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Baculum variation and allometry in the muskrat (*Ondatra zibethicus*): a case for sexual selection

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Abstract Sexual selection is a powerful force that influences the evolution of a variety of traits associated with female mate choice and male–male competition. Although other factors have been implicated, sexual selection may be particularly important in the evolution of the genitalia. Traits under sexual selection typically have high phenotypic variance and positive allometry relative to non-sexual traits. Here, we test the hypothesis that the baculum (os penis) of the muskrat (*Ondatra zibethicus*) is under sexual selection by examining phenotypic variance and allometry relative to non-sexual traits. Muskrats were sampled from Ontario, Canada, and a variety of traits measured. Measurements included baculum length and width, and three non-sexual traits (skull length, skull width, hind foot length). We used coefficient of variation (CV) and allometric slopes calculated using reduced major axis regression to test our hypotheses. Baculum traits had significantly higher CV's relative to non-sexual traits. Baculum traits also showed positive allometry, whereas all non-sexual traits had negative allometric relationships. In addition, baculum width had higher CV's and steeper allometric slopes than baculum length, indicating that, in muskrat, baculum width may be more influenced by sexual selection than baculum length. Positive allometry of the baculum is consistent with other examples of mammalian genitalia, but contrasts with negative allometry found in many insects. Other examples of positive allometry and high phenotypic variance of the baculum have suggested that females may use the baculum as an indicator of male quality. "Good genes" indicator traits may be particularly important in species that mate in an environmental context that prohibits female assessment of male quality. Muskrats mate aquatically, and thus females may be unable to properly assess males prior to copulation.

Keywords Allometry · Good genes · Genitalia · Mammal · Phenotypic variance

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Introduction

Sexual selection is a powerful force influencing the evolution of morphological traits (Andersson 1994). Traits such as ornaments for attracting mates or weapons associated with male–male competition are conspicuous examples of the extravagant traits produced by sexual selection (Andersson 1994), but the tremendous interspecific diversity in genital morphology may also be the result of sexual selection (Hosken and Stockley 2004). Although stabilizing selection has been implicated in explaining reduced intraspecific variation in genital morphology in some insects (Eberhardt et al. 1998; Bernstein and Bernstein 2002; Schulte-Hostedde and Alarie 2006; Fairn et al. 2007), recent evidence in vertebrates indicates that sexual selection may be important for understanding genital evolution (Kelly et al. 2000; Lüpold et al. 2004, but see Hosken et al. 2001).

Exaggerated traits such as ornaments and weapons often show positive allometry and high phenotypic variance (Green 1992; Petrie 1992; Pomiankowski and Møller 1995; Kodric-Brown et al. 2006). Based on these patterns, positive allometry and high pheno-typic variance have been considered a characteristic of sexually selected traits when an increased trait size is directly advantageous for mating success and there is a stronger emphasis on trait growth than on an increase in body size (Bonduriansky and Day 2003). As well, larger males may have more resources to allocate to increasing trait size, which leads to large males having disproportionately larger traits than smaller males (Green 1992). Recent analyses, however, have indicated that positive allometry is not necessarily associated with sexual selection (Bondriansky and Day 2003). Indeed, Bonduriansky and Day (2003) argue that positive allometry should only evolve when the combined effects of sexual and viability selection on trait size and body size results in increased relative fitness for large individuals. Additionally, Bertin and Fairbairn (2007) showed that the allometry and phenotypic variance of a trait under intense directional sexual selection (genitalia) is inconsistent with the patterns of positive allometry and high phenotypic variance associated with sexually selected traits. Contributing to the complexity surrounding this issue are sexual traits such as the accessory glands of the male whirligig beetle (*Dineutus nigrior*) that predict mating success and exhibit positive allometry (Fairn et al. 2007). Thus, although the presence (or absence) of positive allometry and high (or low) phenotypic variance are not necessarily associated with sexually selected traits, it has been suggested that insights into sexual selection can be interpreted from comparisons of allometry and phenotypic variance between sexual and non-sexual traits (Bonduriansky 2007).

