

# Sexual Selection and Genital Evolution in Mammals: A Phylogenetic Analysis of Baculum Length

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**ABSTRACT:** Studies in invertebrate taxa suggest that postcopulatory sexual selection is an important factor in genital evolution. However, despite wide interspecific variation in genital morphology, evidence for an influence of sexual selection on mammalian genitalia is equivocal. Here I conduct phylogenetically controlled comparative analyses across four mammalian orders to assess how one aspect of this variation—male genital length—scales with (a) male body mass and (b) relative testis mass, the latter providing an index of the intensity of sperm competition. In all four orders, baculum (= os penis) length is found to scale only weakly with male body mass. Both baculum and glans penis length in rodents and baculum length in carnivores are found to vary positively with relative testis mass. In contrast, there is no evidence to support an association between baculum length and relative testis mass in either bats or primates. These results suggest that postcopulatory sexual selection influences genital length in at least some mammals, but significant questions remain both as to why selection on the baculum should differ between mammalian groups and as to the precise mechanistic basis through which males benefit from increased genital length.

**Keywords:** allometry, baculum, genitalia, mammals, sexual selection, sperm competition.

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The conspicuous interspecific variability of the mammalian penis has long been of value as a taxonomic tool (e.g., Hooper and Musser 1964a, 1964b), though as in other animal groups the selective pressures underlying such genitalic diversity have not been well understood. Traditional explanations for mammalian genital evolution have cen-

tered on either lock-and-key mechanisms to prevent hybridization or else the idea that genitalia evolve neutrally and interspecific divergence accumulates through pleiotropic effects (see reviews in Patterson and Thaler 1982; Eberhard 1985; Edwards 1993). A growing number of studies in nonmammalian taxa (e.g., Robinson and Novak 1997; Arnqvist 1998; Arnqvist and Danielsson 1999; Coker et al. 2002; House and Simmons 2003; Bertin and Fairbairn 2005) instead support the contention that sexual selection is a powerful force acting on genital morphology (Eberhard 1985). Sexual selection on genitalia may arise either through precopulatory mechanisms to attract females (Langerhans et al. 2005) and attain copulations (Bertin and Fairbairn 2005) or through the postcopulatory processes of sperm competition, cryptic female choice (for “good genes” or “sexy sons”), and/or associated sexual conflict (reviews in Eberhard 1985, 1993; Hosken and Stockley 2004). Assessing the ubiquity and precise nature of sexual selection on genitalia requires the study of these phenomena across the widest possible taxonomic range.

Mammals represent an obvious group in which further studies of genital evolution are required, since to date evidence for a widespread role of sexual selection is equivocal (Hosken and Stockley 2004). Analyses in primates without full control for phylogeny suggest that bacula (= os penes) tend to be larger and genital morphology more complex in species where females typically mate with multiple males (Dixson 1987; Verrell 1992), a pattern repeated in (nonfelid) carnivores (Ferguson and Larivière 2004). However, the degree of penile spinosity in primates does not correlate with sexual selection intensity (Harcourt and Gardiner 1994; but see Stockley 2002). Similarly, in bats, a link between sperm competition and baculum length is not supported once phylogenetic effects are properly controlled for (Hosken et al. 2001). Studies of intraspecific genital allometry (Miller and Burton 2001; Lüpold et al. 2004) are also somewhat at odds with patterns established in invertebrates (e.g., Eberhard et al. 1998; Hosken et al. 2005). Nevertheless, several predictors of baculum size in mammals potentially relevant to the sexual selection hypothesis have been identified, including ex-

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tended copulation durations (Dixson 1987, 1995; Dixson et al. 2004; but see Larivière and Ferguson 2002), latitude (Ferguson and Larivière 2004), and female reproductive tract dimensions (Baumgardner et al. 1982; Patterson and Thaler 1982).

Here, I investigate two aspects of mammalian male genital size—baculum and glans penis length—within an appropriate phylogenetic framework. The study has two aims. First, I provide the most comprehensive analysis to date of interspecific baculum allometry on the basis of data from 403 mammal species across four orders (bats, carnivores, primates, and rodents). Analyses without control for phylogeny suggest a strong correlation between body and baculum size (Dixson et al. 2004), but among several groups of closely related rodents, body size is a relatively poor predictor of baculum size (Best and Schnell 1974; Patterson and Thaler 1982; Patterson 1983).

