

A TEST OF REPRODUCTIVE POWER IN SNAKES

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Abstract. Reproductive power is a contentious concept among ecologists, and the model has been criticized on theoretical and empirical grounds. Despite these criticisms, the model has successfully predicted the modal (optimal) size in three large taxonomic groups and the shape of the body size distribution in two of these groups. We tested the reproductive power model on snakes, a group that differs markedly in physiology, foraging ecology, and body shape from the endothermic groups upon which the model was derived. Using detailed field data from the published literature, snake-specific constants associated with reproductive power were determined using allometric relationships of energy invested annually in egg production and population productivity. The resultant model accurately predicted the mode and left side of the size distribution for snakes but failed to predict the right side of that distribution. If the model correctly describes what is possible in snakes, observed size diversity is limited, especially in the largest size classes.

Key words: *body size; ectotherm; energetics; life history; macroecology; optimal size; reproduction.*

INTRODUCTION

Body size influences nearly every aspect of an organisms' biology and is important in structuring ecological communities (e.g., Peters 1983, Brown 1995). Therefore, body size should be closely tied to fitness, and organisms should show predictable patterns of body size diversity. Frequency distributions of animal body sizes reflect micro- and macroevolutionary processes that have shaped empirical diversity in size and provide ecologists with a comparative tool to investigate such forces (Maurer et al. 1992). For instance, attempts have been made to understand the major forces governing body size by describing and comparing shapes of body size distributions of various clades of organisms (e.g., Hutchinson and MacArthur 1959, Van Valen 1973).

In a similar effort to explain the body size diversity of North American mammals, which show a frequency distribution that is unimodal and right-skewed, Brown et al. (1993) proposed an energetic definition of fitness. They termed this the reproductive power model (RPM) and defined it as the energetic capacity to produce offspring in a mature organism. This capacity is determined by two processes: the rate that energy can be acquired above and beyond maintenance needs and stored as reproductive tissue (acquisition) and the rate that this stored energy can be converted into offspring (conversion). Brown et al. (1993) suggested that the ability of an organism to maximize these rates (and thus

become more fit) is strongly influenced by their body size. For instance, because of their higher mass-specific metabolism, small species must spend more time foraging to supply their homeostatic needs and thus are limited in the rate at which they may acquire resources for reproduction. In contrast, large species have a large capacity to acquire resources but are constrained by the rate they can convert this energy into offspring biomass. When Brown et al. (1993) applied the model, they found that the distribution of reproductive power matched the shape of the frequency distribution of body masses of North American mammals and that reproductive power was maximized at the modal (optimal) body mass.

RPM remains a contentious concept in ecology and researchers have challenged the idea on theoretical and empirical grounds. Fundamentally, some have questioned the existence of a single energetic optimum for a taxonomic lineage, suggesting that multiple "optima" should result from diverse selective forces known to occur among environments (Blackburn and Gaston 1996). Kozłowski (1996, 2002) has argued that RPM ignores the influence of mortality, a critical factor influencing life-history evolution. Additionally, a number of authors have questioned the selection of the allometric equations used in RPM (Blackburn and Gaston 1996, Kozłowski 1996, Perrin 1998). Further, when researchers have tested one prediction of RPM, namely that the slopes of life-history allometries change sign where reproductive power is maximized, empirical data have not supported the prediction (Jones and Purvis 1997, Symonds 1999, Bokma 2001).

Despite these challenges, RPM has accurately predicted the mode of the body size distribution for mammals (Brown et al. 1993, Chown and Gaston 1997), birds (Maurer 1998), and bivalves (Roy et al.

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2000) and has predicted the shape of the distribution for mammals and birds. However, the data required to implement RPM are difficult to generate, largely because studies documenting annual energetic totals of reproduction and population turnover rates, the key variables for examining acquisition and conversion of energy, are rare. For example, a test of RPM in birds (Maurer 1998) was based on acquisition of energy for egg production in only six species of birds. Nevertheless, the most appropriate tests of the generality of RPM must come from large taxonomic groups for which key variables of the model are available.

