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Is baculum size dependent on the condition of males in the polecat *Mustela putorius*?

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Abstract. The allometry between baculum size, body size and body condition was studied in the polecat (*Mustela putorius*). The aim of this study was to investigate whether penis size is dependent on body size. We also calculated the correlation between the size of the baculum and body condition. Our research was based on 107 bacula and skulls from a museum in Slovakia. Individual traits describing the sizes of the body, skull and baculum were moderately to strongly correlated (r between 0.16 and 0.72). Condition was expressed as residuals from a regression analysis of body mass on structural body size. The size of the baculum was correlated with other measurements of body size and with body mass. Analysis revealed that the strongest positive correlation with condition of males was with the size of the baculum. Because the baculum varies between individuals and grows throughout life, the relationship between its size and condition confirms that the baculum may be a suitable indicator of male quality.

Key words: allometry, body size, *os penis*, mustelids

Introduction

The penis bone (also called baculum or *os penis*) is a heterotopic bone which occurs in mammal orders such as carnivores, bats, insectivores and rodents and in some primates. There is no single interpretation of baculum function. For example, some authors suggest that the baculum serves a mechanical role, giving additional support during erection (Kelly 2000). Baryshnikov et al. (2003) suggested that the baculum plays a structural and functional role in protecting the urethra. Additionally, the baculum can also stimulate the reproductive tract of the female during copulation (Dyck et al. 2004, Krawczyk & Malecha 2009).

The shape and size of the baculum vary greatly across species, even in closely related species and therefore have been widely used as diagnostic traits in taxonomy (Hosken et al. 2001, Baryshnikov et al. 2003, Ramm 2007, Malecha et al. 2009). Some authors link this variation to reproductive behaviour. Analysis of the baculum in carnivores (excluding Feliformes) suggested that it tends to be bigger, and

genital morphology more complicated, in species with a multi-male mating system (Ramm 2007). However, it is well known that the baculum also varies markedly between individuals within a species (Reinwaldt 1961, Miller & Burton 2001, Dyck et al. 2004, Ramm et al. 2009). The reason for such morphological differences both between and within species is not clear and two primary hypotheses exist (Lüpold et al. 2004). One is that variation is simply a pleiotropic by-product of phylogenetic divergence. The other group of hypotheses suggests that sexual selection may drive this diversity (Miller et al. 1999, Kelly 2000, Baryshnikov et al. 2003, Ramm 2007). For example, baculum morphology affects the site of sperm deposition or the degree of stimulation of the female reproductive tract during copulation. Hence, the size of the structure may be informative about male quality and useful to females in mate choice (Miller & Nagorsen 2008).

The polecat (*Mustela putorius* Linnaeus, 1958) occurs throughout most of Europe and inhabits many different

habitats, including human settlements (Blandford 1987). In Slovakia it is still a common mustelid and often regarded as a pest. Presently, the species can be hunted in winter (Adamec 2003), but in the past it could be hunted all year round.

The size of the baculum varies between individuals and the bone grows throughout life. The energetic cost of this growth, as well as risk of infection or breakage of the baculum suggests that it is an adaptive trait (Larivière & Ferguson 2002) and that a good physical condition of the male undoubtedly influences the development of the penis bone.

The aim of our study was to analyze relationships between baculum size and body measurements. We also investigated if the size of the baculum was correlated with body condition. Our predictions are that males of better body condition should have bigger

bacula because of the direction of sexual selection which results in morphological adaptation to achieve reproductive success.

Material and Methods

Polecat bones used in this work come from the collection of the Department of Natural History, Šarišské Museum, Bardejov in Slovakia. The polecats were collected by the hunter Tibor Weisz in NE Slovakia, near the town of Bardejov (49°03' N-49°27' N; 20°30' E-21°47' E) in the transition region between the Eastern and Western Carpathians. Polecats were collected during the years 1958-1978, in all months, with a peak between November and March. All specimens were weighed (accuracy 0.1 kg) and measured (accuracy 0.1 mm) by the collector immediately after shooting. He recorded the following variables: body mass (g), body length

