Sexual size dimorphism in mammals

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2.1   Introduction

In this chapter we review the extent and direction of sexual size dimorphism in mammals using body-mass measurements for 1370 mammalian species, constituting almost 30% of those currently known (Wilson and Reeder 1993). Further, we investigate the role of sexual selection through male–male competition as a driver of male-biased sexual dimorphism in mammals. Since theoretical models predict that sexual selection on male size should also have a simultaneous effect on female size (Lande 1980a, 1987; Lande and Arnold 1983), we examine whether fecundity selection on females acts as a counteracting factor that selects for smaller female size (Lindenfors 2002). Finally, we investigate the suggestion that energetic demands placed on females from the need to rear large, successful males can constitute a selection pressure on female size that is correlated with sexual selection on male size (Fairbairn 1997; Lindenfors 2002) and thus explain why more dimorphic species also tend to be larger (Rensch's rule; Rensch 1950, 1959; Abouheif and Fairbairn 1997; Fairbairn 1997; Figure 2.1).

In most sexually reproducing animals, females are larger than males (Andersson 1994; Chapter 1 in this volume), a pattern often explained by fecundity selection on females (Darwin 1871). This is because more space is required for keeping eggs than keeping sperm and because egg production increases with body size (e.g. see Chapter 4 in this volume). Energetic demands on female mammals are comparatively higher than on females in other animal groups since mammals not only need energy for egg production but also for gestation and lactation. Female mammals should therefore be expected to develop a larger energy store and should consequentially be expected to exhibit even larger size differences with males than other animals without such demands.

However, even though there are numerous mammalian species where females are larger than males (Ralls 1976), earlier studies have reported that mammals are generally dimorphic, with a bias toward males (Alexander *et al.* 1979; Weckerly 1998), as is also commonly the case in birds (see Chapter 3 in this volume). In explaining this male size bias, sexual selection is often cited as a possible driver (Darwin 1871). This is especially likely in species where males provide little or no parental investment, as males in these species can increase their reproductive success directly by competing for matings (Trivers 1972, 1985). Sexual selection through male–male competition as an explanation for male-biased size dimorphism has found support in several comparative studies that have shown correlations between different estimates of polygyny and dimorphism. Such correlations have been reported for mammals in general (Alexander *et al.* 1979; Weckerly 1998), but also separately for primates (Clutton-Brock and Harvey 1977; Clutton-Brock *et al.* 1977; Clutton-Brock 1985; Mitani *et al.* 1996; Lindenfors and Tullberg 1998), ungulates (Geist 1974; Pérez-Barbería *et al.* 2002; Jarman 1974, 1983; Loison *et al.* 1999; but see Chapter 12 in this volume), and pinnipeds (Lindenfors *et al.* 2002). Although it is improbable that sexual selection on males is the sole causal agent behind mammal size dimorphism (see e.g. Isaac 2005), these empirical studies indicate that sexual selection can be the important determinant in a significant fraction—if not the majority—of cases where male-biased sexual size dimorphism has evolved in mammals.
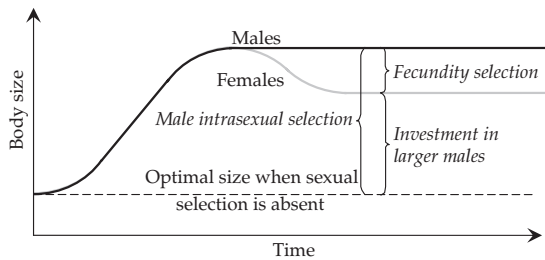
Figure 2.1 An idealized graph of a hypothetical path to male-biased sexual size dimorphism in mammals. Intrasexual competition in males results in larger male body size in species where physical competition is an important determinant of male reproductive success. Due to a genetic correlation between the sexes, female size also increases initially, but this increase is counteracted by fecundity selection, over time resulting in size dimorphism. Female size does not return to its initial level due to increased energetic demands of rearing larger male offspring. Sexual selection and fecundity selection should thus act as antagonistic selection pressures on body size in mammals, at least for females. Adapted from Lindenfors (2002).

If sexual selection acts on males, then what are the expected effects on females? Models indicate that sexual selection on male mass may directly affect female mass due to genetic correlations between the sexes in genes determining body mass (Maynard Smith 1978; Lande 1980a, 1987; Lande and Arnold 1983), but this is expected to only be a temporary phenomenon as female size gradually returns to its initial state due to some opposing natural selection (Lande 1980a; Fairbairn 1997; Reeve and Fairbairn 2001). However, indirect effects on females from selection on males might also be expected from correlated selection on females, because females may need to be larger simply due to the importance of producing larger male offspring (Fairbairn 1997; Lindenfors 2002). For example, sexually selected primate species have significantly longer periods of lactation (even after correcting for body mass; Lindenfors 2002). Resources transferred during lactation are typically more costly than the prenatal costs of gestation (Cameron 1998) and female body mass is positively correlated with milk yield in mammals (Oftedal 1984). For species under sexual selection, offspring production—especially when those offspring are males—should thus involve a longer lactation period, constituting a significant selection pressure to increase female body mass. Females in more polygynous species are therefore expected to

be larger than females in their less polygynous sister taxa.

