

Rensch's rule in large herbivorous mammals derived from metabolic scaling

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Rensch's Rule in Large Herbivorous Mammals Derived from Metabolic Scaling

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ABSTRACT: Rensch's rule, which states that the magnitude of sexual size dimorphism tends to increase with increasing body size, has evolved independently in three lineages of large herbivorous mammals: bovids (antelopes), cervids (deer), and macropodids (kangaroos). This pattern can be explained by a model that combines allometry, life-history theory, and energetics. The key features are that female group size increases with increasing body size and that males have evolved under sexual selection to grow large enough to control these groups of females. The model predicts relationships among body size and female group size, male and female age at first breeding, death and growth rates, and energy allocation of males to produce body mass and weapons. Model predictions are well supported by data for these megaherbivores. The model suggests hypotheses for why some other sexually dimorphic taxa, such as primates and pinnipeds (seals and sea lions), do or do not conform to Rensch's rule.

Keywords: sexual selection, size dimorphism.

Introduction

Rensch's rule describes the tendency across species within a functional or taxonomic group for the ratio of male to female body size at breeding to increase with female body size (Rensch 1950; Reis 1989; Abouheif and Fairbairn 1997; Fairbairn 1997; Dale et al. 2007; Fairbairn et al. 2007). Like other ecological rules (e.g., Bergmann's rule), Rensch's rule is not an absolute law. There are conspicuous exceptions; it does not hold in some groups (Dale et al. 2007; Fairbairn et al. 2007), and in others, an extended version applies, with females being larger than males and the magnitude of sexual dimorphism increasing with decreasing body size (Colwell 2000; Dale et al. 2007). It also lacks a general explanation.

Here we derive a simple model that is based on allometric scaling relationships, which predicts the quantita-

tive form of Rensch's rule in large herbivorous mammals. Our treatment is motivated to account for similar breeding systems that have evolved convergently in three lineages of large herbivorous mammals: bovid and cervid artiodactyls (antelopes and deer, respectively) and macropodid marsupials (kangaroos). In all three taxa, smaller species tend to live in monogamous pairs; in larger species, females tend to aggregate in social groups, and males tend to control these groups and mate with the multiple females (Jarman 1974, 1983; Geist and Bayer, 1988; Croft 1989; Jarman and Coulson, 1989; Geist 1998; Loison et al. 1999; Fisher and Owens 2000; Fisher et al. 2001; Croft and Eisenberg 2006; Lindenfors et al. 2007). Jarman (1983) showed that, in the smallest species of each family, both sexes mature rapidly at similar body sizes and have relatively small weapons, whereas in larger species, life span and time to sexual maturity are longer, and males grow to larger sizes than females and typically possess well-developed ornaments and weapons that are used in contests for mates. Thus, associated with this trend of increasing polygyny are increased longevity, sexual size dimorphism, and weaponry. Our model for Rensch's rule incorporates these salient features of ecology and breeding system as functions of female body size.

The Model

We start from allometric relationships, which are power laws of the form

$$Y = Y_0 M^b, \quad (1)$$

where Y is some dependent variable, such as metabolic rate, somatic growth rate, or death rate; M is adult body mass; Y_0 is a normalization constant; and b is another constant, the allometric or scaling exponent, which is often close to a simple multiple of 1/4 (e.g., Peters 1983; Brown et al. 2004; Savage et al. 2004). Our model is derived as far as possible from metabolic scaling theory and docu-

