



Allometry of the baculum and sexual size dimorphism in American martens and fishers (Mammalia: Mustelidae)

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Genitalia are among the most variable of morphological traits, and recent research suggests that this variability may be the result of sexual selection. For example, large bacula may undergo post-copulatory selection by females as a signal of male size and age. This should lead to positive allometry in baculum size. In addition to hyperallometry, sexually selected traits that undergo strong directional selection should exhibit high phenotypic variation. Nonetheless, in species in which pre-copulatory selection predominates over post-copulatory selection (such as those with male-biased sexual size dimorphism), baculum allometry may be isometric or exhibit negative allometry. We tested this hypothesis using data collected from two highly dimorphic species of the Mustelidae, the American marten (*Martes americana*) and the fisher (*Martes pennanti*). Allometric relationships were weak, with only 4.5–10.1% of the variation in baculum length explained by body length. Because of this weak relationship, there was a large discrepancy in slope estimates derived from ordinary least squares and reduced major axis regression models. We conclude that stabilizing selection rather than sexual selection is the evolutionary force shaping variation in baculum length because allometric slopes were less than one (using the ordinary least squares regression model), a very low proportion of variance in baculum length was explained by body length, and there was low phenotypic variability in baculum length relative to other traits. We hypothesize that this pattern occurs because post-copulatory selection plays a smaller role than pre-copulatory selection (manifested as male-biased sexual size dimorphism). We suggest a broader analysis of baculum allometry and sexual size dimorphism in the Mustelidae, and other taxonomic groups, coupled with a comparative analysis and with phylogenetic contrasts to test our hypothesis. © 2011 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2011, 104, 955–963.

ADDITIONAL KEYWORDS: genitalia – mammal – *Martes* – ordinary least squares regression – reduced major axis regression – sexual selection.

INTRODUCTION

The genitalia are perhaps one of the most obviously variable morphological traits across animals with internal fertilization, whether comparing between distantly related taxa or even closely related species (Hosken & Stockley, 2004). There are several explanations for this diversity, including the lock-and-key

hypothesis (Eberhard, 1985), which proposes that genital differences evolved to prevent hybridization between species, and the pleiotropy hypothesis (Mayr, 1963), which posits that the genitalia have diverged in morphology as a side effect of selection on other traits (pleiotropy) (Hosken & Stockley, 2004). Neither of these hypotheses has been particularly convincing, and recently sexual selection has been identified as a major factor in the evolution of genitalia (Hosken & Stockley, 2004). Sexual selection may be pre-copulatory, resulting in increased attractiveness to mates, but it may also be post-copulatory, and occur

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through sperm competition or cryptic female choice (e.g. through mechanisms such as induced ovulation) (Larivière & Ferguson, 2002; Ramm, 2007). Both pre- and post-copulatory sexual selection (i.e. mating and fertilization) have been linked to the size and shape of the genitalia (House & Simmons, 2003; Ramm, 2007). Thus, although various hypotheses have been proposed, it appears that sexual selection may be particularly powerful in explaining the evolution of genital diversity.