One of the most highly variable primary sex traits in male vertebrates is the baculum, or os penis, that is found in the mammalian orders Chiroptera, Primates, Insectivora, Carnivora and Rodentia (Patterson and Thaeler 1982; Hosken et al. 2001; Lariviere and Ferguson 2002; Ramm 2007). The high degree of interspecific variation has made the baculum a defining taxonomic character (Elder and Shanks 1962; Patterson and Thaeler 1982). Several functional non-exclusive hypotheses have been proposed regarding the evolution of the baculum. Sperm competition occurs when the sperm from multiple males compete to fertilize the ova of a female, and is pervasive in mammals (Gomendio et al. 1998). The baculum may play a role in polyandrous mammals by facilitating the delivery of sperm deep into the female's reproductive tract, or by displacing or removing sperm from other males (Arnqvist 1997; Hosken and Stockley 2004). Sexual conflict can occur when the sexes differ in their reproductive interests—males and females may evolve mechanisms to control fertilization leading to the co-evolution of male and female genitalia (Arnqvist 1997). Cryptic female choice can be important in understanding baculum evolution; females may favor males with large genitalia (if genital size indicates male

quality) or females may engage post-copulatory mechanisms to favor the sperm from high quality males (as determined via the baculum) (Eberhard et al. 1998; Birkhead 1998).

Good-genes sexual selection models predict that females will preferentially fertilize their ova with the sperm of high quality males in order to gain genetic benefits for their offspring (reviewed in Andersson 1994). The baculum may serve as an honest indicator of male genetic quality, particularly if females are unable to assess male quality prior to copulation. For example, when mating occurs in an environment where visual and olfactory acuity is reduced, the assessment of male quality may be compromised (Miller and Burton 2001; Lüpold et al. 2004). In addition, coercive matings may prevent females from engaging in pre-copulatory mate choice (Clutton-Brock and Parker 1995), and thus information gleaned from the baculum may lead to post-copulatory choice. If sexual selection is important under these circumstances, and specifically if females use information from the genitalia to assess male qualities such as body size, then the baculum should show positive allometry and high phenotypic variance in species that engage in coercive or obscured matings. Miller and Burton (2001) found positive allometry and a relatively high variation in the baculum of harp seals (*Phoca groenlandica*), a species that mates aquatically. Kinahan et al. (2007) had similar results, finding positive allometry and high variation for the baculum of the Cape dune mole-rat (*Bathyergus suillus*), a species that engages in subterranean and possibly coercive mating. In addition, among rodents, baculum length is positively related to testis size, indicating that post-copulatory sexual selection may influence bacular evolution (Ramm 2007). Thus, there is evidence that the baculum may be under sexual selection in some circumstances.

The muskrat (*Ondatra zibethicus*) is a semi-aquatic rodent that typically engages in aquatic copulation and is monomorphic (Willner et al. 1982). Although there appears to be some debate regarding the mating system of muskrats (Willner et al. 1982; Marinelli et al. 1997), it appears unlikely that males provide material benefits to females and their offspring under most circumstances (Errington 1963; Forsyth 1999). These characteristics make the muskrat a likely species for possessing phenotypic traits that indicate male genetic quality to female mates during copulation. Here, we assess allometry and phenotypic variance of the baculum relative to other, putatively non-sexual, traits. Although positive allometry may not occur under all conditions of sexual selection (Bonduriansky and Day 2003; Bonduriansky 2007), we test the hypothesis that the baculum of the muskrat may be used as an honest indicator of good genes to female mates during mating as suggested by Miller and Burton (2001) and Kinahan et al. (2007). Based on this hypothesis, we predict that the baculum morphology will demonstrate positive allometry and have a higher coefficient of variation (CV) relative to non-sexual traits.

Methods

Collection and preparation

Bacula (in situ) were obtained from 54 muskrats trapped by fur trappers in the districts of Timmins, Sudbury, Manitoulin Island, North Bay, and Midhurst in the province of Ontario, Canada. The approximate distance between the two furthest districts was 450 km. The skinned animals were frozen until dissection occurred, at which point each carcass was weighed and the penis was removed and then frozen again. The head of every muskrat obtained was removed, and the brain, eyes and tongue dissected out. The skulls remained frozen until all the dissections were complete. The dissected and partially cleaned muskrat

skulls were taken to the 'bug room' at the Royal Ontario Museum (Toronto, Canada) to be thoroughly cleaned by dermestid beetles (*Dermestes* spp).

