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# Sperm competition and brain size evolution in mammals

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## Abstract

The 'expensive tissue hypothesis' predicts a size trade-off between the brain and other energetically costly organs. A specific version of this hypothesis, the 'expensive sexual tissue hypothesis', argues that selection for larger testes under sperm competition constrains brain size evolution. We show here that there is no general evolutionary trade-off between brain and testis mass in mammals. The predicted negative relationship between these traits is not found for rodents, ungulates, primates, carnivores, or across combined mammalian orders, and neither does total brain mass vary according to the level of sperm competition as determined by mating system classifications. Although we are able to confirm previous reports of a negative relationship between brain and testis mass in echolocating bats, our results suggest that mating system may be a better predictor of brain size in this group. We conclude that the expensive sexual tissue hypothesis accounts for little or none of the variance in brain size in mammals, and suggest that a broader framework is required to understand the costs of brain size evolution and how these are met.

## Introduction

Understanding the factors that influence brain size evolution is a subject of longstanding interest within evolutionary biology research, in terms of both structural and functional considerations (Finlay & Darlington, 1995; Barton & Harvey, 2000; Barton, 2006; Byrne & Bates, 2007; Dunbar & Shultz, 2007; Sol *et al.*, 2007; Barrickman *et al.*, 2008; Gonzalez-Voyer *et al.*, 2009). In particular, several, not necessarily incompatible, hypotheses have been proposed to explain selection for relatively large brain size in certain birds and mammals, including ecological hypotheses (Harvey *et al.*, 1980; Barton, 1998; Sol *et al.*, 2005), and the social brain hypothesis (Brothers, 1990; Dunbar, 1998). Other hypotheses focus on potential evolutionary constraints on encephalization in these groups; for example the 'expensive tissue hypothesis' of Aiello & Wheeler (1995) proposes that brain size is constrained by an evolutionary trade-off between investment in energetically expensive brain tissue and other costly organs (e.g. the gut in primates).

More recently, attention has focussed on the possible role of sexual selection in brain size evolution among birds and mammals (Madden, 2001; Garamszegi *et al.*, 2005; Lindenfors *et al.*, 2007). In this context, Pitnick *et al.* (2006) suggested a new 'expensive sexual tissue hypothesis', whereby investment in brain tissue is proposed to trade-off specifically with investment in costly sexually selected traits such as large testes favoured under sperm competition. Sperm competition is a widespread phenomenon where sperm from two or more males compete to fertilize a set of ova (Parker, 1970; Birkhead & Møller, 1998), and is an important driving force in the evolution of diverse male reproductive traits that influence differential fertilization success, from sperm morphology and ejaculate characteristics to copulatory and mate-guarding behaviour (Birkhead & Møller, 1998). In mammals, it is well established that average testis mass (relative to body mass) is positively correlated with the level of sperm competition typically experienced by males (e.g. ungulates, Ginsberg &

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Rubenstein,1990; primates, Harcourt *et al.*, 1981, 1995; bats, Hosken, 1997, 1998; rodents, Ramm *et al.*, 2005). This is because larger testes allow males to invest more sperm in each reproductive event, thereby increasing the probability of winning in sperm competition (Parker *et al.*, 1997; Wedell *et al.*, 2002; see also Preston *et al.*, 2003; Schulte-Hostedde & Millar, 2004).

To date, support for the 'expensive sexual tissue hypothesis' has only been presented for bats, among which Pitnick *et al.* (2006) reported evidence of a negative evolutionary relationship between brain size and testis size as well as a larger brain (relative to body size) for monogamous or polygynous species compared to polygynandrous species (but see Dechmann & Safi, 2009). However, there is more widespread evidence in other mammalian taxa to suggest an association between mating system and brain size: monogamous species generally have larger brains than do species where females mate multiply (primates, Schillaci, 2006; carnivores and ungulates, Shultz & Dunbar, 2007), suggesting that large brain size is often found in species with relatively low levels of sperm competition. Whereas Pitnick *et al.* (2006) argued that various bat species have evolved greater levels of investment in either brain or testis mass, but not both because each of these tissues is energetically expensive to produce (c.f. Aiello & Wheeler, 1995), Shultz & Dunbar (2007) suggest instead that larger brains might be an advantage for monogamous species to optimize mate choice and to avoid cuckoldry. These different interpretations emphasize the importance of considering whether or not correlations are robust to potentially confounding variables and analysis across broader comparative datasets (Barton, 2006; Healy & Rowe, 2007).

Here, we test for evidence of a widespread influence of sperm competition on brain size evolution across a broad taxonomic spectrum of mammals. We use a large dataset, comprising rodents, bats, ungulates, primates, carnivores and insectivores, to look for evidence of a negative relationship between brain size and testis size, as predicted by the expensive sexual tissue hypothesis (Pitnick *et al.*, 2006). Results of our analyses do not support predictions of the expensive sexual tissue hypothesis, and suggest that it does not provide a general explanation for mammalian brain size evolution.

## Materials and methods

### Dataset

We collected data on total brain mass, testis mass, body mass and mating system. When data for continuous variables were available from multiple sources in the literature for the same biological trait in the same species, we used the mean of these data weighted by the sample size provided by each study. Because the different data sources often do not provide information on the sex of each animal measured, previous studies, including Pitnick *et al.* (2006), have used combined measures. We have therefore followed the same procedure here, such that brain and body masses should be considered as an average size for males and females. All data are provided in the Supporting Information.

Data on total brain masses come principally from published reviews [e.g. see Mace *et al.* (1981) and McNab & Eisenberg (1989) for rodents and insectivores, Pitnick *et al.* (2006) for bats, Harvey *et al.* (1980) for primates, Shultz & Dunbar (2006) for ungulates and Gittleman (1986) for carnivores]. This dataset was then supplemented using primary sources identified from *Zoological Record* and the *Mammalian Species* series (see Supporting Information for a complete reference list).