The allometry of the genitalia has raised considerable interest because of the apparent differences in allometric slopes between invertebrates (e.g. the aedeagus in insects) and vertebrates (e.g. the mammalian os penis or baculum). Generally, insect genitalia show negative allometry (Eberhard *et al.*, 1998; Bernstein & Bernstein, 2002; Hosken, Minden & Ward, 2005; Schulte-Hostedde & Alarie, 2006; Bertin & Fairbairn, 2007; Fairn, Schulte-Hostedde & Alarie, 2007), whereas the genitalia of many mammals examined to date show evidence of positive allometry (Miller & Burton, 2001; Lüpold, McElligott & Hosken, 2004; Kinahan *et al.*, 2007; Tasikas *et al.*, 2009; but see Kinahan *et al.*, 2008; Manjerovic *et al.*, 2008; Ramm, Khoo & Stockley, 2010). Several hypotheses have been proposed to explain these patterns. The negative allometry associated with many insects may be the result of selection favouring genitalia that fit the average female: the 'one size fits all' hypothesis (Eberhard *et al.*, 1998). It has been hypothesized that the positive allometry evident in the bacula of some mammals is the result of sexual selection, and that females use baculum size as an index of male quality when assessment of male quality is impossible prior to copulation (Kinahan *et al.*, 2007; Tasikas *et al.*, 2009). For example, if copulations occur in an environment where visual and olfactory acuity is reduced, the pre-copulatory assessment of male quality may be compromised (Miller & Burton, 2001; Lüpold *et al.*, 2004). Similarly, coercive matings may prevent females from exercising pre-copulatory mate choice, and thus the baculum may provide a signal by which females may assess male phenotypic quality. There has been recent criticism, however, of the general conclusion that traits that show patterns of positive allometry are under sexual selection (Bonduriansky & Day, 2003; Bertin & Fairbairn, 2007; Schulte-Hostedde *et al.*, 2011). Thus, interpretations of allometric relationships in the context of sexual selection must be carefully considered (Bonduriansky, 2007). Bonduriansky (2007) suggested that comparing the allometry of putatively sexual and non-sexual traits may provide insight into any role sexual selection plays in the allometry of sexual traits.

Underlying the analysis of body size allometries is the statistical reality that both independent and

dependent variables are measured with error, and this violates the main assumption of ordinary least squares (OLS) regression (e.g., Green, 1999; Schulte-Hostedde *et al.*, 2005). It is generally recommended that an alternative to OLS regression, i.e. reduced major axis (RMA) regression, be employed because it assumes some error in X (the independent variable) (LaBarbera, 1989; Legendre & Legendre, 1998; Green, 1999; Schulte-Hostedde *et al.*, 2005). The differences in slope estimates between OLS and RMA regression can be profound, however, leading to different conclusions (Cuervo & Møller, 2001, 2009 but see Eberhard, Huber & Rodriguez, 1999). RMA slopes need to be interpreted carefully because they are sensitive to variation in the Pearson correlation coefficient (r): RMA slopes are equal to OLS slopes divided by r (Legendre & Legendre, 1998).

Male-biased sexual size dimorphism predominates in mammals (Andersson, 1994; Weckerly, 1998), because of the typically polygynous nature of mammalian mating systems (Clutton-Brock, 1989). Pre-copulatory sexual selection in the form of male–male competition for access to females has driven the evolution of male-biased sexual size dimorphism (Andersson, 1994). Despite the fact that males are larger than females in most mammals, most recent studies of mammalian baculum allometry have been conducted on species that are monomorphic in size [e.g. muskrat (*Ondatra zibethicus*), Schulte-Hostedde (2007); harp seal (*Pagophilus groenlandicus*), Lindenfors *et al.* (2002); house mouse (*Mus musculus*), Schulte-Hostedde (2007)], have female-biased size dimorphism [noctule bat (*Nyctalus noctula*), D. Hosken, pers. comm.], or have limited male-biased size dimorphism [Cape dune mole-rat (*Bathyergus suillus*), Kinahan *et al.* (2007); African ground squirrel (*Xerus inauris*), Manjerovic *et al.* (2008)]. Because of the lack of pronounced male-biased sexual dimorphism in these studied species, we suspect that pre-copulatory sexual selection was relatively weak. In such cases, it is likely that post-copulatory selection is important, either in the context of cryptic female choice or sperm competition, and the baculum should thus exhibit positive allometry (Kinahan *et al.*, 2008). In species in which pre-copulatory selection supercedes post-copulatory selection (such as in species with male-biased sexual size dimorphism), we expect that the baculum should exhibit shallower allometric slopes (Kinahan *et al.*, 2008), consistent with the hypothesis that the baculum is under stabilizing selection in this context (Eberhard *et al.*, 1998).

