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Polarization of skull shapes in adult Lowland European bison, *Bison bonasus bonasus*

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The material consisted of 300 skulls (150 male and 150 female) of adult European bison from the Lowland line aged 5 to 27 years. The specimens belong to the museum collection of the Mammal Research Institute of the Polish Academy of Sciences in Białowieża. On each skull three standard measurements (BP, EctEct, SmSm) were taken. The results were standardized separately for males and females. The sum of three normalized parameters describing each skull was treated as its standardised dimension and then Perkal's natural similarity coefficients were calculated. In adult males a remarkable polarization of skull shapes was observed. In one set of the male specimens the type of a long skull with a broad forehead and narrow face was predominant (27%). In another, opposite and almost equally numerous (24%) set of male specimens, the type of a short skull with a narrow forehead and broad face prevailed. Such a polarization was not found in adult females: the type of a long skull with a narrow forehead and narrow face dominated (28% of the examined material); the remaining variants were evenly distributed.

Introduction

So far scientific research devoted to bison skulls have comprised classical morphological descriptions, post-natal development, and morphometric differences between males and females (Koch 1927, Juśko 1953, Empel 1962). Kobryńczuk (1985) depicted the influence of inbreeding on the shape and size of bison skulls of the Lowland and Lowland-Caucasian lines. Makowiecka (1994) wrote about differences among three bison breeding lines (Białowieża, Pszczyna and Lowland-Caucasian) on the grounds of skull non-metric features. Kobryńczuk and Krasińska (1987) and Krasińska (1988a, 1988b) analyzed the presence of parental traits in skull shapes and body form in hybrids of bison and cattle.

To date differences in skulls of adult bison of the same sex have not been investigated. Usually in bison, age has no or little impact on the elements of the axial skeleton. The aim of this work was to examine whether the contemporary population of bison living in the constant habitat of the Białowieża Forest — representing a similar degree of inbreeding — shows morphologic differentiation (polarization, dichotomy).

Material and methods

Our material consisted of 300 skulls (150 male and 150 female) of adult European bison from the Lowland line aged 5 to 27 years. The specimens belong to the museum collection of the Mammal Research Institute of the Polish Academy of Sciences in Białowieża.

Using the osteometric method by Duerst (1926) and instructions by Empel (1962), Kobryńczuk (1985) and Kobryńczuk *et al*. (2008), the following skull measurements were taken: basal length (Basion–Prosthion, BP), orbital breadth–forehead breadth (Ectorbitale–Ectorbitale, EctEct), and splanchnocranium breadth–face breadth (Supramolare–Supramolare, SmSm). The dimensions were standardised separately for males and females, which allowed us to obtain relative negative (–) or positive (–) values. Following Perkal (1953), the sum of three normalized parameters (BP, EctEct, SmSm) describing any particular skull was treated as its standardised value (*S*). Further, parameter derivatives were Perkal's natural similarity coefficients (l.c.) obtained for individual skulls by subtracting 1/3 of the standardised value (*S)* from each normalized parameter. The natural similarity coefficients are also relative values. Following Perkal (1958) and Kobryńczuk and Kobryń (1981), only the algebraic sings "+" and "–" were used in subsequent analyses. Consequently, for three parameters we obtained a set of six three-sign combinations or variants: the first sign referring to BP (skull basal length), the second to EctEct (forehead breadth), and the third to SmSm (face breadth). A plus (+) means that the value of the parameter is high, whereas a minus (–) that it is low. As a result, the skulls could be classified as long or short with broad or narrow foreheads and broad or narrow faces.

The characteristics of particular variants (skull types) are as follows:

Variant I (+ + –): long skull with broad forehead and narrow face.
Variant II (+ – –): long skull with narrow forehead and narrow face.
Variant III (+ – +) long skull with narrow forehead and broad face.
Variant IV (– – +) short skull with narrow forehead and broad face.
Variant V (– + –) short skull with broad forehead and narrow face.
Variant VI (– + +) short skull with broad forehead and broad face.

