Effects of body size and lifestyle on evolution of mammal life histories

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It has recently been proposed that life-history evolution is subject to a fundamental size-dependent constraint. This constraint limits the rate at which biomass can be produced so that production per unit of body mass is inevitably slower in larger organisms than in smaller ones. Here we derive predictions for how changes in body size and production rates evolve in different lifestyles subject to this constraint. Predictions are tested by using data on the mass of neonate tissue produced per adult per year in 637 placental mammal species and are generally supported. Compared with terrestrial insectivores with generalized primitive traits, mammals that have evolved more specialized lifestyles have divergent mass-specific production rates: (*i*) increased in groups that specialize on abundant and reliable foods: grazing and browsing herbivores (artiodactyls, lagomorphs, perissodactyls, and folivorous rodents) and flesh-eating marine mammals (pinnipeds, cetaceans); and (*ii*) decreased in groups that have lifestyles with reduced death rates: bats, primates, arboreal, fossorial, and desert rodents, bears, elephants, and rhinos. Convergent evolution of groups with similar lifestyles is common, so patterns of productivity across mammalian taxa reflect both ecology and phylogeny. The overall result is that groups with different lifestyles have parallel but offset relationships between production rate and body size. These results shed light on the evolution of the fast–slow life-history continuum, suggesting that variation occurs along two axes corresponding to body size and lifestyle.

allometry | production rate | metabolic ecology | fast-slow

Life history attributes vary with body size (1–3). Small organisms typically are highly productive, live fast, and die young (4). Mass-specific rates of metabolism and production scale as

$$R = R_1 M^{-b},\qquad [1]$$

where R_1 is a normalization constant, M is body mass, and b is an exponent that is generally between 1/4 and 1/3 in mammals (e.g., refs. 5–8). When data for production rates of mammals are plotted on logarithmic axes (Fig. 1*A*), the general scaling relationship predicted by Eq. **1** is observed, but some groups, such as bats, primates, artiodactyls, and whales, contribute substantial variation by having rates consistently lower or higher than the majority. More generally, certain taxonomic and functional groups can be characterized by having normalization constants for mass-specific life-history traits that apparently reflect adaptive changes during the evolutionary history of lineages. Here we interpret these divergences in terms of natural selection. We begin by deriving predictions for how mammals are expected to evolve if subject to a size-dependent constraint on production. These predictions are then tested by using the largest available data set on the life-history attributes of the eutherian mammals.

Theory of Evolution Under a Production Constraint

Life-history evolution is subject to a fundamental size-dependent constraint (9). This constraint limits the rate at which biomass can be produced so that production per unit body mass (termed specific production rate hereafter) is inevitably slower

in larger organisms than in smaller ones. The constraint is thought to be the result of limitations on the ways bodies can be designed (4, 10, 11). Because their specific production rate is higher, smaller animals produce offspring faster than larger ones and so would always be selected if all sizes had the same death rates. However, there are situations in which larger body size is advantageous (9), and this has allowed the evolution of larger body sizes, which has been a general trend in the evolution of the mammals [Cope's rule (12)].

Within this general framework, some evolutionary changes to body design and production rate are possible. How do these come about? Natural selection favors heritable innovations that increase birth rates and decrease death rates (9). The outcome of such an adaptive innovation would be the evolution of a population with a substantially higher or lower normalization constant but a similar exponent, b, for the allometry of mass-specific production rate in Eq. **1**. On the one hand, birth rates directly depend on rates of biomass production, so they may be increased by adaptations to exploit more abundant or reliable food resources. On the other hand, death rates can be reduced by adaptations that affect mortality either directly, or indirectly through changes in ecology. An example of the former would be the acquisition of defensive spines or armor. An example of the latter would be adoption of a volant, arboreal, or fossorial lifestyle, which has the effect of reducing susceptibility to the normal predators of surface-dwelling mammals.

We shall refer to a suite of functionally interrelated traits as a lifestyle. The lifestyle traits may be ecological attributes affecting birth rates through trophic relations or affecting death rates through risk of predation, together with anatomical and physiological attributes affecting resource allocation to fitness components (i.e., reproduction, growth, and survival). So, lifestyles and their associated life history attributes should reflect both the phylogenetic histories of lineages and the ecological conditions that shaped their adaptations.