We tested RPM on snakes, a group that differs from birds and mammals in having ectothermic physiology (Pough 1980), an entirely predatory foraging mode, limbless locomotion, and one of the most extremely elongate body forms known from vertebrates (Pough and Groves 1983). Additionally, snakes exhibit a log-normal body size distribution (Boback and Guyer 2003), rather than the right-skewed size distribution of birds (Maurer 1998) and mammals (Brown et al. 1993). If RPM can accurately predict the distribution of body sizes for snakes, then this would support the idea that diversity of a group of organisms is governed by the allometry of energetics associated with reproductive power.

METHODS

Brown et al. (1993) demonstrated that, within a clade of organisms, reproductive power could be estimated by a model incorporating two rate-limiting processes. Using the convention of Maurer (1998), reproductive power (W), or the capacity to transform energy to reproductive work is

$$W = \frac{AC}{A + C} \quad (1)$$

where A = acquisition and C = conversion. Because reproductive power is strongly influenced by size, Brown et al. suggested that the acquisition and conversion components of RPM could be expressed as allometric functions of body mass (M):

$$\begin{aligned} A &= C_0 M^{b_0} \\ C &= C_1 M^{b_1} \end{aligned} \quad (2)$$

where C_0 , C_1 , b_0 , and b_1 are constants. By combining Eqs. 1 and 2, the distribution of reproductive power within a clade of organisms is as follows:

$$\frac{dW}{dt} = \frac{C_0 M^{b_0} C_1 M^{b_1}}{C_0 M^{b_0} + C_1 M^{b_1}} \quad (3)$$

Brown et al. (1993) argued that the exponents (b_0 and b_1) are fundamental and shared by all organisms. They reasoned that $b_0 = 0.75$ because the rate of energy acquisition in excess of maintenance needs and stored as reproductive tissue should have the same allometric exponent for individual metabolic rate, productivity,

and growth rate (all exponents ~ 0.75 ; Peters 1983, Calder 1984). Further, they reasoned that $b_1 = -0.25$ because conversion of energy to reproductive work should have the same allometric exponent as mass-specific metabolism and other biological conversion processes (approximately -0.25 ; Peters 1983, Calder 1984). In contrast, the coefficients (C_0 and C_1) are taxon specific and describe the ability of each taxon to mobilize resources for activities beyond maintenance under ideal conditions (see Maurer [1998] and Brown et al. [1996] for more discussion of these constants and their units of measure).

We obtained snake-specific estimates of the constants for RPM using data from the literature. For the acquisition (A) portion of RPM, we generated an allometric function for the most costly aspect of producing reproductive tissue for squamates, assumed to be the production of ova prior to ovulation, as in birds (Maurer 1998). Based on a review of egg development in squamates, we assumed that the fastest rate of energy conversion occurs during the final 21 days of vitellogenesis before ovulation, when 90% of egg mass is generated (Saint Girons 1985). Therefore, acquisition was modeled by calculating the proportion of clutch energy (i.e., clutch power measured in watts) generated in the final 21 days of vitellogenesis (see the Appendix for data sources and further explanation of the calculation of clutch power). For all species, we assumed a single clutch per year and that loss of mass between ovulation and the point in time when clutch mass was measured was negligible. For this reason, we used only oviparous species. Although viviparous snakes that are lecithotrophic share some features of development with oviparous species (Stewart 1989, Stewart et al. 1990), we excluded all viviparous species because the prolonged retention of the corpora lutea (Guillette 1987) lengthens date of litter deposition relative to date of clutch deposition in oviparous species.

A power function of clutch watts on maximum body mass was generated using nonlinear regression (PROC NLIN; SAS version 8.2, Statistical Analysis Systems, Cary, North Carolina, USA) and from this we obtained estimates for C_0 (clutch watts when mass = 1 kg) and b_0 (the exponent) for snakes. For comparative purposes, data were log-transformed to linearize the relationship, which allowed us to use an analysis of covariance (ANCOVA) to compare our data to those from birds (Ricklefs 1974) and mammals (Linzell 1972).

