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Research paper

Are size, variability and allometry of the baculum in relation to body length signals of a good condition in male weasels *Mustela nivalis*

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ABSTRACT

In this study we investigated the allometry and variation in the baculum of the weasel *Mustela nivalis* and compared it with head-and-body length, which is not involved in reproduction. The females of many mammalian species select mates in part during intromission and evaluate attributes of the penis that are informative in regard to a male's size or other characteristics. If females benefit by mating with large males by estimation of the size of the male's penis, then positive allometry between penile size relative to body size is realized. Small residuals in the allometric regression may evolve. In species with pre-copulatory selection (manifested as male-biased sexual size dimorphism) baculum allometry may be isometric or exhibit negative allometry. Weasels exhibit a sexual-size dimorphism, with males being larger, and as a result we predicted that baculum size would exhibit negative allometry or isometry. We also tested the hypothesis that baculum size is positively correlated with adult body size and may be used as a reliable indicator of good genes for female mates during breeding. Negative allometry and a relative weak relationship between baculum size and head-and-body length suggest that the baculum is under stabilizing selection for optimal baculum size. We assumed that penile width as related to bacular thickness could be a reliable indicator of quality during copulation.

1. Introduction

Males from the family Mustelidae have been shown to have a heterotopic bone in their penis called a baculum or penis bone (Abramov, 2002; Baryshnikov et al., 2003; Miller and Nagorsen, 2008; Malecha et al., 2009; Krawczyk et al., 2011; Schulte-Hostedde et al., 2011; Vercillo and Ragni, 2011). Bacular morphology in the majority of genera of Mustelidae has been described in several studies (Baryshnikov and Abramov, 1997, 1998; Abramov and Baryshnikov, 2000; Baryshnikov et al., 2003) which proved that the bacula of the Mustelidae tends to be rather simple in structure, with certain more complex projections at the tip, and that bacular length was relatively constant across the whole family of mustelids.

Ramm (2007) showed that the baculum in carnivores (excluding the feliforms) suggests that it tends to be bigger and that genital morphology is more complicated in species with a multi-male mating system. Species of the family Mustelidae are a group in which a multi-male mating system occurs in many species, with only some species having a tendency towards monomorphism, e.g. the European badger *Meles meles* (Lariviére and Jennings, 2009). According to Krawczyk et al. (2011), this is one of the drivers of sperm competition, because it creates circumstances for the development of mechanisms that facilitate post-copulation male competition. Similarly, if a trait is under strong sexual selection, it is not surprising that a limit in baculum growth is found. Nevertheless, based on several studies of baculum size (e.g. Miller et al., 1998, 1999, 2000; Oosthuizen and Miller, 2000; Miller and Burton, 2001; Ramm, 2007; Miller and Nagorsen, 2008; Kinahan et al., 2008 etc.), it has been shown that current evidence on sexual selection in the baculum is limited.

The females of many mammalian species select mates in part during intromission and evaluate the attributes of the penis that are informative about a male's size or other characteristics (Dixson, 1995; Miller and Burton, 2001; Miller and Nagorsen, 2008; Demuth et al., 2009). Nevertheless, these cases occur mainly when females are unable to choose mates before copulating. If females can benefit by mating with large males and can estimate the size of males by the size of the penis, then a positive allometry of penile size relative to body size as well as small residuals in the allometric regression may evolve. Allometry describes the relationship of components of an organism with a change in overall body size and has become the focus of numerous studies on the evolution

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of genitalia (Kinahan et al., 2008). Lüpold et al. (2004) state that sexually selected traits often show positive allometry and exhibit high degrees of phenotypic variation as a result of directional sexual selection. Males in better condition have bigger bacula, which confirms that this bone is potentially a good indicator of viability and quality in males (Demuth et al., 2009; Krawczyk et al., 2011). Baculum size is associated with reproductive behaviour and the mating system (Miller et al., 1998, 1999, 2000; Oosthuizen and Miller, 2000; Miller and Burton, 2001; Ferguson and Lariviére, 2004; Ramm, 2007). Ferguson and Lariviére (2004) showed that the mammalian penis bone likely plays a larger role in monogamous (e.g. Canidae) and multi-male mating systems (e.g. Mustelidae) and can be used as an indicator of genetic quality in males.

Miller and Burton (2001) noted several cases when isometry and a wide scatter about allometric regression (of penile size to body size) might be expected. It is for instance, when choice of mate by females is independent of penile size or if males/females vary in their mating strategies. Similarly, baculum allometry may be isometric or exhibit negative allometry in species with pre-copulatory selection (manifested as a male-biased sexual size dimorphism) over post-copulatory selection (Schulte-Hostedde et al., 2011).

In our study we investigated the allometry and variation in the baculum of the weasel (*Mustela nivalis*) and compared it with a somatic element not involved in reproduction: head-and-body length. We also tested the hypothesis that baculum size is positively correlated with adult body size. If it is true, then bacular size may be used as a reliable indicator of good genes to female mates during breeding and an indicator of male quality, as suggested by Miller and Burton, 2001; Lüpold et al., 2004; Kinahan et al., 2008; Krawczyk et al., 2011. We also predict isometry or negative allometry, because in the weasels occurs male-biased sexual-size dimorphism.