We calculated the distances between all possible pairs (66) of 12 skulls (variants I and IV) according to Perkal (1958) and Kobryńczuk (1985). The shortest distances were selected and on their grounds, a classification tree was constructed (Fig. 1) according to Perkal's natural similarity coefficient (l.c.).

The standardized size of male skulls (*S*) varied from –7.16 for the smallest skull to +3.94 for the largest one. The distances from –7.16 to 0 and 0 and +3.94 were further split in two to produce four value ranges. As a result, male skulls falling within the ranges from –7.16 to –3.58, –3.57 to 0, from 0 to +1.97, and from +1.98 to +3.94 were classified as small, medium-sized, large and very large, respectively.

In the female material the standardised size of skulls varied in the range from –4.84 to +4.46. Here also we created four size categories. Skulls falling within the ranges from –4.84 to –2.42, from –2.41 to 0, from 0 to +2.23, and from +2.24 to +4.46 were classified as small, medium-sized, large and very large, respectively (Tables 1 and 2).

The standardised size was calculated as a derivative of parameters separately for males and females.

Pearson's linear correlation between the standardised size of skulls (*S*) and the age of individual skulls (*A*) was calculated separately for males and females (Figs. 2 and 3). In order to characterize growth rate, separate regression equations were created for both sexes. Skull size was the dependent variable, and age the independent variable.

Results

Of the 150 male skulls, 9 (6%) were classified as small, 54 (36%) as medium-sized, 59 (39%) as large and 28 (19%) as very large. Of the same number of female skulls, 24 (16%) were classified as small, 44 (30%) as medium-sized, 65 (43%) as large, and 17 (11%) as very large

Table 1. Classification of skulls on the basis of age and standardised size.

Age (years)	Number of skulls				Total
	small	medium-sized	large	very large	
Males					
5	7	12	1	2	22
6		8	9	2	19
7	1	8	5	1	15
8		4	10		14
9		4	3	2	9
10		1	3	2	6
11		2	2	3	7
12		6	4	3	13
13		1	4	3	8
14		3	4	7	14
15	1	2	3	1	7
16		2	5	1	8
17			2		2
18		1	2		3
19			1		1
20				1	1
22			1		1
Total males	9	54	59	28	150
Females					
5	9	8			17
6	5	3	1	1	10
7	6		3		9
8			4	1	5
9		3	3		6
10		2	5	2	9
11		5	2	1	8
12	1	2	3	2	8
13		3	4		7
14		3	2	1	6
15	2	2			4
16		1	10		11
17		2	4		6
18			4	1	5
19		1	5		6
20		3	6	1	10
21		2	2	2	6
22		2	1	1	4
23			2		2
24		2	4	1	7
25	1			2	3
27				1	1
Total females	24	44	65	17	150

(Table 1). In males, the rate of small skulls to very large ones was 1:4 (9:28), whereas in females it was 1:0.71 (24:17). It seems that the increase in skull mass at a more advanced age is smaller in females than in males.