For the conversion (C) portion of RPM, we generated an allometric function for relative population productivity for snakes (productivity/biomass; data from Fitch 1963, 1965, 1975, 1999, 2000, Platt 1969, Clark 1970). We chose to define population productivity (P) as the sum of growth productivity and reproductive productivity as defined by (Petrusewicz and Macfadyen 1970). Growth productivity was estimated by obtaining the total mass gained by a population during a year (sum of age-specific growth within a population). Reproductive

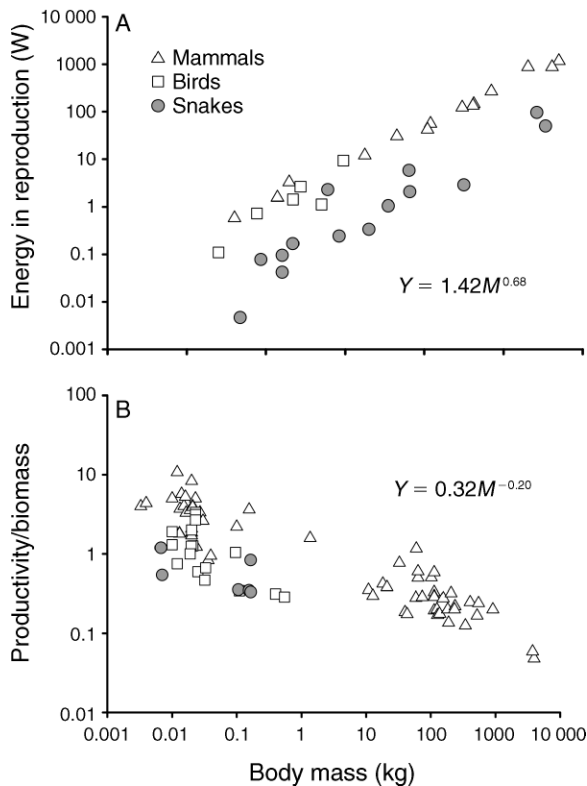


FIG. 1. Allometric relationships used to estimate rate of (A) energy acquisition and (B) energy conversion for snakes and other vertebrate groups. Acquisition is defined as the rate of energy obtained from the environment above and beyond maintenance needs as estimated by clutch power (energy allocated per unit time, in watts). Rate of conversion is defined as the rate of energy converted into offspring as estimated by population productivity (rate of age-specific reproduction + age-specific growth/biomass). Equations for each allometric relationship for snakes are indicated, where M is body mass.

productivity was estimated by obtaining the total mass of offspring produced by a population during a year (sum of age-specific reproduction). To do so, we determined the proportion of reproductive females in each age class and multiplied this by the maximum density of mature females to obtain the maximum number of reproductive females in each age class. Finally, we determined the maximum clutch mass for each age class by multiplying the maximum clutch size of a female in each age class by maximum offspring mass for the species.

Biomass (B) estimates were obtained from the literature and these were divided into the sum of growth and reproductive productivity for each species (productivity/biomass ratio, P/B). Literature values were also used to describe the maximum body mass attained by each species (data available online).² A power function of P/B on maximum body mass was generated using

² (http://www.auburn.edu/cosam/collections/reptiles_amphibians/macroecology/index.htm)

nonlinear regression, and from this regression we obtained estimates for C_1 (P/B when mass = 1 kg) and b_1 (the exponent) for snakes. For comparative purposes, data were log-transformed to linearize the relationship and ANCOVA was used to compare our data to those for birds and mammals (given by Farlow [1976] and utilized by Brown et al. [1993] and Maurer [1998]).