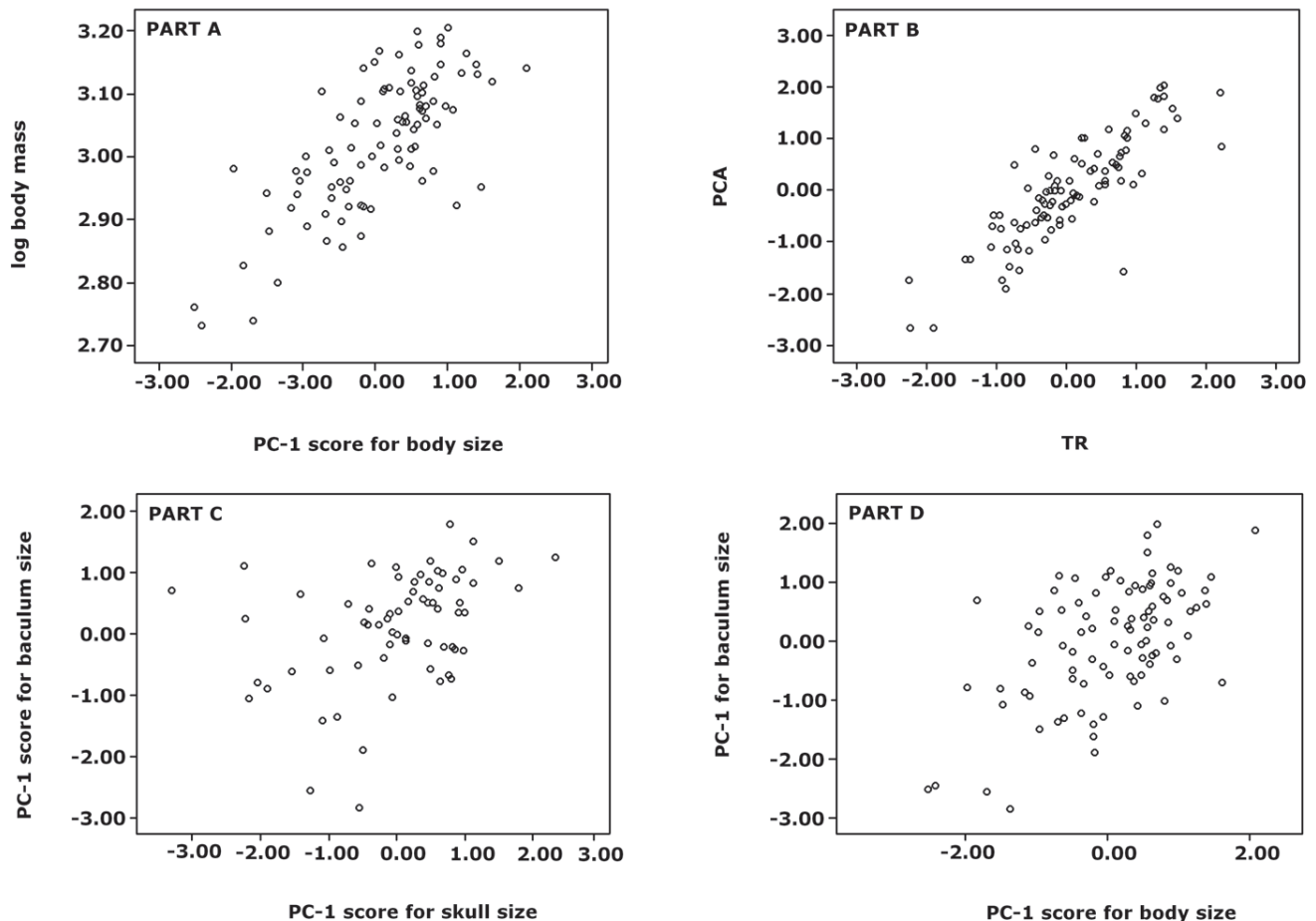


Fig. 1. The relationships between: log body weight and the first principal component from body measurements (PC-1 score for body size) Part A, indices of body condition of polecats calculated using residuals from the regression of log body mass on the first principal component of body measurements (PCA) and a traditional method (TR) Part B, the first principal components derived from baculum (PC-1 score for baculum size) and skull measurements (PC-1 score for skull size) Part C and between the first principal components derived from baculum (PC-1 scored for baculum size) and body measurements (PC-1 score for body size) Part D.

(mm), tail length (mm), foot length (mm) and ear length (mm). Shortly after shooting, the crania and the bacula were removed from the body, immersed into 5 % ammonia solution for at least 24 hours to soften the flesh and then boiled, brushed clean and bleached with hydrogen peroxide. The crania were then washed in water, air-dried and kept in museum boxes.

Bacula and skulls were measured according to standard procedures. We measured bacular length, breadth of baculum base and breadth of bacular apex (after Walton 1968). The following skull measurements were taken: condylobasal length (CbL), braincase breadth (BcB), zygomatic breadth (ZyB), braincase height (BcH), postorbital breadth (PB), mandible length (MdL), height of the mandibular ramus (HRM). Male polecats were aged according to the size and shape of the baculum (Sumiński 1968, Walton 1968) and cranial traits (Buchalczyk & Ruprecht 1977). All measurements were made with an electronic caliper (accuracy 0.1 mm) and all measurements, both for cranial as well as baculum, were highly repeatable (differences between two measured person were very small, not systematically biased to one person and statistically non significant; t-paired test; T value > 0.737 in all cases). For analyses, only data obtained from adults were used (n = 107). However, because of

Table 1. Descriptive statistics of measured traits.