The fisher (*Martes pennanti*) and American marten (*Martes americana*) are carnivores of the family Mustelidae, and are the only members of their genus that are endemic to North America. The two species are superficially quite similar in morphology and life

history, with the most obvious exception being that *M. pennanti* is larger than *M. americana*. Both species have male-biased sexual size dimorphism and are intrasexually territorial (Powell, 1993), but *M. pennanti* is substantially more dimorphic than *M. americana*. These species, like most members of the Mustelidae, are polygynous, which is consistent with the level of sexual dimorphism observed (Moors, 1980). If baculum allometry is affected by the degree of pre-copulatory selection relative to post-copulatory selection, then we predict isometry or negative allometry of the baculum in *M. pennanti* and *M. americana*, with the most dimorphic species (*M. pennanti*) having the lower allometric slope. We also expect that traits that are sexually dimorphic, and presumably under pre-copulatory selection, will have higher allometric slopes than the allometric slopes of the baculum in both species (Schulte-Hostedde *et al.*, 2011).

Fitness-related traits such as those resulting from sexual selection appear to have higher variation than traits unrelated to fitness, or those undergoing weak stabilizing selection (e.g. Merilä & Sheldon, 1999; Tasikas *et al.*, 2009). This is despite the fact that directional selection should erode additive genetic variance, leading to reduced phenotypic variance. This fundamental incongruity has been identified as the 'lek paradox', and resolving this paradox has generated numerous hypotheses (Kotiaho *et al.*, 2008). For example heightened variation in sexually selected traits may be the result of the larger number of loci influencing fitness traits, as compared with traits unrelated to fitness (Pomiankowski & Møller, 1995). Thus, because we expect post-copulatory selection to be weak in *M. americana* and *M. pennanti*, we predicted that baculum size should have relatively low phenotypic variation compared with sexually dimorphic traits. We also expected, however, that phenotypic variance in baculum size should be lower in *M. pennanti* than in *M. americana* because of the greater degree of male-biased sexual size dimorphism in *M. pennanti*.

MATERIAL AND METHODS

SAMPLE COLLECTION

We obtained samples and data from *M. americana* and *M. pennanti* carcass collections made by the Ontario Ministry of Natural Resources (OMNR) during the period from autumn 1972 to winter 1983 in the Algonquin region of central Ontario. An annual harvest for *M. pennanti* and *M. americana* was undertaken by trappers from approximately October to January. Trapping in the region mostly occurred on traplines registered to individual trappers. The

animals in our study were captured by trappers and frozen, skinned carcasses were provided to OMNR each year of the programme. The collected samples were used in extensive management-oriented necropsies at the time of collection, many results of which have been published (e.g., Douglas & Strickland, 1987; Strickland & Douglas, 1987; Strickland, 1994; Fryxell *et al.*, 1999, 2001).

When the necropsies were performed each year on the collected *M. americana* and *M. pennanti* carcasses, the workers at that time took extensive, detailed, and standardized measurements of some features of interest. These included snout-vent length (hereafter body length), zygomatic width, and chest girth, which was the circumference of the skinned carcass around the chest at heart level. All animals were sexed, weighed, and aged using both X-rays of pulp cavity widths and cementum annuli counts. Bacula of males were extracted, cleaned, dried, weighed, and stored in labelled coin envelopes. Thus, we had available to us a data set containing age, sex, weight, length, zygomatic width, and girth for *M. pennanti* and *M. americana* collected over 11 years from central Ontario. We also had a collection of stored bacula for these *M. americana* and *M. pennanti* specimens.

LABORATORY METHODS

The data set contained information about 5360 *M. americana* and 5193 *M. pennanti* specimens collected and necropsied over the years 1972–1983. From this data set, we screened out all juveniles (< 1 year old). To assess sexual size dimorphism, we determined sex differences in body length, chest girth, and zygomatic width. To assess the allometry of the sexually dimorphic traits and the baculum for both species, we restricted our remaining analyses to adult males. We identified the stored bacula for the remaining adult males of both species, and excluded adult males with missing bacula. For the bacula of the remaining males, we measured the total length of each baculum three times using a Mitutoyo Digimatic caliper, accurate to 0.01 mm. We used the median of these measurements for all subsequent analyses. We focused on the length of bacula as our genital trait of interest because it has been shown in other studies to be positively allometric, and is a likely candidate for post-copulatory selection (e.g. Miller & Burton, 2001; Ferguson & Larivière, 2004; Tasikas *et al.*, 2009).