We generated an RPM for snakes by inserting these estimates into Eq. 3. Using a chi-square goodness-of-fit test, the resultant RPM was compared to the observed body mass distribution (Boback and Guyer 2003; distribution based on total lengths of 25% of the world's snake fauna converted to mass using a mass-length regression from Pough [1980]). Additionally, we compared RPMs of snakes to those of mammals, birds, and bivalves (Brown et al. 1993, Maurer 1998, Roy et al. 2000). We calculated skewness and kurtosis for each model by estimating the frequency distribution for each power curve and generating the appropriate statistics and their standard errors (Sokal and Rohlf 1995). Power functions were considered significantly skewed or kurtotic if the absolute value of either divided by its standard error was greater than 2.0 (Reed and Boback 2002).

RESULTS

We estimated maximum rates of energy acquisition from the environment, beyond maintenance needs, by analyzing data of energy invested in a clutch per unit time (watts) for 14 snake species (Appendix). From a power function describing these data, we obtained estimates of $C_0 = 1.42$ and $b_0 = 0.68$ for snakes. When placed on a log-log scale, the distribution of these data was similar in slope but not elevation to those from birds and mammals (Fig. 1A). An analysis of covariance indicated that the slopes were not significantly different among taxonomic groups ($F = 0.84$, $df = 2$, $P = 0.44$). Based on 95% confidence intervals, the slope for birds, mammals, and snakes overlapped the proposed universal slope of 0.75 (Table 1). Intercepts significantly varied among groups ($F = 60.62$, $df = 2$, $P < 0.0001$), with birds and mammals showing relatively higher rates of reproductive tissue formation compared to snakes (Table 1, Fig. 1A).

We estimated rates of energy conversion into reproductive work from data of population productivity of six snake species (Table 2). Applying a power function to these data, we obtained estimates of $C_1 = 0.32$ and $b_1 = -0.20$. When linearized on a log-log plot, the distribution of values for snakes was similar to that of birds and data from both snakes and birds were lower in elevation than data from mammals (Fig. 1B). An analysis of covariance revealed no significant differences in slopes among the taxonomic groups ($F = 1.4$, $df = 2$, $P = 0.25$), and based on 95% confidence intervals, none of these groups differed from the proposed universal slope of -0.25 . However, there was a significant difference in intercepts ($F = 25.96$, $df = 2$, $P < 0.0001$). Mammals had

TABLE 1. Allometric relationships for acquisition (*A*) and conversion (*C*) of energy in snakes, birds, and mammals.

Taxon	Acquisition			Conversion		
	<i>N</i>	Slope	Intercept	<i>N</i>	Slope	Intercept
Universal estimate		0.75			-0.25	
Snakes	14	0.68 (0.13–1.23)	1.42 (–3.00–5.84)	6	-0.20 (–0.59–0.19)	0.32 (–0.19–0.82)
Birds	6	1.92 (0.15–3.68)	10.07 (5.66–14.48)	16	-0.32 (–0.80–0.16)	0.43 (–0.38–1.23)
Mammals	14	0.70 (0.53–0.87)	14.78 (–0.34–29.89)	43	-0.25 (–0.33 to –0.17)	1.26 (0.83–1.69)

Notes: Values are followed by 95% confidence intervals in parentheses. Data for acquisition were obtained as follows: for birds, from energy in egg production (Ricklefs 1974) as utilized in Maurer (1998); for mammals, from maximum milk production (Linzell 1972); and for snakes, from energy in clutches (L. Vitt, *personal communication*; see also Appendix). Data for conversion were obtained from relative population production (productivity/biomass ratio, *P/B*): for birds and mammals, data from Farlow (1976); for snakes, from additional sources (see Table 2 and sources noted throughout the text).

higher *P/B* values than snakes and birds, but only snakes and mammals had nonoverlapping 95% confidence intervals (Table 1, Fig. 1B).