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mented empirical allometric relationships. An overview is given in figure 1. The flow of prediction is shown by the bold symbols and arrows in the central row of figure 1. First, we predict the allometry of group size, N . From this we calculate the difference between the breeding ages of males and females, $t_\delta - t_\varnothing$. Finally, we use this to obtain the ratio of masses of adult males and females, M_δ/M_\varnothing , and hence the magnitude of Rensch's rule. The additional allometric information used in making these predictions is shown in the boxes in the top row of figure 1. In particular, we assume two allometric relationships defining the scaling of death rate and somatic growth rate. Specifically, for female placental mammals, we assume the female adult death rate

$$\mu_\varnothing = 0.49 M_\varnothing^{-1/4}. \quad (2)$$

We use units of kilograms and years throughout. The normalization constant (intercept = 0.49) in equation (2) comes from a regression of data in Sibly et al. (1997) and Ernest (2003); see figure A1. The scaling exponent of $-1/4$ comes from the commonly observed quarter-power scaling of biological rates and times, including death rates in life history (Brown et al. 2004; McCoy and Gillooly 2008; McCoy and Gillooly 2009). For males between the ages of t_\varnothing and t_δ , we assume male somatic growth rate

$$dm/dt = Cm^{3/4}, \quad (3)$$

where m is body mass during growth and C is a normalization constant parameterizing the absolute, size-independent rate of biomass production, whose value is discussed below. The exponent, $3/4$, again reflects commonly observed quarter-power scaling (in this case, of ontogenetic growth rate; Hou et al. 2008; Moses et al. 2008).

The starting point of our model is the allometry of female group size, N (fig. 1). This allometry in principle emerges from the allometry of population density, which scales with body mass to the $-3/4$ power (Damuth 1981, 1987), and the allometry of individual space use or home range size, which scales with body mass to the power 1 (Kelt and Van Vuren 1999, 2001; Jetz et al. 2004). Assuming that females aggregate and share the same home range, the number in the group theoretically should scale with body mass to the power $1 - 3/4 = 1/4$ (Calder 1984). Below some threshold size M_{mono} , however, females do not form social groups but instead live as monogamous pairs and share a territory with a male (Jetz et al. 2004). This gives female group size

$$N = (M_\varnothing/M_{\text{mono}})^g, \quad (4)$$

with Calder's reasoning predicting $g = 1/4$.

The allometry of female group size ultimately determines the allometry of sexual dimorphism, as indicated in figure 1. The key intermediate step is that males adjust

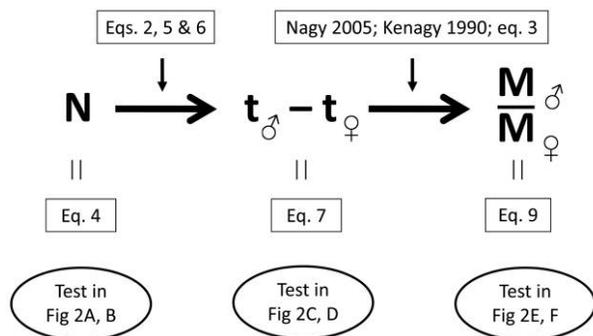


Figure 1: The structure of the model. Key variables are given in boldface type. Group size, N , is predicted first and is used to predict the time difference, $t_\delta - t_\varnothing$, between females breeding for the first time at age t_\varnothing and males breeding for the first time at age t_δ . During this period $t_\delta - t_\varnothing$, males grow larger than females, until the final ratio of their sizes is M_δ/M_\varnothing . The prediction equations for key variables are shown beneath them in square boxes. The ovals below show which figures plot the data in which each prediction equation is tested. Ancillary equations used to derive predictions are shown in the square boxes at the top of the figure.

their life histories in response to variation in female group size to maximize their reproductive success. As group size increases, proportionately fewer males are able to mate, and the intensity of competition among males increases. We assume that, if he is large enough, a single male wins the contests and controls and mates with all of the females in a group. Therefore, as female group size increases, males are selected to grow larger and defer mating until an older age. However, this comes at a cost, both because males delay reproduction and because, as males grow larger than females, they incur higher maintenance requirements and higher death rates. Therefore, the effect of sexual selection on males is a trade-off: larger males can control groups of females and sire more offspring, but this delays reproduction and increases death rates and the energy allocated to maintenance (Blanckenhorn 2000, 2005).

