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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 Pit-

nick *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, λ , 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 than 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.

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

<i>n</i>	ML λ	Variables	Estimate \pm SE	<i>t</i> -value	<i>P</i>
26	< 0.001	Body mass	0.845 \pm 0.065	12.94	< 0.001
		Testis mass	-0.021 \pm 0.06	-0.35	0.729
		SCL	-0.240 \pm 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.

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.

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.

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

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

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

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

<i>Papio anubis</i>	93.5	26400	93.5	High	28; 29
<i>Papio cynocephalus</i>	52	24320	169.1	Low	28; 29
<i>Papio hamadryas</i>	27.1	20170	142.5	Low	28; 29
<i>Papio papio</i>	88.9	31980	165.3	High	28; 29
<i>Papio ursinus</i>	72	31750	214.4	High	28; 29
<i>Pongo pygmaeus</i>	34.2	69000	413.3	Low	28; 29
<i>Presbytis entellus</i>	11.1	17000	135.2	Low	28; 29
<i>Presbytis obscura</i>	4.8	7450	67.6	Low	28; 29
<i>Presbytis cristata</i>	6.2	6580	64	Low	28; 29
<i>Presbytis rubicunda</i>	3.4	6230	92.7	Low	28; 29
<i>Saguinus midas</i>	1.83	570	10.3	High	27; 29
<i>Saguinus oedipus</i>	3.4	520	9	High	28; 29
<i>Saimiri sciureus</i>	3.2	780	24.4	High	28; 29
<i>Theropithecus gelada</i>	17.1	20400	131.7	Low	28; 29
<i>Varecia variegatus</i>	2.63	3471	30.8	Low	3; 29; 38

Ungulates	<i>Aepyceros melampus</i>	120	58500	179	High	31; 32
	<i>Alces alces</i>	106	200000	435	Low	31; 32
	<i>Antilocarpa americana</i>	76	24000	165	High	31; 32
	<i>Capreolus capreolus</i>	43	16850	100	Low	31; 32
	<i>Cephalophus sylvicultor</i>	33.25	45000	170	Low	31; 38
	<i>Cervus elephas</i>	218	90175	311	High	31; 32
	<i>Dama dama</i>	133	56234	215	High	31; 32
	<i>Equus przewalskii</i>	133	361450	586	High	31; 38
	<i>Gazella dorcas</i>	31.46	15000	66	Low	31; 38
	<i>Giraffa camelopardalis</i>	1074	581750	704	High	31; 32
	<i>Hemitragus jemlahicus</i>	26.7	70000	166	High	31; 32
	<i>Hippopotamus amphibius</i>	650	1955000	569	Low	31; 32
	<i>Hylochoerus meinertzhageni</i>	500	200000	140	High	31; 32
	<i>Kobus leche</i>	67.85	123000	223	High	31; 38
	<i>Odocoileus virginianus</i>	76	41960	144	Low	31; 32

<i>Oryx gazella</i>	37.9	130000	274	Low	31; 38
<i>Phaecochoerus aethiopicus</i>	93	68160	132	Low	31; 32
<i>Rangifer tarandus</i>	132	95225	270	High	31; 32
<i>Sus scrofa</i>	36	66900	180	Low	31; 32
<i>Sylviacapra grimmia</i>	21.25	11900	76	Low	31; 38