DATA ANALYSIS

We compared the coefficients of variation (CVs) of the four traits (baculum length, chest girth, zygomatic width, and body length) for both species. The CV was

estimated using untransformed data by dividing the standard deviation by the mean and multiplying by 100 (Zar, 1999). We tested for significant differences in CV between bacula and sexually dimorphic traits using a series of pairwise tests (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. We also used a series of pairwise tests (Zar, 1999) to compare these estimates.

For each species, we then examined the allometry of three traits (baculum length, chest girth, zygomatic width). Miller & Nagorsen (2008) found that *M. americana* exhibited positive allometry in bacula length for individuals ≤ 1 -year old, but not for individuals > 1 -year old. Thus, they concluded that positive allometry was growth related and not the result of sexual selection. We excluded juveniles from our analysis, such that the youngest individuals in the sample analysed were 1.5-years old. Nevertheless, we tested for growth-related positive allometry in the baculum length of both species by dividing the samples into two age groups: those aged 1.5 years and those aged ≥ 2.5 years.

Slope estimates resulting from morphometric comparisons should be made with RMA regression, which accounts for error on the x -axis (LaBarbera, 1989; Schulte-Hostedde *et al.*, 2005). We used OLS regression to test the significance of linear relationships. We used the RMA program (Bohonak, 2004) to carry out reduced major axis regressions, and we used a Microsoft EXCEL spreadsheet written by Dr David Warton (available at <http://www.eco-stats.unsw.edu.au/Software.html>) to determine if the slopes were significantly different from isometry (slope = 1). All other statistical analyses were performed using R (R Development Core Team, 2008).

RESULTS

Sample sizes varied among statistical tests because not every individual had every dimension measured. Males were significantly larger than females for both *M. pennanti* and *M. americana* for body length (*M. americana*, male mean = 40.30 cm, female mean = 35.60 cm, $t_{1045} = 40.23$, $P < 0.001$; *M. pennanti*, male mean = 62.42 cm, female = 51.44 cm, $t_{781} = 57.27$, $P < 0.001$), chest girth (*M. americana*, male mean = 11.79 cm, female mean = 9.60 cm, $t_{453} = 25.4$, $P < 0.001$; *M. pennanti*, male mean = 24.90 cm, female mean = 17.79 cm, $t_{362} = 30.47$, $P < 0.001$), and zygomatic width (*M. americana*, male mean = 4.50 cm, female mean = 3.87 cm, $t_{122} = 10.05$, $P < 0.001$; *M. pennanti*, male mean = 7.86, female mean = 5.81, $t_{195} = 40.0$, $P < 0.001$). Sexual size dimorphism was



Figure 1. Typical bacula of the adult marten (*Martes americana*, above) and fisher (*Martes pennanti*, below).

greater in *M. pennanti* relative to *M. americana* [*M. pennanti* males were 21% longer, have 40% larger chest girth, and 35% wider skulls (zygomatic width) than females; *M. americana* males were 13% longer, had 23% larger chest girth, and 16% wider skulls (zygomatic width) than females].

Both *M. americana* and *M. pennanti* bacula are derived from a common mustelid bacula that was a simple rod-shaped bone lacking a urethral groove and apical embellishments (Baryshnikov, Bininda-Emonds & Abramov, 2003). Both species' baculum had a urethral groove, with a ring-shaped distal tip, and an upward bend that is characteristic of mustelids (Fig. 1). *Martes pennanti* bacula in our sample were much larger, relative to body length, than the *M. americana* bacula (15.9 vs. 8.5% of body length on average, respectively).