We assume that the increased death rate of adult males, μ_δ , can be expressed as a function of female death rate and female body mass as

$$\mu_\delta = \mu_\varnothing (M_\varnothing/M_{\text{mono}})^\theta, \quad (5)$$

where the exponent θ scales male in relation to female death rates. Its value is discussed below.

Although males are capable of breeding earlier, we assume that they first breed at age t_δ , when they are larger than enough other males to control a group of females. We now use the fact that the lifetime reproductive success of males is equal to that of females (Fisher 1930). Lifetime reproductive success of females is $bS_\varnothing/\mu_\varnothing$, and that of males is bNS_δ/μ_δ , where b is the number of offspring produced

per year by individual females and S_δ and S_φ are the survival rates from birth to first breeding of males and females, respectively. Thus

$$bS_\varphi/\mu_\varphi = bNS_\delta/\mu_\delta. \quad (6)$$

We assume that males and females have identical survival rates until t_φ . Subsequently, male death rate increases, so survival rate of males, S_δ , is less than that of females, and we assume $S_\delta = e^{-(\mu_\delta + \mu_\varphi)/2(t_\delta - t_\varphi)} S_\varphi$. Combining with equation (6), recalling equations (2), (4), and (5), and rearranging gives the difference in the age of first reproduction between males and females:

$$t_\delta - t_\varphi = \frac{2(g - \theta) \ln(M/M_{\text{mono}})}{0.49(1 + (M/M_{\text{mono}})^\theta) M^{-1/4}}. \quad (7)$$

This equation predicts how long males have to wait before they can control a group and breed with the females. We assume that the energy available to males is limited by the ecological conditions on the home range and is the same for males and females. A female attains reproductive maturity and stops growing at age t_φ at the ecologically optimal body size. Subsequently, she allocates energy between survival (maintenance) and reproduction, and her total metabolic rate exceeds the standard field metabolic rate (FMR) of $3.1 \times 10^8 M_\varphi^{0.73}$ J/year (Nagy 2005) by approximately 25% because of the cost of reproduction (Kenagy et al. 1990). Therefore, in the period $t_\delta - t_\varphi$, a female uses $5/4 \times 3.1 \times 10^8 M_\varphi^{0.73} (t_\delta - t_\varphi)$ J, and this amount of energy is available to a male over the same period, during which he has to fuel his survival and growth from M_φ to M_δ . The rate of energy expenditure of a male on survival during this period is given by the scaling of FMR as a function of his mass, m , which is $3.1 \times 10^8 m^{0.73}$ J/year. Therefore, over the entire period $t_\delta - t_\varphi$, a male expends $\int_{t_\varphi}^{t_\delta} 3.1 \times 10^8 m^{0.73} dt$ J on survival. The quantity of available energy is the same for both sexes, but the female allocates to reproduction, whereas the male allocates to growth. This means that $5/4 \times 3.1 \times 10^8 M_\varphi^{0.73} (t_\delta - t_\varphi) - \int_{t_\varphi}^{t_\delta} 3.1 \times 10^8 m^{0.73} dt$ J is potentially available to fuel growth from M_φ to M_δ . The metabolic expenditure on growth can be estimated from the energy required to produce a kilogram of mammalian flesh, 2.4 MJ (Hou et al. 2008). Substituting, this gives

$$M_\delta - M_\varphi = \frac{1}{2.4 \times 10^6} [5/4 \times 3.1 \times 10^8 M_\varphi^{0.73} \times (t_\delta - t_\varphi) - \int_{t_\varphi}^{t_\delta} 3.1 \times 10^8 m^{0.73} dt]. \quad (8)$$

The last term can be integrated by approximating 0.73 as 3/4 and using equation (3). Rearranging gives the predicted sexual dimorphism:

$$M_\delta/M_\varphi = 1 + 1.25M_\varphi^{-1/4}(t_\delta - t_\varphi)/(0.008 + 1/C). \quad (9)$$

Predictions of the model are shown in figure 2. The difference in age of first reproduction between males and females, $t_\delta - t_\varphi$, is shown in figure 2C and 2D, and the ratio of masses of breeding males and females, M_δ/M_φ , the magnitude of Rensch's rule, is shown in figure 2E and 2F.

