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Sexual dimorphism in skulls of the lowland European bison, *Bison bonasus bonasus*

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The research was conducted on 600 (311 male and 289 female) European bison skulls of the Lowland line collected between 1967 and 2006. The specimens came from the bison breeding centre in Białowieża (n = 67) and from the free-ranging population of the Polish part of the Białowieża Forest (n = 533). Two indices best differentiating male and female skulls were selected: one being the quotient of the orbital breadth EctEct and the length of the splanchnocranium StP, the second being the quotient of the neurocranium length BSt and the basal skull length BP. Using these indices we constructed an equation which produced negative values for females and positive values for males; 223 (74%) of the male skulls produced positive values consistent with sex, and 82 (26%) produced negative values, indicating female features. Those features were present mainly in skulls of young males (< 4 years old). 230 (80%) of the female skulls had shapes typical of the female sex, whereas 59 (20%) displayed male features.

Introduction

A skull grows in three directions: length, width, and height. According to Empel (1962), this process in bison lasts until they are five years old, i.e. to the moment when sutures in the splanchnocranium and neurocranium become finally ossified. At that time dimorphic cranial features in both sexes settle at an accelerated rate. The aforementioned author had at his disposal 42 skulls of captive-bred bison with known pedigree. In his material, however, there were individuals from the Lowland and Lowland-Caucasian lines. Therefore, the sample was too small and heterogeneous for precise identification of osteometric features that are different in males and females. Material used in earlier research had also been insufficient (e.g. Koch 1927, Juśko 1953, Kobryńczuk *et al*. 1990, Kobryń & Cegiełka 1994). Manifestation of bison sexual dimorphism in bones other than the skull, was investigated by Szara *et al*. (1993, 2003), Kobryńczuk (1998), and Kobryń and Kobryńczuk (1996), who studied sacrum and scapula, metapodials, and sternum respectively. Pucek (1986) presented measurements of 46 skulls of adult bison coming mainly from the free-ranging population living in the Białowieża

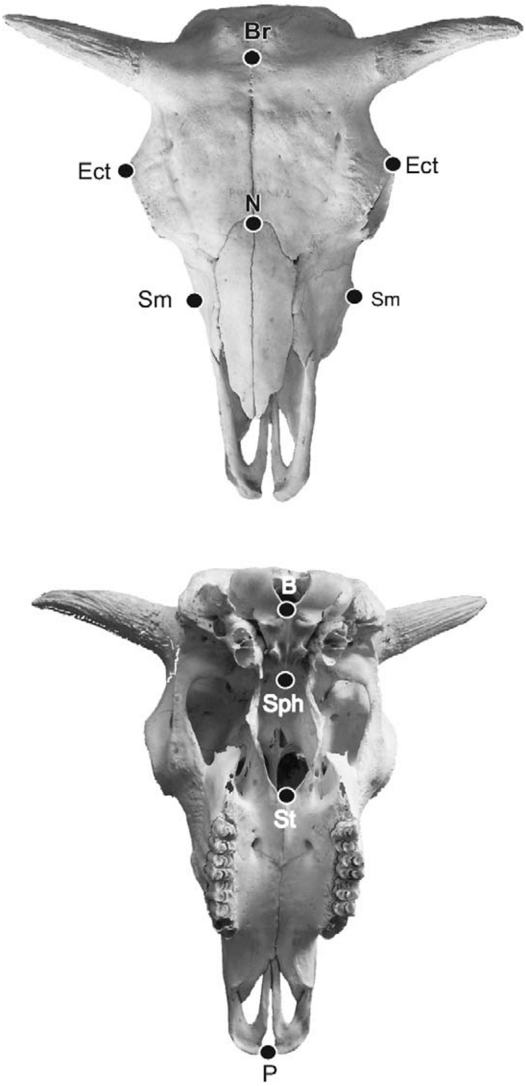

Fig. 1. Measurement points on the skull.

Primeval Forest, but he did not analyze sexual dimorphism in detail.

The aim of this paper was to determine the sexual dimorphism in bison skulls.

Material and methods

Material consisted of 600 bison skulls (311 male and 289 female) aged from one month to 27 years and belonged to the museum collection of the Mammal Research Institute of the Polish Academy of Sciences in Białowieża. Sixty-seven skulls were from individuals that lived at the enclosed bison breeding centre in Białowieża. The remaining 533 skulls belonged to individuals from a free-ranging population in the Polish part of the Białowieża Forest. The skulls were obtained between 1967 and 2006 from dead or killed animals.

Using the osteometric method of Duerst (1926), as well as instructions from Empel (1962) and Kobryńczuk (1985), seven linear dimensions of the skulls were measured (Fig. 1):

1. Basal length: Basion–Prosthion (BP).
2. Length of the splanchnocranium: Staphylon–Prosthion (StP).
3. Length of the neurocranium: Basion–Staphylon (BSt).
4. Orbital breadth: Ectorbitale–Ectorbitale (EctEct).
5. Breadth of the splanchnocranium: Supramolare–Supramplare (SmSm).
6. Height of the splanchnocranium: Staphylion–Nasion (StN).
7. Height of the neurocranium: Sphenobasion–Bregma (SphBr).

