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Muscle Belly Volume of the Pes Joints in the European Bison

[With 5 Tables]

The volume of bellies of muscles acting on the hock joint and digit joints was determined by means of a measuring cylinder in 25 bisons, *Bisons bonasus* (L i n n a e u s, 1758), in different age (13 males and 12 females). The largest belly was found in *m. gastrocnemius* and then in *m. flexor digitorum profundus*. Consecutive places in respect of belly size are occupied in most cases by the following muscles: *m. flexor digitorum superficialis, m. fibularis III, m. extensor digitorum longus, m. extensor digitorum lateralis, m. tibialis anterior* and *m. fibularis longus*. It was found that the ratio of bellies of antagonistic groups of muscles shows only small changes in the postembryonic development of the bison. The mass of analysed muscles is higher in males than in female of te same age.

I. INTRODUCTION

The arrangement of skeleton muscles of the European bison has been the subject of several publications. The problem was briefly outlined by W r ó b l e w s k i (1927), while P o l e i n e r (1932) was the pioneer in the description of extremity muscles in this species. The cutaneous muscles of the bison were studied by Ś w i e ż y ń s k i & P i l a r s k i (1956). A broad morphological characteristics of skeletal muscles (except from some muscles in the head region) was given in the paper by Ś w i e ż y ń s k i (1962). The externall eyeball muscles were elaborated by W ę g r z y n (1962). All these investigations, mainly descriptive, concerned shape, arrangement and attachements of particular muscles.

The present study is an attempt to determine quantitative proportions of selected skeletal muscles occurring in antagonistic groups. For this purpose muscle flexors and extensors of joints of the pes in the bison were used.

II. MATERIAL AND METHOD

The belly volumes of the following muscles were determined during the investigations: 1 — *m. fibularis III*, 2 — *m. tibialis anterior*, 3 — *m. fibularis longus*, 4 — *m. gastrocnemius*, 5 — *m. flexor digitorum profundus*, 6 — *m. flexor digitorum superficialis*, 7 — *m. extensor digitorum longus* (jointly with its deeper head — *m. extensor digiti III*), and 8 — *m. extensor digitorum lateralis* (or *m. extensor digiti IV*).

The material was obtaiened from the bodies of 25 bisons, *Bison bonasus* Linnaeus, 1758 (13 males and 12 females) of different age, starting from foetuses and newborns up to the oldest individuals (Table 1). Their age was established on the basis of the Pedigree Books of European Bisons (Żabiński, 1947—1961; Żabiński & Raczyński, 1961—1971), or of suitable protocols of bison rearing centres. In three cases (Pleśnianka, Pugorka and Plica) the preparations of limbs were fixed according to the method of Pilarski *et al.* (1967), while the remaining material was obtained from fresh corpses. In order to detect some features depending on sexual differences two comparative groups

Table 1

Presentation of the material used.

No.	Bisons name	Pedigree no.	Age Years	Months	Days
		Males			
1.	Po.	2385	—	—	—
2.	Po.	2669	—	—	2
3.	Zo.	2548	—	1	2
4.	Plechton	2402	1	1	18
5.	Plagtur	2398	1	4	18
6.	Pudzik	1876	1	9	24
7.	Zor	2405	2	—	—
8.	Pulman	2119	2	9	9
9.	Puzol	1869	4	9	4
10.	Puzot	1688	5	9	13
11.	Puzonit	1684	6	—	6
12.	No name *		12		
13.	No name *		12		
		Females			
1.	Po.	2113	—	—	—
2.	Patraca	2110	—	—	1
3.	Plikusa	2266	1	4	—
4.	Pleśnianka	857	1	7	19
5.	Pugorka	793	1	8	25
6.	Plica	797	1	11	18
7.	Polga	2115	2	11	12
8.	Puszatka	1870	4	11	14
9.	Puszkotka	1468	8	2	28
10.	Pusłonka	941	15	7	12
11.	Puborka	725	21	—	19
12.	Podwika	736	22	6	13

* Animal was taken from the free-ranging herd.

