CHAPTER ONE

Basic Concepts: Budgets, Allometry, Temperature, and the Imprint of History

SEVERAL COMMON THEMES permeate the field of physiological ecology. Because little can be done in our discipline without touching on them, and because these themes serve as organizing principles later in the book, we devote this chapter to them. It can be read as a guide to the conceptual tools and questions that make animal physiological ecology a coherent field. These conceptual tools and questions also link physiological ecology with ecology at large and make the research that we do with organisms relevant for those who study populations, ecosystems, and the biosphere. Although physiological ecologists quantify the magnitude of a plethora of seemingly disparate traits, we believe that most of these traits can be characterized generally as pools, rates, fluxes, and efficiencies. We begin this chapter by describing how pools, rates, fluxes, and efficiencies can be integrated within the framework of biological budgets. The remaining portion of the chapter is devoted to characterizing how physiological ecologists investigate some of the most important factors that shape physiological traits (or biological budget elements, if you wish) and their variation within and among species. We use the metabolic rate to exemplify the effect of body size and temperature on a trait, and as a trait that is shaped by factors at a variety of time scales. We conclude the chapter by discussing why the evolutionary history of both species and traits needs to be taken into account in comparative studies.

1.1 The Input/Output Budget: A Key Conceptual Framework

A powerful method for organizing a physiological ecology study is to construct a budget. A budget is a detailed accounting of the input and output of energy, or the mass of some substance through an individual, a population, and even an ecosystem (figure 1.1). A budget is not simply an accounting device but a tool that can be used to predict the magnitude of both inputs and outputs. An animal's requirements for energy, nutrients, and water can be predicted from knowledge of minimum obligatory loss rates and from assimilation efficiencies. Perhaps more significantly, budgets can have significant value in ecology because they can allow us to identify limiting factors to the fluxes of energy and materials through organisms. Also, because one organism's waste is another organism's bounty (chapter 10), knowledge about fluxes allows us to find out not only how much of a given resource animals need, but also how much they generate for other creatures. Budgets are important because they specify some of the key physiological questions that are important for ecologists: What are the rates of input and output of energy or matter? What are the efficiencies with which animals assimilate nutrients and energy? What are the patterns of allocation into different parts and functions? And what are the physiological mechanisms that regulate or limit the supply of or demand for energy and materials?

A fundamental reason for the importance of budgets for biologists is that the conservation law for mass and energy is one of the few hard laws that we have available (Kooijman 2000). Equally compelling is the practical utility of