By dividing each dimension by the others we obtained indices which were then analyzed. The most discriminative indices were selected using Wilks' lambda. These indices were used to construct the following equation:

$$S = 12.25\text{EctEct/StP} + 10.60\text{BSt/BP} - 16.61 \quad (1)$$

producing negative values for females, and positive values for males. The smaller the value indicating female features and the greater the value indicating male features are, the more pronounced the dimorphism of the feature is.

Pearson's linear correlation between the animals' age and the value of the result of the equation was calculated. Our hypothesis was that sexual dimorphism should become more pronounced during growth.

Results

Two indices best differentiated between male and female skulls. One was the quotient of the orbital breadth EctEct and the splanchnocranium length StP, the second the quotient of the neurocranium length BSt and the basal length BP of a skull. These indices were used in Eq. 1. Of the 311 male skulls, the positive *S* indicating male features was obtained for 229 (73.6%), and a negative *S* indicating female features for the remaining 82 skulls (26.4%). It means that in the analyzed sample of males aged from 1 month to 21 years almost 3/4 of the individuals had skulls with typical male features and 1/4 had female-like skulls (Table 1 and Fig. 2). In the group of juvenile males — up to 4 years of age — skulls of 75 individuals (24.2% of the examined males) displayed female features. Simultaneously, among adult individuals — over 5 years of age — only 7 skulls (2%) had features typical of females.

In males, the linear correlation between age and *S* was positive and highly significant ($r = 0.333$, $p < 0.01$). It means that in all the skulls male features become increasingly pronounced with age.

Among 289 females there are comparatively more — 230 (80%) — skulls with typically female features, and fewer — 59 (20%) — displaying male features. It means that merely one out of five females had a male-like skull (Table 1 and Fig. 2).

In males, skulls with a shape typical of females appear mainly among juvenile individuals. In females, skulls with featuires typical of the opposite sex are evenly distributed among young and old individuals, hence there was no correlation between age and *S* in females.

Table 1. Cranial features of the European bison.

Age (years)	Number of male skulls			Number of female skulls		
	total	with male features	with female features	total	with male features	with female features
0.10–0.99	55	28	27	70	16	54
1.00–1.99	11	4	7	12	3	9
2.00–2.99	51	22	29	24	5	19
3.00–3.99	15	9	6	17	3	14
4	23	17	6	14	3	11
5	22	22	–	17	4	13
6	19	17	2	10	1	9
7	16	15	1	9	2	7
8	14	14	–	5	2	3
9	9	7	2	6	–	6
10	8	8	–	9	1	8
11	7	7	–	8	2	6
12	13	13	–	8	1	7
13	9	8	1	7	1	6
14	15	15	–	6	1	5
15	7	7	–	5	–	5
16	8	7	1	11	4	7
17	2	2	–	6	2	4
18	3	3	–	6	2	4
19	2	2	–	6	1	5
20	1	1	–	10	1	9
21	1	1	–	7	–	7
22				3	–	3
23				2	1	1
24				7	1	6
25				3	1	2
26				–	–	–
27				1	1	–
Total	311	229	82	289	59	230
Percentage	100	73.6	26.4	100	20.4	79.6