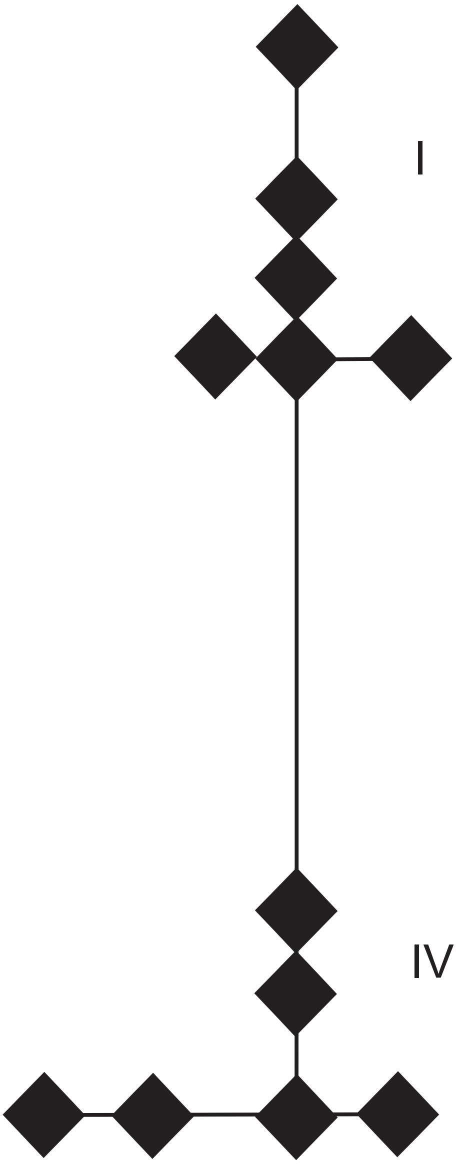

Fig. 1. Classification dendrite for skulls of males of variant I (1, 2, 3, 4, 5, 6) and variant IV (7, 8, 9, 10, 11, 12).

The smallest skulls in both sexes come mostly from individuals betwen 5 and 8 years of age. The very large skulls had a dispersed distribution; they did not come from 17–19-year-old males, probably due to their scarce representation (6 individuals) in the sample. On the other hand, the fact that none of the 21 15–17-year-old females had a very large skull was surprising (Table 1).

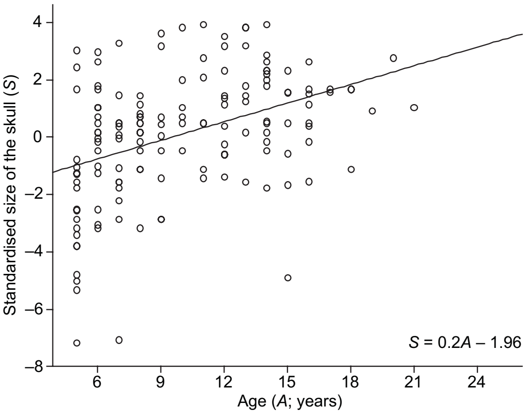

Fig. 2. Correlation between the age of males (*A*) and the standardised size of skulls (*S*).

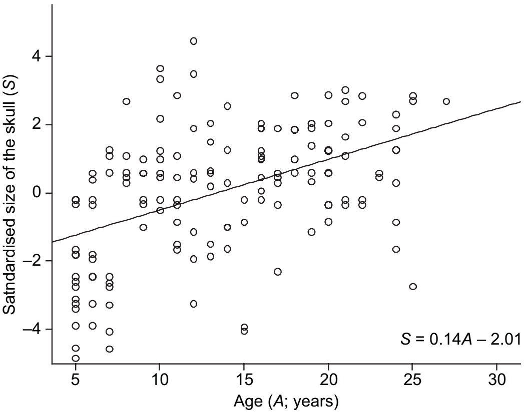

Fig. 3. Correlation between the age of females (*A*) and the standardised size of skulls (*S*).

In males and females, skull size was highly significantly correlated with age ($r = 0.36$ and $r = 0.44$, respectively, $p < 0.01$; Figs. 2 and 3). The regression equations of skull size (S) and age (A) are $S = 0.2A - 1.96$ and $S = 0.14A - 2.01$ for males and females, respectively. In males the regression coefficient ($R = 0.2$) was higher than that in females ($R = 0.14$), which means that in the former the increase in skull mass with time is greater than in the latter (Figs. 2 and 3).

Table 2. Classification of skulls on the basis of variant and standardised size.

Variant	Number of skulls				Total
	small	medium-sized	large	very large	
Males					
I	2	14	20	4	40
II	1	4	6	4	15
III	1	9	10	2	22
IV		12	14	10	36
V	4	6	1	4	15
VI	1	9	8	4	22
Total males	9	54	59	28	150
Females					
I	2	8	11	3	24
II	3	13	21	5	42
III	2	6	8	4	20
IV	7	6	9	1	23
V	5	7	10	1	23
VI	5	4	6	3	18
Total females	24	44	65	17	150

In males, variant I (+ + –) was most frequent being typical for 40 (27%) of the skulls (Table 2). These are long skulls with broad foreheads and narrow faces (Fig. 4). Variant I was accompanied by 15 (10%) "satellite" skulls of variant II (+ – –) and 22 (15%) "satellite" skulls of variant III (+ – +). They are long skulls with narrow foreheads and narrow (variant II) or broad (variant III) faces. The majority of male skulls (51%, $n = 77$) were long (variants I, II and III; Table 2).