0 and I were distinguished among males and females (Table 2). Group 0 included foetuses just before birth and newborns. Group I included individuals aged from 1 year and 4 months to 4 years and 11 months. The mean age of the male individual in the first group is 2.55 years, and female — 2.43 years, hence these groups of males and females are nearly in the same age and the mean values obtained for them can be compared.

It was intended to preserve constant conditions of preparation and conservation of the studied objects, but this was not always possible. The material from bisons is in principle accidental, obtained in various circumstances.

After accurate preparation of flexors and extensors of the pes joints at the height of the leg their bellies were isolated in order to determine the volume by dipping them into a measuring cylinder. The bellies were separated from the tendons by a transverse cutting in the place of ending of muscle fibres, as clearly visible from outside.

Table 2

The list of representative of compared groups.

Group	Males	Females
0	1. Po. 2. Po.	1. Po. 2. Potraca
Avg. age, years	0.00	0.00
I	1. Plagtur 2. Pudzik 3. Zor 4. Pulman 5. Puzol	1. Plikusa 2. Pleśnianka 3. Pugorka 4. Plica 5. Polga 6. Puszatka
Avg. age, years	2.55	2.42

After measuring the volume the appearance of connective tissue and tendon stroma in individual bellies were estimated by macroscopic observation.

In the present investigations *m. interosseus medius* was not taken into account although it contains some muscle fibres (Świeżyński, 1962; Kobryńczuk, 1972) and exerts an effect of the joints of the digits. However, its muscle fibres in adult individuals are embedded with tendon mass which dominants over the contractile element and hence with the employed method the muscle could not be examined. Also *m. extensor digitorum brevis* and *m. soleus* were neglected in the investigations. In the bison these two muscles represent small structures (Świeżyński, 1962), have a negligible functional significance and their omission in this study should be without effect on the final conclusions.

III. RESULTS

In the group of flexors of the hock joint the highest volume of the belly was found for *m. fibularis III* in both sexes (Table 3). The second place in this respect is occupied by *m. tibialis anterior* in all females and males, except Zor. The third is *m. fibularis longus*, although in Zor it precedes *m. tibialis anterior*. The relative belly volumes of these muscles, in the quoted above order, amount on the average to 50 : 30 : 20 in male foetuses and newborns, and to 50 : 33 : 17 in the corresponding

Table 3

Volumes of the bellies of flexors and extensors of pes joints (cm^3).

Name of animal	*Musculi articulationis tarsi*				*Musculi articulationum digitorum*			
	flexores			*extensor*	*flexores*		*extensores*	
	m. fibularis III	*m. tibialis anterior*	*m. fibularis longus*	*m. gastrocnemius*	*m. flexor digitorum profundus*	*m. flexor digitorum superficialis*	*m. extensor digitorum longus*	*m. extensor digitorum lateralis*
Males								
Po.	12	7	5	78	37	20	15	10
Po.	25	15	10	130	55	24	20	18
Zo.	25	15	8	130	70	30	20	14
Plechton	40	14	11	200	110	50	30	40
Plagtur	70	40	27	460	220	90	75	60
Pudzik	210	65	47	810	365	220	75	100
Zor	160	25	40	750	380	190	110	90
Pulman	100	35	20	620	300	170	70	50
Puzol	130	55	40	880	400	250	80	85
Puzot	220	90	60	1130	640	300	150	160
Puzonit	230	65	60	1130	600	360	160	145
No name	280	100	75	1300	620	300	200	180
No name	290	90	78	1380	710	400	230	220
Females								
Po.	12	7	5	90	37	20	14	9
Potraca	15	11	4	85	40	24	15	11
Plikusa	45	26	14	345	156	75	42	32
Pleśnianka	50	26	20	405	195	100	55	41
Pugorka	150	50	45	675	300	180	60	75
Plica	105	42	32	640	310	155	72	71
Polga	140	40	32	590	300	140	70	55
Puszatka	170	70	50	940	460	250	150	120
Puszkotka	160	78	55	1000	520	290	140	100
Pusłonka	300	105	100	1480	780	360	240	210
Puborka	175	90	67	1070	517	260	150	125
Podwika	170	50	45	900	470	130	150	200

group of females. In all other males this ration corresponds to 61 : 22 : 17, and in females to 58 : 24 : 18. From these considerations it appears that the belly volume of *m. fibularis III* in the youngest individuals equals the sum of its two synergists. In older individuals this proportion, especially in males, shifts to the favour of *m. fibularis III*, this fact indicating a higher rate of postembryonic development of the muscle.