If the above innovations in ecology or nutritional physiology are advantageous, they can give rise to a new adaptive radiation, with speciation and diversification in body size and other attributes to exploit the new lifestyle. Diversication of body size, however, will still be subject to the fundamental size-dependent production constraint described above.

Transient effects of adaptive changes that increase production or decrease mortality are increased fitness and population growth. After adaptive changes have occurred, though, birth and
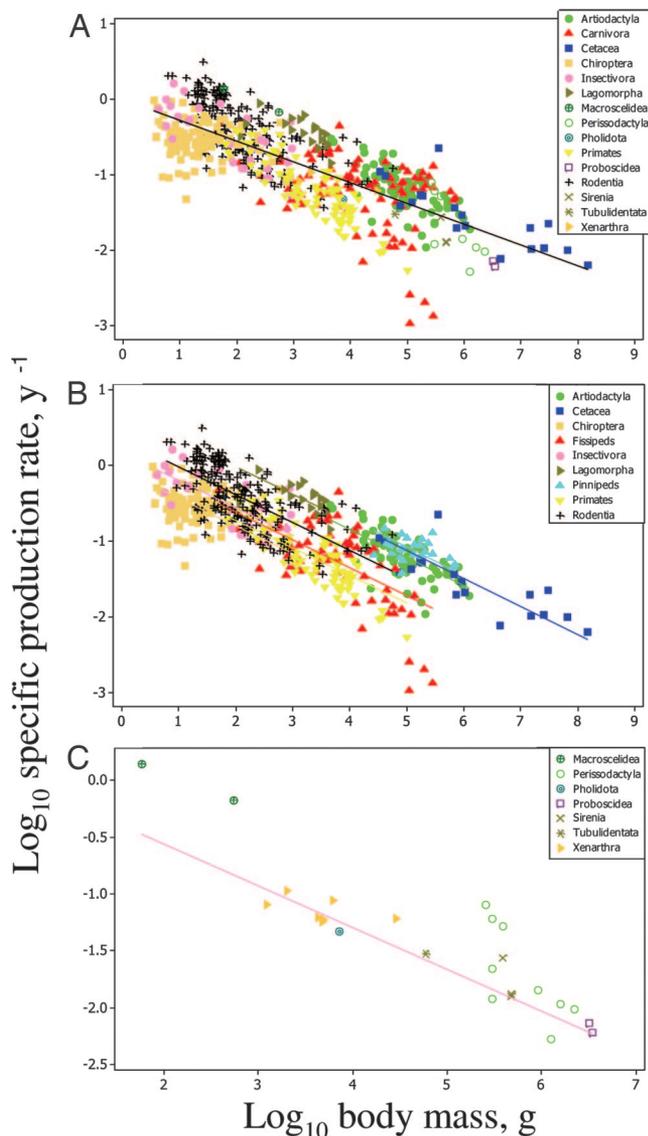
Fig. 1. Specific production rates of 637 mammal species as a function of body mass. (*A*) The whole data set, showing the different orders. (*B*) Plot for the species in orders with ≥10 data values. Symbols as in *A*, except that the Carnivora have been split into suborders Fissipedia (red triangles) and Pinnipedia (blue triangles) (compare Fig. 3*B*). The lines are fitted by GLM so as to have the same slopes, and they are color-coded according to taxon. (*C*) Plot for the species in the orders not shown in *B*. Symbols are as in *A*. The pink line, shown for purposes of comparison, is for Insectivora (see text).

death rates are adjusted by "ecological compensation" (13, 14), so that population growth rate returns to zero. The mechanisms by which this occurs are the subject of population ecology (see, e.g., ref. 15) and do not concern us here. However, it is important for our arguments that ecological compensation does not negate the initial adaptive changes in vital rates. This assumption is valid if the adaptive change in lifestyle permanently changes either production or mortality rate, and then the ecological compensation subsequently adjusts the opposing rate so that the population growth rate returns to zero.

Here we provide a quantitative analysis and adaptive interpretation of the allometric scaling of mass-specific production in eutherian mammals. Based on the above theory and ref. 9, we make the following specific predictions:

1. Allometric equations fitted to mammals grouped by lifestyle will have generally similar slopes but may have different normalization constants. The regressions for certain groups will be displaced from each other as predicted below.

