.

The variability in a population can be calculated as a subtraction: one minus the loss of variability caused by inbreeding ($1/2\ N_e$) which is proportional to effective population size (Falconer, 1974). This dependence is presented in Fig. 1. When a population is created from two animals there is then 75% of the initial variability in it.

The variability can be kept on the same level or even increased by proper breeding *i.e.* when participation of all ancestors is equalized in a gene pool of the population (Ralls, Ballou, 1986; Bouman & Bouman, 1979). Nei *et al.* (1975) stated that after the bottleneck the variability in a population can increase with proper breeding.

The aim of this paper was the determination of the level of variability in European bison, *Bison bonasus*, Linnaeus, 1758, by the evaluating the proportion of 12 ancestral genes and comparing this proportion between selected large breeding centers of European bison and between lines (LC and LB). For each of those lines the influence of inbreeding on longevity and reproduction traits of females was studied.

2. MATERIAL AND METHOD

The material for this analysis included data taken from the Pedigree Book of European bison about all bison with known origin born before 1985. The proportion of genes of 12 ancestors was determined for each individual as a mean of those value for its parents.

The individual with parents having values, for example of 0.236 and 0.542 of genes of one ancestor would have a value equal to $(0.236+0.542)/2=0.389$. This calculation started from 12 ancestors.

In order to describe the existing European bison population, the composition of the gene pool for animals born between 1980 and 1984 was calculated as the mean participation of each of 12 ancestors. The results obtained were compared to those of Slatis (1960) who dealt with bison living in 1954. The results of both works were compared using the rank correlation of Spearman.

In the twenties there was a serious bottleneck in the species. At this time there were only 54 bison in the world which traced their origin back to only 12 ancestors (Slatis, 1960). The Caucasian bison subspecies was represented by only one male — Kaukasus (no. 100). The progeny of this male and females makes the lowland-Caucasian line (LC). Pure lowland bison are in the Białowieża line (LB), which includes the Pszczyna line (LP) based on only 2 ancestors. These lines are described by Kobryńczuk (1986). I have used his abbreviations. The proportion of each ancestor in both lines from 1945 to 1984 was determined in 5-year periods.

In some larger closed breeding centers the proportion of ancestral genes was determined, and for those places the index of participation of ancestros (V) was determined. This index made it possible to compare the equalization of composition of gene pool in each center and was calculated using formula:

$$V = \left[\frac{\Sigma p_i^2 - 10000/k}{k \times (k-1)} \right]^{1/2}$$

where:
V — index of participation of ancestors;
p_i — proportion of i ancestor in percent;
k — number of ancestors.

3. RESULTS

Table 1 and Fig. 2 present the participation of ancestors in the existing population of European bison (both lines together) and, for comparison, in the population living in 1954 (Slatis, 1960). Both results were similar, that means that the proportion of ancestor genes did not change significantly during 30 years. The coefficient of rank correlation (0.86) is high and significant. It means that the range of participation of ancestors did not differ between the two periods.

The mean level of inbreeding for bison born before 1985 exceeded 20% (Olech, 1987). An increase in the inbreeding level can be identified with an increase of homozygosity and mating individuals with similar proportions of ancestor genes in genotypes. In the entire population there was no directional change of frequency of ancestral genotypes, what means that the gene pool did not change.

The effective numbers of founding herds and percent of lost genetic variability are presented in Table 2 for both lines of European bison.

Table 1
The proportion of genotypes of 12 ancestors of European bison and division
of those ancestors into three genetic lines: (a) animals living on 31.12.1954
(Slatis, 1960), (b) 876 animals born 1980—1984. LB — Białowieża line,
LP — Pszczyna line, LC — lowland-Caucasian line. LB and LP = lowland bison.

Number, name of ancestor with division into lines	Sex	Proportion of ancestors genes	
		(a)	(b)
LP 45 Plebejer	M	26.4	27.0
42 Planta	F	18.8	19.3
89 Bilma	F	9.6	10.1
87 Bill	M	7.2	7.7
LB 16 Plavia	F	9.1	7.7
15 Begrunder	M	8.2	7.1
147 Bismarck	M	0.9	0.6
100 Kaukasus	M	6.1	6.7
96 Gatczyna	F	6.3	5.7
LC 95 Garde	F	3.8	3.5
35 Plevna	F	2.7	3.2
46 Placida	F	0.9	1.3

The differences between lines were rather low (7.3% in LB and 4.4%
in LC). The loss of variability in the Białowieża line was larger because
of the smaller number of ancestors.

