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The Offspring-Size/Clutch-Size Trade-Off in Mammals

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ABSTRACT: The Smith-Fretwell model for optimal offspring size assumes the existence of an inverse proportional relationship (i.e., trade-off) between the number of offspring and the amount of resources invested in an individual offspring; virtually all of the many models derived from theirs make the same trade-off assumption. Over the last 30 years it has become apparent that the predicted proportionality is often not observed when evaluated across species. We develop a general allometric approach to correct for size-related differences in the resources available for reproduction. Using data on mammals, we demonstrate that the predicted inverse proportional relationship between number of offspring and offspring size is closely approached after correcting for allocation, though there is a slight curvature in the relationship. We discuss applications for this approach to other organisms, possible causes for the curvature, and the usefulness of allometries for estimating life-history variables that are difficult to measure.

Keywords: offspring size, clutch size, trade-off, eutherians, allometry.

The trade-off between the number of offspring produced and the investment per offspring is important to many theoretical models of life history (e.g., Smith and Fretwell 1974; Stearns 1992; Roff 2003). The classic Smith-Fretwell (1974) model argues that for a reproductive individual with R resources to divide among its offspring, the number of offspring (C) that individual can produce will be inversely proportional to the investment per offspring (I): $C \propto R/I$. Because the investment per offspring can be approximated by offspring size (Smith and Fretwell 1974; Charnov 1993), this trade-off is typically assessed by evaluating relationships between clutch size and individual

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offspring mass, effectively assuming that R is constant. Several cross-species data sets (see examples in Stearns 1992; Charnov 1993; Molles 2001; Roff 2003) show negative relationships between C and I but do not show the proposed proportionality. This deviation from the expected trade-off is expected if R varies greatly among species and particularly if R and I covary (e.g., species with greater R also have larger offspring, as is commonly observed within many taxa; Charnov 1993).

Some life-history models (Charnov 1993, 2001; Charnov et al. 2001) predict that reproductive allocation per unit time scales across species as female body mass (m) raised to the 0.75 power. This relationship has received strong empirical support in a variety of taxa (Charnov et al. 2001), including mammals (e.g., Brody 1945; Charnov 1993; Charnov 2001; Ernest et al. 2003). Furthermore, for mammals, it is known that I is almost proportional to m, resulting in positive covariation between I and R (Charnov 1993). Therefore, a more general version of the size/number trade-off across species should be $C/R \propto I^{-1}$; that is, clutch size (C) per unit allocation (R) varies as I^{-1}. If R is indeed proportional to $m^{0.75}$, as theory and data suggest, then yearly clutch size divided by $m^{0.75}$ ought to be inversely proportional to the mass of an individual offspring:

$$\frac{C}{m^{0.75}} \propto I^{-1}. \tag{1}$$

Here, we demonstrate this offspring-size/clutch-size trade-off using a data set containing life-history information for 14 orders of eutherian mammals, resulting in a strong, general test of the effects of size-dependent reproductive allocation on the trade-off between number of offspring and individual offspring mass.

Methods

While offspring size at independence is a more complete measure of parental investment, we also present here results utilizing neonate size. Even though weaning size is proportional to offspring size at birth (see Ernest 2003), we opted to conduct analyses for both measures of parental investment for a variety of reasons. First, data for neonate

size are more numerous. Second, while birth is effectively an instantaneous process, weaning is a gradual process, and deciding at what point during this process to measure the size of the offspring is highly subjective. The ambiguity concerning when weaning occurs introduces considerable error into weaning mass estimates. Finally, our estimates of clutch size are based on neonate litter sizes and not on the actual number of individuals weaned, potentially resulting in increased error in our calculations. Because neither measurement of I is perfect, we present here results for both.

Data on neonate mass, weaning mass, maternal mass, litter size, and litters per year were obtained from a recently published data set on mammalian life history (Ernest 2003). While the data set contains life-history information for 1,447 species of eutherian mammals, only 532 species had information for neonate mass, maternal mass, litter size, and litters per year; substituting weaning mass for neonate mass yielded life-history information for 303 species. While only a subset of the 1,447 species in the database contained the data necessary for this study, it still provided us with data for species from 14 orders of mammals: Artiodactyla, Carnivora, Cetacea, Insectivora, Lagomorpha, Macroscelidea, Perissodactyla, Pholidota, Primates, Proboscidea, Rodentia, Sirenia, Tubulidentata, and Xenarthra. Reproductive allocation per unit time (R) was estimated from maternal mass (m) using the equation $R \propto m^{0.75}$. Annual litter size (C) was calculated by multiplying litter size by litters per year.