The penile tissues of the 54 muskrats were then thawed to dissect the bacula out of the surrounding tissues. Following the protocol of Kinahan et al. (2007) the extracted penile tissue was placed into a solution of potassium hydroxide (KOH) pellets mixed with distilled water at a concentration of 0.05 g ml^{-1} and left to soak for a 24-h period. The bacula were then dissected out of the surrounding tissue and placed into a 70% ethanol (EtOH) solution for preservation. Juveniles were removed based on criteria presented in Elder and Shanks (1962). Adult muskrat baculum have a larger proportion of bone than the more cartilaginous juvenile baculum, and only those bacula which had little to no cartilage in the distal and proximal parts were classified as adult and included in the sample. These criteria left us with a sample of 39 adult males (Sudbury $n = 8$, Midhurst $n = 7$, Manitoulin Island $n = 4$, Timmins $n = 16$, North Bay $n = 4$).

Measurements

Prior to dissection of the muskrats, measurements were made of body length (nose to base of tail) [with a tape measure (±0.5 cm)], and hind foot length [with a ruler applied to the base of the foot (±1 mm)]. Four measurements (±0.01 mm) were made of each of the bacula including: total length, central length (length excluding proximal projections), central width and base width (see Fig. 1). Two measurements (±0.01 mm) were made of the skulls of each of the muskrats. First, skull length was measured from the premaxillary to the occipital condyle. Second, skull width was measured across the zygomatic arches. The sample size for muskrat skulls was one less than the sample size of the baculum (38 rather than 39) because one of the skulls was damaged and could not be measured. The
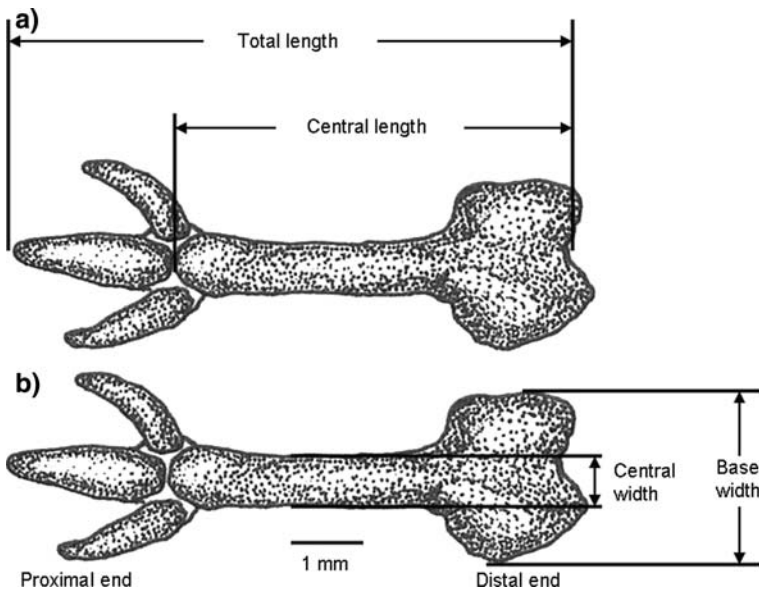

Fig. 1 Line drawing indicating the four traits measured of the muskrat baculum [length (**a**) and width (**b**) and their associated landmarks]. (Figure by DT)

same Mitutoyo Absolute Digimatic Solar (Toronto, ON, CAN) digital calipers were used. Body size measurements were performed by SL whereas the skull and baculum measurements were performed by DT. Each of the baculum and skull measurements was replicated three times and the average of these three values used. These measurements were found to be highly repeatable ($r^2 > 0.78$; $P < 0.001$).

To determine if there was any geographic variation in our samples, we performed an ANOVA on four muskrat measurements, body length, body mass, baculum base width and baculum central length. All four of the ANOVA tests showed no significant differences among the districts ($F < 1.2$; df = 4,34; $P > 0.05$). All of the individuals were subsequently pooled into one sample.