My second and principal aim is then to assess the influence of sperm competition on the evolution of genital length in 128 species across these four mammalian orders. It is important to note here that the substantial variation in genital length among mammals represents only one aspect of genital divergence; different aspects of genital morphology may be subjected to different selection (e.g., Arnqvist and Danielsson 1999; Stockley 2002; House and Simmons 2003; Bertin and Fairbairn 2005). While baculum length may often reflect overall genital size (e.g., Bradley and Schmidly 1987), data on the relationship between genital length and complexity in mammals are equivocal (app. A in the online edition of the *American Naturalist*). These additional aspects of genital morphology should therefore ideally be investigated separately, and a more definitive assessment of the influence of sperm competition (or other forms of sexual selection; see below) on mammalian genital morphology must await data on these other aspects of genital design. Nevertheless, several suggestions have been made as to why genital length may be directly relevant to the outcome of sperm competition. Longer genitalia could, for example, optimize the site of ejaculate deposition (Parker 1970, 1984). Alternatively, they could provide greater stimulation to the female reproductive tract (Dixson 1987; Kelly 2000), influencing sperm transport (Toner and Adler 1986) as well as subsequent female remating behavior and reproductive physiology (review in Huck and Lisk 1986). Finally, they might protect the urethra from damage during (more vigorous) copulation (Dixson 1995; Stockley and Preston 2004). Studies in nonmammalian taxa confirm that variation in male genital size can be an important paternity-biasing mechanism (e.g., Córdoba-Aguilar 2002; Rodriguez et al. 2004).

I employ relative testis mass as a proxy measure of sperm competition level, since both theory and empirical data

across a wide range of taxa suggest that this measure is a reliable indicator of variation in sperm competition intensity (Parker et al. 1997; Wedell et al. 2002), including in three out of the four mammalian orders studied here (Harcourt et al. 1981; Hosken 1997, 1998; Ramm et al. 2005). However, this approach comes with one important caveat. While a correlation of genital (baculum or glans penis) length with relative testis mass is entirely consistent with sexual selection via sperm competition acting on genital length, to the extent that their intensity co-varies, such a finding could equally result from the action of other forms of sexual selection and/or sexual conflict (Hosken and Stockley 2004). It should also be stressed that the absence of a correlation with relative testis mass does not preclude a possible influence for these alternative sexual selection mechanisms. Adaptations to sperm competition frequently give rise to sexual conflict (Stockley 1997), though the costs and benefits to females of variation in genital morphology are largely unknown (but see Crudgington and Siva-Jothy 2000; Hosken et al. 2003). Similarly, cryptic female choice (via sexy sons or good genes) could also influence genital evolution (see Eberhard 1985; Hosken and Stockley 2004), though in this case the direction of selection on genital length is especially difficult to predict. For example, intromittent organ size in waterfowl correlates positively with sperm competition level (Coker et al. 2002), but in most other bird groups, an intromittent organ is lacking; this absence may be explained by female choice if it enables females to regain control over fertilization (Briskie and Montgomerie 1997). In other groups, female choice for longer genitalia may be more plausible (e.g., Rodriguez et al. 2004). Thus, in the analyses that follow, positive evidence for sperm competition influencing genital length in a particular group must be broadly interpreted in favor of genital length being sexually selected, while the absence of such evidence cannot be used to conclude the opposite. Alternative methods are better suited to distinguishing the precise sexual selection mechanisms acting on genitalia (Hosken and Stockley 2004).

## Methods

### *Data Collection*

Data sets were compiled from the extensive literature on penile morphology (Hooper 1958, 1959, 1960, 1962; Burt 1960; Hooper and Hart 1962; Hooper and Musser 1964a, 1964b; Best and Schnell 1974; Morrissey and Breed 1982; Lidicker and Yang 1986; Lidicker and Brylski 1987; Contreras et al. 1993), on the basis of the availability of data for independent variables. Data on male body mass and testis mass were taken from the same sources as genitalic traits wherever possible, but where necessary, additional

data were obtained from Kenagy and Trombulak (1986), Pierce et al. (1990), Silva and Downing (1995), or Breed (1997). Baculum data for nonrodent taxa were obtained from Dixson et al. (2004), with additional data on testis mass for bats from Hosken et al. (2001), for primates from Harcourt (1991), and for carnivores from Kenagy and Trombulak (1986) or *Mammalian Species* articles (Loughlin et al. 1987; Pasitschniak-Arts 1993; Verts et al. 2001). Where data were available from multiple sources, (unweighted) mean values were used. All data were log transformed before analysis (Freckleton 2000).