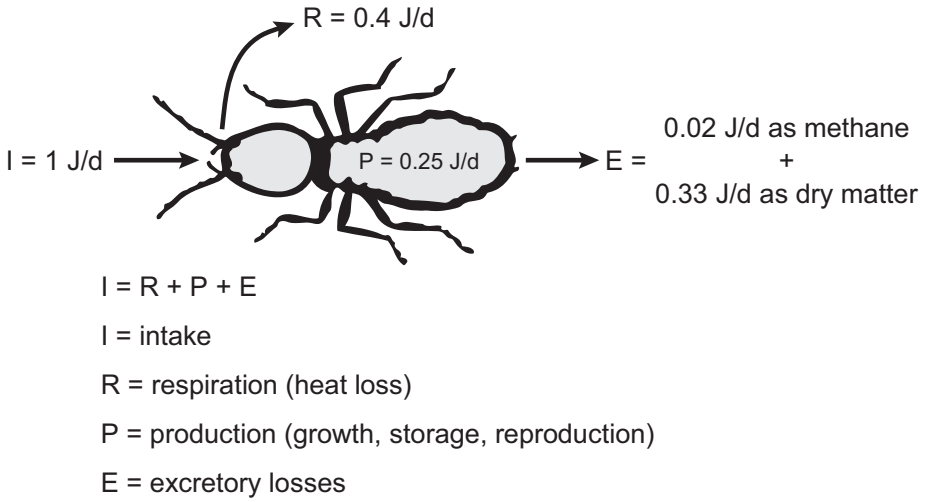

Figure 1.1. A simple input/output budget for energy in a termite. The primary input is chemical potential energy in the food (I). The primary outputs include both chemical potential energy in excretory wastes (E) and new tissue produced (P), and heat evolved during respiration (R). Note that, of the total energy ingested only a fraction is assimilated, and of the fraction assimilated only a fraction is used in catabolic processes (R) or anabolic processes (P). Energy or material budgets can be used to estimate the ecological impacts of animals, such as this 3.5 mg termite. Based on these numbers, one estimates that in a savanna ecosystem in Western Africa with 4000 termites per square meter, termites breakdown 77 g wood per meter per year or at least 15% of the woody litter, and produce 48 mmol methane gas per year per square meter. Methane, a product of microbial fermentation in the termite, is one of the principal greenhouse gases, and termites worldwide may account for up to 15% of total production. (Based on data in Wood and Sands 1978 and Bignell et al. 1997.)

the approach. Budgets allow us to construct models that link mass and energy flow in individuals to population, community, and life history phenomena. Although we will emphasize individual organisms in this chapter, the same principles apply to collections of them. For example, budgets allow quantification of the flow of toxicants through ecosystems (Cairns and Niederlehner 1996), and plant physiological ecologists use community level budgets to estimate the impact of plant communities and animal communities on the composition of the atmosphere (Griffiths 1997). Budgets are one of the tools that allow physiological ecologists to scale up their measurements from individuals to the biosphere (Van Gordingen et al. 1997).

1.1.1 Pools, Fluxes, and Residence Times

The input/output format of a budget is straightforward and should be intuitive to anyone who handles a bank account. The size of the pool is the capital and the inputs and outputs are profits and expenditures, respectively. An expression for the flow of chemical potential energy through an invertebrate, for example, might include an energy input rate for feeding and energy output rates for digestive wastes, heat, and new tissue (e.g., progeny, figure 1.1). The chemical potential energy in food, digestive wastes, and new tissue is measured by bomb calorimetry, whereas the heat produced is typically measured by respirometry, which is also called indirect calorimetry (box 1.1). Although we will use the term "metabolic rate" as shorthand for the rate at which an animal catabolizes organic materials (usually aerobically) to generate energy, this term is strictly incorrect. Catabolism (breakdown) and anabolism (synthesis) collectively constitute metabolism. Perhaps we should use the term "respiration rate" instead. However, the term metabolic rate is so firmly entrenched that attempting to dislodge it probably confuses more than it enlightens.

The first law of thermodynamics, the conservation law for energy, requires that the rate of energy input equal the sum of the rates of outputs. A budget, or a balance equation, is an arithmetic expression of this principle (figure 1.1). Knowledge about the flow of materials through a system is necessary in the construction of a budget, but it is not sufficient. One must also know the sizes of the pools of energy and materials in an organism.

The change in the size of a pool of energy or material in an animal is an immediate consequence of the balance between inputs and outputs:

$$\frac{d\,(\text{size of the pool})}{dt} = \text{input rate} - \text{output rate}. \tag{1.1}$$

Box 1.1 Respirometry: The Measure of Heat Production Based on Oxygen Consumption and/or Carbon Dioxide Production

The reason oxygen or carbon dioxide can be used to measure heat production is because we understand the stoichiometry of catabolic reactions and therefore we can relate gas exchange directly to heat production. To illustrate this, consider the stoichiometry of the oxidation of 1 mole of palmitic acid—a fatty acid common in vertebrates:

$$CH_3(CH_2)_{14}COOH + 23\ O_2 \rightarrow 16\ CO_2 + 16\ H_2O$$

reaction's heat of combustion = 10,040 kJ

reaction consumes O_2 and produces CO_2

(23 moles O_2) × (22.4 liters O_2/mole at 760 torr and O^oC) = 515 liters O_2 STP

(16 moles CO_2) × (22.4 liters/mole) = 358 liters CO_2 STP

Therefore, 10,040/515 = 19.5 kJ/liter O_2

10,040/358 = 28.0 kJ/liter CO_2

Consult table 1.1 for average values of heat produced per gram of substrate and unit gas exchanged for each substrate.

TABLE 1.1
Average values of heat produced per gram of substrate and per unit gas exchanged for each substrate

Substrate	*kJ/g substrate*	*kJ/liter O_2*	*kJ/liter CO_2*	$RQ = \frac{CO_2\ formed}{O_2\ consumed}$
Carbohydrate	16.9	20.9	20.9	1.00
Fat	39.5	19.7	27.7	0.71
Protein (urea as end product)	23.6 (18.0)[a]	18.8[b]	23.1[b]	0.81[b]
Protein (uric acid as end product)	23.6 (17.76)[a]	18.4[b]	24.8[b]	0.74[b]

The last column in the table gives the respiratory quotient (RQ) which is the ratio of CO_2 produced to O_2 consumed. This can usually tell the investigator what fuel is being oxidized.