Measured trait	Mean	SD	n
Body			
Body mass (g)	1083	254	102
Body length (mm)	399.0	24.6	101
Tail length (mm)	141.8	13.2	98
Foot length (mm)	59.48	3.70	100
Ear length (mm)	26.38	2.47	101
Skull			
CbL	66.46	3.04	82
BcB	30.47	1.09	79
ZyB	40.92	2.43	73
BcH	25.02	1.30	83
PB	17.32	0.91	84
MdL	41.66	2.30	92
HRm	20.65	1.58	93
Baculum			
Length	39.50	4.15	99
Breadth	4.87	1.44	100
Distal width	5.18	0.58	100

some problems with the material (e.g. broken bones), sample sizes differed slightly between analyses (see also comments in Demuth et al. 2009).

Because features describing body size, baculum size and skull size are strongly inter-correlated (see Tables into Results section), to reduce number of multiple comparisons and to explain overall body size parameters we performed principal component analysis (PCA) with VARIMAX rotation for all three datasets. The dataset for body measurements PCA excluded body mass, because it changed seasonally and daily and generally is rather a measure of condition than of structural body size (Blandford 1987, Piersma & Davidson 1991, Brzeziński & Romanowski 1997). Before analysis, measurements were log transformed to reduce intra-sample variation and to improve normality.

Body condition was estimated as the residuals from a regression of log body mass on the first principal component from the body measurements. This was compared to the alternative traditional measure based on the residuals from a regression of log body mass on log body length.

Results

Descriptive statistics

The descriptive statistics of studied traits are presented in Table 1. The first principal components based on body measurements (PC-1 score for body size), baculum measurements (PC-1 score for baculum size) and skull measurements (PC-1 score for skull size) explained 59.0, 67.0 and 69.7 % of the total variance in their datasets, respectively. Body mass was highly positively correlated with the first principal component from body measurements ($r = 0.696$, $n = 94$, $P < 0.0001$; Fig. 1). The resulting values of body condition were correlated positively with the traditionally used condition index (Blackwell 2002) ($r = 0.843$, $n = 94$, $P < 0.001$; Fig. 1). The index of body condition ranged from -2.68 to 2.02 and averaged -0.00 ± 0.99 ($n = 94$). The descriptive statistics of studied traits are presented in Table 1.

Correlation between variables

Variables within the three groups of measurements (body, skull, baculum) were strongly correlated (Tables 2, 3 and 4), and majority of them were still strongly significant after Bonferroni correction for multiple comparisons (details are provided in table headings).

Correlations between body condition and baculum size

Baculum size was correlated with other metrics describing the size of males (Table 5, Fig. 1). Body condition of individuals showed the strongest correlation

Table 2. Correlation matrix of the body measurements. Correlation coefficients upper value, significance lower value, values significant at $P < 0.05$ are emboldened.

	Body length	Tail length	Foot length
Tail length	0.440 0.0001	-	-
Foot length	0.690 0.0001	0.598 0.0001	-
Ear length	0.190 0.059	0.221 0.03	0.454 0.0001

Table 3. Correlation matrix of the skull measurements. Correlation coefficients upper value, significance lower value, values significant at $P < 0.05$ are emboldened. All correlations are also significant after Bonferroni correction for multiple comparisons.

	CbL	BcB	ZyB	BcH	PB	MdL
BcB	0.668 0.0001	-	-	-	-	-
ZyB	0.708 0.0001	0.700 0.0001	-	-	-	-
BcH	0.690 0.0001	0.659 0.0001	0.643 0.0001	-	-	-
PB	0.299 0.0001	0.494 0.0001	0.469 0.0001	0.425 0.0001	-	-
MdL	0.887 0.0001	0.677 0.0001	0.712 0.0001	0.680 0.0001	0.317 0.0040	-
HRM	0.825 0.0001	0.700 0.0001	0.682 0.0001	0.683 0.0001	0.380 0.0001	0.767 0.0001

Table 4. Correlation matrix of the baculum measurements.

	Length	Width
Width	0.756 0.0001	-
Distal width	0.508 0.0001	0.339 0.0001

Table 5. Correlations between the three first principal components from baculum, skull and body measurements and body condition. Correlation coefficients upper value, significance lower value, values significant at $P < 0.05$ are emboldened.