However, fecundity in mammals has been shown to decrease with increased body size (e.g. Boyce 1988; Harvey *et al.* 1989; Lee *et al.* 1991; Purvis and Harvey 1995). Both interspecific studies (e.g. Boyce 1988; Harvey *et al.* 1989; Lee *et al.* 1991; Purvis and Harvey 1995) and theoretical models (e.g. Charnov 1993) predict that there is a trade-off between somatic growth and reproduction. Growth to a large size takes time and energy, so life-history relationships with body mass are often thought of as physiologically constrained allometries, with resulting trade offs between body size and reproduction (Roff 1992; Stearns 1992; Charnov 1993). Increased female size due to sexual selection on males should therefore decrease female fecundity. Such effects already identified are smaller litter sizes in more dimorphic mammals (Carranza 1996) and longer interbirth intervals in more polygynous haplorhine primates (Lindenfors 2002).

When increases in male mass are correlated with smaller increases in female mass, a correlation between size and size dimorphism is produced (Figure 2.1), a pattern termed Rensch's rule (Abouheif and Fairbairn 1997; Fairbairn 1997): the tendency for size dimorphism to scale with body size (Rensch 1950, 1959). To test the scenario described above, we examine support for Rensch's rule in mammals by presenting the first analysis of allometry for sexual size dimorphism across all mammals as well as separately within each order (Abouheif and Fairbairn 1997). Note that our outlined model is not falsified if Rensch's rule is not supported (Lindenfors and Tullberg 2006); but that the presence of Rensch's rule nevertheless would provide a first indication that there exists parallel—but not equal—selection pressures on males and females. We also test whether more polygynous species are more dimorphic and have larger males and females than less polygynous species. To test for possible counteracting selection on females, we conduct life-history analyses to attempt to identify fecundity costs of larger female size due to sexual selection on males, but also costs of sexual selection per se, after the effects of body size have been removed. Finally, we examine

whether there is a detectable increased investment in offspring in more sexually selected species, because of both their larger size and the effects of sexual selection on its own.

2.2   Materials and methods

We obtained data on adult body mass for males and females, mating systems, variables indicating female fecundity (age at first birth, gestation length, litter size, interbirth interval, birth rate, maximum longevity), and variables indicating investment in individual offspring (neonatal mass and weaning age) from the PanTHERIA v.1 database (K.E. Jones, J. Bielby, A. Purvis *et al*., unpublished work). PanTHERIA has been compiled to summarize comparative variables among all mammal species and contains over 100 000 lines of data from over 3300 sources collected over a 2-year period by a collaboration of three academic institutions. Source papers were found systematically from relevant journals and secondary sources (e.g. *Journal of Mammalogy*, *Mammalia*, *Journal of Zoology*; Hayssen *et al*. 1993). Further sources for particular variables, clades, or individual species were found using the electronic search engine Web of Science (http://isi3. isiknowledge.com). Entries were checked for inconsistencies and complemented when additional data were required (Kitchener 1991; Creel and Macdonald 1995; Nowell and Jackson 1996; Mills and Hofer 1998; Smith and Jungers 1997; Smith and Leigh 1998; Creel and Creel 2002; Lindenfors 2002; Pérez-Barbería *et al*. 2002, Sunquist and Sunquist 2002; Macdonald and Sillero-Zubiri 2004). All variables were $\log_{10}$-transformed prior to analysis to meet the assumption that the data were normally distributed.

We used a composite dated supertree phylogeny of 4497 mammal species for our phylogenetic comparative analyses (Bininda-Emonds *et al*., 2007). This phylogeny was compiled by combining previously published mammal supertrees (Purvis 1995; Bininda-Emonds *et al*. 1999; Jones *et al*. 2002; Grenyer and Purvis 2003; Cardillo *et al*. 2004; Price *et al*. 2005) with new interordinal and intraordinal supertrees constructed by Matrix Representation with Parsimony, using procedures outlined elsewhere (Bininda-Emonds *et al*. 2004; Cardillo *et al*.

2004). The supertree used here is the preliminary version also used by Cardillo *et al*. (2005). Branch lengths were $\log_{10}$-transformed to best meet the assumptions of the computer program CAIC (Purvis and Rambaut 1995).