Because the slopes from the allometric relationships for clutch power and population productivity for snakes did not differ from the proposed universal slopes (Table 1), we followed Brown et al. (1993) and Maurer (1998) and generated an RPM for snakes using universal slopes and snake-specific constants (*C*₀, *C*₁). Using these values, maximum reproductive power is attained for a 676-g snake. The resulting RPM matches the mode in the empirical distribution of body masses for the world’s snake fauna (380 g) more closely than in the other taxonomic groups for which such data are available (Table 3). However, the RPM predicts a right skew to reproductive power and, therefore, does not mimic the log-normal distribution of body size in snakes ($\chi^2 = 266$, *P* = 0.99; Fig. 2A). A right-skewed RPM is consistent with all taxonomic groups tested thus far and all four groups have similar values for skew and kurtosis (Fig. 2B).

Because RPMs for the four taxa examined to date differ in volume of potential reproductive power (mammals and snakes > birds > mollusks) and position (snakes shifted to right of all others; Fig. 2B), we explored the combination of taxon-specific constants that could result in such differences. We further explored the combination of exponents required to generate log-normal and left-skewed distributions. First, we used the universal exponents and held *C*₁ constant at 1.0 while adjusting *C*₀ (1, 10, and 100). This generated RPMs that differed in volume and mode but that emerged from similar positions along the right side of the model (Fig. 3A). Second, we used the universal exponents and held

*C*₀ constant at 1.0 while adjusting *C*₁ (1, 10, and 100). This generated RPMs that differed in volume and mode but that emerged from similar positions along the left side of the model (Fig. 3B). The maximum reproductive power attained by altering *C*₁ was much greater than that attained by altering *C*₀. Finally, we held *C*₀ and *C*₁ constant at 1 while adjusting the exponents from the universal values, through values of *b*₀ = 0.75 and *b*₁ = –0.75 to values of *b*₀ = 0.25 and *b*₁ = –0.75. This generated RPMs that were right-skewed, log-normal, and left-skewed, respectively (Fig. 3C).

DISCUSSION

Using snake-specific constants, we found that RPM predicted the mode of the body size distribution for the world’s snakes. This is the fourth taxonomic group for which this is so (Brown et al. 1993, Maurer 1998, Roy et al. 2000). Therefore, this portion of RPM appears to consistently predict the body size with the greatest scope for speciation for major taxonomic radiations. Further, the groups that have been examined appear to have had sufficient time over which to accumulate this richness. However, this argument requires that size distributions for these taxonomic groups are accurately described from extant taxa and that their modes have not changed with time. Because an examination of fossil mammals by Alroy (1998, 2003) generally confirms that the size distribution for extant mammals created by Brown and Nicoletto (1991) accurately reflects the distribution including relatively recent fossils, we assume that fossil data generally support evaluation of patterns generated by extant taxa.

In addition to accurately predicting the mode of the snake size distribution, RPM accurately predicted the

TABLE 2. Key variables for determination of conversion of energy into reproductive work for snakes.

Species	Mass (kg)	<i>P</i> _{gro} (g·ha ⁻¹ ·yr ⁻¹)	<i>P</i> _{rep} (g·ha ⁻¹ ·yr ⁻¹)	<i>P</i> _{gro} + <i>P</i> _{rep}	<i>B</i> (g/ha)	<i>P/B</i>
<i>Carphophis vermis</i>	0.0067	253.7	825.0	1078.7	906.2	1.190
<i>Diadophis punctatus</i>	0.0070	1023.9	3453.1	4476.9	8268.4	0.541
<i>Thamnophis sirtalis</i>	0.1060	477.2	743.7	1221.0	3449.5	0.354
<i>Agkistrodon contortrix</i>	0.1550	165.5	305.0	470.5	1356.4	0.347
<i>Heterodon nasicus</i>	0.1640	327.3	79.2	406.4	487.1	0.834
<i>Coluber constrictor</i>	0.1650	501.1	724.7	1225.8	3703.1	0.331

Notes: *P*_{gro} = growth productivity; *P*_{rep} = reproductive productivity; *B* = biomass; *P/B* = productivity/biomass ratio.