2. Material and methods

The penile bones of the weasel *Mustela nivalis* used in this study were from the collection of the Department of Natural History at the Saris Museum in Bardejov, Slovakia. The important feature of these datasets is that all of the specimens were collected and evaluated by the same person "Tibor Weisz", the main collector at the museum. The second advantage is the fact that all the individuals were hunted from several localities near the town of Bardejov, i.e. from one "small" area in north-eastern Slovakia, (49° 17′N, 21° 17′E, Western Carpathians) in the years 1961–1982. Information about the locality, date and age was obtained from the catalogue and protocol cards attached to the evidence in the museum collections (see Hromada et al., 2015). Nevertheless, according to Krawczyk et al. (2011), we asked whether the data obtained from the museum collections were sufficient for our analysis. Several possible sources of errors were considered. As a result, smaller penis bones (from younger individuals; damaged during preparation or storage) were excluded and only the data obtained from adult males were used for the evaluation (n = 285).

Specimens were assigned to the age class adult based on baculum weight and the presence of a baculum protuberance (van Soest and van Bree, 1970; Grue and King, 1984; Elsasser and Parker, 2008).

The descriptive statistics of the studied variables are presented in Table 1. The length of the penis bones were taken with a digital calliper with the accuracy of 0.01 mm, and their weight was taken with digital scales to the nearest 0.01 g. All specimens were measured and evaluated as recommended by several authors (Malecha et al., 2009; Čanády, 2013; Čanády and Čomor, 2013, 2015). The measurements collected are described in Fig. 1a–b and include: LeBa – length of baculum (1–1′), DvThp – dorsoventral thickness

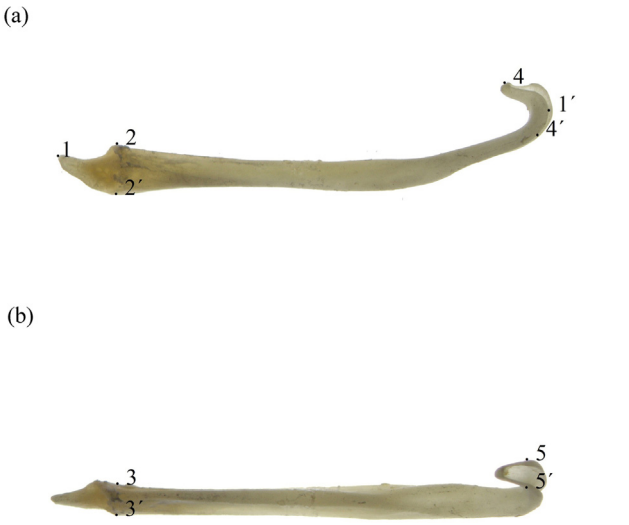

Fig. 1. Baculum measures used in the study. Lateral (a), dorsal (b) views of weasels, *Mustela nivalis*. Measures: LeBa – length of the baculum (1–1′), DvThp – dorsoventral thickness of proximal end (2–2′), LtLtThp – laterolateral thickness of proximal end (3–3′), SH – length of distal tip i.e. hook (4–4′), LtLtThH – laterolateral thickness of distal tip i.e. hook (5–5′).

of the proximal end (2–2′), LtLtThp – laterolateral thickness of the proximal end (3–3′), SH – size of the distal tip, i.e. hook (4–4′), LtLtThH – laterolateral thickness of the distal tip, i.e. hook (5–5′) and finally WeBa – weight of the baculum. We also used data from two somatic measurements: body weight (W) and head-and-body length (HBL) obtained from the protocol cards attached to the evidence in the collections.

The obtained dataset (untransformed data) was evaluated using the following statistical parameters: minimum and maximum (min–max), mean (M), standard deviation (SD), standard error of the mean (SE) and coefficient of variation (CV). Moreover, it should be also noted that the mass is a cubic variable and length is linear. Therefore, we compare the cube root of bacular mass with bacular length measures to assess relative variation for these variables. Normal distribution was tested by three normality tests (the Kolmogorov-Smirnov test, the D'Agostino-Pearson omnibus K^2 test and the Shapiro-Wilk *W*-test). Moreover, morphometric variation was examined by means of multivariate methods (Principal component analysis – PCA). The correlations between the baculum measurements and body size (weight and head-and-body length) were analysed using the Pearson correlation coefficient (r_p).

Before our allometry analysis, the measurements were $\log_{10}$ transformed to reduce the intra-sample variation and to improve the normality. We investigated the allometric (log-log) relationships in two steps. First, ordinary least squares regression (OLS) was used to determine whether the slopes differed from zero. If the slopes were significant, we proceeded by using the reduced major axis regression (RMA) to test for deviations from isometry. According to Miller et al. (2000), Schulte-Hostedde et al. (2011) the RMA regression is generally preferable to simple linear regression in allometric studies because there is no distinction between the explanatory and response variables and because all variables are measured with an error. Moreover, above-mentioned authors showed that both types of regression are identical when $r = 1$, because in the reduced major axis the regression slope = b/r where b is the slope in the simple linear regression.

All analyses were performed using MS Excel 2003 for Windows XP and the statistical analysis system GraphPad Prism, version 5.01 (GraphPad Software, Inc., San Diego, California, USA). The ordinary least square (OLS) regression and the reduced axis major (RMA)