Results and Discussion

Correcting the number of offspring by the resources available for reproduction results in a relationship between the number of offspring and offspring size that is extremely close to the predicted slope of -1 (fig. 1). This similarity to the theoretically predicted value is especially striking when compared to the relationship for the same data uncorrected for reproductive allocation (fig. 2). Our data, when uncorrected for reproductive allocation (i.e., not divided by $m^{0.75}$), show not only higher variability around the relationship but also a slope substantially shallower than -1 (fig. 2; see also Stearns 1992; Molles 2001). Indeed, because offspring size at birth is almost proportional to the mother's size, figure 2A shows the expected $\approx -1/4$ scaling relationship between yearly litter size and mother mass reported for mammals (Charnov 1993). Overall, given our use of an allometric equation to approximate R and various issues with our measures of I, the closeness to proportionality in figure 1 is noteworthy since we have clearly ignored the details in the parental-resource transfer and the offspring-growth processes, both before and after birth.

One interesting result that emerges from our analysis is a mild deviation from the predicted power-law relationship between C/R and I. Careful inspection of figure 1 reveals what could be a curve or break in the relationship that is most apparent at a neonate size of approximately 1,000 g (or 7 natural-log units). This curvature can also be seen in the weaning data at around 8 natural-log units (fig. 1B). Refitting the log-transformed data with a second-order polynomial showed that there is indeed statistically significant curvature in the relationship ($P < .001$ for both weaning and neonate data). However, the addition of the quadratic term improved the fit of the regression by only 0.3% (neonate: $r^2 = 0.943$ vs. 0.946; weaning: $r^2 = 0.946$ vs. 0.949). Though the increase in r^2 is slight, it is possible that the process generating this secondary pattern explains the discrepancy between our empirical results and the theoretically predicted slope of -1. Potential reasons for this slight deviation from the model include first, an interaction between seasonality and body size that differentially constrains large animals to one litter per year, potentially altering the relationship for large versus small mammals; second, an interaction between phylogeny and body size, resulting in a slightly different relationship for large animals than small animals because of evolutionary constraints; third, a slight curvature in the relationship between production and body size, as suggested by Kozlowski and Weiner (1997); and finally, some other complexity in how R varies with body size, possibly caused by the parent-offspring resource transfer, ontogenetic growth of the offspring, and other R-related issues mentioned above. It is also interesting to note that the slope from the plot utilizing weaning data is actually further from the predicted relationship than that from the plot utilizing neonate data. While this may reflect the additional error in the weaning data or the mismatch between neonate clutch size and weaning mass, another possibility is that it reflects some added biological complexity introduced during the transfer of resources from mother to offspring through lactation. While in-depth investigation of the residual variation is beyond the scope of this study, further quantification of the pattern, study of its causes, and evaluation of similar patterns in other taxa should prove insightful. However, despite the pattern in the residuals, the fact that our slope deviates from the predicted Smith-Fretwell slope by only ∼3%–9%, depending on how I is calculated, is noteworthy and represents a substantial improvement in our understanding of resource/offspring trade-offs in mammals.