In group 0 the sum of volumes of hock flexor bellies is in males 1.37 times higher than in females. In group I the quotient is equal to 1.21.

The relative share of bellies of the discussed muscles in the mass of all examined muscle units is always smaller than that of the hock extensor in all individuals. It is also smaller than the share of the group of digit flexors, but higher (except two cases in males and 1 female) from the share of digit extensors (Table 4).

The mass of the belly in *m. gastrocnemius*, the main extensor of the hock joint, is conspicuously higher from the mass of its antagonists (Table 3). In males below 2 or above 7 years of age this proportion is expressed by the figure 75 : 25, while in the age group 2—7 years the ratio is more favourable to the hock extensor and amounts to 80 : 20.

Table 4

Mean relative share of muscle bellies in groups of flexors and extensors of pes joints in relation to the whole analysed muscle system.

Musculi articulationis tarsi						*Musculi articulationum digitorum*					
flexores			*extensor*			*flexores*			*extensores*		
$\bar{x}$	s	V	$\bar{x}$	s	V	$\bar{x}$	s	V	$\bar{x}$	s	V
Males											
13.8	1.6	11.6	43.1	1.7	3.9	31.6	2.1	6.6	11.6	1.8	15.5
Females											
13.0	1.2	9.2	43.9	1.7	3.9	31.8	1.5	4.7	11.4	2.0	17.5

In females below 2 years of age the ratio of the belly of *m. gastrocnemius* to its antagonists is higher (78 : 22) than in older individuals (76 : 24). Hence in all cases the extensor of the hock joint is almost three times larger than the group of flexors.

The volume of the belly of *m. gastrocnemius* in both compared groups (0 and I) is 1.18 times higher in males than in females. The percentage share of the active part of this muscle in the sum of the discussed units is the highest (Table 4).

In the group of flexors of digit joints *m. flexor digitorum profundus* has always a larger belly than that of *flexor digitorum superficialis* (Table 3). In male individuals below 2 years of age the ratio of the volume of these units amounts to 69 : 31; in older males the mass of *m. flexor digitalis superficialis* increases at a faster rate and in consequence this ratio amounts to 65 : 35. In females during the whole postembryonic development the ratio of the belly volume in both flexors of the digit joints remains fairly constant oscillating around the value of 66 : 34. In group 0 the mass of bellies of analysed muscles is 1.11 and in group I 1.18 times higher in males than in females.

The percentage proportion of flexors of the digit joints is in the discussed muscles considerable, and exceeded only by the share of *m. gastrocnemius*.

In 10 cases of males and 11 cases of females *m. extensor digitorum longus* has a larger belly than *m. extensor digitorum lateralis* (Table 3). In the remaining cases the reverse situation is observed. In the small youngest males the ratio of the volume of these bellies amounts on the average to 57 : 43, and in the remaining males it changes to the favour of *m. extensor digitorum lateralis* to reach the value of 51 : 49. In the youngest four females this ratio is 58 : 42, in the remaining ones — 52 : 48. In group 0 the sum of bellies volume of extensors of digit joints is 1.28 times higher in males than in females, and in group I this quotient is even lower and amounts to 1.13. The percentage share of bellies of both digit extensors in the all analysed muscles is the smallest except two cases in males and one in female (Table 4).

The ratio of the volume of digit flexors to extensors is rather high. For the 5 youngest and 2 oldest males it amounts to 71 : 29 on the average, and in the remaining individuals — 77 : 23. In females only in the case of foetuses and newborns this ratio is analogous to the youngest and oldest males (71 : 29), while in the remaining 10 females it is equal to 74 : 26.

In the compared groups the sum of the belly volume of all analysed muscle units is alvays higher in males than in females (1.20 times in group 0, 1.18 times in group I).

It should be noted that the mass of the discussed muscles is not proportional to age. Among males the example of Pulman may be given: in this case the total mass of bellies of analysed muscles is smaller that of younger Zor (Table 3). The same can be said about Puzonit, and among females about Plica, Polga and Podwika.