The lowland-Caucasian line is open because an animal from this line
has to have only one parent from this line, the second can be from the
pure lowland line. This means that there is a continuous supply of low-
land bison genes. The Białowieża line is closed because only offspring
of 2 Białowieża animals can be recognized as being Białowieża line.
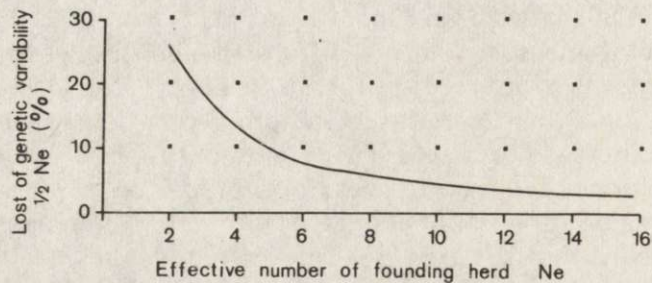As to whether the line is closed or open depends on the number of

Fig. 1. The value of genetic variability lost in comparison to initial variability after bot-
tleneck depends on effective number of founding herd.

Table 2

The effective number of founding herds and loss of variability (%) in lowland-Caucasian and Białowieża (with Pszczyna) lines of European bison (*Bison bonasus*) after bottleneck.

Line	Number of ancestor		Ne	Loss of variability
	males	females		
Lowland-Caucasian	5	7	11.67	4.4%
Białowieża	4	3	6.86	7.3%

ancestors which create the gene pool of the line. The Białowieża line contains genotypes of seven individuals (Nos 42, 45, 87, 89, 15, 16, 147) and the lowland-Caucasian line, 12 (except those which are in LB are five more: 100, 95, 96, 35, 45) (Table 1, Fig. 3).

The number of ancestors and whether the line is open or not influences the level of inbreeding of animals in the line (Table 3). The bison from LC have smaller inbreeding coefficients. It confirms the results of Olech (1987) about the relationship between the inbreeding level and the degree of migration into population.

There were differences between the lines as to the influence of inbreeding on reproduction traits and viability. The percent of deaths in the first month of life was in both lines similar: 11.25% for LB, and 11.95% for LC. The percent of deaths before the second birthday was less in the Białowieża line (22.83%) than in the lowland-Caucasian line 23.84%. This difference was insignificant.

The mean values of reproduction traits and inbreeding depression in both lines of bison are presented in Table 4. Inbreeding had a significant influence on reproduction traits in lowland-Caucasian females while in the Białowieża line the depression was smaller, and almost for all traits, insignificant. Using the regression line the hypothetical
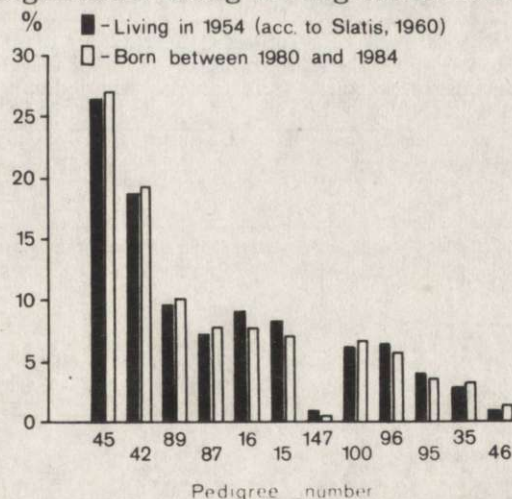
Fig. 2. The participation of 12 ancestors in European bison (*Bison bonasus*) population: (a) living in 1954 (acc. to Slatis, 1960); (b) born between 1980 and 1984.

values for not inbred females were determined (Table 4). The noninbred
Białowieża females theoretically should live longer (almost 1 year), but
have older age of first calving (1.5 months), have less offspring (1.6
less) and longer intervals between calvings (3 months longer).

Table 3
The mean inbreeding coefficient in two lines (lowland-Caucasian and Białowieża)
of European bison (*Bison bonasus*).