2. Insectivores will exhibit intermediate relationships. This is because they include the most ancient surviving eutherian mammal lineage, and most representatives retain primitive traits of the ancestral stocks from which other eutherian groups have evolved. Consequently, insectivores can be viewed as a baseline from which to assess the adaptive displacements of other groups, toward both higher and lower production rates, as discussed below. Fissiped carnivores should have similarly intermediate production rates, because most representatives are relatively unspecialized flesh eaters of generalized body form.

3. Compared with insectivores, grazing and browsing herbivores should have higher normalizations, resulting in higher production rates than most other mammals of comparable size. This is because the various morphological, physiological, and ecological adaptations that allowed these mammals to acquire, ingest, and digest green vegetation gave access to an abundant and generally reliable food resource that could fuel high rates of production.

4. Similarly, marine mammals should have high rates of production, because invasion of the marine realm made available abundant, reliable, high-quality food resources in the form of fish and invertebrates. Normalizations for pinniped carnivores (seals, sea lions, and walruses) and both odontocete (toothed) and mysticete (baleen) whales should be substantially higher than those for the baseline insectivores and the terrestrial carnivores.

5. Groups that have been able to lower death rates by adopting habits and invading habitats where predation is low should have relatively low production rates as a result of ecological compensation (13, 14). The reasoning here is that a major innovation affecting life history evolution was a shift to a lifestyle or environment that reduced predation. Specifically, at least five functional groups are predicted to have lower normalization constants than the baseline: (*i*) flying bats; (*ii*) arboreal mammals, including primates and arboreal squirrels; (*iii*) fossorial forms, including moles among the insectivores and among the rodents, several different clades that are fossorial and spend the vast majority of their lives in burrows below ground; (*iv*) several different lineages of desert-dwelling rodents, especially those that have evolved enlarged ears or bipedal locomotion to detect and avoid predators (16–18); and (*v*) very large mammals, including megaherbivores and bears, which have escaped most predators by virtue of their size.

6. Predictions may be complicated when the above factors tending to increase and decrease production rates are offsetting. So, for example, sloths might be expected to have high rates, because they are folivorous and low rates because they are arboreal, and rhinos and elephants might be expected to have high rates because they are folivorous but low ones because they have reduced predation by evolving extremely large body size. In such cases, the observed production rates might be expected to be somewhat intermediate, lower than those of other folivores but higher than those expected just on the basis of the reduced mortality alone.

7. The observed relationships will be better explained, and the predictions will be better supported when the data are analyzed by lifestyle as well as by phylogeny. This follows directly from the assumption that the shifts in normalization constants reflect adaptive life history evolution. So adaptation of different lineages to similar ecological regimes are predicted to result in convergent life history evolution. For example, we predict that arboreal squirrels and the multiple clades of rodents that have independently evolved fossorial

Table 1. Descriptive statistics and allometric relationships for the principal taxonomic groupings referred to in the text

	No. of species	Median body mass, g	Minimum body mass, g	Maximum body mass, g	Normalization constant at 1 g	± SE	Slope (regression coefficient)	±SE
Mammalia	612	483	4	149,000,000	0.007	0.031	−0.275	0.009
Artiodactyla	75	71,500	4,550	1,258,333	0.610	0.041	−0.364	0.048
Carnivora	96	12,025	50	716,667			−0.212	0.048
Fissipedia	71	4,500	50	286,367	0.103	0.034	−0.461	0.059
Pinnipedia	25	101,250	27,000	716,667	0.750	0.059	−0.116	0.075
Cetacea	18	813,000	32,500	149,000,000	0.696	0.076	−0.301	0.053
Chiroptera	105	17	4	888	−0.069	0.048	−0.085	0.045
Insectivora	28	102	4	957	0.170	0.058	−0.361	0.066
Lagomorpha	19	2,121	115	4,506	0.713	0.060	−0.208	0.076
Perissodactyla	9	384,000	257,000	2,233,333	0.420	0.108	−0.823	0.280
Primates	81	3,495	66	101,386	0.005	0.032	−0.506	0.034
Rodentia	190	97	6	55,000	0.337	0.034	−0.378	0.032

The normalization constants and and regression coefficients (slopes) for the class Mammalia, in the top row, were obtained by regression. The other normalization constants were obtained by GLM fitting lines of common slope to the data in Fig. 1B. The consensus slope of these fitted lines was −0.366 ± 0.017. The slopes in the penultimate column were obtained by separate regressions.

and desert-dwelling lifestyles will have lower production rates than more closely related rodents in other functional groups. The same logic can be applied to make and test finer predictions or to explain individual species or genera that are obvious outliers. For example, is the sea otter more productive than terrestrial mustelid carnivores of comparable size? Do the highly arboreal dormice (family Myoxidae) have production rates that are more similar to those of arboreal squirrels than to related myomorph rodents?