[a] The energy value per g for the average protein measured in a bomb calorimeter is about 23.6 kJ/g (Robbins 1993). However, protein's energy value to the animal depends on the excretion product of the animal because urea and uric acid have different combustible energy values which are subtracted from the combustion value of protein (see chapter 7 also).

[b] The energy value per unit gas for protein depends on the excretion product of the animal because urea and uric acid have different combustible energy values which are subtracted from the combustion value of protein.

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Notice that the range in kJ/liter O_2 is very small; a value of 19.7 kJ/liter is customarily used and this results in an error of only 7% in the estimation of heat production. In contrast, kJ/liter CO_2 varies quite a bit with metabolic substrate. Therefore, the calculation of heat production from CO_2 production requires knowledge of the substrates being catabolized.

How is gas exchange actually measured? Aquatic animals are kept in closed containers of water, and the concentration of dissolved O_2 is periodically measured. Terrestrial animals are kept in closed containers and the concentration of O_2 and/or CO_2 in the air is measured, or air is pumped through the container and its flow rate and the change in O_2 and/or CO_2 between inflow and outflow are measured. It is even possible now to measure CO_2 and hence heat produced by free living animals by measuring the turnover of isotopes of oxygen and hydrogen. This method, called the doubly labeled water method, is described in chapter 13.

For example, an animal's body water is the result of the dynamic equilibrium between the rate at which water is gained by ingestion (in food and by drinking) and metabolic production and the rate at which it is lost by evaporation and in saliva, urine, and feces (chapter 12). For nongrowing animals, one can often make the assumption that the size of a given pool is in steady state. This assumption, together with the assumption that the "contents" of the pool are well mixed, allows establishing some useful equalities. At steady state the flow rate into the pool equals the flow rate out of the pool. You will find that some scientists call these rates the "fluxes" in and out of the pool. These fluxes equal the size of the pool divided by the average residence time of the material in the pool:

$$\text{input rate} = \text{output rate} = \frac{\text{size of the pool}}{\text{average residence time}} \tag{1.2}$$

Note that the reciprocal of residence time is the fraction of materials in the pool that turns over per unit time. This fractional turnover rate (or rate constant) plays a very important role in physiological ecology.

The ingredients of equations 1.1 and 1.2 summarize much of what physiological ecologists do. As we will see, a physiological ecologist interested in measuring the field metabolic rate of an animal needs to measure the animal's body water and the fractional turnover of two components in this pool: oxygen and hydrogen (see chapter 13). An ecotoxicologist interested in determining

the output rate of a toxicant into an animal may need to measure the amount of toxicant in an animal (the pool) and its residence time (see chapter 9). Note that ecologists of a variety of persuasions also tend to think in terms of pools, rates, and fluxes. For example, a population ecologist can visualize a population as consisting of a pool of individuals. The birth, death, immigration, and emigration rates are the determinants of the input and output fluxes into and from the population. In a similar fashion, ecosystem ecologists spend a lot of time measuring the pools, fluxes, and residence times of energy and materials in ecosystems. If you are an ecologist, or would like to become one, then it is a good idea to become thoroughly familiar with the basic mathematics of pools, fluxes, and residence times. In box 1.2 we provide a basic introduction. Harte's (1985) wonderful little book *Consider a spherical cow* gives a more detailed account.

Box 1.2 Pools, Fluxes, and Residence Times

Imagine for a moment that your favorite organism is a well-mixed container full of a material that you are interested in (carbon, nitrogen, calcium, etc.). To keep things simple, let us assume that the amount (A) of this material in the organism is neither growing nor shrinking ($dA/dt = 0$). Let us denote by ρ_{in} and ρ_{out} the fractional rates at which the material enters and leaves the pool. At steady state, $\rho_{in} = \rho_{out} = \rho$. We have used the word "fractional" when referring to ρ_{in} and ρ_{out} because these numbers represent the fraction of A that gets in and out of the organism per unit time. Therefore, the units of ρ are time^{-1}. The fluxes of the material in and out of the organism are F_{in} and F_{out} and equal $F_{in} = \rho_{in} \cdot A$ and $F_{out} = \rho_{out} A$, respectively. The average time that it takes to fill up the pool of material in the organism (τ) must satisfy the following equation: $F = \rho \cdot A = A/\tau$. Therefore, $\tau = \rho^{-1}$. If the material within the organism represents a well-mixed pool, then we can say a good deal more about τ.