Data and Empirical Evaluation

We have compiled and analyzed relevant data for bovids, cervids, and macropodids. Data were obtained from multiple sources in the published literature, available in Dryad. Sufficient standardized data are available for all three taxa to analyze female group size, N ; the age difference between females and males breeding for the first time, $t_\delta - t_\varphi$; and the magnitude of sexual dimorphism, M_δ/M_φ , all as functions of female body size (fig. 2). The allometries of Bovidae and Cervidae are indistinguishable and are plotted in the upper row of figure 2, the allometries of Macropodidae are in the lower row. Assumptions and predictions of the model are evaluated empirically as follows:

1. Female group size: The smallest females with group size of one weigh approximately 1 kg in macropodids and approximately 10 kg in bovids and cervids. Therefore, we used $M_{\text{mono}} = 1$ kg for macropodids and $M_{\text{mono}} = 10$ kg for bovids and cervids. Linear regression of the log-log data shown in figure 2A and 2B gives exponents (\pm SE) of 1.09 ± 0.05 for bovids and cervids ($P < .001$, $R^2 = 0.77$) and 0.55 ± 0.06 for macropodids ($P < .001$, $R^2 = 0.75$). Both exponents are substantially and significantly higher than the value of 0.25 predicted by Calder (1984). Given this discrepancy, we used the exponents from the fitted regression equation for each group to complete the model (fig. 1).

2. Female death rate: Equation (2) predicts that death rates of adult females scale as $\mu_\varphi = 0.49M^{-1/4}$. Analysis by McCoy and Gillooly (2008) of data for 323 mammal species gave a similar exponent but higher normalization constant: $\mu_\varphi = 1.20M^{-0.24}$, with a standard error for normalization constant of 1.07 and a standard error for scaling exponent of 0.01. Their data for 41 species of Bovidae and Cervidae give $\mu_\varphi = 1.4M^{-0.23}$. Our data are from field studies of survival rate in Sibly et al. (1997), whereas their data are based on estimates of the maximum longevity of captive animals, under the assumption that the mortality rates of wild animals are approximately 2.5 times greater. Our analysis suggests that their correction factor of 2.5 may overestimate death rates of ungulates in the wild.

3. Age of breeding and male death rate: Difference in age of breeding between the sexes is plotted as a function of M_φ in figure 2C and 2D. The model predictions (solid