For *M. americana*, CV' for chest girth was significantly higher than baculum length and zygomatic width (Table 1). CV' was equal between baculum length and zygomatic width. For *M. pennanti*, CV' for both chest girth and zygomatic width was greater than CV' for baculum length. In addition, the CV' for baculum length was significantly lower in *M. pennanti* than in *M. americana* ($Z = 6.66$, $P < 0.05$).

There was a positive, linear, and relatively weak relationship between baculum length and body length in *M. americana* (OLS, $F = 39.03$, $N = 837$, $P < 0.001$, $r^2 = 0.045$) (Fig. 2). OLS regression indicated that the *M. americana* baculum exhibited negative allometry, but this was in sharp contrast to RMA slope estimates, which indicated positive allometry for the *M. americana* baculum (Table 2). When divided into two groups by age, the relationships found in the combined sample were upheld for both individuals aged 1.5 years ($F = 20.59$, $N = 384$, $P < 0.001$, $r^2 = 0.051$) and individuals aged ≥ 2.5 years ($F = 18.25$, $N = 453$, $P < 0.001$, $r^2 = 0.039$) (Table 2).

Table 1. Descriptive statistics for traits from male martens and fishers (≥ 1.5 years old) sampled in Ontario, Canada, from 1972 to 1983. All measurements are cm.

Morphological trait	n	\bar{X}	SD	CV (%)	CV'
<i>Marten</i>					
Baculum length (cm)	837	3.41	0.19	5.55 ^a	5.42 ^a
Chest girth (cm)	540	11.69	0.90	7.70 ^b	6.75 ^b
Zygomatoc width (cm)	83	4.46	0.24	5.33 ^a	5.09 ^a
Body length (cm)	837	40.30	1.75	4.35 ^c	–
<i>Fisher</i>					
Baculum length (cm)	321	9.93	0.41	4.08 ^a	3.87 ^a
Chest girth (cm)	178	24.59	2.68	10.90 ^b	8.85 ^b
Zygomatoc width (cm)	80	7.86	0.46	5.86 ^c	5.74 ^c
Body length (cm)	321	62.50	3.10	4.96 ^d	–

a, b, c, d, different letters indicate significant differences between traits within a species.

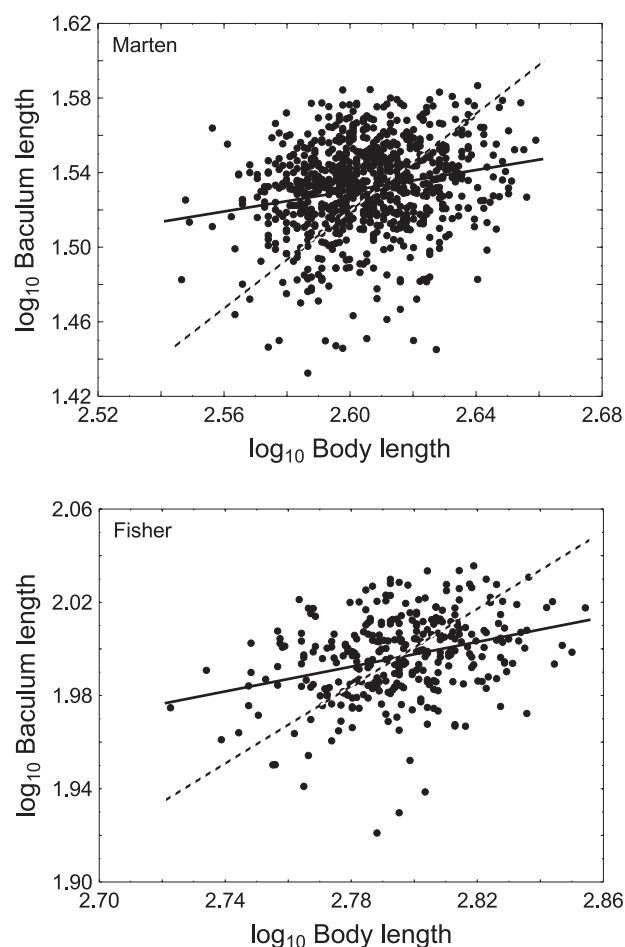


Figure 2. Scatterplots of baculum length (cm) compared with body length (cm) for martens (*Martes americana*) and fishers (*Martes pennanti*) collected in Ontario, Canada, during 1972–1983. Both variables are \log_{10} transformed. The solid line is the slope calculated from an ordinary least squares regression, and the dashed line is the slope calculated from a reduced major axis regression.