Phylogenetic methods (see below) require an estimate of the phylogenetic relationships between species included in the data set. Phylogenies for rodents were constructed from various sources (Stangl and Baker 1984; Watts et al. 1992; Watts and Baverstock 1995; Engel et al. 1998; Liu et al. 2001; Herron et al. 2004; Jaarola et al. 2004; Steppan et al. 2004, 2005) and, for bats, carnivores, and primates, from the supertrees in Jones et al. (2002), Bininda-Emonds et al. (1999), and Purvis (1995), respectively. Phylogenetic relationships between orders were inferred from Liu et al. (2001). Branch lengths were generally unavailable, and so unit branch lengths were assumed (Freckleton et al. 2002).

#### *Comparative Analyses*

To control for potential nonindependence in the data due to shared ancestry (Felsenstein 1985; Harvey and Pagel 1991), data were analyzed using the phylogenetic general linear model (PGLM) procedure described by Gage and Freckleton (2003). This method is equivalent to the generalized least squares approach (Martins and Hansen 1997; Pagel 1999). Briefly, the method employs a maximum likelihood (ML) framework to first estimate an index of phylogenetic dependence,  $\lambda$ , based on the extent to which traits co-vary according to their degree of shared ancestry (Pagel 1999; Freckleton et al. 2002). This degree of shared ancestry was extracted from the phylogeny as a variance-covariance matrix using APE (Paradis et al. 2004). Likelihood ratio tests assess whether  $\lambda$  differs significantly from 0 and hence whether the data exhibit significant phylogenetic dependence (with a  $\lambda$  value of 1 indicating that the data are structured according to a Brownian model of trait evolution; see Felsenstein 1985; Freckleton et al. 2002). Maximum likelihood estimates of regression slopes for the independent variables can then be obtained while simultaneously controlling for phylogenetic associations by reference to an internal matrix of expected covariances based on this ML estimate of  $\lambda$  (for further details of the model, see Gage and Freckleton 2003). In general, only models with  $\lambda$  set to its ML value are reported (Freckleton et al. 2002).

#### *Interspecific Allometry of Baculum Length*

The phylogenetically controlled regression of baculum length on male body mass for rodents was obtained using data on baculum length and male body mass from 88 species collected from the literature (all data, together with sources, are given in app. B in the online edition of the *American Naturalist*). This was then compared with data from Dixson et al. (2004) on 315 species of bats, carnivores, and primates, reanalyzed to obtain phylogenetically controlled regression slopes. The principal aim of this analysis is to assess whether baculum length does indeed scale with body mass after control for phylogeny, for which tests based on the slopes from the PGLM are appropriate. A secondary question is then to assess the form of this relationship (where one exists). Since the assumption of no error in the  $x$  variable is violated, alternative methods may give more reliable slope estimates (Harvey and Pagel 1991). Where the PGLM analysis suggested a nonzero slope, I therefore also calculated the reduced major axis slope of baculum length on body mass. Because of the differing dimensions of the  $x$  and  $y$  variables, a slope estimate of  $b = 1/3$  would be expected under isometry. This combined analysis of 403 mammal species represents the most comprehensive study of interspecific baculum allometry to date. In addition to ML estimates of  $\lambda$  (see above), I also investigated the phylogenetic signal for (absolute and relative) baculum size by calculating the autocorrelation index, Moran's  $I$ , at three taxonomic levels: species within genera, genera within families, and families within orders (Gittleman and Kot 1990). Values were calculated using APE (Paradis et al. 2004).

#### *Sexual Selection and Genital Length*

Data on baculum and glans penis length (together with male body and testis mass) were collated from the literature for 45 and 31 rodent species, respectively (see app. B). Multiple regression was used with (log-transformed) male body mass and testis mass entered as the independent variables, a significant effect of the latter being taken as evidence that sperm competition influences genital length (Gage and Freckleton 2003).

Intraspecific sample sizes on which these analyses are based were often small, which may be problematic (see Harmon and Losos 2005). To explore the effects of small sample sizes per species ( $N_{ps}$ ), I repeated the baculum analyses on progressively smaller subsets of the data by excluding species for which baculum length was based on only one or two individuals (mean  $N_{ps}$  for whole data set = 9.18;  $N_{ps} = 1$  for seven species,  $N_{ps} = 2$  for eight species, and  $N_{ps} \geq 3$  for 30 species). I also conducted separate analyses of the two rodent families best represented

in the data set (Muridae,  $N = 34$ ; Heteromyidae,  $N = 6$ ). Too few data were available to conduct analogous analyses for glans penis length.