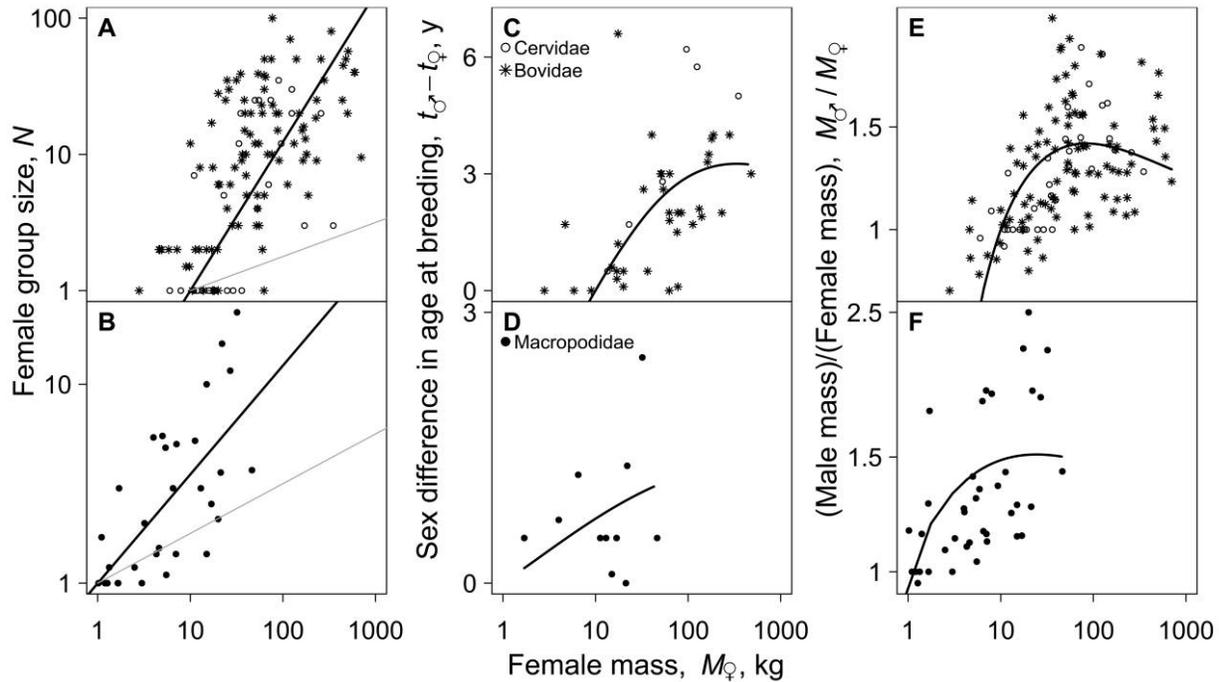


Figure 2: Model predictions and empirical tests of the key allometric relationships (see fig. 1). Model predictions are shown as solid lines except in panels *A* and *B*. Data for Bovidae (asterisks) and Cervidae (open circles) are shown in the upper row, and data for Macropodidae (closed circles) are shown in the lower row; for values and sources, see Dryad. The left-hand column (*A*, *B*) tests the prediction for the allometry of female group size N . The theoretical prediction is $N = (M_{\text{♀}}/M_{\text{mono}})^{0.25}$, shown as faded lines. Fitted regressions are solid lines corresponding to $N = (M_{\text{♀}}/M_{\text{mono}})^g$ with $g = 1.09 \pm 0.05$ in *A* and $g = 0.55 \pm 0.06$ in *B*. These values are used in the model predictions in *C*, *D*, *E*, and *F*. *C* and *D* test the prediction for the difference in age of first reproduction between males and females, $t_{\text{♂}} - t_{\text{♀}}$. *E* and *F* test the predicted allometry of the ratio of masses of adult males and females, $M_{\text{♂}}/M_{\text{♀}}$ (Rensch's rule).

lines) come from equation (7), which gives the difference in age of breeding as a function of $M_{\text{♀}}$ and θ , where θ is the exponent relating male to female death rates in equation (5). We used nonlinear least square regression (Gauss-Newton algorithm in *R*) to fit equation (7) to the data in figure 2*C* and 2*D*. The model predictions fit the data well, giving values (\pm SE) of $\theta = 0.60 \pm 0.03$ for bovids and cervids and $\theta = 0.40 \pm 0.03$ for macropodids ($P < .001$, $R^2 = 0.73$ and $P < .001$, $R^2 = 0.56$, respectively). Few data are available with which to compare these values, but there is clearly a substantially higher death rate among males than among females in highly sexually dimorphic species (Georgiadis 1985; Owen-Smith 1993; Jorgenson et al. 1997; Catchpole et al. 2004). From data in Owen-Smith's (1993) study of greater Kudu (Bovidae) we calculated that $\mu_{\text{♂}}$ was approximately $6.6\mu_{\text{♀}}$. In this species, females weigh approximately 200 kg, suggesting that $\theta \approx 0.63$, close to our fitted value for *Cervidae* and *Bovidae* of 0.60. Thus, the limited data that are available support the model assumption that an increased male death rate is an

emergent outcome of sexual selection for large male body size.