Chest girth in *M. americana* also exhibited negative allometry based on OLS regression ($F = 40.56$, $N = 540$, $P < 0.001$, $r^2 = 0.070$), but was isometric based on RMA regression (Table 2). Zygomatoc width was not related to body length (Table 2).

Bacula length in *M. pennanti* also had a positive but weak relationship with body length (OLS, $F = 35.69$, $N = 321$, $P < 0.001$, $r^2 = 0.101$) (Fig. 2), and exhibited negative allometry based on both OLS and RMA regression (Table 2). Similar results were obtained when we split the *M. pennanti* sample into two groups by age: individuals aged 1.5 years ($F = 20.39$, $N = 168$, $P < 0.001$, $r^2 = 0.109$) and individuals aged ≥ 2.5 years ($F = 12.83$, $N = 153$, $P < 0.001$, $r^2 = 0.078$). In contrast, chest girth exhibited positive allometry but zygomatoc width had contrasting results, depending on the regression model used. OLS regression indicated negative allometry and RMA regression indicated positive allometry for zygomatoc width (Table 2).

DISCUSSION

The allometry of genitalia has been of recent interest because of the realization that variation in the size and shape of genitalia may be heavily influenced by sexual selection (Hosken & Stockley, 2004). Traits under sexual selection are predicted to exhibit positive allometry (Green, 1992; Petrie, 1992; Pomiankowski & Møller, 1995; Kodric-Brown, Sibly & Brown, 2006; but see Bonduriansky, 2007), and there is substantial evidence that the mammalian baculum exhibits positive allometry in a variety of species, ostensibly because of the baculum's importance in post-copulatory selection (Miller & Burton, 2001; Lüpold *et al.*, 2004; Kinahan *et al.*, 2007; Ramm, 2007; Tasikas *et al.*, 2009; but see Kinahan *et al.*, 2008; Manjerovic *et al.*, 2008; Ramm *et al.*, 2010).

Table 2. Ordinary least squares (OLS) and reduced major axis (RMA) regression slopes and 95% confidence intervals for relationships between traits and snout–vent lengths in male martens (*Martes americana*) and fishers (*Martes pennanti*) sampled in Ontario, Canada, from 1972 to 1983

Morphological trait	<i>N</i>	<i>r</i> ²	OLS slope	95% CI (OLS)	RMA slope	95% CI (RMA)
<i>Martes americana</i>						
Baculum length	837	0.045	0.28	0.19–0.36	1.30	1.22–1.39
Baculum length (1.5 years)	384	0.051	0.31	0.17–0.45	1.39	1.26–1.53
Baculum length (\geq 2.5 years)	453	0.039	0.25	0.13–0.31	1.28	1.16–1.39
Chest girth	540	0.070	0.57	0.40–0.75	1.08	0.99–1.17
Zygomatic width	83	0.040	0.28*	–0.03–0.59	–	–
<i>Martes pennanti</i>						
Baculum length	321	0.101	0.26	0.17–0.35	0.83	0.79–0.92
Baculum length (1.5 years)	168	0.109	0.26	0.14–0.38	0.80	0.68–0.91
Baculum length (\geq 2.5 years)	153	0.078	0.24	0.11–0.37	0.86	0.72–0.99
Chest girth	178	0.341	1.17	0.93–1.41	2.00	1.78–2.27
Zygomatic width	80	0.089	0.38	0.11–0.65	1.27	1.03–1.57

*Indicates OLS slope was not significantly different from 0 (i.e. $P > 0.05$). Unless otherwise noted, all comparisons are for individuals \geq 1.5-years old.