For our analyses, we have used a $\log_{10}$-transformed ratio of male to female body mass as our measure of sexual size dimorphism but for comparisons with other studies in this volume we also show the size dimorphism index (SDI) of Lovich and Gibbons (1992) in Table 2.1. When describing the distribution of dimorphism in mammals, we placed an arbitrary cut-off point at 10% size difference between the sexes to term a species dimorphic (equivalent to $\log_{10}$(male mass/female mass) of ± 0.0414). To statistically test for the presence or absence of dimorphism, we used paired *t* tests where male mass was paired against female mass.

Mating system was used as an indication of the strength of sexual selection on males. Species were classified as having one of three mating systems which were ordered into degrees of increasing potential sexual selection through direct male–male competition (polyandrous/monogamous, polygynandrous, and polygynous) and treated as a discrete variable. The influence of sexual selection was analyzed utilizing the BRUNCH option in CAIC (Purvis and Rambaut 1995) which functions as normal independent contrasts (Felsenstein 1985) but allows the incorporation of a discrete independent variable, in this case mating system. When BRUNCH is used, only contrasts at nodes where the sister species differ in mating system are included in the final analysis. In this manner, "more" or "less" sexually selected taxa were compared, where polygynandrous species ended up as being either more or less polygynous depending on whether its sister taxa were monogamous or polygynous. Polytomies were handled using zero-length branches.

When checking for the presence or absence of Rensch's rule, we follow Abouheif and Fairbairn (1997), by first performing an independent contrasts analysis and then regressing male mass contrasts on to female mass contrasts, and finally testing for a deviation from a slope of 1.0. The alternative method of regressing size dimorphism on female size is to be avoided for statistical

Table 2.1 Summary of the patterns of dimorphism found in mammals. Dimorphism is given as the standard size ratio and, in parenthesis, as the SDI of Lovich and Gibbons (1992), calculated as (mass of the larger sex/mass of the smaller sex) − 1, with the sign arbitrarily given as negative when males are larger and positive when females are larger. Mammals and the majority of mammalian orders are, on average, male-biased dimorphic (average size ratio > 1.0, SDI < 0, $P < 0.05$), even if there exist a few orders with no significant dimorphism ($P > 0.05$) or female-biased dimorphism (Lagomorpha, average size ratio < 1.0, SDI > 0, $P < 0.05$). P values represent the significance of paired t tests where male body mass was paired with female body mass. Although analyses indicate that size dimorphism increases with size in mammals as a whole (Rensch's rule), upon closer inspection this only applies separately in Primates and Diprotodontia. The presence of Rensch's rule was tested using the procedure following Abouheif and Fairbairn (1997). Dashes indicate orders with too few data points for statistical analysis ($n < 3$ for tests of the presence of dimorphism; $n < 10$ for tests of the presence of Rensch's rule).

Order	Number of recognized species	Number of species with body mass data	Average dimorphism (SDI)	Sexual size dimorphism (*P* value)	Rensch's rule
		Mammalia			
All mammals	4629	1370	1.184 (−0.176)	≪ 0.001	Yes
		Subclass Prototheria			
Monotremata (monotremes)	3	2	1.273 (−0.273)	–	–
		Subclass Metatheria			
Didelphimorphia (American marsupials)	63	13	1.323 (−0.323)	0.002	No
Paucituberculata (shrew oppossums)	5	2	1.840 (−0.840)	–	–
Microbiotheria (Monito del monte)	1	1	1.044 (−0.044)	–	–
Dasyuromorphia (Dasyuroids)	63	24	1.465 (−0.464)	≪ 0.001	No
Peramelemorphia (bandicoots and bilbies)	21	9	1.496 (−1.496)	0.015	–
Notoryctemorphia (marsupial moles)	2	0	–	–	–
Diprotodontia (kangaroos, etc.)	117	63	1.306 (−0.298)	≪ 0.001	Yes
		Subclass Eutheria			
Insectivora (insectivores)	428	59	1.048 (−0.040)	0.081	No
Macroscelidea (elephant shrews)	15	5	0.964 (−0.020)	0.142	–
Scandentia (tree shrews)	19	1	–	–	–
Dermoptera (colugos)	2	0	–	–	–
Chiroptera (bats)	925	354	0.999 (0.017)	0.091	No
Primates (primates)	233	198	1.247 (−0.246)	≪ 0.001	Yes
Xenarthra (sloths, armadillos, and anteaters)	29	4	0.914 (−0.054)	0.216	–
Pholidota (pangolins)	7	3	1.767 (−0.825)	0.001	–
Lagomorpha (rabbits and pikas)	80	21	0.930 (0.087)	0.012	No
Rodentia (rodents)	2015	295	1.092 (−0.085)	≪ 0.001	No
Cetacea (whales, dolphins, and porpoises)	78	10	1.414 (−0.395)	0.082	No
Carnivora (carnivores)	271	180	1.476 (−0.472)	≪ 0.001	No
Tubulidentata (aardwark)	1	0	–	–	–
Proboscidea (elephants)	2	2	1.900 (−0.900)	–	–
Hyracoidea (hyraxes)	6	1	1.111 (–0.111)	–	–
Sirenia (dugongs and manatees)	5	0	–	–	–
Perissodactyla (horses, rhinos, and tapirs)	18	8	1.164 (−0.152)	0.156	–
Artiodactyla (antelopes, camels, pigs, etc.)	220	115	1.340 (−0.335)	≪ 0.001	No