For testis mass, the data utilized in our study come mainly from published reviews [e.g. Kenagy & Trombulak (1986) for rodents, insectivores and carnivores; Pitnick *et al.* (2006) for bats; Harcourt *et al.* (1981) for primates and Ginsberg & Rubenstein (1990) for ungulates]. Again, this dataset was supplemented using information from primary sources identified from *Zoological Record* and the *Mammalian Species* series (see Supporting Information). For each species, combined testis mass (hereafter testis mass) is the average mass of both (right and left) testes, measured from multiple adult males in reproductive condition.

For each species, we attempted to utilize body mass data obtained from the same study as brain mass. When this source did not provide information on body mass, we used information from testis mass sources to complete our dataset. In bats, body mass values are the same as those collated by Pitnick *et al.* (2006) and summarized in their electronic Appendix S1. However, these authors provide two body masses for each species, one based on the source from where they obtained brain mass data and one from the source where they obtained testis mass data. As these two body masses were strongly correlated ($r = 0.96$; $P < 0.001$) and because there was no significant difference between them for each species ($t_{74} = -1.61$, $P = 0.11$), we here present results only for analyses using the body mass data which originates from the same sources as the brain mass data. This choice is more appropriate for our analysis as brain mass is always included as the dependent variable in all tests of the expensive sexual tissue hypothesis. Unless otherwise stated, all of our results remain qualitatively unchanged if the alternative body mass measure is used instead.

For mating system, we employed a dichotomous classification to distinguish between species that are likely to experience relatively high vs. relatively low levels of sperm competition. Our classification was based on the number of males with which a female typically mates within a single reproductive bout. Thus, species in which females typically mate with more than one male per reproductive attempt were classified as 'high sperm competition' (including species with polyandrous, polygynandrous and promiscuous mating systems) and those

in which females typically mate with only one male per reproductive attempt were classified as 'low sperm competition' (including species with polygynous and monogamous mating systems). This classification allows us to test the hypothesis of an evolutionary correlation between level of sperm competition and brain mass across all mammals in our dataset for which mating system data were collated (165 species) in a single model. Sources used to identify the level of sperm competition of each species are provided in the Supporting Information.

### Comparative methods

To control for nonindependence between species due to shared ancestry (Harvey & Pagel, 1991), data were analysed using the phylogenetic general linear model (PGLM) procedure described by Gage & Freckleton (2003), using a variance–covariance matrix extracted using APE (Paradis *et al.*, 2004). The main principle of this method is the employment of maximum likelihood to estimate an index of phylogenetic dependence, $\lambda$, which assesses the degree to which shared ancestry explains the data (see Freckleton *et al.*, 2002), and then incorporation of this into the analysis to control for the phylogenetic effect (Gage & Freckleton, 2003). We used information from published supertrees to construct phylogenies for bats (Jones *et al.*, 2002), primates (Purvis, 1995), carnivores (Bininda-Emonds *et al.*, 1999), insectivores (Grenyer & Purvis, 2003) and rodents (Bininda-Emonds *et al.*, 2007). For ungulates, we used the tree compiled by Shultz & Dunbar (2006) based on three different sources (Gatesy *et al.*, 1997; Flagstad *et al.*, 2001; Murphy *et al.*, 2001). Branch lengths were largely unknown, so unit branch lengths were assumed throughout (Freckleton *et al.*, 2002). In all cases, brain mass and testis mass were log-transformed prior to analysis, and log-transformed body mass was included in all analyses as a covariate (Harvey & Krebs, 1990).

We constructed a series of models to investigate potential effects of testis mass and sperm competition level on brain size evolution. In a general model including species from the full range of taxa investigated (bats, rodents, ungulates, primates, carnivores and insectivores), we looked for an influence of sperm competition (based on relative testis mass or sperm competition level) on total brain mass. We then conducted the same test for each taxon separately, except for insectivores due to the small number of species ($n = 7$) available for this group in our dataset. Finally, because of differences between groups reported by Pitnick *et al.* (2006), we also re-analysed these data to test the expensive hypothesis separately in echolocating (formerly Microchiroptera) and nonecholocating (formerly Megachiroptera) bats.

In each analysis, brain mass was entered into the PGLM as the dependent variable, with body mass plus testis mass or mating system as the independent variables. We confirmed that testis mass is related to sperm competition level as expected (see Introduction), by conducting further tests with testis mass as the dependent variable and body mass and sperm competition level as the independent variables. We also conducted tests with only body mass as an independent variable to compare the Akaike's Information Criterion (AIC) of these models with the AIC of the model described above. If an investigated variable (testis mass or mating system) has a significant effect on brain size evolution, we expect the AIC of these models to be smaller that the AIC of the model with only body mass as the independent variable. Again, these analyses were conducted both within each mammalian group for which sufficient data were available and across the dataset as a whole.

## Results

No significant negative relationship was found between testis mass and total brain mass, either across all species in the dataset, or within each of the mammalian orders tested separately (Table 1a). Indeed, in rodents, we found a marginally nonsignificant positive relationship between testis mass and brain mass ($n = 89$, $t = 1.86$, $P = 0.07$). Overall then, our analysis provides no evidence for the evolutionary trade-off between testis size and brain size predicted by the expensive sexual tissue hypothesis.

Next, we looked for evidence that brain size differs between species according to whether they typically experience 'high' or 'low' levels of sperm competition, where sperm competition levels were assessed on the basis of mating system classifications rather than testis size *per se* (see Methods). Here, as expected, species classed as having a 'high' sperm competition level had significantly larger relative testis mass compared to those classed as having a 'low' sperm competition level, both across the dataset as a whole ($n = 141$, $t = 6.17$, $P < 0.0001$) and within four of the five taxonomic groups investigated separately (bats: $n = 28$, $t = 5.45$, $P < 0.0001$; rodents: $n = 21$, $t = 3.69$, $P = <0.01$; ungulates: $n = 28$, $t = 2.47$, $P = 0.02$; primates: $n = 41$, $t = 0.27$, $P < 0.01$; carnivores: $n = 23$, $t = 1.67$, $P = 0.11$; for a possible explanation of the carnivore result, see Iossa *et al.*, 2008). However, consistent with our results for testis mass, we found no significant difference in total brain mass between species with contrasting levels of sperm competition based on mating system classifications, either across all the mammalian species in our dataset or within each of the groups analysed separately (Table 1b). Bats were the only exception to this pattern; as previously reported by Pitnick *et al.* (2006), for this group we found that high levels of sperm competition are associated with smaller brains (Table 1b).