These studies have focused on mammals that do not exhibit the male-biased sexual size dimorphism typical in mammals (Andersson, 1994).

Mammals in which post-copulatory selection predominates should show positive allometry of the genitalia, and conversely mammals in which pre-copulatory selection predominates should exhibit isometry or negative allometry (Kinahan *et al.*, 2008). Thus we predicted that baculum length would exhibit negative allometry or isometry in *M. americana* and *M. pennanti* because of the strength of pre-copulatory selection surmised from the high degree of male-biased sexual size dimorphism found in these species. The allometric slope for baculum length in *M. pennanti* was negative for both OLS and RMA regression, but for *M. americana*, the allometry of the baculum varied depending on the regression model used. OLS regression indicated negative allometry, whereas RMA regression indicated positive allometry. Slope estimates for chest girth showed similar patterns in the *M. americana*: OLS slopes indicated negative allometry, yet RMA slope estimates indicated positive allometry. In *M. pennanti*, chest girth exhibited positive allometry regardless of the regression model, zygomatic width exhibited negative allometry with OLS regression, and positive allometry with RMA regression. These discrepancies between regression models must be addressed in order to evaluate these tests of our initial predictions.

The RMA regression is considered appropriate when both dependent and independent variables are measured with error (Legendre & Legendre, 1998). Indeed, slope estimates can differ between OLS and RMA

regression, leading to different conclusions based on the regression model used (see Cuervo & Møller, 2001, 2009). Although it is not unusual for slope estimates to differ substantially between RMA and OLS regression (e.g. Kinahan *et al.*, 2007), it is unclear which is the biologically relevant result when the slope estimates are variable with respect to the form of allometry that is being measured. Although statistically significant, the relation between baculum length and body length in both *M. americana* and *M. pennanti* was remarkably weak: only 4.5–10.1% of the variation in baculum length was explained by variation in body length. The statistical significance of these shallow slopes was the result of the substantial sample sizes of both *M. americana* and *M. pennanti* bacula. For example, typical sample sizes from recent studies of bacular allometry have ranged from $N = 10$ to $N = 69$ (Miller & Burton, 2001; Lüpold *et al.*, 2004; Kinahan *et al.*, 2007, 2008; Tasikas *et al.*, 2009; Ramm *et al.*, 2010), and the statistical power required to detect 5–10% of the variation in body length explained by baculum length ranged from 0.096 to 0.153 for $N = 10$, and 0.362 to 0.647 for $N = 50$ (Cohen, 1988). In contrast, sample sizes of $N = 300$ – 800 have statistical power > 0.99 to detect $r^2 = 0.05$ – 0.1 .

Arguably, baculum length provides little information to the female in respect of body size: if large male size was desirable because it indicated male quality, then baculum size would be an inefficient signal for females to use (Miller & Nagorsen, 2008). The original hypothesis explaining the positive allometry of the baculum found in some mammals argued that in situations where females are unable to engage in

pre-copulatory mate choice (e.g. in forced copulations, and in aquatic or subterranean mating contexts), females may glean information from the baculum, preferentially fertilizing her ova with the sperm from a high-quality male (i.e. a male of large body size) (Miller & Burton, 2001; Kinahan *et al.*, 2007; Tasikas *et al.*, 2009). Allometric slope estimates from monomorphic mammals reflect this view. For example, the RMA slope of baculum allometry is 3.19 in *Bathyergus suillus* (Kinahan *et al.*, 2007) and 1.7 in *Ondatra zibethicus*. Both of these examples are substantially steeper than the slopes obtained in *M. americana* and *M. pennanti*. Our modified hypothesis explained that in situations when pre-copulatory selection overrides post-copulatory selection, as is typically the case in mammals with male-biased sexual size dimorphism, baculum size should exhibit negative allometry, and shallower slopes should be evident in species with more pronounced sexual size dimorphism. Negative allometry is consistent with stabilizing selection for an optimal baculum size (Eberhard *et al.*, 1998). The negative allometry and generally weak relationship between baculum length and body length are consistent with this prediction. In addition, the allometric slopes for baculum length were generally shallower in the most dimorphic species (*M. pennanti*) when compared with the least dimorphic species (*M. americana*), indicating some support for our hypothesis.