TABLE 3. Characteristics of body mass distributions and maximum reproductive power predictions for the four taxonomic groups studied to date.

Taxon	Minimum (g)	Maximum (g)	Mode (g)	Maximum reproductive power
Mammals	3	489 178	50	100
Birds	1.6	160 572	12	33
Bivalves	0.00003	137	1.7	9
Snakes	1.3	338 744	380	676

Note: Maximum reproductive power is calculated using the following formula (Brown et al. 1993): $M = (-C_1 b_1 / C_0 b_1)^{1/(b_0 b_1)}$.

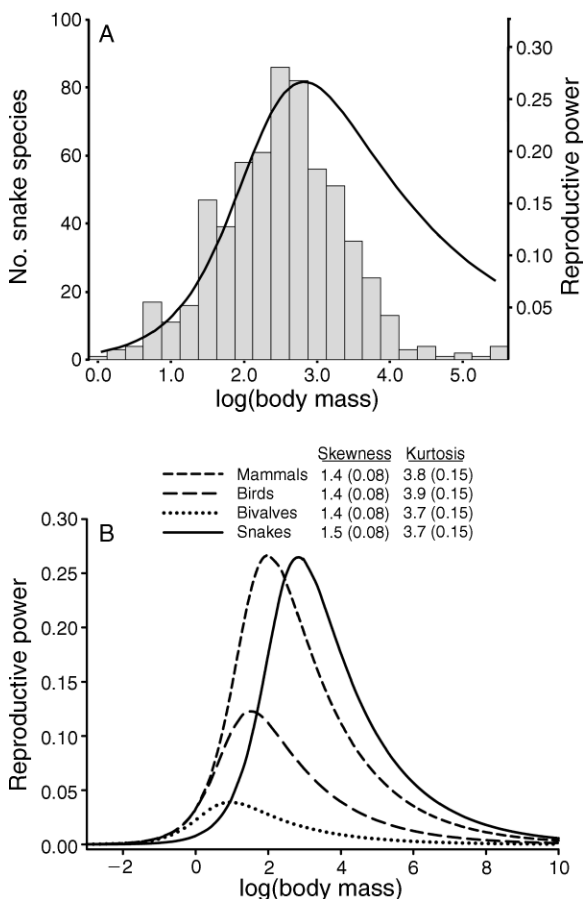


FIG. 2. Reproductive power for snakes as compared to (A) a frequency distribution of approximately one-quarter of the world's snake fauna (Boback and Guyer 2003) and (B) power functions generated for other animal groups, based on log₁₀-transformed body mass, originally measured in grams. Skewness and kurtosis values (with SE) for each of the distributions were calculated assuming a sample size of 1000 for each of the taxonomic groups. Positive values of skewness indicate positive (or right) skew whereas negative values indicate negative (or left) skew. Positive values of kurtosis indicate leptokurtosis whereas negative values indicate platykurtosis.