Further analyses for bats reveal that the relationship between brain and testis mass is significant and negative for echolocating species (Table 1a), and 'low' sperm competition species in this group have larger brains than

**Table 1** Phylogenetic general linear model analysis of total brain mass in relation to (a) testis mass and (b) sperm competition level classification (SCL), a dichotomous variable based on the degree of female promiscuity.

| | (a) Testis mass | | | | | | (b) SCL | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Taxon | *n* | ML $\lambda$ | Variables | Estimate ± SE | *t*-value | *P* | *n* | ML $\lambda$ | Variables | Estimate ± SE | *t*-value | *P* |
| Mammals | 277 | 0.999 | Body mass | 0.50 ± 0.02 | 24.22 | < 0.001 | 165 | 0.999 | Body mass | 0.56 ± 0.02 | 43.22 | < 0.001 |
| | | | Testis mass | 0.03 ± 0.02 | 1.32 | 0.186 | | | SCL | −0.02 ± 0.06 | −0.35 | 0.72 |
| Bats* | 75 | 0.997 | Body mass | 0.70 ± 0.03 | 22.12 | < 0.001 | 38 | 0.906 | Body mass | 0.73 ± 0.03 | 20.91 | < 0.001 |
| | | | Testis mass | −0.04 ± 0.02 | −1.60 | 0.112 | | | SCL | −0.19 ± 0.07 | −2.39 | 0.02 |
| Echolocating bats | 61 | 0.896 | Body mass | 0.74 ± 0.04 | 19.76 | < 0.001 | 32 | < 0.001 | Body mass | 0.77 ± 0.04 | 19.87 | < 0.001 |
| | | | Testis mass | −0.07 ± 0.03 | −2.69 | 0.009 | | | SCL | −0.31 ± 0.08 | −3.90 | < 0.001 |
| Nonecholocating bats | 14 | < 0.001 | Body mass | 0.61 ± 0.03 | 18.78 | < 0.001 | 6 | < 0.001 | Body mass | 0.69 ± 0.02 | 27.11 | < 0.001 |
| | | | Testis mass | 0.09 ± 0.03 | 2.8 | 0.017 | | | SCL | −0.30 ± 0.08 | −3.72 | 0.03 |
| Rodents | 89 | 0.937 | Body mass | 0.38 ± 0.02 | 14.19 | < 0.001 | 21 | 0.999 | Body mass | 0.42 ± 0.04 | 10.36 | < 0.001 |
| | | | Testis mass | 0.05 ± 0.03 | 1.86 | 0.07 | | | SCL | 0.19 ± 0.12 | 1.60 | 0.13 |
| Ungulates | 28 | 0.999 | Body mass | 0.52 ± 0.06 | 7.64 | < 0.001 | 28 | 0.999 | Body mass | 0.45 ± 0.05 | 8.26 | < 0.001 |
| | | | Testis mass | −0.06 ± 0.07 | −0.71 | 0.48 | | | SCL | 0.14 ± 0.12 | 1.19 | 0.24 |
| Primates | 43 | 0.739 | Body mass | 0.63 ± 0.05 | 11.71 | < 0.001 | 41 | 0.800 | Body mass | 0.60 ± 0.049 | 12.08 | < 0.001 |
| | | | Testis mass | −0.001 ± 0.004 | −0.26 | 0.80 | | | SCL | −0.27 ± 0.20 | −1.36 | 0.18 |
| Carnivores | 35 | 0.999 | Body mass | 0.56 ± 0.06 | 9.84 | < 0.001 | 36 | 0.651 | Body mass | 0.58 ± 0.03 | 16.87 | < 0.001 |
| | | | Testis mass | 0.05 ± 0.08 | 0.63 | 0.53 | | | SCL | 0.02 ± 0.13 | 0.18 | 0.86 |

The group 'mammals' is composed of bats, rodents, ungulates, primates, carnivores and insectivores. In each model, body mass is included as a covariate.

*Note that the results for bats differ slightly from Pitnick *et al.* (2006). The relationship between testis mass and brain mass was negative for bats, but did not reach statistical significance in our analysis, either in the model presented or with $\lambda$ set to 0 or 1, or with branch lengths set according to Jones *et al.* (2005). The most likely explanation for this difference is the way in which the two different methods handle polytomies. In particular, owing to a poorly resolved phylogeny, the family Vespertillionidae contributes five independent contrasts to the analysis of Pitnick *et al.* (2006), despite the fact that 18 species from this family are included in the analysis; there is no obvious correlation between brain mass and testis mass in Vespertillionidae, a result which has a proportionately greater influence on our overall result.

'high' sperm competition species (Table 1b). For each model where the relationship between brain mass and testis mass or mating system was significant (Table 1a,b), the AIC increased when the tested variable was removed from the model (not shown) which confirms the importance of testis mass or mating system to explain variation in brain size. (As expected, the AIC decreased when we removed the tested variable in the models where they do not have a significant effect.) For the 26 echolocating species for which data on both testis mass and mating system are available, both trends are still apparent when the two explanatory variables are analysed separately (testis mass: $n = 26$, $t = -2.00$, $P = 0.06$; sperm competition level: $n = 26$, $t = -2.82$, $P < 0.01$). However, when both are combined in the same model, only sperm competition level (based on mating system classifications) approaches significance (Table 2). These patterns are strengthened if the alternative body mass measure (based on testis mass data sources – see methods) is used, resulting in a significant effect of sperm competition level ($P = 0.03$, not shown). The nonecholocating species also differ in brain size according to mating system classification (Table 1b), but in contrast to echolocating species there is a significant positive relationship between brain and testis mass.