The corrected coefficient of variation (CV') was lower for baculum length than chest girth (one sexually dimorphic trait) and the same as zygomatic width in *M. americana*, and the CV' of baculum length was lower than chest girth and zygomatic width in *M. pennanti*. In addition, CV' for baculum length was higher in *M. americana* than *M. pennanti*. These patterns are in accordance with our initial predictions: in the most dimorphic species (*M. pennanti*), phenotypic variation was highest among sexually dimorphic traits relative to baculum length, and phenotypic variance of the baculum was highest in the least dimorphic species (*M. americana*). Fitness-related traits often have greater variation than traits unrelated to fitness (Pomiankowski & Møller, 1995), and thus if the baculum was important in terms of post-copulatory selection, it would be expected to be relatively highly variable. This does not appear to be the case with *M. americana* and *M. pennanti*: CV values obtained for these two species are substantially lower than that found for *Ondatra zibethicus* (11.3% for total baculum length and 25.6% for central width; Tasikas *et al.*, 2009) and *Bathyergus suillus* (18.9%; Kinahan *et al.*, 2007). Indeed, the CV values of *M. americana* and *M. pennanti* bacula are more consistent with those found in insects and spiders (e.g. $\bar{X} = 6.5\% \pm 3.4$, $N = 61$; Eberhard *et al.*, 1998);

$\bar{X} = 5.8\% \pm 3.1$, $N = 13$; Hosken *et al.*, 2005), which conform to the 'one size fits all' model of genital evolution.

If the weight of evidence suggests that variation in baculum size is not consistent with a trait under sexual selection, what is the source of bacular variation? The bacula of the Mustelidae tend to be rather simple in structure with some more complex projections at the tip (Baryshnikov *et al.*, 2003). Arguably, this suggests that the function of the baculum is to support the penis and protect the urethra during prolonged copulation (Baryshnikov *et al.*, 2003). There is evidence of baculum fractures in the Mustelidae, indicating that the physical load on these structures is substantial (Baryshnikov *et al.*, 2003). If the function of the baculum is associated with structural support, then stabilizing selection may be operating on baculum size. This hypothesis would explain the relatively low variation in bacular length, and the weak relationship between baculum length and body size. Alternatively, coevolution between males and females may dictate the allometry of the male baculum. For example, female size may be limited by energetics, and thus optimized by natural selection. Male genital size may be a response to this, leading to the prediction that male and female genitalia should covary spatially.

The results of this study are not consistent with other studies of mammals that implicate sexual selection as an important factor in explaining variation in baculum morphology. Allometric slopes that are less than one (using the OLS regression model), a very low proportion of variance in baculum length explained by body length, a general pattern of lower allometric slopes for baculum length compared with sexually dimorphic traits, and low phenotypic variability all point to stabilizing selection, rather than sexual selection, as the evolutionary force shaping variation in *M. americana* and *M. pennanti* baculum length. We hypothesize that this pattern is because post-copulatory selection plays a smaller role than pre-copulatory selection (manifested as male-biased sexual size dimorphism). In some ways, the Mustelidae are an ideal group to test this hypothesis. The baculum in the Mustelidae are relatively simple in shape, and thus easily measured. There is substantial variation across species in sexual size dimorphism, with males being over twice as heavy as females in some species (e.g. *Mustela erminea*), and with some species tending toward monomorphism (e.g. *Meles meles*) (Moors, 1980). A broader analysis of baculum allometry and sexual size dimorphism in the Mustelidae, coupled with a comparative analysis and phylogenetic contrasts would be the next logical step to test our hypothesis. More broadly, we predict that male-biased sexual size dimorphism is associated with negative allometry and isometry of the genitalia,

regardless of taxa, and further research should be conducted across taxonomic groups to test the generality of our hypothesis.

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