When the discussed muscles are arranged in the order from the smallest to the largest belly the following picture is obtained for both sexes: 1 — *m. gastrocnemius*, 2 — *m. flexor digitorum profundus*, 3 — *m. flexor digitorum superficialis*, 4 — *m. fibularis III*, 5 — *m. extensor digitorum longus*, 6 — *m. extensor digitorum lateralis*, 7 — *m. tibialis anterior*, 8 — *m. fibularis longus*.

Only the first two muscles hold their position in all cases (Table 5), while other muscles may shift forward or backward in the order. The highest fluctuations were found in both sexes for *m. extensor digitorum longus* (Table 5), which in 16% of males occupies 4th position in respect of belly size, in 54% it is on the 5th place and in 30% on 6th place (one individual corresponds to approximately 8% of the whole material, both in males and females).

In 92% of females *m. flexor digitorum superficialis* occupies 3rd position in respect of size (Table 3), and in 8% as far as 6th position. The latter value was found in 23 years old Podwika, in which this muscle showed signs of underdevelopment. In effect in this individual hypertrophy of *m. flexor digitorum profundus* was observed, and curiously enough this was accompanied by shifting *m. extensor digitorum lateralis* to 3rd position from 6th one found in most cases of bisons.

Table 5

Arrangement of pes muscles in order of decreasing masses of their bellies.

Name of muscle	Position							
	1	2	3	4	5	6	7	8
	Per cent of cases							
Males								
1. *m. gastrocnemius*	100							
2. *m. flexor digitorum profundus*		100						
3. *m. flexor digitorum superfic.*			92	8				
4. *m. fibularis III*			8	68	16			
5. *m. extensor digitorum longus*				16	54	30		
6. *m. extensor digitorum lat.*					30	62	8	
7. *m. tibialis anterior*						8	84	8
8. *m. fibularis longus*							8	92
Females								
1. *m. gastrocnemius*	100							
2. *m. flexor digitorum profundus*		100						
3. *m. flexor digitorum superfic.*			92			8		
4. *m. fibularis III*				75	25			
5. *m. extensor digitorum longus*				25	67	8		
6. *m. extensor digitorum lat.*			8		8	84		
7. *m. tibialis anterior*							92	8
8. *m. fibularis longus*							8	92

IV. DISCUSSION

The belly consists of not only muscle fibres but also of connective tissue network, part of the tendon forming characteristic streaks, as well as vessels and nerves. The quantitative proportion of muscle fibres to non-contractile elements may be different in particular muscles, hence the muscles can be divided into dynamic and statodynamic (Klimov, 1960). The direction of the course of muscle fibres is a characteristic feature, while their number is proportional to effective work of the muscle. Due to this fact the volume or mass of all constituents of a belly are not strictly proportional to the energy potential of the muscle but give only a rough approximation.

A beam, corresponding to the skeleton of the pes, behaves as a single--arm lever during the action of hock flexors. The axis of the turn goes through *articulatio tarsocruralis*, while *tuberositas ossis metatarsalis III* corresponds to the point of force application, and phalanges to the point of force resistance. These two points lie on one side on the axis of the analysed lever.

During contraction of *m. gastrocnemius* the same beam behaves as two-armed lever, *articulatio tarsocruralis* being also its axis. The point of force application of *m. gastrocnemius* is on the *tuber calcanei*, above the axis of the turn, while the point of force resistance corresponds to *facies flexoriae* of both third phalanges lying below the axis of turn of this lever.

From author's investigations it appears that in a close approximation the belly mass of *m. gastrocnemius*, the main hock extensor, is three times higher than that of its antagonists. This fact does not mean however, that the bison puts only three times more strength in the extension of this joint than in its bending. Other muscles cooperating with *m. gastrocnemius* should be also taken into consideration. Such function is fulfilled mainly by two flexors of digits in those situations when extension of the hock joint is accompanied by bending of digit joints, as it always occurs during extension of a limb during walking. On the other hand, during pulling out of the foot from swampy ground or deep snow the extension of the hock joint takes place without help of flexors of digits. Thus when two muscles of digit flexors cooperate with *m. gastrocnemius* the ratio of mass of hock joint extensors to flexors changes from 3 : 1 (in both sexes) to 5.4 : 1 in males and 5.8 : 1 in females.