reasons (e.g. Atchley *et al.* 1976; Ranta *et al.* 1994; Sokal and Rohlf 1995; but see Smith 1999), but also for conceptual reasons, because male and female body sizes are what selection acts on—not dimorphism *per se*. We use major-axis regressions through the origin as there is no reason *a priori* to put males or females on the *x* or *y* axis. For life-history analyses, ordinary regression analyses were carried out by placing female body mass on the *x* axis. For analyses of only continuous variables, the independent contrasts method (Felsenstein 1985), as implemented by the CRUNCH option in the computer program CAIC (Purvis and Rambaut 1995), was used.

2.3   Results

2.3.1   General patterns

We collected sex-specific body-mass data for 1370 species, constituting almost 30% of the 4629 extant and recently extinct mammalian species described (Wilson and Reeder 1993). The variances of male and female body masses were not significantly different (Cochran $P = 0.150$; Figure 2.2a), indicating that neither female nor male body mass is more variable. The distribution of body masses is significantly different from a normal distribution for both sexes (Kolmogorov–Smirnov $P < 0.01$).

With the cut-off point at a 10% size difference in either direction, we found that mammals on average are male-biased size dimorphic (average male/female mass ratio = 1.184; paired *t* test $P \ll 0.001$; Table 2.1) with males larger than females in 45% of species (Figure 2.2b; Table 2.1). The majority of mammalian orders are also significantly male-biased dimorphic (average male/female mass ratio > 1.0; $P < 0.05$). Some orders exhibit no significant size dimorphism, and one (Lagomorpha) is significantly female-biased dimorphic on average (average male/female mass ratio < 1.0; $P < 0.05$; Table 2.1). The distribution of dimorphism in mammals is significantly different from a normal distribution (Kolmogorov–Smirnov $P < 0.01$), probably because the distribution is not phylogenetically corrected (see Lindenfors 2006).

A major-axis regression on male and female body mass contrasts revealed a significant allometric relationship between male and female body mass. This implies that size dimorphism increases with body mass in mammals in general, which supports Rensch's rule (Table 2.1; Figure 2.3), and that—contrary to our previous result—male body mass is more variable than female. However, further analyses of mammalian orders only finds support for Rensch's rule in Primates and Diprotodontia (Table 2.1).
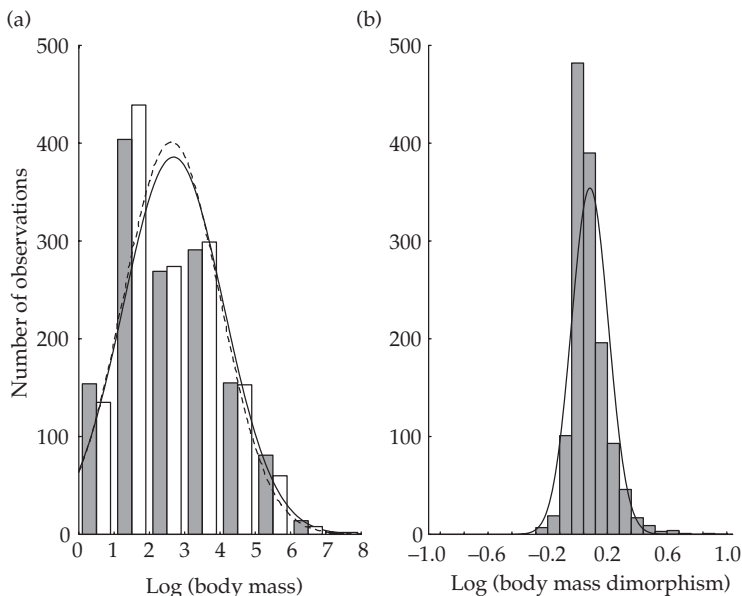

Figure 2.2   The distribution of (a) body mass and (b) sexual size dimorphism in mammals, where one species provides one observation. Sexual size dimorphism is measured as the log (male mass/female mass). The distributions of dimorphism and body mass for both sexes are significantly different from the normal distribution. In (a) the variances of body masses in males (shaded bars, continuous line) and females (open bars, striped line) are equal. Mammals are male-biased dimorphic, with an average male/female mass ratio of 1.184.
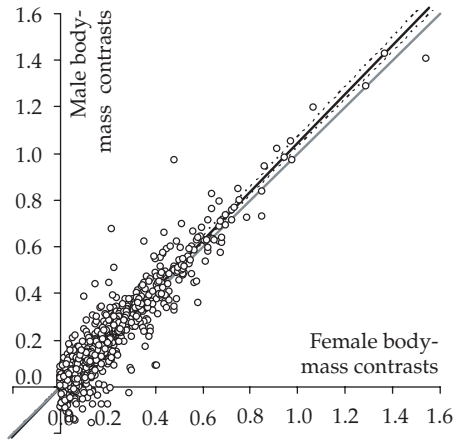
Figure 2.3 Major-axis regression through 0 (thick black line) on male and female body-mass contrasts in mammals. The 95% confidence intervals (thin dashed lines) exclude the slope of 1 (thick grey line), indicating that the relationship between male and female body mass is allometric, in extension indicating that body-mass dimorphism increases with increasing body mass in mammals, that Rensch's rule applies in mammals.