## Discussion

No significant negative relationship was found between testis and brain mass across mammals in our dataset, or within any mammalian order investigated separately (bats, rodents, ungulates, primates and carnivores). Hence, we find no general evidence in support of the expensive sexual tissue hypothesis as applied to mammalian taxa. As similarly argued by Hladik *et al.* (1999) in relation to the expensive tissue hypothesis of Aiello &

**Table 2** Phylogenetic general linear model analysis for echolocating bats of total brain mass in relation to body mass, testis mass and sperm competition level classification (SCL), a dichotomous variable based on the degree of female promiscuity.

| *n* | ML $\lambda$ | Variables | Estimate ± SE | *t*-value | *P* |
|---|---|---|---|---|---|
| 26 | < 0.001 | Body mass | 0.845 ± 0.065 | 12.94 | < 0.001 |
| | | Testis mass | −0.021 ± 0.06 | −0.35 | 0.729 |
| | | SCL | −0.240 ± 0.131 | −1.834 | 0.080 |

Compared to results described in Table 1, body mass, testis mass and SCL are here tested simultaneously in the same model.

Wheeler (1995), it is not immediately obvious why the energetic costs of any two specific costly organs should impact directly on one another, instead of producing more diffuse effects on investment in a range of other costly organs or activities (Barton, 2006). Aiello & Wheeler's (1995) expensive tissue hypothesis has also received mixed support beyond their original analyses for anthropoid primates. For example, Jones & MacLarnon (2004) reported evidence of a positive relationship between relative brain size and intestine length in bats, rather than the negative evolutionary relationship predicted, and Isler & van Schaik (2006) found no compelling evidence that the size of other energetically expensive organs (e.g. heart, lungs, gut) is systematically traded off against brain size in birds. Moreover, the mammalian brain is a highly complex organ with a large number of components and neuronal connections involved in many functions (Laughlin *et al.*, 1998); thus, a simple energetic trade-off between any organ and overall brain mass may be unlikely (Hladik & Pasquet, 2003).

Consistent with the results for relative testis mass, we find no evidence that total brain mass differs according to level of sperm competition based on our mating system classification across all mammals tested, or within each group tested separately except for bats (see below). Similarly, Schillaci (2006) found no interspecific differences in brain size of primates according to levels of female promiscuity. Here, it is important to note that our 'level of sperm competition' classification, like the mating system classification of Schillaci (2006), is based on levels of female promiscuity, whereas earlier studies have placed greater emphasis on aspects of social organization. In primates for example, bigger brains are found in harem and multi-male species compared to solitary and pair-bonded species (Shultz & Dunbar, 2007), whereas sperm competition is high only in multi-male species (Harcourt *et al.*, 1995). Consequently, primate brain size appears to correlate more closely with sociality than with sperm competition (see also Shultz & Dunbar, 2007).

The only mammalian group for which we find evidence of a negative relationship between testis mass and brain mass was the echolocating bats (see also Pitnick *et al.*, 2006). Might the expensive sexual tissue hypothesis then be applied as a special case to this group? Echolocating bats (which are typically insectivorous) are smaller compared to nonecholocating bats (which feed primarily on fruit) and so small body size could be one source of energetic constraint. This seems unlikely, however, because the other group in our analysis with small body size, rodents, actually exhibited a positive trend in the relationship between testis mass and brain mass. Alternatively, the energetic costs of flight and echolocation are also substantial (Arita & Fenton, 1997; Winter & von Helversen, 1998) and so might act as a specific constraint in echolocating bats (Pitnick *et al.*, 2006). However, although perhaps not directly comparable to bats (Winter & von Helversen, 1998), evidence for birds tends not to support the idea that flight constrains investment in encephalization (Iwaniuk *et al.*, 2004). Moreover, our results for echolocating bats suggest that mating system may be a better predictor of brain size than testis size *per se* (see also Shultz & Dunbar, 2007). That is, when we tested simultaneously for an effect of both testis size and mating system classification on brain size in echolocating bats, only mating system approached significance. Hence on the basis of this analysis, we find limited support for the expensive sexual tissue hypothesis even in echolocating bats. Similarly, Dechmann & Safi (2009) reported that brain mass and testis mass in bats are no longer correlated after accounting for foraging strategy.

More broadly, there are a number of difficulties associated with applying the comparative method to understand patterns of brain size evolution, particularly in relation to hypotheses about sexual selection (Healy & Rowe, 2007). Importantly, specific parts of the brain may vary independently of whole brain size (the 'mosaic brain evolution' hypothesis; Barton & Harvey, 2000), and studies which seek to explain variation in the size of specific parts of the brain may often be more informative than those which focus on total brain size, particularly if such parts can be assigned a reasonably discrete function (Krebs, 1990; Barton, 1998, 2004; Healy & Rowe, 2007). Secondly, comparative analyses of brain components measured separately in males and females are also relevant to understanding potential effects of sexual selection on encephalization (Lindenfors *et al.*, 2007), as sex differences in brain structure have already been established (Jacobs *et al.*, 1990; Gahr *et al.*, 2008). In zebra finches and canaries for example, the high vocal centre and the robust nucleus of the archistriatum, which are two subregions of the brain involved in singing, are larger in males than in females (MacDougall-Shackleton & Ball, 1999). Therefore, it seems likely that natural or sexual selection may influence male and female brains differently (Garamszegi *et al.*, 2005), and if sexual selection favours a larger overall brain size in males than in females, the effect of sperm competition on encephalization might be underestimated when using an average measure. Hence, to be tested rigorously, hypotheses involving a putative role of sexual selection in brain size evolution should be tested with sex-specific data on brains or brain components.