Results

Mass-specific production rate is plotted against adult body mass on log scales for all 637 species in Fig. 1A. The different orders are color-coded. It is immediately apparent that specific production rate declines with adult body mass, and the data can be fitted with an allometric scaling relation of the form of Eq. **1**, which gives specific production rate = $0.98 M^{-0.28}$. This accords with the hypothesis of a general metabolic constraint because of body size acting on mammalian life history (4). The slope of the fitted regression line, −0.28 ± 0.01 (SE), is intermediate between the theoretically predicted values of −1/4 and −1/3 (4, 8) but closer to the former. It is also apparent that there is a variation of >1 order of magnitude among species of the same body size. Indeed, the fitted regression accounts for only 59% of the variation (R^2_{adj}), which is not large considering that the variation in body mass spans ≈8 orders of magnitude. As shown by the clustering of the values for different orders, this variation is not randomly distributed but related in systematic ways to the different taxonomic and functional groups.

We now analyze this variation in the context of evaluating the above predictions:

1. Allometric equations fitted to different taxonomic or lifestyle groups of mammals have generally similar slopes but different normalization constants. This was tested by using the General Linear Model (GLM) to fit lines of common slope to the different taxa (Fig. 1B; the residuals were normally distributed). The prediction of similar slopes was generally supported, accounting for 72.1% of the variation in the data (R^2_{adj}). This rises by only 1.7% if the slopes are allowed to vary, although this is statistically significant ($F_{8,594} = 6.1$, $P < 0.001$). Primates had a steeper slope than the consensus (−0.51), whereas chiroptera, pinnipeds, and lagomorpha had shallower slopes (−0.09, −0.12, and −0.21, respectively; Table 1). The consensus slope was −0.37 ± SE 0.017. This is greater than the theoretically predicted value of −1/4 ($z = 7.1$,

$P < 0.001$) but not significantly different from −1/3 (4, 8). The prediction of different normalization constants is supported qualitatively by observing that the parallel lines fitted to the taxa in Fig. 1B are often widely separated. This is quantified in Fig. 2 and Table 1, which show that the normalization constants, calculated by fitting lines of common slope to the data of Fig. 1B, vary by almost 1 order of magnitude, from −0.1 for chiroptera to 0.7–0.8 for lagomorphs, pinnipeds, and cetaceans. To control for lack of independence among species, we repeated these analyses using genus and family means and found similar relationships. The consensus slopes were −0.33 ± SE 0.02 and −0.28 ± SE 0.04 using genus and family means, respectively. The conclusions about normalization
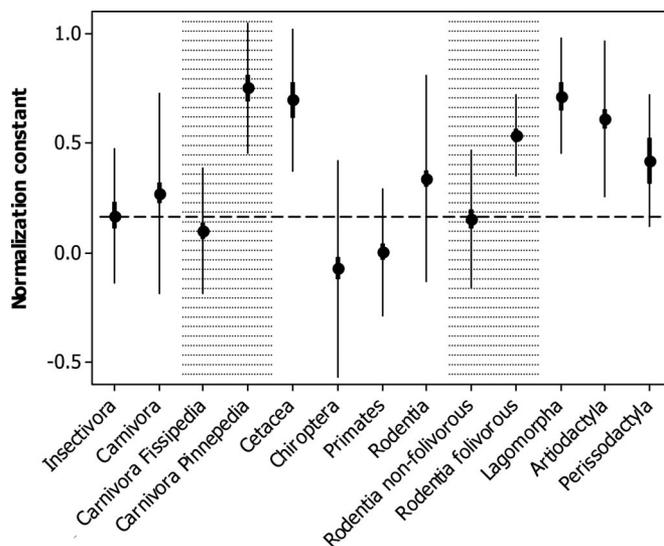
Fig. 2. Normalization constants for the major taxonomic and lifestyle groupings [mean, SE (thick bars) and SD (thin bars)], obtained by using GLM to fit lines of common slope to the data in Fig. 1B. Normalization constants measure the vertical displacement of the regression lines (i.e., y intercepts) (see Table 1). SDs are presented to show the variation within each grouping (see text). The dashed horizontal line, shown for purposes of comparison, is the normalization constant for Insectivora. Symbols on shaded backgrounds depict subgroups of carnivores and rodents based on lifestyle. "Rodentia nonfolivorous" refers to rodents that are arboreal, fossorial, or desert dwelling (see SI Table 2 for classification).