2.3.2 Sexual selection

We tested for the effects of sexual selection using mating system as a three-state unordered categorical variable, testing for differences in dimorphism between "more" and "less" sexually selected sister taxa utilizing the BRUNCH option in CAIC. These tests revealed that a higher degree of sexual selection was associated with a higher degree of male-biased dimorphism. Further, more polygynous taxa also had larger males and females than their less polygynous sister taxa. These patterns only hold separately in the mammalian orders of Primates and Artiodactyla (Table 2.2).

2.3.3 Fecundity selection

Since we were also interested in the female aspect of male-biased size dimorphism, we analyzed the relationship between female mass and several life-history characters using independent contrasts. Our results confirmed the pattern reported in earlier research (e.g. Boyce 1988; Harvey *et al*. 1989; Lee *et al*. 1991; Purvis and Harvey 1995), that all life-history traits are slower or energetically more costly in larger species of mammals (Table 2.3).

Table 2.2 Results from the BRUNCH algorithm in CAIC using mating system as a three-state unordered discrete character enabling comparisons of "more" and "less" sexually selected sister taxa (see text for an explanation of these categories). A significant difference between sister taxa differing in degree of polygyny is indicated by $P < 0.05$ (in bold; values close to significance are in italics). There is a significant effect of sexual selection on dimorphism as well as male and female body mass in mammals in general, but this pattern is no longer significant if Primates and Artiodactyla are excluded from the comparisons.

Variable	Number of comparisons	*t* value	*P*
Artiodactyla			
Dimorphism	15	2.015	*0.064*
Male mass	15	2.297	**0.038**
Female mass	15	2.124	*0.052*
Carnivora			
Dimorphism	10	1.594	0.146
Male mass	10	1.462	0.178
Female mass	10	1.059	0.317
Chiroptera			
Dimorphism	9	−0.057	0.956
Male mass	9	−0.629	0.547
Female mass	9	−0.696	0.506
Mammalia			
Dimorphism	69	3.360	**0.001**
Male mass	69	3.199	**0.002**
Female mass	69	2.764	**0.007**
Diprotodontia			
Dimorphism	4	−0.508	0.647
Male mass	4	−0.354	0.746
Female mass	4	−0.273	0.802
Primates			
Dimorphism	20	3.670	**0.002**
Male mass	20	3.090	**0.006**
Female mass	20	2.645	**0.016**
Rodentia			
Dimorphism	5	1.151	0.314
Male mass	5	1.036	0.358
Female mass	5	0.917	0.411
Mammalia except Artiodactyla and Primates			
Dimorphism	33	1.451	0.110
Male mass	33	1.272	0.256
Female mass	33	1.050	0.304

Repeating these analyses over several mammalian orders complicated the picture in that not all life-history traits in all orders were correlated with body mass (Table 2.4). This was particularly true

for small-bodied orders such as Rodentia and Insectivora, but particularly the aerial Chiroptera. It is likely that flight adaptations play an important role in Chiropteran life-history evolution (Jones and MacLarnon 2001).

We further carried out analyses using the BRUNCH option in CAIC, with mating system indicating the strength of sexual selection and the life-history variables given in Table 2.4 as indicators of female fecundity. We used General Linear Models (GLMs) to enable the inclusion of female body mass as a covariate in subsequent tests (see below). These analyses revealed no effect of sexual selection on female fecundity in mammals (GLM, $P > 0.5$ for all variables). Separately analyzing three orders where sexual selection is a probable cause of dimorphism revealed no life-history correlates of mating system in Artiodactyla or Primates, while several correlates were found in Carnivora (GLM, age at female sexual maturity, $F = 10.612$, $P = 0.011$; litter size, $F = 40.899$, $P = 0.001$; birth rate, $F = 8.263$; $P = 0.026$; maximum longevity, $F = 5.318$, $P = 0.058$). These patterns in Carnivora remained significant after including female mass as a covariate, indicating an extra effect above that of size alone (GLM, age at female sexual maturity, $F = 6.238$, $P = 0.044$; litter size, $F = 420.350$, $P \ll 0.001$; birth rate, $F = 9.112$, $P = 0.032$; maximum longevity, $F = 15.538$, $P = 0.013$). Interestingly, in Primates the interbirth interval was indicated to be significantly longer in more polygynous species after the inclusion of mass (GLM, $F = 5.251$, $P = 0.045$).