## Conclusions

We conclude that there is no general trade-off between testis mass and brain mass in mammals, and consequently that there is no evidence that the expensive sexual tissue hypothesis can provide a general explanation for the evolution of mammalian brain size. Moreover, as noted by Dunbar & Shultz (2007), energetic or developmental explanations are mainly aimed at identifying constraints on brain size evolution, rather than the

selection pressures through which individuals might benefit from larger brains. Although the energetic costs of large brains must indeed be somehow accommodated, there is perhaps no reason to assume that this is achieved through a simple and invariant mechanism, such as a trade-off against the size of another organ. Instead, there may be a variety of complex and varying trade-offs among body size, life histories, energy acquisition rates, and energy allocation to a range of organs of which the brain is just one (Isler & van Schaik, 2006; Barrickman *et al.*, 2008). We suggest, therefore, that understanding the costs of brain size evolution requires a broader approach to these trade-offs than has commonly been used in the past.

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## Supporting information

Additional Supporting Information may be found in the online version of this article:

**Appendix S1** Sperm competition and brain size evolution in mammals.

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# Supplementary Online Material

## Sperm competition and brain size evolution in mammals

Jean-François Lemaître, Steven A. Ramm, Robert A. Barton and Paula Stockley

Testes mass, body mass, brain mass and sperm competition level for rodents, primates, ungulates, carnivores and insectivores*. Testes mass (TM) is the average combined mass of both (right and left) testes, measured from multiple adult males in reproductive condition; brain mass (BrM) is total brain mass, measured as an average from different adult individuals; body mass (BM) data were obtained from the same source as brain mass data where possible; sperm competition level (SCL) is a dichotomous classification based on mating system. Species classified as having relatively high sperm competition include those with polyandrous, polygynandrous, and promiscuous mating systems, and those classified as having relatively low sperm competition include species with polygynous and monogamous mating systems. When data were available from multiple sources in the literature for testes mass, body mass and brain mass, we used the mean of these data weighted by the sample size provided by each study. All brain and body mass data should be considered as an average size for males and females.

| | *Species Name* | TM (g) | BM (g) | BrM (g) | SCL | Sources |
|---|---|---|---|---|---|---|
| Rodents | *Aethomys chrysophilus* | 0.862 | 117 | 1.84 | | 1; 2 |
| | *Aethomys hindei* | 2.768 | 146.3 | 2.01 | | 1; 2 |
| | *Aethomys namaquensis* | 1.476 | 79.4 | 1.48 | | 1; 2 |
| | *Ammospermophilus leucurus* | 2.14 | 106 | 2.92 | High | 1; 3; 4 |
| | *Apodemus flavicollis* | 0.891 | 32.3 | 1.29 | | 1; 2 |
| | *Apodemus sylvaticus* | 0.788 | 18.6 | 1.17 | | 1; 2 |
| | *Arvicola terrestris* | 0.78 | 144.15 | 1.865 | | 1; 3; 4 |
| | *Cavia aperea* | 0.95 | 524.9 | 5.86 | Low | 1; 5 |
| | *Cavia porcellus* | 4.1 | 971 | 4.3 | | 3; 4; 6 |
| | *Chaetodipus formosus* | 0.21 | 20.9 | 1.13 | | 1; 4 |
| | *Chinchilla lanigera* | 5.2 | 432 | 5.5 | | 3; 4 |
| | *Chiropodomys gliroides* | 0.38 | 25.3 | 1.29 | | 1; 2 |
| | *Clethrionomys glareolus* | 0.646 | 17.9 | 1.11 | High | 1; 3; 4 |
| | *Cynomys leucurus* | 4.88 | 992.1 | 6.28 | | 1; 8 |
| | *Cynomys ludovicianus* | 0.928 | 793.75 | 6.6 | | 1; 3; 9 |
| | *Dasyprocta leporina* | 5.03 | 2800 | 20.3 | | 3; 10 |
| | *Dicrostonyx groenlandicus* | 0.092 | 68.4 | 1.31 | | 1; 11 |
| | *Dipodomys merriami* | 0.45 | 37.9 | 1.64 | | 1; 3; 4; 12 |
| | *Dipodomys microps* | 0.4 | 60 | 1.8 | | 1; 3; 4; 12 |
| | *Dipodomys ordii* | 0.53 | 54 | 1.97 | | 1; 4; 12 |
| | *Dipodomys panamintinus* | 0.52 | 74 | 1.54 | | 4; 12 |
| | *Galea musteloides* | 2.77 | 375 | 3.31 | High | 1; 5 |
| | *Gerbillus pyramidum* | 0.81 | 40.9 | 1.47 | | 1; 13 |
| | *Jaculus jaculus* | 0.58 | 55.2 | 1.8 | | 1; 3; 14 |
| | *Lophuromys flavopunctatus* | 1.138 | 60 | 1.6 | | 1; 2 |
| | *Marmota monax* | 7.4 | 4199 | 11.24 | High | 1; 3; 4 |
| | *Megadontomys thomasi* | 2 | 77 | 2.01 | | 3; 15 |