Finally, I assessed the influence of sperm competition on baculum length in three additional taxa, reanalyzing data for bats from Hosken et al. (2001) to confirm phylogenetic dependence and conducting novel phylogenetic analyses of baculum length in carnivores and primates on the basis of data collated by Dixson et al. (2004). All data (together with sources) for these analyses are given in appendix B. The scarcity of data currently precludes an analysis of glans penis length in these taxa, and possible sample size effects were not explored.

## Results

### *Interspecific Baculum Allometry*

All results are presented in table 1. When analyzed without regard to phylogeny, interspecific allometry explains nearly

two-thirds of the variation in baculum length. Previous estimates of the allometric slope based on 315 species of bats, carnivores, and primates (Dixson et al. 2004) are not much altered by the addition of 88 rodent species in this study (slope before = 0.42; slope after = 0.38). However, significant positive Moran's  $I$  values (fig. 1) and ML estimates of  $\lambda = 1$  (table 1) indicate that these results may be unreliable and that phylogenetic effects must be taken into account. After control for phylogeny, the relationship between baculum length and body mass is substantially weaker ( $r^2$  before = 0.62;  $r^2$  after = 0.12), and the allometric slope estimate (0.20) is substantially reduced; within the bat lineage, the relationship is lost altogether (Hosken et al. 2001). This alteration in the allometric slope after control for phylogeny is not uncommon (see Harvey and Pagel 1991; Nunn and Barton 2000) and results from the distorting effect of fitting lines across distinct groups that differ in relative baculum length. Intraorder allometric

**Table 1:** Phylogenetically controlled comparative analyses of mammalian genital length

Component, taxon, and species	$N$	ML $\lambda$	Intercept $\pm$ SE	Body mass $\pm$ SE	Testis mass $\pm$ SE	$r^2$	RMA slope $\pm$ SE
Glans:							
Rodents:							
All	31	1.00***	1.630 $\pm$ .216***	.066 $\pm$ .042 <sup>†</sup>	.133 $\pm$ .038**	.63	
Baculum:							
Rodents:							
All	88	.98***	.888 $\pm$ .218***	.244 $\pm$ .028***	...	.45	.362 $\pm$ .028
All	45	1.00***	1.434 $\pm$ .237***	.145 $\pm$ .036***	.111 $\pm$ .042*	.64	
$N_{ps} \geq 2$	38	1.00***	1.531 $\pm$ .285***	.129 $\pm$ .041**	.095 $\pm$ .045*	.63	
$N_{ps} \geq 3$	30	1.00***	1.556 $\pm$ .364***	.116 $\pm$ .051*	.097 $\pm$ .049 <sup>†</sup>	.62	
Muridae	34	1.00***	1.661 $\pm$ .199***	.046 $\pm$ .037 <sup>†</sup>	.148 $\pm$ .037***	.57	
Heteromyidae	6	1.00 <sup>†</sup>	3.886 $\pm$ .307**	-.250 $\pm$ .067*	.650 $\pm$ .066**	.98	
Bats:							
All	163	1.00***	-.021 $\pm$ .530 <sup>†</sup>	.143 $\pm$ .076 <sup>†</sup>	...	.02	
All	52	1.00**	.158 $\pm$ .713 <sup>†</sup>	.141 $\pm$ .140 <sup>†</sup>	-.006 $\pm$ .108 <sup>†</sup>	.01	
Primates:							
All	69	1.00***	1.143 $\pm$ .442*	.143 $\pm$ .050*	...	.09	.467 $\pm$ .050
All	21	1.00**	1.324 $\pm$ .883 <sup>†</sup>	.155 $\pm$ .140 <sup>†</sup>	.056 $\pm$ .162 <sup>†</sup>	.02	
Carnivores:							
All	83	1.00***	.783 $\pm$ .557 <sup>†</sup>	.200 $\pm$ .044***	...	.19	.458 $\pm$ .044
All	10	.98*	3.143 $\pm$ .577***	-.120 $\pm$ .061*	.786 $\pm$ .156**	.73	
Mammals:							
All	403	1.00***	.848 $\pm$ .391 <sup>†</sup>	.195 $\pm$ .026***	...	.12	.568 $\pm$ .026
All	128	1.00***	2.013 $\pm$ .484***	.005 $\pm$ .042 <sup>†</sup>	.205 $\pm$ .056***	.14	
All	403	$\lambda = 0^a$	-.285 $\pm$ .094**	.380 $\pm$ .015***	...	.62	
All	128	$\lambda = 0^a$	1.808 $\pm$ .299***	-.008 $\pm$ .057 <sup>†</sup>	.439 $\pm$ .070***	.57	