2.3.4 Increased investment in offspring

Finally we examined whether there is an increased investment in offspring in species under more sexual selection. The BRUNCH option in CAIC showed that this effect could be found for weaning age, which was higher in mammals under greater sexual selection because of their larger mass (GLM, $F = 0.352$, $P = 0.034$). Separately analyzing the three orders in which sexual selection correlates with size dimorphism revealed larger neonates in Carnivora (GLM, $F = 4.275$, $P = 0.070$), whereas Primates have higher weaning ages in species under greater sexual selection (GLM, $F = 11.658$,

Table 2.3 Results of regressions through the origin on independent contrasts of the relationship between nine life-history variables and female body mass separately in mammals. N refers to the number of contrasts. All life-history characters are significantly correlated with female body mass.

Variable	N	B	t	R^2	P
Mammalia					
Female maturity	490	0.170	10.216	0.176	0.000
Gestation length	606	0.076	10.673	0.158	0.000
First birth	291	0.190	10.974	0.293	0.000
Litter size	844	−0.035	−2.965	0.010	0.003
Interbirth interval	637	0.158	6.483	0.062	0.000
Birth rate	631	−0.190	−6.674	0.066	0.000
Maximum longevity	521	0.123	5.617	0.057	0.000
Neonate mass	562	0.665	22.238	0.468	0.000
Weaning age	581	0.129	7.732	0.093	0.000

$P = 0.006$). We then added mass as a covariate and tested for an effect of sexual selection above that caused by size increase alone. These analyses again showed that weaning age is significantly longer in species under more sexual selection, even after removing the effects of the increased mass (GLM, $F = 3.583$, $P = 0.039$). As above, no effect of sexual selection on female life histories was found in Artiodactyla, whereas Carnivora again had larger neonates (GLM, $F = 12.965$, $P = 0.010$), and Primates had higher weaning ages in species under greater sexual selection (GLM, $F = 5.251$, $P = 0.045$).

2.4 Discussion

Generally, we found that mammals exhibit significant male-biased sexual size dimorphism, thus corroborating the results of earlier comparative studies (e.g. Greenwood and Wheeler 1985; Reiss 1989; Abouheif and Fairbairn 1997; Loison *et al.* 1999). Examining mammal orders separately, most taxa with sufficient numbers of species for statistical analyses also conform to this pattern; notable exceptions are Lagomorpha and Chiroptera, the former being significantly female-biased dimorphic and the latter showing a tendency ($P = 0.091$) in the same direction. The overwhelmingly largest mammal order—Rodentia, containing 45% of the extant mammal species—is,

Table 2.4 Results of regressions through the origin on independent contrasts of the relationship between nine life-history variables and female body mass separately in seven mammalian orders as well as in all mammals except Artiodactyla, Carnivora, and Primates. *N* refers to the number of contrasts. Neonate mass and age at weaning are correlated with body mass in all examined orders.