4. Growth trajectories: The model assumes that females stop growing at reproductive maturity, but in species where group size is >1 and $M > M_{\text{mono}}$, males continue to grow. This is supported by Georgiadis' (1985) study of 11 species of African ruminants, and we have found high-quality data on growth rates as a function of age for three species: white-tailed deer (Fuller et al. 1989), red deer (Clutton-Brock et al. 1982, 1988), and moose (Solberg and Sæther 1994). These data strongly support the model assumption that, in sexually dimorphic species, females virtually stop growing once they reach sexual maturity, whereas males continue to grow, but at decreasing rates, throughout life.

5. Sexual size dimorphism and male growth rate: We used nonlinear least square regression to fit equation (9) to the data in figure 2*E* and 2*F*. The model predictions fit the data well, giving values of male growth rate (\pm SE) $C = 0.35 \pm 0.03$ $\text{kg}^{1/4}/\text{year}$ for bovids and cervids and

$0.97 \pm 0.13 \text{ kg}^{1/4}/\text{year}$ for macropodids (fig. 2E, 2F; $P < .001$, $R^2 = 0.60$ and $P = .001$, $R^2 = 0.58$, respectively).

Discussion

Using four parameter values (M_{mono} , g , θ , and C) estimated from the data, our model makes assumptions and predictions that are consistent with analyses based on large data sets for all three groups. Therefore, the model provides a quantitative explanation for Rensch's rule in these large herbivorous mammals.

Calder's theoretical prediction of $M^{1/4}$ scaling of female group size, based on the allometry of metabolic rate and home range size in mammals (Calder 1984; Jetz et al. 2004), was not supported (fig. 2A, 2B). The fitted exponents are substantially and significantly greater than 0.25 for both groups: 1.09 for bovids and cervids, 0.55 for macropodids (fig. 2A, 2B). The empirical regressions, although highly significant, left considerable unexplained residual variation. To some extent, both the higher exponent and the magnitude of variation may reflect lack of comparability across studies because of differences in methodology and because of our representation of each species with a single value of (average female) body size and (maximum) group size. Much of the variation, however, undoubtedly reflects real differences in group size among species with similar body sizes. These differences probably reflect variability in habitat quality, stability, and mobility of female groups and characteristics of the breeding system (Jarman 1974, 1983). There is a need both to revisit Calder's theory for allometric scaling of space use and group size, especially as it applied to large herbivorous mammals, and to obtain more and better data to evaluate and perhaps modify the theory.

With this qualification, our model appears to capture the fundamental role of female group size and its relationship to foraging ecology in accounting for Rensch's rule in large herbivorous mammals. We used empirical values for four parameters of the model: the constant, M_{mono} , in equations (4) and (5) for the average body size of monogamous species (i.e., where female group size = 1); the exponent g in equation (4) for scaling of female group size with female body mass (see above); the exponent θ in equation (5) for scaling male relative to female death rates; and the normalization constant, C , in equation (3) for scaling of growth rate. After such parameterization, the model predicted the data for both differences between sexes in age of first breeding (fig. 2C and 2D) and sexual size dimorphism (fig. 2E and 2F). Thus, the model makes predictions for Rensch's rule in large herbivorous mammals that are in reasonable agreement with the data. However, mechanistic models such as ours, which make multiple predictions for disparate traits, re-

quire more sophisticated evaluation procedures than are currently available (White et al., forthcoming). For example, all four fitted parameters contribute to the prediction of sexual dimorphism in equation (9), so the fitting procedure would ideally fit all four parameters simultaneously to all the data in figure 2. Phylogenetic correction during model fitting would also be desirable, but techniques have not yet been devised to allow phylogenetic fitting of nonlinear regressions. In our defense, we note that, when species data are spread out over orders of magnitude variation in body mass, phylogenetically corrected and uncorrected analyses tend to give similar results. For example, in a thorough analysis of Rensch's rule in varanid lizards, Frydlova and Frynta (2010) found that the results remained virtually unchanged after performing a phylogenetically informed analysis.