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|---|---|---|---|---|---|
| *Melomys cervinipes* | 2.782 | 70 | 1.9 | | 1; 2 |
| *Melomys rubex* | 1.872 | 49.7 | 1.86 | | 1; 2 |
| *Melomys rufescens* | 1.342 | 54.7 | 1.88 | | 1; 2 |
| *Mesembriomys gouldii* | 5.498 | 1110 | 5.18 | | 1; 2 |
| *Mesocricetus auratus* | 3.17 | 13.3 | 1.12 | | 1; 3; 4 |
| *Micromys minutus* | 0.15 | 6.4 | 0.88 | | 1; 2 |
| *Microtus agrestis* | 0.804 | 22.3 | 1.16 | | 1; 4 |
| *Microtus arvalis* | 0.424 | 30.4 | 1.14 | | 1; 4 |
| *Microtus californicus* | 0.27 | 43.15 | 1.37 | Low | 3; 4 |
| *Microtus montanus* | 0.38 | 39.85 | 1.28 | High | 1; 3; 16 |
| *Microtus ochrogaster* | 0.52 | 43.9 | 1.3 | Low | 1; 3; 16 |
| *Microtus pennsylvanicus* | 0.58 | 37.15 | 1.36 | High | 1; 3; 16 |
| *Microtus pinetorum* | 0.07 | 24.9 | 1.15 | Low | 1; 16 |
| *Mus musculus* | 0.119 | 14 | 0.44 | Low | 2; 6; 17 |
| *Myocastor coypus* | 4.4 | 9070 | 17.68 | | 1; 18 |
| *Neotoma micropus* | 1.206 | 378.3 | 3.25 | | 1; 19 |
| *Notomys alexis* | 0.045 | 37 | 1.55 | | 1; 2; 3; 4 |
| *Ondatra zibethicus* | 5.31 | 1236.5 | 5.76 | Low | 1; 3; 4 |
| *Perognathus longimembris* | 0.07 | 8.15 | 0.93 | | 1; 3; 4; 12 |
| *Peromyscus boylii* | 0.3 | 16.3 | 1.37 | | 1; 15 |
| *Peromyscus californicus* | 0.2 | 34.2 | 1.54 | | 1; 15 |
| *Peromyscus crinitus* | 0.12 | 14.7 | 0.875 | | 1; 3; 15 |
| *Peromyscus eremicus* | 0.232 | 20.65 | 0.885 | | 1; 3; 15 |
| *Peromyscus gossypinus* | 0.68 | 26.6 | 1.42 | | 1; 15 |
| *Peromyscus leucopus* | 0.25 | 21.8 | 1.24 | | 1; 15 |
| *Peromyscus maniculatus* | 0.393 | 20.95 | 0.88 | High | 1; 3; 4 |
| *Peromyscus megalops* | 1.48 | 71 | 1.8 | | 1; 3; 15 |
| *Peromyscus mexicanus* | 0.43 | 53.4 | 1.63 | | 1; 15 |
| *Peromyscus polionotus* | 0.1 | 14 | 1.12 | Low | 1; 15; 20 |
| *Peromyscus truei* | 0.47 | 30 | 1.36 | | 1; 3; 15 |
| *Podomys floridanus* | 0.58 | 27.3 | 1.54 | | 1; 15 |

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|---|---|---|---|---|---|
| *Praomys tullbergi* | 1.43 | 37.2 | 1.45 | | 1; 21 |
| *Pseudomys australis* | 2 | 50 | 1.75 | | 1; 2 |
| *Rattus exulans* | 1.893 | 42.1 | 1.69 | | 1; 22 |
| *Rattus fuscipes* | 4.262 | 135.7 | 2.22 | | 1; 2; 3 |
| *Rattus lutreolus* | 4.434 | 92.85 | 2.23 | | 1; 2; 3 |
| *Rattus norvegicus* | 4 | 269 | 2.09 | | 4; 7 |
| *Rattus rattus* | 3.467 | 150 | 1.92 | | 2; 3 |
| *Rattus sordidus* | 3.522 | 158 | 2.29 | | 2; 3 |
| *Rattus tunneyi* | 4.865 | 243 | 2 | | 2; 3 |
| *Rhabdomys pumilio* | 0.909 | 55 | 1.28 | | 2; 3 |
| *Sciurus aestuans* | 2.6 | 626.75 | 7.44 | | 1; 3; 4 |
| *Sciurus carolinensis* | 5.18 | 574.5 | 7.76 | High | 1; 4 |
| *Sciurus niger* | 6.9 | 809.9 | 9.31 | | 1; 4 |
| *Sciurus vulgaris* | 2.81 | 331.8 | 6.34 | High | 1; 4 |
| *Sigmodon hispidus* | 1.73 | 140.25 | 1.455 | | 1; 3; 4 |
| *Spermophilus beecheyi* | 9.05 | 587.25 | 5.71 | High | 1; 3; 4 |
| *Spermophilus beldingi* | 2.5 | 263 | 3.87 | | 3; 23 |
| *Spermophilus lateralis* | 3.25 | 166 | 3.6 | High | 1; 3; 4 |
| *Spermophilus townsendii* | 0.624 | 199 | 2.65 | | 1; 24 |
| *Spermophilus tridecemlineatus* | 1.27 | 175 | 3.02 | | 3; 25; 26 |
| *Tamias amoenus* | 0.62 | 50.8 | 1.98 | High | 1; 4 |
| *Tamias minimus* | 0.72 | 45.3 | 2.19 | High | 1; 4 |
| *Tamias palmeri* | 0.86 | 60.8 | 2.58 | | 1; 4 |
| *Tamias panamintinus* | 7.8 | 51.2 | 2.42 | | 1; 4 |
| *Tamias striatus* | 1.7 | 93.65 | 2.73 | | 1; 3; 4 |
| *Tamias townsendii* | 0.82 | 89.4 | 3.03 | High | 1; 4 |
| *Tatera afra* | 7.74 | 65 | 2.15 | | 1; 4 |
| *Tatera brantsii* | 5.31 | 91.7 | 2.15 | | 1; 4 |
| *Tatera indica* | 6.41 | 139.85 | 2.43 | | 1; 3; 4 |
| *Uranomys ruddi* | 0.348 | 33.6 | 1.36 | | 1; 2 |