Correcting for differences in reproductive allocation can also explain another life-history pattern that has been reported for mammals. Blueweiss et al. (1978) first noted that there was a tight relationship between log-transformed total litter mass and log-transformed maternal body mass (m). However, Blueweiss et al. (1978) had no theoretical
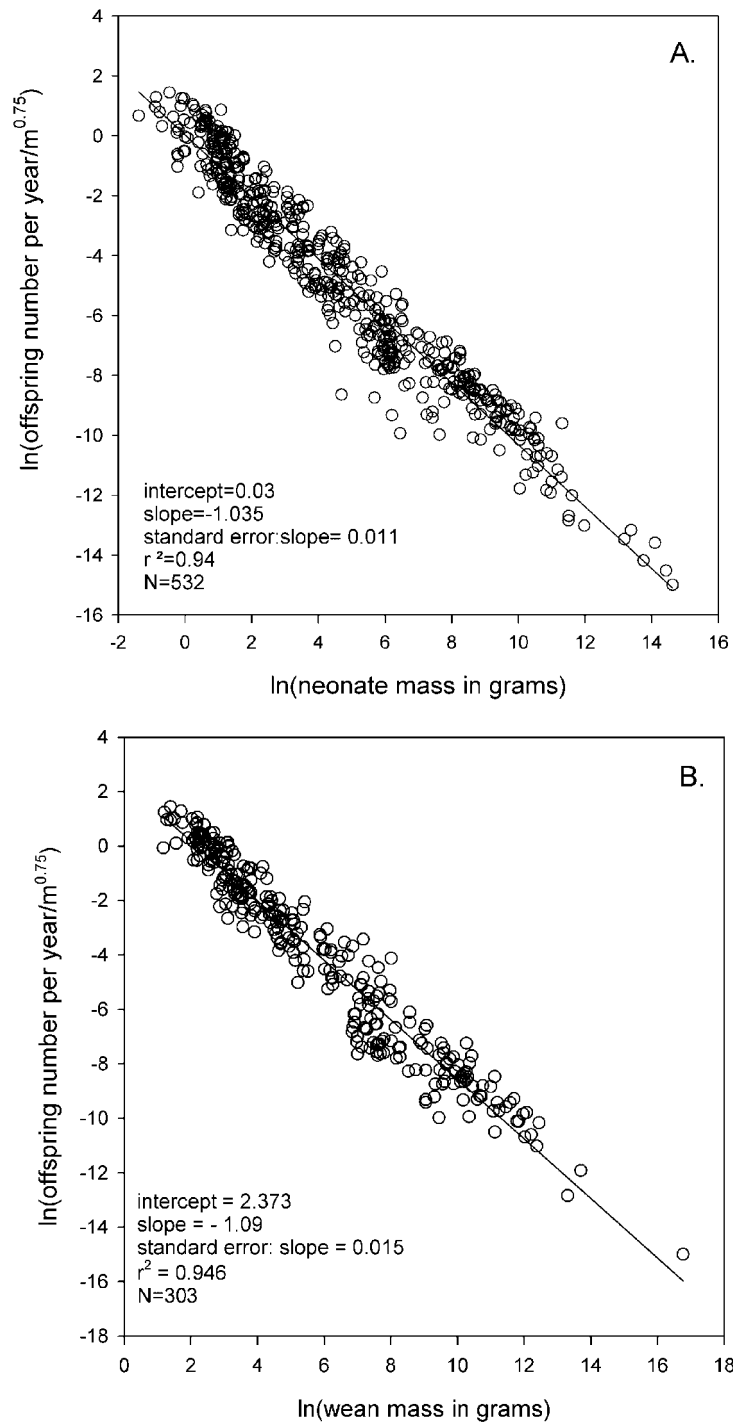
Figure 1: Correction for species-level differences in R changes the slope of the relationship between offspring size and offspring number to more closely reflect the predicted slope of -1. *A*, Relationship using neonate mass for *I*. Slope for the corrected relationship is -1.03 (95% confidence interval [CI]: -1.01 to -1.05). While the CI for the corrected plot does not statistically include the predicted value of -1, it approaches the predicted value to within 1%. Because R was estimated from $m^{0.75}$, small differences between the theoretically predicted and empirical exponents could cause a slight deviation from -1; an exponent <0.75 would reduce the fitted slope. The exact -1 slope would result from an exponent of 0.72. It is also worth noting that because of the lack of phylogenetic independence in our data, our CIs may be overly narrow. *B*, Relationship using weaning mass for *I*. Slope $= -1.09$ (95% CI: -1.12 to -1.06).
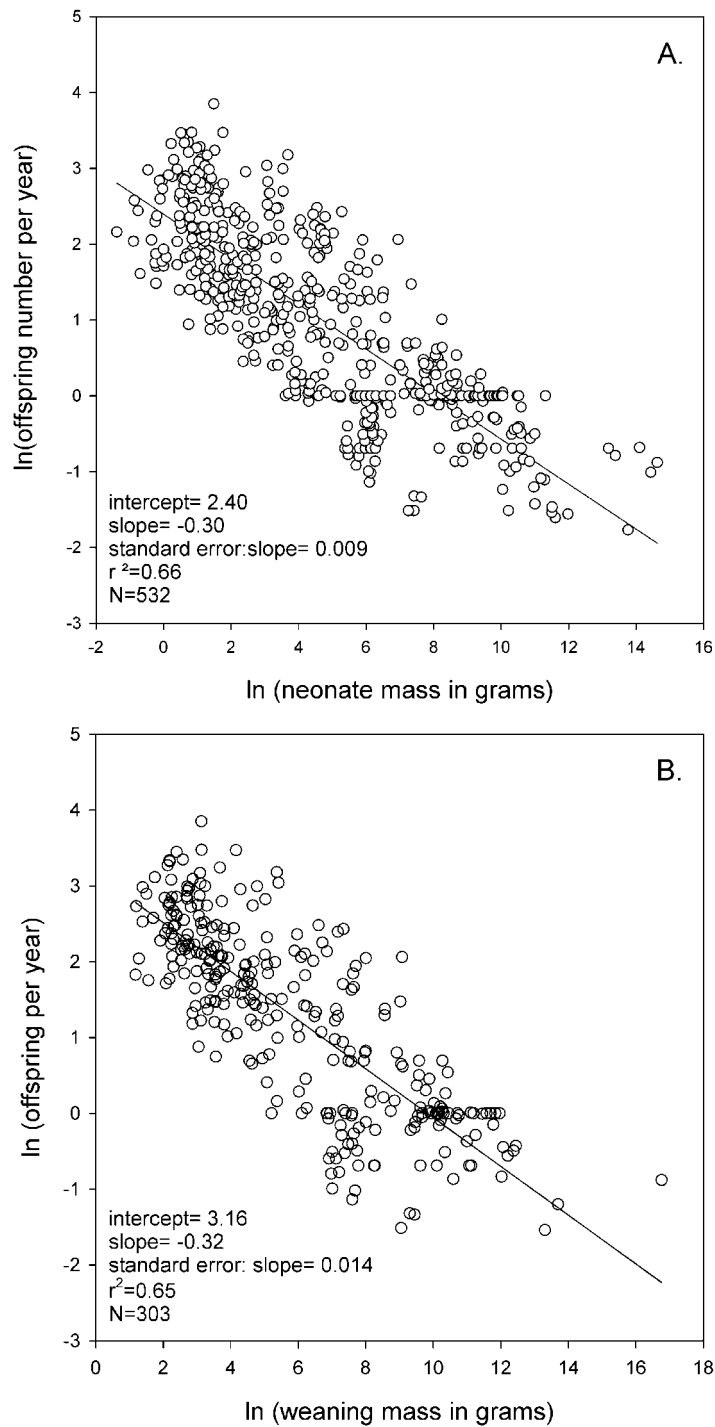
Figure 2: Relationships between C and I (i.e., C not corrected by $m^{0.75}$) are negative but not close to the predicted slope of -1. *A,* Relationship using neonate mass for I. Slope $= -0.30$ (95% confidence interval [CI]: -0.28 to -0.31). *B,* Relationship using weaning mass for I. Slope $= -0.32$ (95% CI: -0.29--0.35).