Note: Analyses are adjusted for phylogenetic dependence according to maximum likelihood (ML) estimates of  $\lambda$  (see "Methods"), and asterisks following the  $\lambda$  estimate refer to tests of  $H_0: \lambda = 0$  (phylogenetic independence). Note also that results for bats replicate those obtained previously by Hosken et al. (2001) using independent contrasts. Where the phylogenetic analysis suggested a nonzero slope in the body mass analyses, reduced major axis (RMA) slopes were also calculated (last column).

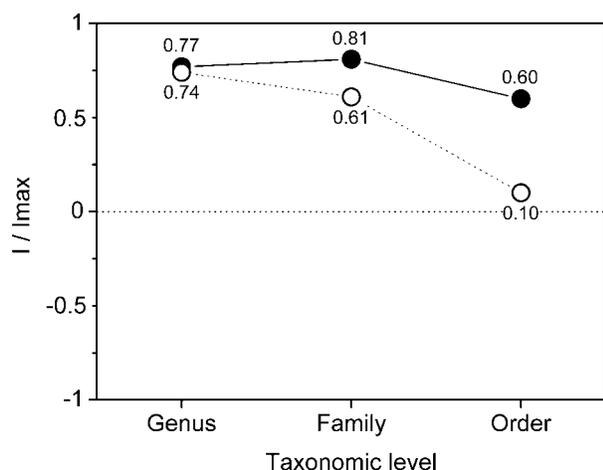
<sup>a</sup>  $\lambda$  constrained to 0 (phylogenetic independence).

\*  $P < .05$ .

\*\*  $P < .01$ .

\*\*\*  $P < .001$ .

<sup>†</sup> Not significant ( $P > .05$ ).



**Figure 1:** Phylogenetic correlogram of absolute (solid symbols) and relative (open symbols) baculum length in mammals. The Y-axis represents rescaled Moran's  $I$  values to permit comparison across taxonomic levels. All values are significantly different from 0 ( $P < .05$ ), and positive values indicate that species within each grouping are more correlated than would be expected by chance (Gittleman and Kot 1990).

slope estimates without control for phylogeny were much closer to the phylogenetically controlled global estimate (bats: 0.314; carnivores: 0.269; primates: 0.212; rodents 0.190; all  $P < .001$ , not shown). In models that also include testis mass (see below), a positive association between baculum length and body mass is lost in all but the rodent lineage.

#### *Sexual Selection and Rodent Genital Length*

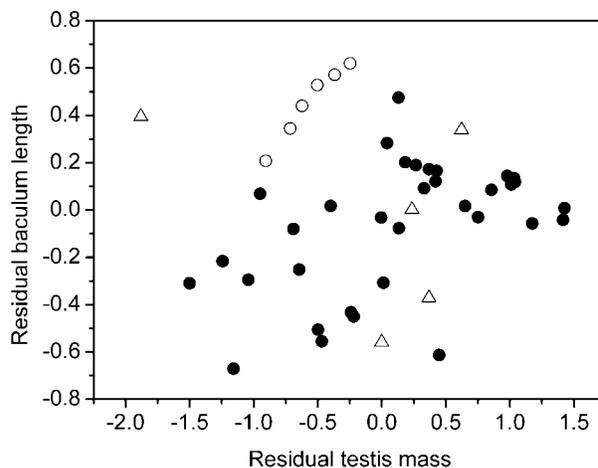
All results are presented in table 1. Data for both glans penis length and baculum length displayed strong phylogenetic dependence (ML estimate of  $\lambda = 1$  in each case). After control for phylogeny, both glans penis length and baculum length were found to be influenced by interspecific variation in sperm competition level, as indicated by the significant and positive effect of testis mass on both genital size measures in multiple regression analyses once body mass variation is taken into account.