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|---|---|---|---|---|---|---|
| Primates | *Aloutta palliata* | 23 | 7260 | 55.1 | High | 28; 29 |
| | *Aotus trivergatus* | 1.2 | 1020 | 18.2 | Low | 28; 29 |
| | *Ateles geoffroyi* | 13.4 | 7940 | 110.9 | High | 27; 29 |
| | *Avahi laniger* | 2.29 | 1300 | 7.4 | Low | 2; 29; 38 |
| | *Callithrix jacchus* | 1.3 | 320 | 7.9 | High | 27; 29 |
| | *Cebuella pygmaea* | 0.33 | 130 | 4.15 | High | 27; 29 |
| | *Cebus apella* | 4.64 | 3000 | 10 | High | 27; 29 |
| | *Cercophitecus ascanius* | 3 | 5360 | 67 | High | 27; 29 |
| | *Cercopithecus aethiops* | 13 | 4950 | 59.8 | High | 28; 30 |
| | *Cheirogaelus major* | 2.3 | 340 | 6.8 | | 27; 29 |
| | *Colobus polykomos guereza* | 10.7 | 10250 | 76.6 | Low | 28; 29 |
| | *Erythrocebus patas* | 7.2 | 10000 | 108 | High | 27; 29 |
| | *Galago senegalensis* | 1.66 | 220 | 4.8 | High | 3; 29; 38 |
| | *Galagoides demidovii* | 0.85 | 70 | 3.4 | High | 27; 29 |
| | *Gorilla gorilla* | 29.6 | 169000 | 505.9 | Low | 28; 29 |
| | *Hylobates agilis* | 6.32 | 6000 | | Low | 28 |
| | *Hylobates lar* | 5.5 | 5500 | 107.7 | Low | 28; 29 |
| | *Hylobates moloch* | 6.1 | 5440 | 113.7 | Low | 28; 29 |
| | *Lagothrix lagothrica* | 11.2 | 5220 | 96.4 | High | 28; 29 |
| | *Leontopithecus rosalia* | 1.48 | 550 | | Low | 27 |
| | *Loris tardigradus* | 1.8 | 270 | 6.8 | | 27; 29 |
| | *Macaca arctoides* | 48.15 | 10510 | 76.8 | High | 28; 29 |
| | *Macaca fasciularis* | 35.2 | 4420 | 69.2 | High | 28; 29 |
| | *Macaca mulatta* | 46.2 | 9200 | 95.1 | High | 28; 29 |
| | *Macaca nemestrina* | 66.7 | 9980 | 106 | High | 28; 29 |
| | *Macaca radiata* | 48.2 | 8650 | 104.1 | High | 28; 29 |
| | *Microcebus murinus* | 2.49 | 70 | 1.78 | High | 27; 29 |
| | *Miopithecus talapoin* | 5.2 | 1250 | | High | 27 |
| | *Nasalis larvatus* | 11.8 | 20640 | 94.2 | Low | 28; 29 |
| | *Nycticebus coucang* | 1.2 | 1058 | 12.2 | High | 3; 29; 38 |
| | *Pan troglodytes* | 118.8 | 44340 | 410.3 | High | 27; 29 |

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|---|---|---|---|---|---|---|
| | *Papio anubis* | 93.5 | 26400 | 93.5 | High | 28; 29 |
| | *Papio cynocephalus* | 52 | 24320 | 169.1 | Low | 28; 29 |
| | *Papio hamadryas* | 27.1 | 20170 | 142.5 | Low | 28; 29 |
| | *Papio papio* | 88.9 | 31980 | 165.3 | High | 28; 29 |
| | *Papio ursinus* | 72 | 31750 | 214.4 | High | 28; 29 |
| | *Pongo pygmaeus* | 34.2 | 69000 | 413.3 | Low | 28; 29 |
| | *Presbystis entellus* | 11.1 | 17000 | 135.2 | Low | 28; 29 |
| | *Presbystis obscura* | 4.8 | 7450 | 67.6 | Low | 28; 29 |
| | *Presbytis cristata* | 6.2 | 6580 | 64 | Low | 28; 29 |
| | *Presbytis rubicunda* | 3.4 | 6230 | 92.7 | Low | 28; 29 |
| | *Saguinus midas* | 1.83 | 570 | 10.3 | High | 27; 29 |
| | *Saguinus oedipus* | 3.4 | 520 | 9 | High | 28; 29 |
| | *Saimiri sciureus* | 3.2 | 780 | 24.4 | High | 28; 29 |
| | *Theropithecus gelada* | 17.1 | 20400 | 131.7 | Low | 28; 29 |
| | *Varecia variegatus* | 2.63 | 3471 | 30.8 | Low | 3; 29; 38 |
| Ungulates | *Aepyceros melampus* | 120 | 58500 | 179 | High | 31; 32 |
| | *Alces alces* | 106 | 200000 | 435 | Low | 31; 32 |
| | *Antilocarpa americana* | 76 | 24000 | 165 | High | 31; 32 |
| | *Capreolus capreolus* | 43 | 16850 | 100 | Low | 31; 32 |
| | *Cephalophus sylvicultor* | 33.25 | 45000 | 170 | Low | 31; 38 |
| | *Cervus elephus* | 218 | 90175 | 311 | High | 31; 32 |
| | *Dama dama* | 133 | 56234 | 215 | High | 31; 32 |
| | *Equus przewalskii* | 133 | 361450 | 586 | High | 31; 38 |
| | *Gazella dorcas* | 31.46 | 15000 | 66 | Low | 31; 38 |
| | *Giraffa camelopardalis* | 1074 | 581750 | 704 | High | 31; 32 |
| | *Hemitragus jemlahicus* | 26.7 | 70000 | 166 | High | 31; 32 |
| | *Hippopotamus amphibus* | 650 | 1955000 | 569 | Low | 31; 32 |
| | *Hylochoerus meinertzhageni* | 500 | 200000 | 140 | High | 31; 32 |
| | *Kobus leche* | 67.85 | 123000 | 223 | High | 31; 38 |
| | *Odocoielus virginianus* | 76 | 41960 | 144 | Low | 31; 32 |