Our model implies that Rensch's rule is observed in large herbivorous mammals, such as deer, antelope, and kangaroos, because females form social groups of increasing size with increasing body size, and a single male that lives long enough and grows large enough can control a group and monopolize the matings. Therefore, an important parameter is how the number of females in a group varies with female body size. This scaling of group size reflects the role of ecological factors, especially foraging, predator avoidance, and information exchange. Even in herbivorous mammals, there is much variation, discussed above, and there are also exceptional species that violate assumptions of the model. For example, zebra and wildebeest are large but exhibit little or no sexual dimorphism in body size. However, these species typically occur in large herds, where it is difficult for single males to control groups of females. When this is taken into account, these species may actually support the model.

We urge caution in extrapolating from our model for large herbivorous mammals to make predictions about Rensch's rule and the correlates and causes of sexual size dimorphism in other taxa. However, some speculation is warranted. Primates are another group that exhibits Rensch's rule (Smith and Cheverud 2002; Gordon 2006). Most components of our model seem to apply, at least qualitatively, to primates: females occur in social groups; group size scales positively with body size; and larger, older, dominant males mate with more females. There are also differences, however. In particular, somewhat different ecological factors (information exchange and predation risk) likely account for body size-dependent aggregation into social groups, which often include multiple subordinate males as well as females.

The model also offers insights into why some other taxa are exceptions to Rensch's rule. For example, some pinnipeds (seals, sea lions, and walruses) are highly sexually dimorphic in body size, but the magnitude of dimorphism

is not correlated with body size (being highest in fur and elephant seals, which are among the smallest and largest pinnipeds, respectively; authors' unpublished data compilation and analysis). In these marine mammals, the magnitude of dimorphism is strongly related to harem size, but the limited terrestrial sites where females mate and give birth are related to habitat and predator avoidance strategies and not to foraging ecology.

The relevance of our model to other cases is less clear. Hummingbirds exhibit an "extended" Rensch's rule, with females being larger than males and the magnitude of sexual dimorphism increasing with decreasing body size (Colwell 2000; Dale et al. 2007). At least in this case, male reproductive success seems to depend less on dominance in aggressive interactions and more on agility in courtship displays. In such cases, biomechanical analyses support the inference that smaller males are more agile and better able to execute tight turns and complicated manoeuvres (Dial et al. 2008). Some groups that exhibit Rensch's rule, such as varanid lizards, seem to differ from large herbivorous mammals and hence from our model in so many ways that extrapolation is unwarranted (Frydlova and Frynta 2010).

The values of the parameter C used to generate prediction lines in figure 2E and 2F are extremely low ($0.35 \text{ kg}^{1/4}/\text{year}$ for bovids and cervids and $0.97 \text{ kg}^{1/4}/\text{year}$ for macropodids). C is the proportionality constant relating somatic growth rate to body size (eq. [3]). If males continued to grow as fast as females throughout their lives, they would mature much earlier or attain much larger sizes (Georgiadis 1985), and C would be on the order of $3 \text{ kg}^{1/4}/\text{year}$ (see "Appendix"). However, male and female growth rates are similar only up until the size at which females stop growing. In dimorphic species, although males continue to grow, their growth rates are substantially

reduced, which is probably attributable in part to the costs of maintaining the large bodies and weapons used to compete for mates. These costs are likely to be higher in species with larger weapons, and this may explain why C is lower for bovids and cervids, in which males grow horns or antlers, than for macropodids, which do not have such obvious weaponry.