Variable	N	B	t	R^2	P	N	B	t	R^2	P
			Artiodactyla					*Carnivora*		
Female maturity	60	0.169	2.514	0.097	0.015	117	0.140	4.619	0.155	0.000
Gestation length	64	0.116	5.851	0.352	0.000	132	0.142	4.937	0.157	0.000
First birth	44	0.214	3.723	0.244	0.001	42	0.233	5.750	0.446	0.000
Litter size	66	−0.048	−2.049	0.061	0.044	149	0.036	1.092	0.008	0.277
Interbirth interval	58	0.008	0.163	0.000	0.871	119	0.109	3.565	0.097	0.001
Birth rate	57	−0.108	−2.252	0.083	0.028	119	−0.076	−1.680	0.023	0.096
Maximum longevity	64	0.113	3.016	0.083	0.004	131	0.157	5.251	0.175	0.000
Neonate mass	65	0.863	23.447	0.896	0.000	115	0.565	6.195	0.252	0.000
Weaning age	59	0.212	3.223	0.152	0.002	124	0.117	2.673	0.055	0.008
			Chiroptera					*Insectivora*		
Female maturity	40	0.201	2.274	0.117	0.028	13	0.207	0.991	0.076	0.341
Gestation length	81	−0.046	−1.069	0.014	0.288	25	0.130	2.867	0.255	0.008
First birth	33	0.086	0.975	0.029	0.337	4	0.158	0.661	0.127	0.556
Litter size	184	−0.010	−0.744	0.003	0.458	36	0.010	0.137	0.000	0.982
Interbirth interval	120	−0.018	−0.633	0.003	0.527	28	0.158	0.640	0.015	0.528
Birth rate	118	0.004	0.447	0.002	0.656	27	−0.030	−0.076	0.000	0.940
Maximum longevity	42	−0.102	−0.716	0.012	0.478	25	0.365	3.186	0.297	0.004
Neonate mass	97	0.923	13.662	0.660	0.000	21	0.845	9.454	0.817	0.000
Weaning age	73	0.213	1.985	0.052	0.051	19	0.103	1.745	0.145	0.098
			Diprotodontia					*Primates*		
Female maturity	34	0.109	2.193	0.127	0.035	74	0.070	1.150	0.018	0.254
Gestation length	26	−0.066	−1.346	0.068	0.190	94	0.017	1.036	0.011	0.303
First birth	21	0.104	2.126	0.184	0.046	78	0.071	1.382	0.024	0.171
Litter size	57	−0.127	−3.581	0.186	0.001	101	−0.051	−1.910	0.035	0.060
Interbirth interval	37	0.149	2.598	0.158	0.013	81	0.174	3.502	0.133	0.001
Birth rate	37	−0.276	−4.580	0.368	0.000	79	−0.373	−6.556	0.355	0.000
Maximum longevity	39	0.227	3.224	0.215	0.003	85	0.100	2.238	0.056	0.028
Neonate mass	21	0.581	7.556	0.741	0.000	78	0.607	12.544	0.671	0.000
Weaning age	38	0.275	9.168	0.694	0.000	86	0.340	4.324	0.180	0.000
			Rodentia				*Mammals except Artiodactyls, Carnivores, and Primates*			
Female maturity	81	0.171	3.461	0.130	0.001	239	0.174	8.069	0.215	0.000
Gestation length	113	0.117	6.786	0.291	0.000	329	0.002	0.157	0.000	0.875
First birth	38	0.258	5.016	0.405	0.000	130	0.180	7.694	0.314	0.000
Litter size	160	−0.040	−1.313	0.011	0.191	540	−0.078	−8.069	0.108	0.000
Interbirth interval	106	0.162	1.526	0.022	0.130	381	0.067	2.234	0.013	0.026
Birth rate	106	−0.146	−1.240	0.014	0.218	378	−0.142	−0.044	0.042	0.000
Maximum longevity	75	0.186	3.852	0.167	0.000	254	0.166	8.310	0.214	0.000
Neonate mass	103	0.788	26.422	0.872	0.000	308	0.804	32.671	0.777	0.000
Weaning age	105	0.115	3.907	0.128	0.000	315	0.168	9.945	0.240	0.000

however, significantly male-biased dimorphic. It is likely that the data we were able to examine are biased toward larger species, as these tend to be better studied than smaller species, which may affect the overall pattern we report.

A non-phylogenetic analysis indicated no significant difference between the variances of male or female body masses, thus giving no apparent indication of which sex changes size more often. Contrary to this result, our phylogenetic analysis of the relationship between size dimorphism and body mass (Rensch's rule) revealed a significant correlation between mass and mass dimorphism. This puts the focus on males for understanding size dimorphism in mammals, since male contrasts were significantly larger than female. Our result is also the first where Rensch's rule has been confirmed across such a high-taxon level (class Mammalia). Since Rensch's rule is based on empirical observations of patterns in the animal world (D.J. Fairbairn, personal communication), this broadens the generality of the rule. However, in contrast to an earlier study (Abouheif and Fairbairn 1997), we only found support for Rensch's rule on the level of order in Diprotodontia and Primates. Also, as has been shown elsewhere, the presence/absence of Rensch's rule can be due to factors not relating to the rule itself (Lindenfors and Tullberg 2006). More revealing is therefore to analyze the data for drivers of size dimorphism.

Since our results show that mammals exhibit male-biased sexual dimorphism and since this dimorphism has been shown in several mammal groups to relate to sexual selection on males (Geist 1974; Jarman 1974, 1983; Clutton-Brock and Harvey 1977; Clutton-Brock et al. 1977; Alexander et al. 1979; Clutton-Brock 1985; Mitani et al. 1996; Lindenfors and Tullberg 1998; Weckerly 1998; Loison et al. 1999; Lindenfors et al. 2002; Pérez-Barbería et al. 2002), we have here focused on male-biased dimorphism and its relation to sexual selection on males. Using mating system as a proxy for the strength of sexual selection indicates that mammals under greater sexual selection pressure are indeed more dimorphic. The same analysis applied to body mass reveals that species under more sexual selection have larger males, but

also larger females, than do species under weaker sexual selection. Thus, we found sexual selection to be an important cause of sexual dimorphism, but also of large size itself.