Carnivores	<i>Acinonyx jubatus</i>		58560	111.05	High	33; 34
	<i>Alopex lagopus</i>	4.06	3190	35.52	Low	33; 35; 36
	<i>Bassariscus astutus</i>		840	16.44	High	33; 36
	<i>Canis aureus</i>	13.3	8760	72.24		33; 35
	<i>Canis latrans</i>	15.4	10490	88.23	Low	33; 35; 36
	<i>Canis lupus</i>	27.38	33110	131.63	Low	33; 35; 36
	<i>Canis mesomelas</i>		7690	56.83	Low	33; 37
	<i>Chrysocyon brachiurus</i>	12.68	23100	120.3		33; 35
	<i>Crocuta crocuta</i>	9.85	66020	144.03		33; 35
	<i>Cryptoprocta ferox</i>	11.15	9490	32.14	High	33; 38
	<i>Cuon alpinus</i>	6.35	17640	94.63	Low	33; 38
	<i>Cynictis penicillata</i>	1.98	590	10.49		33; 35
	<i>Enhydra lutris</i>		27940	125.21	High	33; 36
	<i>Felis chaus</i>	4.62	7030	39.25		33; 35
	<i>Felis silvestris</i>	1.38	4660	37.34	High	33; 35
	<i>Gulo gulo</i>	17	11130	78.26	High	33; 35; 36
	<i>Herpailurus yagouaroundi</i>		7460	40.04	High	33; 36
	<i>Leopardus pardalis</i>		13460	63.43	High	33; 36
	<i>Lutra canadensis</i>	18	7320	52.98	High	33; 35; 36
	<i>Lutra lutra</i>	4.05	8670	42.1	Low	33; 38
	<i>Lynx lynx</i>	7.2	11030	70.11		33; 35
	<i>Lynx rufus</i>		6110	57.97	High	33; 36
	<i>Martes americana</i>		860	15.8	High	33; 36
	<i>Martes pennanti</i>	7.76	3460	31.82	High	33; 35; 36
	<i>Meles meles</i>	14.4	13970	57.45	High	33; 35

<i>Mellivora capensis</i>	54	8080	72.97		33; 35
<i>Mephitis mephitis</i>	5.05	2360	10.28	Low	33; 35; 36
<i>Mustela erminea</i>	2.64	131.5	4.05	High	3; 33; 36
<i>Mustela frenata</i>	1.88	230	4.01	High	33; 35; 36
<i>Mustela nigripes</i>		580	8.5	High	33; 36
<i>Mustela nivalis</i>	0.43	70.5	1.83	High	3; 33; 36
<i>Mustela putorius</i>	3.14	1030	8.25		33; 35
<i>Mustela vison</i>	4.95	837.5	7.85	High	3; 33; 35
<i>Nyctereutes procyonoides</i>	9.18	7460	28.5		33; 35
<i>Panthera leo</i>	55	124235	219.815		3; 33; 35
<i>Panthera onca</i>	27.5	85630	151.41	High	33; 35; 38
<i>Panthera tigris</i>	24.4	184085	290.33	Low	3; 33; 38
<i>Potos flavus</i>		2050	28.365	High	3; 33; 39
<i>Procyon lotor</i>	13.72	6170	40.04		33; 36
<i>Puma concolor</i>		50400	125.21	High	33; 35
<i>Spilogale putorius</i>	5.4	540	5	High	33; 35; 36
<i>Suricata suricatta</i>	1.3	730	10.28		33; 35
<i>Taxidea taxus</i>	35.56	4060	48.91	High	33; 35; 36
<i>Urocyon cinereoargenteus</i>	5.07	3630	40.85	Low	33; 35; 36
<i>Urocyon littoralis</i>		2050	27.66	Low	33; 36
<i>Ursus americanus</i>		109950	259.82	High	33; 36
<i>Ursus arctos</i>	92	298870	336.97	High	33; 35; 36
<i>Vulpes velox</i>		2200	32.14	Low	33; 36
<i>Vulpes vulpes</i>	9	4760	45.46	Low	3; 4; 33

Insectivores	<i>Erinaceus europaeus</i>	2.31	812.5	3.635		1; 3; 4; 6
	<i>Neomys fodiens</i>	0.21	16.25	0.305		1; 3; 4
	<i>Scalopus aquaticus</i>	2.2	39.8	1.32		1; 3; 4
	<i>Sorex araneus</i>	0.28	7.5	0.25	High	3; 4; 40
	<i>Sorex cinereus</i>	0.1	3.9	0.17		1; 3; 4
	<i>Sorex minutus</i>	0.1	3.9	0.15		1; 4

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