Surprisingly, our calculations clearly show that highly dimorphic male bovids, cervids and macropodids allocate only a very small fraction of their total metabolic energy to growing additional biomass, including both body and weapons. It is likely that this qualitative result also holds for other sexually dimorphic mammals and other vertebrates. The vast majority of metabolic energy is apparently spent on maintenance (including survival). An important caveat is that males of sexually dimorphic species also expend energy on potentially costly breeding behaviors, including courtship of females and aggressive contests with other males. Because reproductively successful males do tend to be larger and to have more elaborate weapons and ornaments (Kodric-Brown et al. 2006), this raises interesting, still unanswered questions about the energetic basis of sexual size dimorphism and how it relates to sexual selection and life history.

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APPENDIX
Supplemental Figures

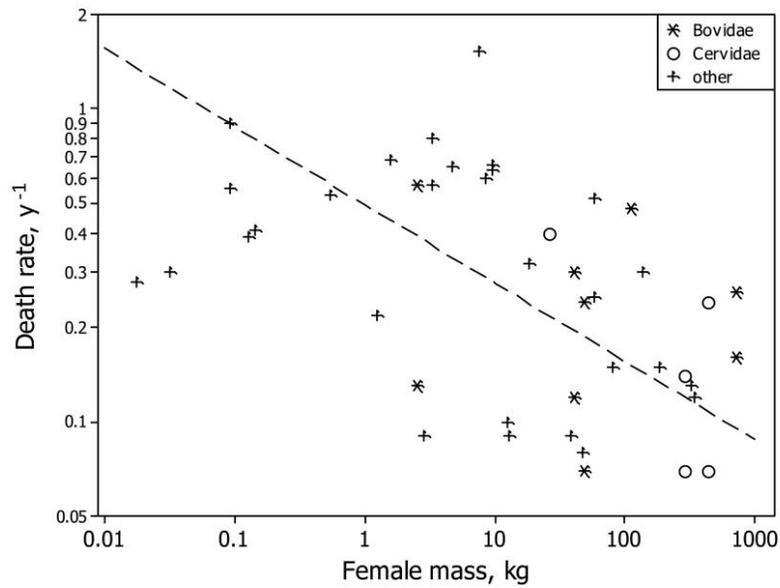


Figure A1: Death rates of young adult female placental mammals in relation to body size. Data are from Sibly et al. (1997). These rates are estimated from field studies of populations, and some species are represented more than once. The line is the fitted line with slope $-1/4$.

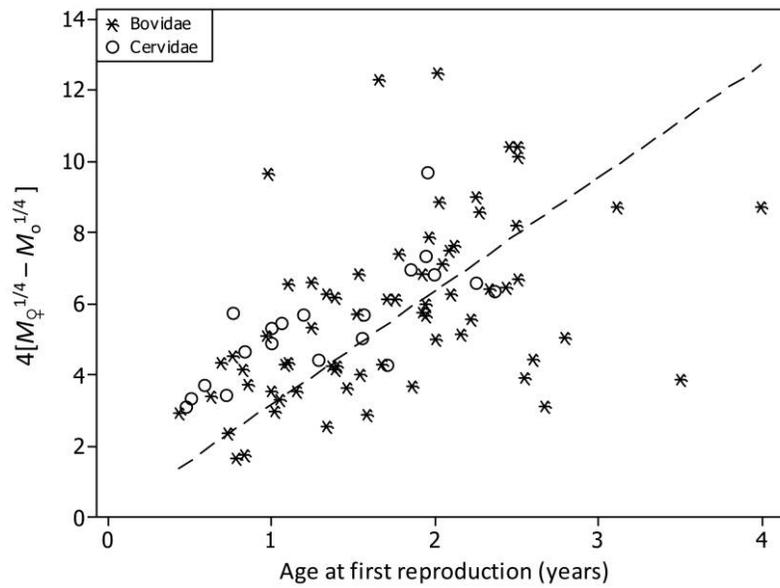


Figure A2: $4[M_{\text{♀}}^{1/4} - M_{\text{♂}}^{1/4}]$ plotted against $t_{\text{♀}}$. The slope of the fitted line gives C .

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