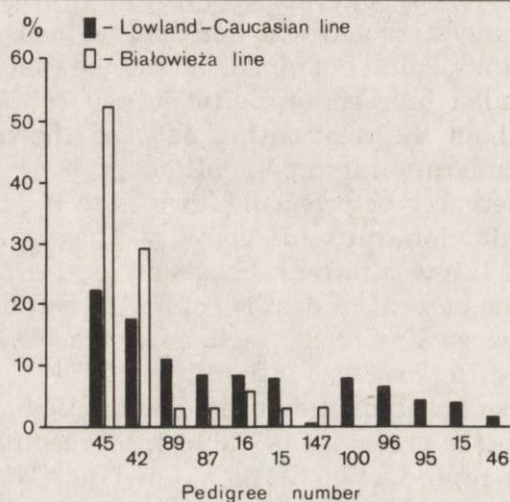| Line	Number	Mean inbreed. coefficient ± s.e.
Lowland-Caucasian	3537	0.193±0.002
Białowieża	890	0.324±0.007

Fig. 3. The participation of 12 ancestors in European bison (*Bison bonasus*) population
born between 1980 and 1984: LC — Lowland-Caucasian line, LB — Białowieża line.

Table 4
Mean values of length of life and some reproductive traits of females in both lines (LB
and LC), inbreeding depression for those traits, and determined values of those traits for
not inbred females using the regression line. *$p \leq 0.05$; **$p \leq 0.01$.

Trait	Line	N females	Mean∓SE	Inbreeding depression for 1%	Determined value for not inbred females
Length of life (days)	LC	798	2029.1∓88.1	−18.0**	2377.4
	LB	231	2412.7∓178.8	−7.5	2593.8
Number of offspring per female	LC	680	4.95∓0.14	−0.03*	5.46
	LB	200	4.71∓0.25	0.04*	3.82
Age of first calving (days)	LC	680	1542.3∓16.7	5.8**	1437.9
	LB	200	1555.2∓25.8	2.6	1489.5
Mean interval between calvings (days)	LC	557	565.2∓8.8	2.6**	518.8
	LB	169	600.9∓22.5	−0.1	604.6

This means that inbreeding had a less depressing influence in the Białowieża line probably caused by a smaller frequency of detrimental genes that were probably eliminated during many years of breeding in closed herd. The animals react to higher homozygosity by higher mortality of young and those which live are "resistant" to inbreeding. This is probably how inbreeding influences the European bison population.

The proportion of ancestors in lines changed a little with time (Table 5). In the lowland-Caucasian line there was a decrease in proportion of ancestor genes. This is characteristic only for this line of ancestors, for example Kaukasus — 100 (the only one from the Caucasian subspecies of European bison) and some females (35, 95, 96). There was an increase in the participation of ancestors 42 and 45, which founded the Pszczyna line.

The lowland-Caucasian line animals compose the majority of the species and are bred in most places except Poland. In Poland all closed breeding centers (reservations and Zoos) have pure lowland European bison from the Białowieża (sometimes Pszczyna) line. The proportions of ancestor genotypes in different places were not the same (Table 6).

To evaluate the equality of participation of all ancestors the index V

Table 5

The proportion of ancestor genotypes in both lines (LC and LB) of European bison (*Bison bonasus*) in five years periods from 1945 to 1984.

Pedigree No. of ancestor	Years							
	1945—49	50—54	55—59	60—64	65—69	70—74	75—79	80—84
Lowland-Caucasian line (12 ancestors)								
45	10.4	17.1	19.8	20.1	21.1	20.6	21.3	22.4
42	9.6	14.1	16.0	16.4	17.1	16.8	17.1	17.6
89	12.1	12.1	11,8	12.2	12.0	12.4	11.1	11.2
87	8.4	9.3	8.9	9.0	8.9	9.1	8.4	8.4
16	14.0	10.9	9.5	9.3	8.8	8.9	8.7	8.4
15	13.1	10.4	8.9	8.8	8.4	8.4	8.3	7.9
147	0.0	0.7	0.4	0.4	0.4	0.4	0.5	0.4
100	10.2	8.0	7.9	7.4	7.5	7.5	8.2	7.8
96	11.1	8.5	7.6	7.6	7.2	7.2	6.7	6.6
95	6.1	4.8	4.5	4.4	4.2	4.2	4.2	4.1
35	4.1	3.2	3.4	3.0	3.3	3.4	4.0	3.7
46	1.0	1.1	1.4	1.2	1.2	1.2	1.7	1.5
Białowieża line with Pszczyna line (7 ancestors)								
45	55.8	54.5	44.0	46.4	48.8	51.2	52.9	55.6
42	31.4	33.3	33.5	33.5	31.2	30.4	29.8	29.6
89	2.6	3.5	6.6	5.6	4.7	4.0	3.3	2.5
87	2.6	3.5	6.6	5.6	4.7	4.0	3.3	2.5
16	3.0	2.6	4.6	4.4	5.3	5.3	5.4	4.9
15	2.1	1.3	2.3	2.2	2.7	2.6	2.7	2.5
147	2.6	1.3	2.3	2.2	2.7	2.6	2.7	2.5

Table 6

The proportion of ancestor genotypes in European bison born 1975—1984 in large breeding centers divided into lines and value of ind (V) of proportion of ancestors in those centers.