	PC1_baculum	PC1_skull	PC1_body
PC1_skull	0.431 0.0001	-	-
PC1_body	0.559 0.0001	0.724 0.0001	-
Body condition	0.394 0.0001	0.261 0.035¹	0.016 0.877

¹ This correlation is non-significant in case of use of Bonferroni correction for multiple comparisons.

with baculum size (Table 5, Fig. 2). Correlation with body condition was even more significant when the analysis included both first principal components from body measurements and skull measurements (partial correlation $r = 0.517$, d.f. = 59, $P < 0.0001$).

Discussion

As predicted, we found correlations between baculum size and other body size traits (both body measurements and cranial bones). However, we must first ask whether the data obtained from museum collections are reliable? There are several possible sources of error that should be considered. There is a possibility that smaller penis bones could have been damaged during preparation or storage at the museum. To minimise such errors we only analyzed bones from adult specimens.

We showed a correlation between the size of the baculum and other body dimensions in the polecat. Moreover, baculum size was positively correlated with an index of male condition. Some authors consider that larger (especially heavier) males are favoured by sexual selection, i.e. mate with more females (e.g. De Marinis 1995). Covering long distances in search of mates and a violent and prolonged sexual act (as in polecats) are very energy-expensive processes, and can cause a significant loss of fat reserves (Brzeziński & Romanowski 1997).

Females of many mammal species choose their mate during copulation through assessment of the penis, which carries information about the characteristics of the male (Miller & Burton 2001). The size and shape of the baculum probably affect the structure of the

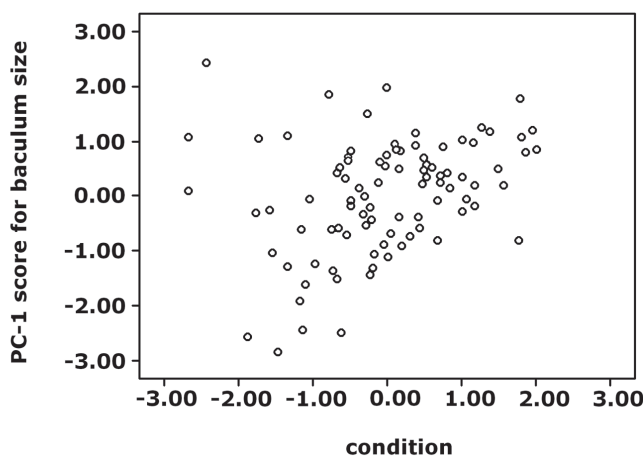


Fig. 2. The relationship between the first principal component derived from baculum measurements (PC-1 score for baculum size) and body condition.

penis, hence females could detect a different stiffness, size and shape of penis during copulation. This suggests an important role in intraspecific selection during copulation. Moreover, the length and stiffness of the penis aid penetration and sperm deposition and the morphological characteristic of the distal tip assists in removing or damaging sperm of previous males during copulation (Ferguson & Larivière 2004, Eberhardt 2009, Tasikas et al. 2009).

Mustelidae are a group where a multi-male mating system occurs in many species. This is one of the drivers of sperm competition, because it creates circumstances for the development of mechanisms to facilitate postcopulation male competition. Therefore, if a trait is under strong sexual selection, is not surprising that there occurs a limit to baculum growth. The baculum in some cases could be a burden for an animal and there are numerous cases of bone fractures, which may lead to complications, even death (Reinwaldt 1961, Kierdorf 1996). Since it is known that holders of exaggerated

features achieve success, they are preferred by females as breeding partners (Zahavi 1975). This risk of losses, for example fracture of the baculum, are outweighed by the benefits of increased reproduction caused by a greater attractiveness to the opposite sex (Radwan 1996).

Evidence that females choose partners during mating can be shown by the characteristic aggressive behaviour of males during copulation by polecats (Brzeziński & Romanowski 1997). Aggression during copulation in relation to females should inevitably lead to the development of an internal mechanism for selection of the best partners by females (Miller & Burton 2001). There are a few suggestions that the length of the baculum is one of the elements of an arms race in sperm competition. Longer penis size can optimize the deposition of the ejaculate and provide more stimulation to the female reproductive system affecting the transport of sperm (Ramm 2007). Males in better condition have bigger bacula which confirms that this bone is potentially a good indicator of viability and quality in males. Hence, females can assess male quality during copulation, especially when visual and olfactory experience is reduced. We should, however, take into account that previous studies were (like the present work) correlational and to confirm most of the results it would be necessary to carry out controlled experiments to show a real impact of the condition and baculum size on the reproductive success.

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