explanation for this pattern. Because litter mass is simply $I \times C$, we can explain the relationship documented by Blueweiss et al. (1978) using a simple rearrangement of our equation (1): $IC \propto m^{0.75}$. Blueweiss et al. (1978) observed an exponent of 0.82 in their empirical data, which is very close to the theoretically predicted value.

While we demonstrate only for mammals how correcting for mass-related variation in R results in the predicted inverse proportionality between C and I, our method for getting at R to normalize the number of offspring among species can probably be applied to many other taxa. However, because rates of resource acquisition and allocation for ectotherms are highly dependent on temperature, $m^{0.75}$ should be multiplied further by an exponential temperature correction (Gillooly et al. 2002; Charnov and Gillooly 2004). This temperature correction was unnecessary for homeothermic mammals because their body temperatures are all very similar.

In conclusion, these results show that by correcting—even if only coarsely—for species-level differences in R caused by differences in body size, we can closely approach the theoretically predicted relationship between C and I. Furthermore, the use of the function $R \propto m^{0.75}$ to correct for differences in resource allocation demonstrates the strengths of applying well-known allometric relationships to life-history problems (Charnov 1993), especially to estimate difficult-to-obtain variables (like R). This approach is especially useful because, for most organisms, body mass is relatively easy to measure in the field, and the relationship between body mass and production is known for a large variety of taxa. Interestingly, there are slight deviations from the predicted form of the relationship in our results, and investigating these deviations should prove to be an additional and interesting avenue for research, eventually helping in our understanding of the trade-offs between C and I, given constraints on R. Despite our use of a coarse approximation of R, our results very closely approach -1 and point to the usefulness of correcting for species-level differences in R, although they suggest that future models for growing offspring should perhaps explore why the cost to the parent is not exactly proportional to offspring mass. However, in general, our simple approach demonstrates that across widely varying species of mammals, there is strong evidence for the predicted trade-off between offspring size and number of offspring.

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