A. Lowland-Caucasian line

Breeding centers of European bison	Pedigree No. of ancestor												V
	45	42	89	87	16	15	147	100	96	95	35	46	
Okskij zapoviednik	34.3	26.2	9.9	9.9	5.0	5.0	0.0	2.5	4.9	2.5	0.0	0.0	14.3
Prioksko-terrasnyj	38.3	27.2	8.4	8.1	5.2	4.5	0.4	2.1	3.7	1.9	0.2	0.0	17.3
Topolcianky	23.3	23.3	16.9	12.0	4.9	4.9	0.0	4.3	6.1	3.1	1.2	0.0	8.8
Avesta	13.3	12.6	20.4	13.0	8.4	8.3	0.0	6.9	10.1	5.1	1.8	0.0	4.4
Berlin	6.5	3.9	0.0	0.0	18.6	18.6	0.0	19.9	12.2	6.3	13.7	0.4	7.4
Hardehausen	18.2	14.7	4.2	4.2	9.5	8.9	1.1	13.8	5.9	5.8	8.0	5.8	3.0
Springe	18.1	17.0	12.3	10.0	9.5	8.9	2.4	7.0	5.9	4.0	3.0	2.1	3.5
Whipsnade	34.4	21.9	7.0	6.1	8.6	6.1	2.5	4.8	3.3	2.0	2.8	0.7	11.8
Amsterdam	0.0	0.0	0.0	0.0	37.4	29.1	0.0	8.4	16.7	8.4	0.0	0.0	20.0
Duisburg	13.4	9.2	3.1	2.2	14.3	13.4	0.0	16.2	7.5	6.0	10.3	4.4	3.4
Damerover Werder	25.0	24.5	14.4	13.2	5.4	5.4	0.0	3.2	5.7	2.9	0.3	0.0	9.6
Sababurg	26.0	21.3	11.6	9.5	6.3	6.3	0.0	6.0	6.2	3.6	2.4	0.9	7.6

B. Białowieża and Pszczyna line

Breeding centers of European bison	Pedigree No. of ancestor							V
	45	42	89	87	16	15	147	
Białowieża	45.5	27.8	4.2	4.2	9.2	4.6	4.6	18.6
Pszczyna	65.3	30.6	0.6	0.6	1.4	0.7	0.7	44.0
Niepołomice	53.2	30.0	2.6	2.6	5.8	2.9	2.9	27.6
Smardzewice	50.8	28.5	2.5	2.5	7.9	3.9	3.9	40.7
Borki	49.4	28.6	3.7	3.7	7.4	3.7	3.7	22.6
Prioksko-terrasnyj	58.4	32.3	3.8	3.8	0.8	0.4	0.4	35.4

was used. This parameter was determined for animals from large breeding centers taking into consideration both lines separately (Table 6). If proportion of all ancestors would be equal then index V would equal 0. When the value of this index is smaller, the proportion of ancestors genes is more equal. Animals from Hardehausen, Springe and Duisburg have the most equal participation of all ancestors.

4. DISCUSSION

Slatis (1960) determined the participation of 12 ancestors of European bison living in 1954. After 30 years the frequency of ancestor genes did not radically change and for animals born in 1980—1984 it was similar. It showed that the genotype of each ancestor was not lost from the gene pool of the species. The composition of this gene pool can be used to measure variability in the population of European bison. Variability did not change.

This tendency to maintain the variability level applies to the whole population of bison. In different places the proportion of ancestors is quite different. For example in Hardehausen, Springe and Duisburg there is a much more equalized proportion of ancestor genotypes for animals born in those places than in the entire population. This shows that it is not only possible to maintain the variability but in can be increased by proper breeding.

Two lines which were distinguished in this paper differ from each other by the number of ancestors after the serious bottleneck in the twenties. The Białowieża line is completely closed and has genotypes of 7 ancestors which caused a lower variability level than in the lowland-Caucasian line. The second one has genotypes of 12 ancestors and is open, meaning that genes from the Białowieża line are still added to the gene pool of the lowland-Caucasian line. This created the level of inbreeding of animals in each lines. Białowieża line bison are more inbred than the lowland-Caucasian line. But because the LC line is open, the genotypes characteristic for this line have now lower frequency (mainly genotypes of Kaukasus — 100). The participation of ancestors 42 and 45 (Planta and Plebejer) doubled. This way it is possible to loose genotypes of ancestors from the gene pool. Proper breeding should equalize the participation of all ancestral genotypes, and this can limit the inflow of lowland blood to the lowland-Caucasian line.