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|---|---|---|---|---|---|---|
| | *Oryx gazella* | 37.9 | 130000 | 274 | Low | 31; 38 |
| | *Phaecochoerus aethiopicus* | 93 | 68160 | 132 | Low | 31; 32 |
| | *Rangifer tarandus* | 132 | 95225 | 270 | High | 31; 32 |
| | *Sus scrofa* | 36 | 66900 | 180 | Low | 31; 32 |
| | *Sylviacapra grimmia* | 21.25 | 11900 | 76 | Low | 31; 38 |
| Carnivores | *Acinonyx jubatus* | | 58560 | 111.05 | High | 33; 34 |
| | *Alopex lagopus* | 4.06 | 3190 | 35.52 | Low | 33; 35; 36 |
| | *Bassariscus astutus* | | 840 | 16.44 | High | 33; 36 |
| | *Canis aureus* | 13.3 | 8760 | 72.24 | | 33; 35 |
| | *Canis latrans* | 15.4 | 10490 | 88.23 | Low | 33; 35; 36 |
| | *Canis lupus* | 27.38 | 33110 | 131.63 | Low | 33; 35; 36 |
| | *Canis mesomelas* | | 7690 | 56.83 | Low | 33; 37 |
| | *Chrysocyon brachiurus* | 12.68 | 23100 | 120.3 | | 33; 35 |
| | *Crocuta crocuta* | 9.85 | 66020 | 144.03 | | 33; 35 |
| | *Cryptoprocta ferox* | 11.15 | 9490 | 32.14 | High | 33; 38 |
| | *Cuon alpinus* | 6.35 | 17640 | 94.63 | Low | 33; 38 |
| | *Cynictis penicillata* | 1.98 | 590 | 10.49 | | 33; 35 |
| | *Enhydra lutris* | | 27940 | 125.21 | High | 33; 36 |
| | *Felis chaus* | 4.62 | 7030 | 39.25 | | 33; 35 |
| | *Felis silvestris* | 1.38 | 4660 | 37.34 | High | 33; 35 |
| | *Gulo gulo* | 17 | 11130 | 78.26 | High | 33; 35; 36 |
| | *Herpailurus yagouaroundi* | | 7460 | 40.04 | High | 33; 36 |
| | *Leopardus pardalis* | | 13460 | 63.43 | High | 33; 36 |
| | *Lutra canadensis* | 18 | 7320 | 52.98 | High | 33; 35; 36 |
| | *Lutra lutra* | 4.05 | 8670 | 42.1 | Low | 33; 38 |
| | *Lynx lynx* | 7.2 | 11030 | 70.11 | | 33; 35 |
| | *Lynx rufus* | | 6110 | 57.97 | High | 33; 36 |
| | *Martes americana* | | 860 | 15.8 | High | 33; 36 |
| | *Martes pennanti* | 7.76 | 3460 | 31.82 | High | 33; 35; 36 |
| | *Meles meles* | 14.4 | 13970 | 57.45 | High | 33; 35 |

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|---|---|---|---|---|---|---|
| | *Mellivora capensis* | 54 | 8080 | 72.97 | | 33; 35 |
| | *Mephitis mephitis* | 5.05 | 2360 | 10.28 | Low | 33; 35; 36 |
| | *Mustela erminea* | 2.64 | 131.5 | 4.05 | High | 3; 33; 36 |
| | *Mustela frenata* | 1.88 | 230 | 4.01 | High | 33; 35; 36 |
| | *Mustela nigripes* | | 580 | 8.5 | High | 33; 36 |
| | *Mustela nivalis* | 0.43 | 70.5 | 1.83 | High | 3; 33; 36 |
| | *Mustela putorius* | 3.14 | 1030 | 8.25 | | 33; 35 |
| | *Mustela vison* | 4.95 | 837.5 | 7.85 | High | 3; 33; 35 |
| | *Nyctereutes procyonoides* | 9.18 | 7460 | 28.5 | | 33; 35 |
| | *Panthera leo* | 55 | 124235 | 219.815 | | 3; 33; 35 |
| | *Panthera onca* | 27.5 | 85630 | 151.41 | High | 33; 35; 38 |
| | *Panthera tigris* | 24.4 | 184085 | 290.33 | Low | 3; 33; 38 |
| | *Potos flavus* | | 2050 | 28.365 | High | 3; 33; 39 |
| | *Procyon lotor* | 13.72 | 6170 | 40.04 | | 33; 36 |
| | *Puma concolor* | | 50400 | 125.21 | High | 33; 35 |
| | *Spilogale putorius* | 5.4 | 540 | 5 | High | 33; 35; 36 |
| | *Suricata suricatta* | 1.3 | 730 | 10.28 | | 33; 35 |
| | *Taxidea taxus* | 35.56 | 4060 | 48.91 | High | 33; 35; 36 |
| | *Urocyon cinereoargentus* | 5.07 | 3630 | 40.85 | Low | 33; 35; 36 |
| | *Urocyon littoralis* | | 2050 | 27.66 | Low | 33; 36 |
| | *Ursus americanus* | | 109950 | 259.82 | High | 33; 36 |
| | *Ursus arctos* | 92 | 298870 | 336.97 | High | 33; 35; 36 |
| | *Vulpes velox* | | 2200 | 32.14 | Low | 33; 36 |
| | *Vulpes vulpes* | 9 | 4760 | 45.46 | Low | 3; 4; 33 |
| Insectivores | *Erinaceus europaeus* | 2.31 | 812.5 | 3.635 | | 1; 3; 4; 6 |
| | *Neomys fodiens* | 0.21 | 16.25 | 0.305 | | 1; 3; 4 |
| | *Scalopus aquaticus* | 2.2 | 39.8 | 1.32 | | 1; 3; 4 |
| | *Sorex araneus* | 0.28 | 7.5 | 0.25 | High | 3; 4; 40 |
| | *Sorex cinereus* | 0.1 | 3.9 | 0.17 | | 1; 3; 4 |
| | *Sorex minutus* | 0.1 | 3.9 | 0.15 | | 1; 4 |

| | | | | |
|---|---|---|---|---|
| *Sorex palustris* | 0.15 | 11.9 | 0.31 | 1; 4 |

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*Data for bats are not reproduced here and were taken from the single source:

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