This pattern only holds across all mammals and was not found within different orders (except for Primates and Artiodactyla). This lack of support may in some cases be due to a low statistical power, as sample sizes in some orders were small. The lack of a relationship between dimorphism and mating system is particularly interestingly in Carnivora as this order contains a large number of species and the most dimorphic mammal known (southern elephant seal, *Mirounga leonina*). Previous carnivore studies have found a significant relationship between canine dimorphism and mating system (Gittleman and Van Valkenburgh 1997). Also, a study on pinnipeds using harem size instead of mating system showed that sexual selection drives sexual dimorphism in pinnipeds (Lindenfors et al. 2002). It is therefore possible—or even probable—that sexual selection is also an important driver of size dimorphism in carnivores, but that our measurement of mating system is too crude to detect a relationship. This also acts as a cautionary note for the other orders where the influence of sexual selection could not be validated.

By confirming sexual selection on males as a correlate of male-biased dimorphism in mammals, however, we have only managed to explain half of the pattern. To make a dimorphic species, it is important also to explain what maintains smaller size in females (Lindenfors 2002). Our life-history analysis of female mammals confirmed that large size slows down and increases the expenditure of reproduction (Boyce 1988; Roff 1992; Stearns 1992; Charnov 1993). Thus, as fecundity is an important selection pressure on female size, it is not in the females' interest to grow larger (Lindenfors 2002).

Separate analyses of each mammalian order confirms the general pattern. Generally, the more variation in body mass that exists in an order, the more tight is the relationship between body mass and fecundity. For example, in Rodentia, Chiroptera, and Insectivora, many of the analyzed life-history variables are not at all correlated with body mass. This can be a statistical effect where the

relationship becomes more detectable as more variation is included, but it can also indicate that, at small sizes, body mass is not a major determinant of life histories. In Chiroptera, for example—which is the order where our results indicate the fewest correlations between body mass and life histories—flight adaptations may play an important role (Myers 1978; Jones and MacLarnon 2001).

If sexual selection is the cause of size dimorphism through selection on males, and if female size is also greater in species under greater sexual selection, then females should be expected to pay some sort of life-history price for their larger size (Lindenfors 2002). Our results indicate that in general it is age at weaning that is later in species under more sexual selection. Interestingly enough, this result remains even if the effects of body mass are removed. Further, an earlier study has reported that, contrary to theoretical predictions, the ratio of weaning weight to adult weight scales with adult body mass (Purvis and Harvey 1995). These results indicate that mammals under more sexual selection wean at a later age and consequentially also at a larger size. Weaning age and body weight are especially important because resources transferred during lactation are typically more energetically costly than the prenatal costs of gestation (Cameron 1998), and female body mass is correlated with milk yield in mammals (Oftedal 1984). Thus, a longer suckling period constitutes a significant selection pressure on female size.

We did not find that the higher weaning age resulted in a longer interbirth interval, a result that we expected. It has been shown previously in primates (Lindenfors 2002) that higher weaning age corresponds with a longer interbirth interval, a result replicated in this study for primates but not for mammals overall. It is not unlikely, however, that our result outside primates stems from the low number of comparisons available when simultaneously utilizing mating system and interbirth interval. Future studies may shed more light on this question.

Overall, our results indicate that much of the male-biased dimorphism in mammals is caused by sexual selection on males. We also suggest that fecundity selection on females explains the female part of sexual size dimorphism. Nevertheless,

females were found to be larger in more sexually selected species, most probably because a selection pressure correlated to sexual selection on males through the demands of lactation.

This review also highlights that there is ample variation in mammalian sexual size dimorphism left to explain. Although it is probable that much of the male-biased dimorphism we have not been able to explain here will also be tied to sexual selection on males, we still have no satisfying general answer for what causes female-biased dimorphism in mammals.

2.5 Summary

This chapter explores the pattern of sexual size dimorphism in mammals and the processes that underly its evolution. We find that, on average, male mammals are the larger sex (average male/female mass ratio 1.184), with males being at least 10% larger than females in over 45% of species. Most mammalian orders are also have male-biased sexual dimorphism, although some orders do not show any bias or are significantly female-biased (Lagomorpha). Sexual size dimorphism increases with body size across mammals (Rensch's rule), suggesting that there are parallel selection pressures on both male and female size. We found support for the hypothesis that male-biased dimorphism relates to sexual selection on males through male–male competition for females. We draw this conclusion from a positive correlation between the degree of sexual selection, as indicated by mating systems and the degree of male-biased size dimorphism. The degree of sexual selection was also positively correlated with male and female size across mammals. Further, a parallel selection pressure on female mass is identified in that age at weaning is significantly higher in more polygynous species, even when correcting for body mass. We also explore the processes maintaining smaller female size in sexually dimorphic species and confirm that reproductive rate is lower for larger females, indicating that fecundity selection selects for smaller females in mammals. Although the patterns we discuss hold across mammals as a whole, there is considerable variation across orders and many of these

relationships are not significant. Further work is still needed to more closely investigate the pattern of sexual dimorphism and processes driving sexual dimorphism in different clades.

2.6   Acknowledgments

2.7   Suggested readings

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