The influence of inbreeding on longevity and reproduction traits was different in both lines. The inbreeding depression was much smaller in the Białowieża line than in the lowland-Caucasian line. This may indicate that bison from the Białowieża line are better adapted to inbreeding and this is the reason to keep this line separate.

REFERENCES

1. Bouman I. & Bouman J., 1979: Captive breeding of the Przewalski horse; survival of its Przewalski-like descendants or the conservation of the Przewalski horse? Foudation for the preservation and protection of the Przewalski horse.
2. Falconer D., 1974: Dziedziczenie cech ilościowych. PWN Warszawa.
3. Foose T. J. & Foose E., 1983: Demographic and genetic status and management. [In: „The biology and management of an extinct species Pere David's deer", B.B. Bech & C. M. Wenner (eds)], Noyes publications, Park Ridge, New Jersey: 133—186.
4. Foose T.J., Lande R., Flesness N.R., Rabb G. & Read B., 1986: Propagation plans. Zoo Biology, 5: 139—146.
5. Frankel O. H., 1983: The place of management in conservation. [In: „Genetics and conservation." Ch. Shonewald-Cox, S. Chambers, B. MacBryde & W.L. Thomas (eds)], INC Menlo Park, California.
6. Kobryńczuk F., 1985: The influence of inbreeding on the shape and size of the skeleton of the European bison. Acta theriol. 30: 379—422.
7. Nei M., Maruyama T. & Chakraborty R., 1975: The bottleneck effect and genetic variability in population. Evolution 29: 1—10.
8. Olech W., 1987: Analysis of inbreeding in European bison. Acta theriol. 30: 373—387.
9. Ralls K. & Ballou J., 1986: Captive breeding programs for population with a small number of founders. Trends Ecol. Evol., 1: 19—22.
10. Senner J. W., 1980: Inbreeding depression and survival of population. [In: „Conservation biology". M.E. Soule & B.A. Wilcox (eds)] Sinauer Ass. Inc., Massachussets.
11. Slatis M. A. 1960: An analysis of inbreeding in the European bison. Genetics, 45: 275—287.

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UDZIAŁ ZAŁOŻYCIELI WE WSPÓŁCZESNEJ POPULACJI ŻUBRÓW

Streszczenie

Pula genowa współcześnie żyjącej populacji żubrów zawiera genotypy 12 założycieli. W oparciu o dane rodowodowe zaczerpnięte z Księgi Rodowodowej Żubra oceniono udział tych przodków w liniach i wybranych ośrodkach hodowli zamkniętej żubrów.

Wyniki dotyczące zwierząt urodzonych w latach 1980—1984 porównano z zaczerpniętymi z pracy Slatisa (1960) i stwierdzono, że w populacji żubrów proporcje genów 12 założycieli populacji nie uległy istotnym zmianom w puli genowej całego gatunku na przestrzeni 30 lat, co świadczy o utrzymaniu zmienności genetycznej w tym gatunku na niezmienionym poziomie (Tabela 1, Ryc. 2).

Żubry zostały podzielone na dwie linie zgodnie z podziałem w Księdze Rodowodowej Żubrów. Różna liczba założycieli dwóch wyróżnionych linii (białowiesko-kaukaskiej i nizinnej) (Ryc. 3) oraz stopień zamknięcia linii ma istotny wpływ na poziom inbredu w każdej z nich. Poziom inbredu w otwartej linii białowiesko-kaukaskiej jest niski (0.193), a w linii żubrów nizinnych znacznie większy (0.324) (Tabela 3). W linii białowisko-kaukaskiej zauważa się niepokojący spadek udziału założycieli charakterystycznych tylko

dla tej linii (głównie samca Kaukasusa z 10.2% do 7.8%) i dwukrotny wzrost udziału
przodków o numerach 42 i 45 (Planta i Plebejer) (Tabela 4).

Aby utrzymać obecny poziom zmienności, a nawet go zwiększyć, należy dalszą hodow-
lę w obrębie każdej z linii oprzeć na planowanym wyrównaniu udziału wszystkich zało-
życieli. Oceniono wyrównanie składu puli genowej żubrów z kilku większych ośrodków
zamkniętej hodowli. Wśród tych ośrodków na czoło pod względem wyrównania udziału
wszystkich założycieli wysuwają się hodowle w Hardehausen, Springe i Duisburgu (Ta-
bela 5).