Fig. 3. Specific production rate as a function of body mass for species grouped by lifestyle. Grazers and browsers (*A*); baleen and toothed whales and pinnipeds (*B*); terrestrial (fissiped) and marine (pinniped) carnivores (*C*); rodents (*D*); frugivorous and nectarivorous (green symbols) and insectivorous (black symbols) bats in the families containing more than five species (*E*). The Phyllostomidae, which include carnivorous, insectivorous, and fruit-eating species (http://animaldiversity.ummz.umich.edu), are not shown. The pink line shown in each image, for purposes of comparison, is for Insectivores. Some exceptional cases are highlighted: 1, crab-eating fox (*C. thous*); 2, African civet (*Civettictis civetta*); 3, sea otter (*E. lutris*); 4, African wild dog (*L. pictus*); 5, bears of the family Ursidae; 6, naked mole rat (*H. glaber*). See text for discussion.

constants also were little affected by using genus or family means [supporting information (SI) Fig. 5].

2. Insectivores and terrestrial carnivores exhibit intermediate relationships. This can be seen in Fig. 1*B*, where the pink and red regression lines of insectivores and fissiped carnivores have very similar slopes and normalizations. They are above the bat and primate lines but below those for most other groups (see also Table 1).

3. Grazing and browsing foliovores have higher production rates than most other mammals of comparable size. This prediction is supported by the data in Fig. 3*A*, which shows that almost all artiodactyls, lagomorphs, perissodactyls, and rodents lie

above the insectivore line. It is also apparent in the high normalization constants of the lagomorphs, artiodactyls and rodents in Fig. 2 and Table 1; all are above the insectivore line. Some of the rodents are arboreal or fossorial and others are not specialized foliage eaters, which increases the variation and lowers the normalization constant for the order Rodentia as a whole, as discussed below.

4. Marine mammals have high rates of production. This prediction is supported by the fact that data points for seals and sea lions and baleen and toothed whales all lie well above the insectivore line (Fig. 3*B*). The pinniped marine carnivores have some of the highest rates of all mammals and are more productive than their terrestrial fissiped relatives (Fig. 3*C*).

5. Groups that have adopted habits and invaded habitats where predation is low have low production rates; these groups include flying bats, arboreal mammals, such as primates, arboreal squirrels, and dormice, and fossorial mammals, such as moles, pocket gophers, and other subterranean rodents. This prediction is supported by Figs. 1*B* and 2 and Table 1, which show that bats and primates have the lowest productivity of the major groups, and by Fig. 3*D*, which shows that arboreal, fossorial, and desert rodents are less productive than their folivorous relatives. Fossorial moles, Family Talpidae, are only slightly and not significantly less productive than the other insectivores, but this may be confounded by the fact that some other insectivores possess traits (odors, spines, and aquatic) that may also confer protection from predation and hence low death rates. The largest bears (Family Ursidae) have production rates well below other fissiped carnivores (Fig. 3*C*).

6. When the factors tending to increase and decrease production rates are offsetting, the groups tend to have intermediate relationships, and to deviate from their closest relatives in the predicted direction. Thus megaherbivore elephants (Proboscidea) and rhinos (the largest Perissodactyls) have production rates considerably lower than most folivorous mammals (Figs. 1*C* and 3*A*). Insectivorous bats generally have lower production rates not only than terrestrial insectivores but also than frugivorous and nectarivorous bats (Fig. 3*E*). Arboreal folivorous sloths have lower production rates than most herbivore groups but not conspicuously lower than their xenarthran relatives, some of which, however (armadillos), are armored.