Analyses of baculum length based on the smaller data sets—with reduced measurement error but also reduced power (Freckleton et al. 2002; Harmon and Losos 2005)—in general support the above conclusions (though for  $N_{ps} \geq 3$ , the testis mass effect is marginally nonsignificant;  $P = .058$ ). The taxonomic utility of the baculum is predicated on its high interspecific variability (one component of which is length), and the risk of intraspecific measurement error producing spurious results may therefore be quite low (Harmon and Losos 2005; see also Best and

Schnell 1974). Within-family analyses also support this conclusion. For both Muridae and Heteromyidae, testis mass is a highly significant predictor of baculum length, though bacula are in general larger relative to body mass in the latter family (fig. 2). While analyses based on so few data should be interpreted with caution, there is some evidence that both the slope and intercept for the relationship between testis mass and baculum length differ between these two families (main effect of “family”:  $-0.454 \pm 0.203$ ,  $P < .05$ ; “family”  $\times$  testis mass interaction:  $-0.124 \pm 0.050$ ,  $P < .05$ ).

#### *Sexual Selection and Baculum Length in Other Mammals*

All results are presented in table 1. The analysis for bats confirms that these data exhibit strong phylogenetic dependence (ML estimate of  $\lambda = 1$ ) and therefore amounts to a justification and replication of results obtained using independent contrasts by Hosken et al. (2001), that is, that sperm competition does not influence baculum length. This pattern was repeated for primates, whereas the analysis for carnivores supported an association between sperm competition level and baculum length. Overall, this pattern results in a weak but highly significant correlation between relative testis mass and baculum length among the 128 rodent, bat, carnivore, and primate species in the complete data set. The slope estimate for this relationship is substantially reduced compared with the case where  $\lambda$  is constrained to 0 (table 1).



**Figure 2:** Residual plot of baculum length on testis mass (after control for body mass) to illustrate interfamily differences in relative baculum length. Solid circles represent Muridae, and open circles represent Heteromyidae. Additional taxa (three Sciuridae, one Geomyidae, and one Castoridae) are represented by triangles. For phylogenetically controlled slope estimates, see table 1.

## Discussion

### *Interspecific Allometry of Baculum Length*

In contrast to analyses without control for phylogeny (Dixson et al. 2004), this analysis suggests that baculum length is only weakly correlated with male body mass, in keeping with earlier results among closely related rodent species (e.g., Best and Schnell 1974; Patterson and Thaler 1982; Patterson 1983). These results thus add to the evidence that genital size in mammals evolves to a large extent independently of body size. Previous authors have interpreted this pattern in rodents as evidence that the baculum is subject to direct selection (Patterson and Thaler 1982; Patterson 1983), and a weak correlation between genital and body size across species has also been reported for other taxa (e.g., Rodriguez et al. 2004).

### *Genital Length in Rodents Is Sexually Selected*

Analyses presented here reveal that the relative length of two male genital components—the glans penis and underlying baculum—evolves in parallel with levels of sperm competition among rodents. Thus, higher levels of sperm competition appear to favor increased genital length. However, as pointed out in the first section of this article, the precise mechanism of sexual selection acting on genitalia cannot readily be inferred from comparative data alone. In addition to the potential for sperm competition per se to produce this relationship, multiple mating by females also frequently gives rise to sexual conflict (Stockley 1997; Arnqvist and Rowe 2005) and is a prerequisite for cryptic female choice, either for good genes or sexy sons (Eberhard 1985; Hosken and Stockley 2004). While the absence of a correlation with relative testis size could not have excluded these additional selection pressures (or indeed the possibility that genitalia function as defensive adaptations to sperm competition; see Stockley 2002), nor can the positive association found here. Conservatively, I therefore conclude that any or all of these processes may be relevant; they are of course unlikely to be mutually exclusive (Eberhard 1985; Hosken and Stockley 2004). Given the many potential sexually selected benefits to males of longer genitalia (see first section of this article), further studies will be required before the comparative trend established here can be fully understood.

### *Selection on Baculum Length Differs between Mammalian Orders*

Bacula occur in bats, carnivores, insectivores, primates, and rodents. Variation in baculum length in four out of five of these orders was investigated here. The very limited data in carnivores tend to support the comparative trends

established for rodents (see also Ferguson and Larivière 2004), but the small sample size for this group makes this conclusion provisional at best. More confidently, analyses in bats do not support a link between sperm competition and baculum length (Hosken et al. 2001; but see Lüpold et al. 2004). Similarly, a previously reported comparative trend toward larger bacula in primate species with multimale mating systems (Dixson 1987; Verrell 1992) appears to be contradicted by the present phylogenetically controlled results using relative testis mass to infer variation in sperm competition level.