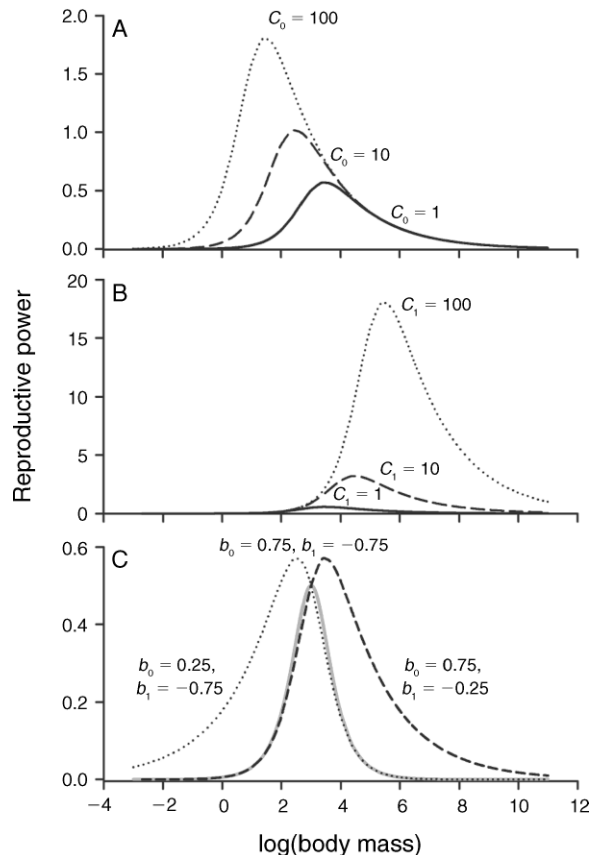


FIG. 3. Testing the flexibility of the reproductive power model by holding all constants the same and then (A) varying C_0 ; (B) varying C_1 ; and (C) varying the universal constants (b_0 , b_1). C_0 and b_0 are the intercept and exponent, respectively, from the allometric function for energy acquisition ($A = C_0 M^{b_0}$). C_1 and b_1 are the intercept and exponent, respectively, from the allometric function for energy conversion ($C = C_1 M^{b_1}$). Brown et al. (1993) argued that b_0 and b_1 are universal for all organisms ($b_0 = 0.75$, $b_1 = -0.25$), whereas C_0 and C_1 are taxon-specific constants. Reproductive power is regressed on log₁₀-transformed body mass, originally measured in grams.

body size distribution from the modal-sized species to the smallest species, as it has for the other three radiations examined (Brown et al. 1993, Maurer 1998, Roy et al. 2000). Since the data required for the acquisition portion of RPM are from energetics associated with acquiring energy beyond homeostatic needs, and because all groups examined to date (including snakes) conform to the slope expected from allometry (Brown et al. 1993), current data are consistent with the hypothesis that diversity below the modal size is limited by taxon-specific rates of obtaining energy for reproduction.

RPM did not predict the diversity of snake body sizes from the modal-sized species to the largest species. Failure of RPM to predict this portion of a size distribution was also true for bivalves (Roy et al. 2000), a group that, like snakes, does not have a right-skewed size distribution. Population productivity (rela-



PLATE 1. An (invasive) adult Burmese python (*Python molurus*) shown thermoregulating during the morning hours of 7 January 2008 in Everglades National Park, Dade County, Florida, USA. If the reproductive power model is accurate, the diversity of large-bodied snakes, exemplified by the Burmese python above, is limited. We suggest that this may be due to constraints on foraging mode or the biomechanics of limbless locomotion. Photo credit: S. M. Boback.

tive to standing crop biomass, the P/B ratio) in snakes, as with all other groups examined to date, conformed to the slope predicted by Brown et al. (1993). Therefore, the physiological processes proposed to limit the right side of the size distribution is consistent among all animal groups examined, even if the potential for size evolution is not actually met in some groups.

We see four explanations for the failure of RPM to predict size distributions in all taxa. First, the right-skewed size distribution might not be as universal as implied by previous authors (reviewed by Kozłowski and Gawelczyk 2002). Second, both groups in which RPM predicts body size distributions are endotherms, whereas both groups in which RPM fails to predict body size distributions are ectotherms. Thus RPM, or the equations upon which it is based, might only apply to endothermic organisms. Pough (1980) argued that mass-specific metabolic rate rises so rapidly in small-bodied endotherms that it is virtually impossible to supply individuals smaller than 3–5 g with enough energy to survive. In contrast, ectotherms are relatively unconstrained at the small end of the body size distribution. Thus, we could predict that physiological differences