7. The patterns of production in eutherian mammals reflect the evolutionary influence of both ecology and phylogeny. Observed relationships are best explained and predictions most strongly supported when the data are analyzed by lifestyle (Fig. 2), which accounts for substantial variance in the normalization constants (40% in the carnivores, comparing fissipeds and pinnipeds, $F_{1,94} = 61.4$, $P < 0.001$; 38% in the rodents, comparing folivores with nonfolivores, $F_{1,108} = 67.1$, $P < 0.001$. Fig. 2 shows how variation at the order level is reduced substantially by separating the component functional groups (shown on shaded backgrounds). Life history adaptations associated with divergent lifestyles also appear to explain several data points for individual species that are outliers with respect to their relatives (see numbered points in Fig. 3). As predicted, the sea otter (*Enhydra lutris*) has a higher production rate than any of the 21 terrestrial mustelids. Perhaps similarly, the crab-eating fox (*Cerdocyon thous*) has a higher rate than any other canid. Other outliers call for explanation. The high rates of production of the naked mole rat (*Heterocephalus glaber*) and African wild dog (*Lycaon pictus*) suggest that "helpers" increase the productivity of the single reproductive female within a social group. Overall, it is apparent that production rates of species with divergent lifestyles are often quite different from their closest relatives

Fig. 4. The two major axes of the slow–fast life-history continuum, body mass, and lifestyle. To the well known axis of allometric variation due to body size, we have added a second orthogonal axis based on ecological lifestyle. Here the solid line represents an unspecialized ancestral condition, the dashed line depicts a more productive ''live fast die young'' lifestyle, and the dotted line shows a lifestyle with a lower death rate, slower life history, and consequently lower production.

and convergently similar to distantly related mammals with similar behaviors and ecologies.

Discussion

In general, the data for mammalian life histories support theoretically predicted relationships between rates of mass-specific production and lifestyle. Compared with the baseline set by generalized primitive terrestrial insectivores and carnivores or by their nearest relatives, groups that have specialized on abundant and reliable food sources (most notably grazing and browsing herbivores and marine mammals) have high production rates. Also, groups that have specialized in ways that reduce predation (most notably flying bats, arboreal primates, arboreal, fossorial, and desert rodents and the largest bears) have low production rates. These patterns are often deeply rooted in eutherian mammalian phylogeny, where they presumably reflect lifestyle innovations in ancient lineages. Evidence of convergent evolution reflecting ecological adaptations comes from two patterns (*i*) similar production rates in distantly related mammals that have adopted similar lifestyles, and (*ii*) divergent production rates in closely related mammals that have adopted divergent lifestyles.

These results shed light on the evolution of the fast–slow life-history continuum, suggesting the existence of a second major axis of variation, orthogonal to that of body size, as shown in Fig. 4. This new axis corresponds to variation in lifestyle. So animals that "live fast and die young" can be distinguished from those that live more slowly and die older in two ways. Living fast and dying young is a general property of smaller as opposed to larger animals. Within size classes, the groups that live faster and die younger are more productive (dashed line in Fig. 4). Those that live more slowly and die older have reduced death rates because of protection from predators and compensatingly lower production rates (dotted line). Together, the two axes accounted for 72% of the variation in production rate in the analysis of Fig. 1*B*. This suggests that the fast–slow continuum occurs in two dimensions, represented by the two axes of body size and lifestyle, in Fig. 4.

Future efforts to extend, evaluate, and synthesize life history and metabolic theory should consider constraints due not only to phylogenetic history but also to ecological factors. We have used the term "lifestyle" to characterize suites of interrelated ecological, physiological, and behavioral traits to evaluate preliminary hypotheses about how they have influenced the evolution of production. Because production and mortality must be

compensatory, our lifestyle axis of variation is similar, but inverse to the mortality axis identified by earlier workers (2, 3).