Overall, it seems likely that multiple factors influence genital evolution and that their relative importance will undoubtedly vary between groups. For example, since male genitalia must ultimately “fit” female genitalia, variation in female genital size is also likely to influence selection on male genital size (Eberhard 1985; Eberhard et al. 1998). Across species, this may result in the correlated evolution of male and female genital size (e.g., Ilango and Lane 2000; Rodriguez et al. 2004; but see Ramos et al. 2005). These effects were not considered here but might repay further investigation across mammals since a correlation between male and female genital dimensions in rodents has already been established (Baumgardner et al. 1982; Patterson and Thaler 1982; see also Fooden 1967).

Behavioral correlates of genital size observed in other mammals (Dixson 1987, 1995; Dixson et al. 2004) also merit further attention. Patterns of copulatory behavior in rodents have been shaped by sperm competition (Stockley and Preston 2004), but preliminary analyses conducted here failed to support a link with baculum length and three measures of copulatory behavior: intromission number, ejaculation number, and ejaculation latency (app. C in the online edition of the *American Naturalist*). Previous studies in other mammals have found an association between elongated bacula and the evolution of prolonged, single intromission copulatory patterns (Dixson 1987, 1995; Dixson et al. 2004). Rodents exhibit complex and diverse copulatory behavior, often involving multiple intromissions and ejaculations (Dewsbury 1975), and future studies should aim to include measures of intromission duration before any firm conclusions about the interplay between behavioral and anatomical male adaptations can be drawn.

A further factor likely to vary between mammalian groups is the degree to which the site of ejaculate deposition in the female tract is critical to fertilization success. Bearing in mind the correlation between male genitalia and female reproductive tract length in rodents (Baumgardner et al. 1982; Patterson and Thaler 1982), longer bacula could ensure that sperm and/or copulatory plugs are optimally positioned in the female reproductive tract (the position of the latter being critical to maximize sperm transport; Toner et al. 1987) or could facilitate the removal

of previously deposited plugs (e.g., O'Hanlon and Sachs 1986). Since female bats store sperm for prolonged periods (Racey 1975), the site of initial ejaculate deposition may be less critical, but whether genital morphology influences sperm storage is unknown. Primate data are not easily interpreted in this context, but given previous results in this group (Dixson 1987; Verrell 1992), the conclusion that sperm competition does not favor longer genitalia must also be treated with caution. A final factor that might help explain interorder differences is that the extent of bacular expression on the surface of the penis may also vary between groups (Patterson 1983), meaning that the correlation between genital length and baculum length will also vary (see also Lüpold et al. 2004).

#### *The Evolution of Animal Genitalia*

While the male genitalia of many animal groups have clearly been influenced by postcopulatory sexual selection (Robinson and Novak 1997; Arnqvist 1998; Arnqvist and Danielsson 1999; Córdoba-Aguilar 2002; House and Simmons 2003; Bertin and Fairbairn 2005), results from this and previous analyses (Dixson 1987; Verrell 1992; Harcourt and Gardiner 1994; Hosken et al. 2001; Stockley 2002; Ferguson and Larivière 2004) suggest that the situation in mammals is not straightforward. This study addresses only one aspect of genital morphology, male genital length, and different genital components have frequently been found to be subject to different selection pressures (e.g., Arnqvist and Danielsson 1999; House and Simmons 2003; Bertin and Fairbairn 2005). The various other aspects of penile morphology recognized to vary substantially between closely related mammals (e.g., baculum shape, penile spines and other embellishments) therefore need not be subject to the same selection pressures (see also Stockley 2002). In addition, the limitations of the comparative method in distinguishing between postcopulatory processes must also be acknowledged (Hosken and Stockley 2004; but see Eberhard 2004a, 2004b). Nevertheless, the comparative analyses conducted here provide phylogenetically controlled evidence that at least one aspect of genital morphology (male genital length) has been shaped by postcopulatory sexual selection in at least one mammalian lineage. Future work in this area should now seek to establish the mechanistic basis through which sexual selection favors increased genital length in rodents, together with the reasons as to why this is apparently not a pervasive trend across all mammals.

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