In bisons, similarly to other *Paraxonia*, the hock consists of two joints almost equivalent in respect of mobility (Kobryńczuk, 1972). These two joints are: *articulatio talocruralis*, the turn axis of which was considered as the axis of the analysed lover, and *articulatio intertarsea proximalis*, formed mainly by *trochlea distalis tali* and *os centroquartale*. When the second joint operates the axis of the discussed lever moves in the direction of digits. This elongates the force arm of the hock extensor, shortens the force arm of flexors and the construction of the whole simple machine of the foot becomes more favourable to the hock extensor. It is difficult to establish in which conditions the *Paraxonia* utilize *articulatio intertarsea proximalis*. Most likely the functioning of this joint is rather limited during normal walking but becomes important in such situations as fighting with antlers in *Ruminantia* or burrowing in *Suidae*.

The participation of digit muscles in the biomechanics of digits is easier for the analysis since apart from *m. interosseus medius* they do not cooperate with other muscle groups in the pelvic limb. In relation to digit muscles the phalanges behave as one-arm levers. Since none of the digit flexors end on the proximal phalanges, *articulationes metatarsophalangeae* are bended by the pressure of *ossa sesamoidea phalangum proximalium* exerted from the back by the tendons of these flexors during their contraction.

The relation of belly volumes of the analysed muscles, both within groups and between groups, oscillates around rather constant values during the postembryonic life of the bison. This indicates that the effort related to the body locomotion throughout the life exerts almost identical effect on the development of antagonistic groups of muscles. Apart from few exceptions, such as *m. interosseus medius*, the number of myocytes remains constant during the postembryonic life of the animal (E w y, 1969). They can only change their mass in relation to work or training. Their initial stage of development observed in the newborns gradually increases in proportion to functional tasks imposed upon muscles.

Analysing small variations in volumetric relations of the studied muscles it can be observed that *m. fibularis III* prevails in older age over its two synergists. Also *m. flexor digitorum superficialis* increases the mass of its belly in a higher degree than *m. flexor digitorum profundus* cooperating with it. Moreover, the development of *m. extensor digitorum lateralis* is more favourable in comparison with *m. extensor digitorum communis.*

When comparing the relation of volume of antagonistic muscle groups acting on the hock *m. gastrocnemius* in males aged 2—7 years prevails over its antagonists in a higher degree than other muscles. The group of digit flexors increases its mass in the postembryonic life of males more considerably than the group of digit extensors. The reverse situation is observed in females.

However, all these fluctuations in relative values are small. It can be supposed that some muscle units are inhibited in their development by limited space (*m. tibialis anterior, m. fibularis longus, m. extensor digitorum longus*), other are stimulated by a particular type of work such as the fight of males with antlers (*m. gastrocnemius, m. flexor digitorum superficialis*).

On transverse and longitudinal sections of bellies of the analysed muscles it was found that the tendon matrix is more developed in these muscles which are situated on the back side of the leg. This might indicate that such muscles as *m. gastrocnemius* and *m. flexores digitorum* have rather statodynamic character and participate in the specific fixative system of the pes joints of the bison.

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OBJĘTOŚĆ MIĘŚNI STOPY ŻUBRA

Streszczenie

Zbadano przy pomocy menzurki objętość brzuśców mięśni obsługujących staw stępowy i stawy palców 25 żubrów *Bison bonasus* (L i n n a e u s, 1758) w różnym wieku (13 samców i 12 samic). Stwierdzono, że największy brzusiec posiada *m. gastrocnemius* a następnie *m. flexor digitorum profundus*. Kolejne miejsca pod względem wielkości brzuśców zajmują najczęściej następujące jednostki: *m. flexor digotorum superficialis, m. fibularis III, m. extensor digitorum longus, m. extensor digitorum lateralis, m. tibialis anterior* i *m. fibularis longus*. Stwierdzono, że stosunki objętości brzuśców mięśni zespołów antagonistycznych wykazują w życiu pozapłodowym żubra niewielkie wahania. Masa analizowanego umięśnienia jest zawsze większa u samców niż u rówieśnych samic.