Despite the clarity of the patterns, they can be regarded as preliminary in the sense that there is much room for additional research, both theoretical and empirical. In particular, three issues deserve attention. First, a more explicit phylogenetic analysis should shed much light on the relationships between ecology and evolutionary history mentioned above. Second, there are significant variations among the allometric slopes of some taxa (Table 1). This could reflect the history of body size and life history evolution of divergent body sizes, suggesting hypotheses that could be tested by phylogenetic analysis. Third, it should be illuminating to explore more deeply the relationship between diet, metabolism, and life history in the light of other studies that have pointed out relationships between these attributes but given them somewhat different but not necessarily conflicting interpretations (e.g., refs. 19–25). Notable among these is McNab's analysis of associations between food habits and energetics in placental mammals (21), although this has been criticized for confounding dietary with phylogenetic effects (25, 26). McNab concluded that in animals of the same food habit metabolic rate scales as $M^{0.75}$, but arboreal species had lower normalizations than terrestrial ones, and burrows and predator defenses of large invertebrate-eating predators were associated with lower normalizations. He also found that among vertebrate- and invertebrate-eating mammals, aquatic species had relatively high metabolic rates, which he attributed to the need to maintain body temperature. Given the close association between rates of metabolism and production, these patterns agree with those reported here. However, there are also differences. Our preliminary hypothesis for the relationship between diet, metabolism, and production is that high rates of energy acquisition and mass-specific metabolism are required to fuel high rates of production. However, low mass-specific metabolic rates are not always associated with lower production, because death rates can be reduced by adaptations, such as ones that reduce predation, that do not much affect metabolic rates. So, for example, multiple lineages of fossorial and desert rodents have unusually low metabolic rates (27–29), whereas volant bats and arboreal rodents and primates do not (7, 30, 31). Further work on food availability and dietary quality is also required, but care must be taken to avoid circularity in characterizing food availability and quality (32).

More generally, the theory and data presented here suggest exciting possibilities for integrating physiology and life history, ecology and evolution. The life history evolves in response to both intrinsic physiological and extrinsic environmental factors that affect birth and death rates. Birth rates are affected by the availability of food resources in the environment, and the rate at which these resources can be ingested, assimilated, and allocated to reproduction. Death rates are affected proximally primarily by predation, but predation risk depends ultimately on many traits and tradeoffs associated with lifestyle and habitat. Exploration of these relationships should contribute to the further synthesis of metabolic and life-history theories.

Materials and Methods

We made preliminary tests of the predictions using recent compilations of mammalian life history data for placental non-volant mammals (33) (www.esapubs.org/archive/ecol/E084/093/default.htm) and for Chiroptera by K. E. Jones (personal communication). The data sets record litter size, litters per year, neonate and weaning masses, and adult body mass. We considered two possible methods of estimating production rate: mass of neonate tissue produced per female per year or mass of weanling tissue produced per female per year. Ideally, the latter method would use the number of offspring weaned as one of the variables in the calculation, but this information is hard to obtain

and is not in the database, so the only option would be to use litter size as a surrogate. Because the ratio of neonate to weanling mass does not vary with the logarithm of body mass (GLM taking account of the taxonomic groups in Fig. 1B, $F_{1,149} = 1.78$, nonsignificant) and differs only from 0.10 to 0.30 among lifestyle groups, calculating production rates by the two methods and using litter size gives similar results, as shown in SI Fig. 6 (compare Fig. 1B). We used the neonate method for calculating production rates in this article because there were many more measurements of neonate mass than of weaning mass, measurements of weaning mass were imprecise, and no data on the sizes of litters actually weaned.

Therefore, production rate was estimated here as the mass of neonate tissue produced per adult female per year, and this was calculated as the product of litter size, litters per year, and neonate mass. The units are grams per year. This value was divided by adult body mass in grams to obtain mass-specific production rate, in units of y^{-1}. Values were calculated for 637 species, representing 374 genera, 94 families, and 15 orders, for which data on litter size, litters per year, neonate mass, and adult body size were available. Our analysis does not include monotremes or marsupials, which are long-divergent lineages with dramatically different reproductive biologies, egg-laying and pouch-rearing, respectively. Data manipulation and statistical analyses were performed by using Minitab 14.1 (Minitab, State College, PA)

We analyzed the data by using the level of taxonomy that seemed most appropriate. Only 8 orders, Artiodactyla, Carnivora, Cetacea, Chiroptera, Insectivora, Lagomorpha, Primates, and Rodentia, contained ≥ 10 species, and these were analyzed separately. We also singled out particular taxonomic (e.g., suborder or families) or functional groups (e.g., arboreal or fossorial rodents) for focused comparisons where appropriate. We followed the taxonomic classification of Wilson Reader (34), which is a relatively recent reorganization that incorporates modern phylogenetic information.

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