Statistical analysis

The coefficient of variation (CV) was calculated using untransformed data (Zar 1999). CV was calculated for each of the four baculum measurements, as well as the hind foot length and skull length and width. This allowed a direct comparison of the baculum with putatively non-sexual traits. Comparisons between the CV of the baculum and putatively non-sexual traits, as well as among baculum measurements were made using a series of pairwise tests for difference between two coefficients of variation (Zar 1999). Eberhard et al. (1998) describe a correction for CV that calculates CV of y should x be held constant. This corrected CV (CV′) is an alternative measure of dispersion that accounts for variation in the allometric slope of sexual and non-sexual traits.

Allometric slopes were determined for each of the four baculum measurements, and three putatively non-sexual traits—the two skull measurements and hind foot length. For the allometric analysis, the log_{10} transformed measurements of these traits were plotted against the log_{10} transformed body length measurements. Ordinary Least Squares (OLS) regression has been widely used for regression analysis, but has several assumptions associated with it that make OLS regression unsound for allometric investigations. OLS requires that X and Y are not interdependent and that there is no error in X, because X is set by the researcher whereas reduced major axis regression assumes some error in X (LaBarbera 1989; Legendre and Legendre 1998; Schulte-Hostedde et al. 2005). Because the measurement of body length was made with possible error, we used RMA (model II) regression to determine whether the slopes of the various measured muskrat traits differed from isometry (Lüpold et al. 2004; Kinahan 2007). A Microsoft Excel spreadsheet written by D. Warton (available at http://www.web.maths.unsw.edu.au/~dwarton/programs.html) was used to determine if the RMA slopes were significantly different from isometry (slope = 1). All other statistical analyses were performed using STATISTICA 6.1 (StatSoft, Inc., Tulsa, OK, USA).

Results

Coefficient of variation

The four baculum measurements had relatively higher CV values (>9%) than the three putatively non-sexual traits (<5%) of hind foot length, skull width and skull length (Table 1). Baculum width had the highest CV of all the traits, at 25.6%, while hind foot length had the lowest CV at 3.5%. We tested for homogeneity of coefficients of variation

Table 1 Descriptive statistics [including coefficient of variation (CV)] of baculum and non-sexual traits from male muskrats

Morphological trait	n	$\bar{X}$	SD	CV (%)	CV′
Baculum traits					
Base width	39	2.98	0.69	23.0	18.6
Central width	39	0.81	0.21	25.6	20.6
Total length	39	5.60	0.63	11.3	8.5
Central length	39	8.76	0.80	9.2	7.4
Non-sexual traits					
Skull width	38	37.97	1.91	5.0	3.0
Skull length	38	61.63	2.59	4.2	2.5
Hindfoot length	39	81.15	2.83	3.5	3.2

All measurements are in mm

(Zar 1999) and found significant heterogeneity among all traits measured ($\chi^2 = 176.23$, df = 6, $P < 0.001$). We conducted a series of pair-wise comparisons to test for differences between coefficients of variation (Zar 1999) of baculum and putatively non-sexual traits, and to test for differences among baculum traits. The coefficients of variation for all bacular traits were significantly higher than putatively non-sexual traits [$F > 3.3$; df = 39,39; df = 39,38 for comparisons with skull measurements (see "Methods"); $P < 0.001$]. Within baculum traits, the coefficients of variation for bacular central length and total length did not differ ($F = 1.52$; df = 39,39; $P > 0.10$), nor did the coefficients of variation of the central width and base width of the baculum differ ($F = 1.24$, df = 39,39; $P > 0.40$). However, the comparison of the coefficients of variation between both baculum length and width traits revealed that baculum base width and central width were significantly higher than baculum central length and total length ($F > 3.78$; df = 39,39; $P < 0.001$). The adjusted CV for each trait was similar when compared with the raw CV values—genital traits had larger adjusted CV values relative to non-sexual traits (Table 1).