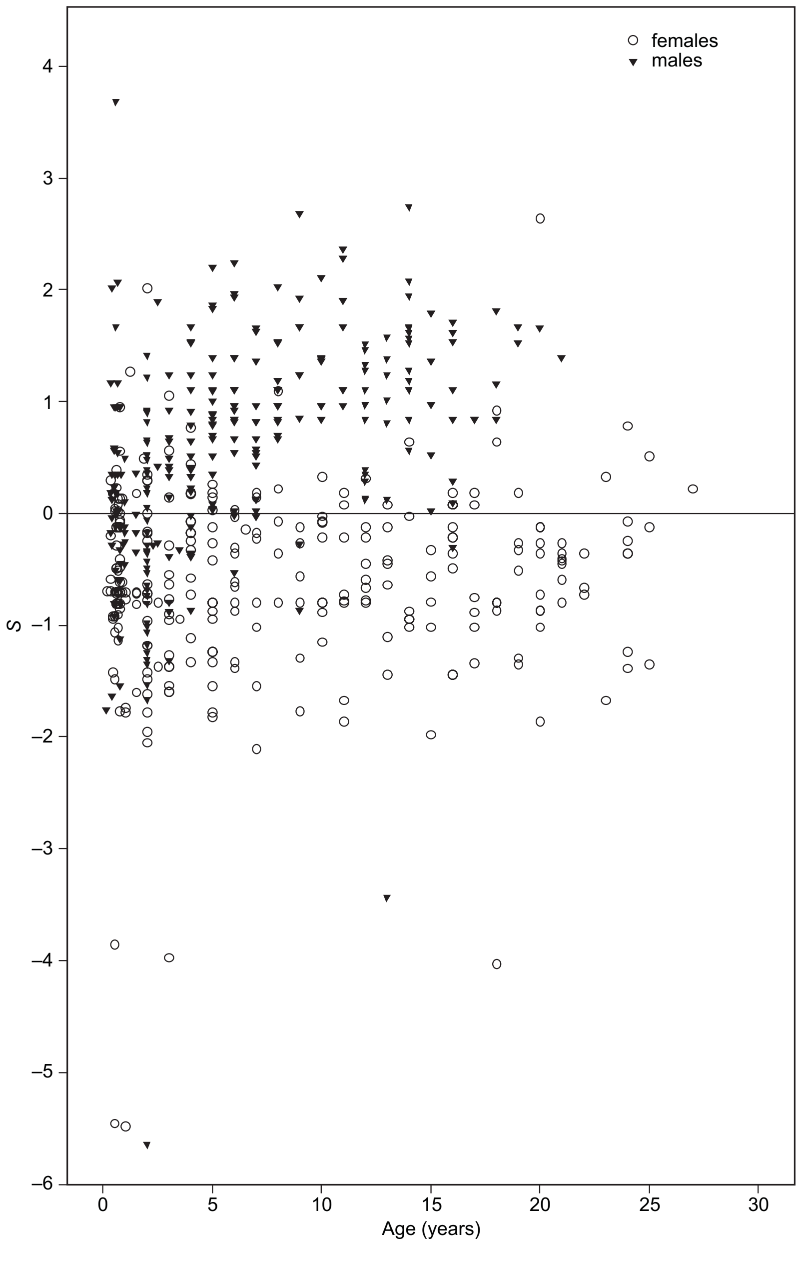

Fig. 2. Relation between age and S (*see* Eq. 1).

Discussion

The value of S (Eq. 1) is positive when the orbital breadth EctEct and length of the neurocranium BSt are comparatively large, and the length of the splanchnocranium StP and basal length of the skull BP are small. In the opposite situation, the skull is female-like (Fig. 3). The calculations show that the difference between EctEct/StP for males and females is much larger than that for BSt/BP. In spite of this, the influence of the latter index in Eq. 1 is almost equivalent to EctEct/StP, because its elements — BSt and BP — are less variable than EctEct and StP.

Henryk Bojanus (Roskosz & Empel 1965) was the first to study bison cranial morphology, and then Koch (1927), Empel (1962), and Juśko (1953) paid attention to the conspicuously large orbital breadth in bison males. There has even emerged a saying that male bison have a tele-

Fig. 3. Typical skull of a male (left) and a female (right).

scopic orbit. In males of the European bison, the shape of the cornual processes is different from that in females (Kobryń & Cegiełka, 1994).

In nearly all adult males (over 5 years of age) the shape of the skull is settled and presents typically male features.

The question arises why the skulls of some adult female bison have male characteristics, and why — in their juvenile period — the skulls did not undergo the process of restructuring in the direction typical to the sex? Firstly, we considered inbreeding as a reason. Contemporary bison of the Lowland (Bialowieża) line descend from only seven ancestors (Slatis 1960, Olech 1989). Moreover, genes of three founders (genealogical numbers 15, 16 and 147) were transmitted to the offspring from the ancestor F 524 BESTE. The share of one pair of founders — M 45 PLEBEJER and F 42 PLANTA — is the highest and amounts to over 80% (Olech 2003). The consequence of such a small number of founders is inbreeding. The world population of the European bison is highly homozygous. At the same time, the inbreeding coefficient of the Lowland bison of known pedigree is high and in the last 10 years estimated to be on average 48% (Olech 2003, 2006). Inbreeding may influence the skull shape of current female bison of the Białowieża line as is the case for individuals of the Lowland-Caucasian line. In those, the shape of the skull approximates that of one of the progenitor — the bull KAUKASUS (pedigree number 100) (Kobryńczuk 1985). Similarly, it is believed that some dental pathologies in bison of the Early Holocene prairie population result from inbred reproduction. In small, inbred bison populations, recessive features could appear in phenotypes and — in extreme cases, as a consequence of prolonged inbred chaos — could lead to increased mortality (McDonald 1981). The fact that all the female bison of the Białowieża line have copies of the same chromosome Y, originating from the same founder M 45 PLEBEJER (Olech 2006), may be connected with another fact that skulls of adult males of the Lowland line are more homogeneously built than those of females. However, the presence of male-like skulls in some mature females does not necessarily suggest pathology. This may also result from individual variability in the cranial parameters of female bison, which could indicate that the homozygosity in bison is not as high as is theoretically calculated. The results of our research show that despite persistent inbreeding in the contemporary bison population there are no traces of homogeneity. This is supported by high morphometric variability of the skull, especially among females. This seems to be a positive prognosis for the future of *Bison bonasus*.

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