between the two groups might allow ectotherms a smaller value for the slope (and/or a greater intercept) of the acquisition portion of the reproductive power model. However, our results are inconsistent with this prediction since snakes conform to the predicted slope (and show a lower intercept) for this portion of the model and the fit of the model is strongest for snakes below the modal size. Thus, the log-normal distribution of snake body sizes does not appear to result from a broadening of the scope for small size relative to the modal size. Instead, the distribution appears to be created by a narrowing of the size distribution relative to the predictions generated by the allocation (conversion) portion of the reproductive power model (from modal to largest size). Because of their reliance on anaerobic physiology, ectotherms exhaust rapidly and are relatively easy for endothermic predators to catch (Pough 1983). Indeed, many bird and mammal species prey on snakes and a notable number of these specialize on them (e.g., Secretary Birds, *Sagittarius serpentarius*; Roadrunners, *Geococcyx californicus*; Laughing Falcons, *Herpetotheres cachinnans*; Greene 1997). If predation affects large snake species more than small ones, then this size-

biased predation might explain why the snake distribution is truncated in the largest size classes and thus why snakes fail to fulfill the promise of the reproductive power model.

A third constraint that might limit the size distribution of snakes relative to their potential energetic fitness is foraging mode. The two groups whose body size distributions conform to predictions of RPM (birds and mammals) include a broad range of foraging modes, whereas the two groups that do not conform to RPM predictions exhibit restricted foraging modes (gape-limited predation in snakes, filter-feeding in bivalves). Those snakes that fill the distribution above the modal size are dominated by large constricting colubrids and boids that apprehend prey from ambush locations (Pope 1961, Montgomery and Rand 1978, Slip and Shine 1988). Many of the largest snakes have diets consisting largely of terrestrial mammals that, because of prey mobility, are difficult for a snake to capture. Ungulates dominate the mammals available for the largest snakes to eat. Because these mammals are social, travel in large groups, and have low population densities (Damuth 1981), they are likely challenging for a slow-moving ambush predator, like a snake, to apprehend. These capture difficulties compound a problem associated with the decreasing diversity of large mammals available for large predatory snakes and potentially limit the scope of diversification available to large snakes.

A final explanation for why snakes fail to achieve the body sizes implied by RPM is physical properties associated with limbless locomotion. In describing the log-normal size distribution for snakes, we (Boback and Guyer 2003) suggested that, if snakes are constrained by static irregularities of objects required for lateral undulation, and if these irregularities are log-normally distributed (like many physical objects in the universe, Brown 1995), then the snake size distribution should reflect a similar shape. The largest snakes (boas and pythons; see Plate 1) typically employ rectilinear locomotion whereby the body is oriented in a straight line and motion of the lateral muscles ratchets the belly scales propelling the body forward in a caterpillar-like movement. This type of locomotion may be typical of big snakes in part because their massive bodies are less easily flexed laterally, a movement necessary for lateral undulation (Greene 1997). If this constraint generally affects size distributions, then similar functional effects of locomotion should be evident in other groups. The physical features of flight create a constraint envelope that accurately reflects the size distribution of birds (Pennycuik 1986). We know of no similar analysis for mammals or bivalves.

Relative to the other three groups examined to date, snakes achieve the largest modal size and have an RPM that is shifted to the right. Because snakes frequently feed on species within the bird and mammal distributions, they need to be larger than those organisms to overpower and consume them (Mushinsky 1987). This

results in a shift of RPM of snakes to a distribution centered on larger body sizes. Alternatively, competition from other terrestrial vertebrates could also have played a role in shaping the snake size distribution. All snakes are carnivores and thus competition from relatively large carnivorous birds and mammals may be responsible for the truncation of the right side of the snake size distribution. Preliminary evaluation of RPMs in the other three taxa suggests that variation in attainable reproductive power is constrained largely by differences in energy conversion rather than energy acquisition. This explains the consistent position of the left side of the RPMs of bivalves, birds, and mammals, but differing peaks of their RPMs. Overall, the association of body size distributions with RPM indicates that a consistent set of physiological principles constrain body size distributions from the mode to the smallest species. A more complicated set of variables shapes size distributions from the mode to the largest species.

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APPENDIX

Data used for the determination of acquisition of energy for reproduction in snakes (*Ecological Archives* E089-085-A1).