Allometry

All allometric slopes (for both bacular and putatively non-sexual traits) were significantly greater than 0 as calculated by OLS regression ($P < 0.001$) and thus RMA regression was employed to estimate allometric slopes. The RMA slopes ($P < 0.01$) were significantly greater than 1 for each of the four baculum measurements (Table 2). The 95% confidence intervals for these four measurements were all above 1.00. In addition, the lower bound of the 95% confidence interval for allometric slopes of baculum central width and base width were greater than the upper bound of the 95% confidence interval for allometric slopes of baculum central length and total length (Table 2). This indicates that the allometric slopes are steeper for measures of baculum width than baculum length.

The RMA slopes were found to be significantly less than 1 ($P < 0.02$) (negative allometry) for all three of the putatively non-sexually selected traits: hind foot length, skull width and skull length. The 95% confidence intervals for these three measurements were all below 1.00.

Table 2 Summary statistics for reduced major axis (RMA) regression of male muskrat traits

Morphological trait	r^2	RMA slope	95% CI	F	P
Baculum traits					
Base width	0.349	3.35	2.57–4.37	132.4	<0.001
Central width	0.352	3.72	2.86–4.86	170.3	<0.001
Total length	0.353	1.72	1.32–2.25	18.7	<0.001
Central length	0.435	1.40	1.09–1.79	7.5	0.009
Non-sexual traits					
Skull width	0.651	0.785	0.644–0.958	6.13	0.018
Skull length	0.633	0.659	0.537–0.807	18.2	<0.001
Hind foot length	0.146	0.537	0.395–0.730	18.6	<0.001

The coefficient of determination (r^2), the allometric slope calculated using RMA regression between the morphological trait of interest and body length (RMA slope), the calculated 95% confidence intervals of the slope estimates (95% CI), and the F and P values associated with the tests for difference from isometry (slope = 1) are presented

Discussion

The positive allometry and high phenotypic variance exhibited by the muskrat baculum, especially when contrasted with the negative allometry and low phenotypic variance found in non-sexual traits, are consistent with patterns of genital allometry and variation found in other mammals (Miller and Burton 2001; Lüpold et al. 2004; Kinahan et al. 2007). In mammals such as the harp seal and Cape dune mole-rat (Miller and Burton 2001; Kinahan et al. 2007), the baculum exhibited positive allometry and relatively high phenotypic variation. While it is not possible to compare our results to Miller and Burton (2001) (they used OLS regression to estimate allometric slopes and did not compare coefficients of variation), Kinahan et al. (2007) report higher CV for baculum length and steeper allometric slopes than found in muskrat. This apparent trend among some mammals is contrasted sharply with patterns found in insects and other invertebrates that indicate negative allometry in genital size (e.g., Eberhardt et al. 1998; Bernstein and Bernstein 2002; Schulte-Hostedde and Alarie 2006; Bertin and Fairbairn 2007; Fairn et al. 2007). The basis for these profound differences between mammals and insects is unclear, but differences in the form of sexual selection may be responsible. Eberhard et al. (1998) proposed the "one size fits all" hypothesis to explain the pervasive presence of negative allometry of the genitalia among many insects. The "one size fits all" hypothesis suggests that male genitalia are under stabilizing selection to facilitate copulation with as many females as possible, regardless of female size (Eberhard et al. 1998). Clearly, this hypothesis is not relevant to mammals that exhibit positive allometry of the genitalia.

It has been suggested that positive allometry in male genitalia of mammals is associated with a "good-genes" model of sexual selection that may be particularly adaptive in the context of cryptic female choice (Miller and Burton 2001; Lüpold et al. 2004; Kinahan et al. 2007). Both harp seals and Cape dune mole-rats live in environments in which visual acuity is reduced (aquatic and subterranean environments) and thus they, with the muskrat, are consistent with the hypothesis that the baculum facilitates female mate choice in these kinds of environment. Similarly, male penis length (but not baculum length) exhibited positive allometry and high phenotypic variance in noctule bats (*Nyctalus noctula*), perhaps because males mate with females while they are hibernating, and females

preferentially store sperm from males with longer penises and that are of higher quality (Lüpold et al. 2004). This model may be particularly appropriate for muskrats because they are monomorphic and exhibit no competition or display for mates, and males likely do not offer direct benefits to mates or offspring (Errington 1963; Forsyth 1999). Females may need to assess male quality because mating is coercive or because the environment prevents the female from assessing male quality because of sensory deprivation (e.g., aquatic or subterranean mating). Muskrats are an unlikely candidate for coercive mating because males and females are the same size (Willner et al. 1982). It is more likely that females are unable to assess male quality before copulation because mating is aquatic, and thus females may employ the baculum as an index of male quality.