The opposite cranial type i.e. variant IV (– – +) was typical to 36 (24%) of the male skulls. They are short with narrow foreheads and broad faces (Fig. 5). The "satellite" variants, V and VI, included 15 (10%) and 22 (15%) of the skulls, respectively. The common feature of these two variants are broad foreheads, but the former (V) has narrow, while the latter (VI) broad faces. Short skulls (variants IV–VI, $n = 73$) were typical to 49% of the male skulls (Table 2).

Analyzing the results for male skulls of variants I and IV (Fig. 1 and Table 3), we observed small differences between skulls within a given variant and, simultaneously, remarkable differences between the two variants. This indicates a dichotomy of skull shapes.

Variant II — long skulls with narrow foreheads and narrow faces — dominated the female sample (42 skulls, 28%) while the remaining variants (I, III, IV, V and VI) were almost equally represented (24, 20, 23, 23 and 18 skulls, respectively). As variant II prevailed in females,

Fig. 4. Skull of a typical male of variant I.

variant V was not sufficiently numerous (only 23 skulls) to constitute the opposite set.

Discussion

Our results clearly show the existence of polarization in skull shapes in adult males of the Białowieża population of the European bison. Females of this population display only one cluster. In male bison, the standard deviation of the cranial length (BP) is 3.27% while in females it is 2.81%. The standard deviation of the forehead breadth (EctEct) in males is 5.79% and in females it is 5.59%, so the difference is small. However, in case of face breadth (SmSm) the deviation in males is 5.61%, whereas in females it is as much as 7.28%. Therefore, we conclude that it is the variability in face breadth in both sexes that results in two dominant variants in males and only one in females.

Fig. 5. Skull of a typical male of variant IV.

Consequently, adult females of the European bison of the studied population, are characterized by greater individual variability in some cranial dimensions. This is also confirmed by the results of Kobryńczuk *et al*. (2008).

Values deviating the most from 0 *in plus* and *in minus* are the cranial basal length (BP) and face breadth (SmSm), respectively (Table 3). EctEct deviates from 0 to a lesser degree. The basal length (BP) is the sum of the splanchnocranium (StP) and neurocranium (BSt) lenghts. Greater variability is typical in the former. If we also consider variability in face breadth (SmSm), which is significant in the dichotomy, we conclude that plasticity of the skull is mainly due to changes in the splanchnocranium. Since the

Table 3. Perkal's coefficients of male skulls representing variant I (1, 2, 3, 4, 5, 6) and variant IV (7, 8, 9, 10, 11, 12). Meaurements of skull: BP = Basion–Prosthion, EctEct = Ectorbitale–Ectorbitale, SmSm = Supramolare–Supramolare.

Variant I						Variant IV					
Skull no.	Age	Animal breeding number	BP	EctEct	SmSm	Skull no.	Age	Animal breeding number	BP	EctEct	SmSm
1	5	150474	+84	+18	–102	7	5	155748	–43	–2	+45
2	5	152347	+76	+12	–64	8	5	160871	–31	–56	+87
3	5	168711	+82	+38	–120	9	12	164029	–56	–36	+92
4	12	163678	+75	+20	–95	10	14	158542	–74	–1	+75
5	12	156631	+64	+74	–138	11	14	162468	–53	–11	+64
6	18	168708	+60	+49	–109	12	16	163969	–32	–22	+54

splanchnocranium length is correlated with total length of the row of premolar and molar teeth, the longer the row, the longer the splanchnocranium, and *vice versa*. In contrast, face breadth (SmSm) is limited by rows of premolar and molar teeth on both sides.

The process of dental development depends on the kind of food an animal eats — in case of the bison it is more or less lignified food. Since bison living in the Białowieża Primeval Forest occupies identical habitats, the effect of diet can be disregarded. Consequently, the existing differences in the structure of the splanchnocranium is possibly of genetic origin.

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