Clearly, patterns of allometry and phenotypic variance cannot provide information about the form of sexual selection, and alternative mechanisms that affect the evolution of genitalia cannot be excluded. In particular, a comparative analysis of baculum morphology and testis size found a positive correlation between baculum length and relative testis size in both rodents and carnivores (Ramm 2007). Thus sperm competition may also influence the evolution of baculum and genital size.

If the baculum of male muskrats is acting to indicate genetic quality, then mate assessment by females should be occurring during copulation. In order for females to prevent paternity of offspring by males of low genetic quality (those with a disproportionately small baculum), females would have to evolve post-copulatory mechanisms to minimize the probability of her ova being fertilized by sperm from poor quality males. Tactics such as detachment from males prior to ejaculation, expelling deposited sperm, forcing sperm into competition through rapid successive mating, and/or cryptic female choice via sperm manipulation would allow females to maintain control over mate selection and resulting paternity of offspring (Neff and Pitcher 2005). For example, Pizzari and Birkhead (2000) found that if female feral fowl (*Gallus gallus*) are coerced into mating with poor quality males, they will eject the deposited sperm before successful fertilization can occur. This manipulation may allow female fowl to control mating success and bias paternity of their offspring towards higher quality mates, despite mating with low quality males (Pizzari and Birkhead 2000). If female selection of mates is done post-copulation, then we predict that significant post-copulatory choice should be evident in females of species such as the muskrat, harp seal and Cape dune mole-rat that may use the baculum as an indicator of male genetic quality (Miller and Burton 2001; Kinahan 2007).

Comparison of the coefficients of variation and allometric slope indicate that baculum width may be more strongly influenced by sexual selection than baculum length. Although both baculum width and length had steeper allometric slopes and higher coefficients of variation than putative non-sexual traits, measures of baculum width were more variable and had steeper slopes than measures of baculum length. This may be indicative of the functional role of the muskrat baculum and the ability of the female to detect individual differences in male genital morphology through the female reproductive tract. For example, females may be more sensitive to baculum width than length and utilize that sensitivity to discriminate between mates, which might lead to stronger selection for baculum width. A wider baculum might also play a structural role that helps ensure successful completion of copulation once mating has commenced and increase the male's likelihood of successful paternity. The hypothesis that baculum width may be more important than baculum length in assessing male quality also suggests the reduced importance of sperm competition and the use of the baculum to aid in the placement of sperm deep in the female's reproductive tract. Under such circumstances, baculum length would be expected to be more important than baculum width. Interestingly, Miller and

Burton (2001) also found that baculum width (thickness at midshaft) had a steeper allometric slope than baculum length.

There are several research directions suggested by our results. First, given the positive allometry and high phenotypic variation in the baculum of the muskrat, what are the consequences for female genitalia? Kinahan (2007) examined female genitalia in Cape dune mole-rats and concluded that female genitalia exhibited positive allometry, supporting the hypothesis of co-evolution between the sexes. Nonetheless, it should be advantageous for a male to mate with any encountered female, especially if costs (e.g., provisioning of material benefits) are low. Thus, it may be important to consider the fitness consequences of compatibility between males with large genitalia and females with small genitalia. Second, morphological evidence of sexual selection predicts that males with disproportionately large bacula will have enhanced reproductive success relative to other males. The question could be answered with the use of imaging technology such as ultrasound or X-ray for the measurement of the baculum, in combination with molecular techniques to assess male paternity in a mark-recapture study of muskrat populations. Finally, Ramm (2007) suggested that baculum length evolves with sperm competition pressure in rodents. If this is true, and baculum size is under sexual selection, then males that invest heavily in ejaculates (relatively large testes) should have large bacula, and have concomitant paternity success.

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