In a well-mixed pool of material, the time that each molecule stays in the organism is distributed as a negative exponential. That is, the probability density function of the age (x) of the molecules found in the pool at any given time is given by

$$f(x) = \rho e^{-\rho t} \qquad (1.2.1)$$

Equation 1.2.1 implies that the expectation for the time that a molecule stays in the organism (or pool) equals $\tau = 1/\rho$, which is why the reciprocal of the fractional input rate is called the "average residence time". The variance in residence time (or age) of the molecules in the pool is given by $\sigma^2 = 1/\rho^2$. You will often find that people use the "half-life" ($\tau_{1/2} = \ln(2)/\rho = 0.69/\rho$)

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instead of the average residence time to characterize how long molecules stay in the pool. The half-life estimates the median of the distribution of residence times, or ages, of molecules in the pool. Thus, 50% of all molecules stay in the pool for less than $\tau_{1/2}$ and 50% of the molecules stay longer. Because the negative exponential density function is asymmetrical and skewed to the left $\tau_{1/2}$ is smaller than τ. The theory that we have outlined here applies to well-mixed pools in which all the material is in a single compartment. These systems are referred to as having "one-compartment, first-order kinetics." Many physiologically and ecologically important systems satisfy these assumptions, or are close enough to satisfying them for the theory to apply reasonably well. We will apply this theory in chapter 4, when we talk about guts as chemical reactors, in chapter 8 when we discuss how the isotopic signature of a diet is incorporated into an animal's tissues, and in chapters 9, 12, and 13, when we describe how we measure toxicant and water turnover and the doubly labeled water method to estimate metabolic expenditure. In chapter 4 (box 4.2) we describe how you can use appropriate markers to estimate ρ. If probability density distributions intimidate you (or if you have no idea what they are), we strongly recommend that you read the first four chapters of the very nice introduction to probability theory for biologists by Denny and Gaines (2000).

Pool sizes and turnover or residence times vary within and among species with body size in a somewhat predictable pattern. Allometry is the term that refers to these patterns of change in some parameter with change in body size. In a subsequent section of this chapter we will examine allometry in some detail.

1.1.2 Efficiency

A useful metric that allows interpretation of the elements of a budget is efficiency. Efficiency is a ratio that describes the magnitude of one of the outputs relative to an input. All the inputs and outputs within a budget or balance equation must have the same units, and therefore efficiencies are either unitless proportions, or expressed as percentages if multiplied by 100. Throughout this book we will describe several efficiency indices that we believe are useful. Here we emphasize digestive efficiency only because it illustrates how the budget for a whole organism can be profitably viewed as made up of the combination of

budgets of several subsystems. We will reexamine digestive efficiency in more detail in chapter 3.

The input/output format can be applied at different levels of a system or organism. Within the main system in figure 1.1, for example, one can specify several subsystems, each of which can have its associated subbudget. These subsystems allow the tracking of the flow of energy and materials through an animal, and hence allow the dissection of patterns of resource allocation (figure 1.1). For example, in a slightly more detailed view of the fate of ingested energy, we can define first a subsystem that represents the gastrointestinal tract (GIT). The input to it is food intake in kJ/d. Outputs include energy losses in feces plus an output representing the energy in kJ/d absorbed and retained in the animal, which is called digestible energy. With this framework we can define the apparent digestive efficiency of one of the components of an animal's diet as the ratio between output rate and input rate in the GIT. We will define digestive efficiency more rigorously and discuss why we call this digestibility "apparent" in chapter 3. Briefly, digestive efficiency is interesting to ecologists because a low efficiency translates into more time and effort spent collecting food to meet a fixed required net input: The animal retains a small fraction of the nutrients that it ingests. Furthermore, if food intake rate is fixed, for example if the gut's volume imposes limitations on the maximal amount that can be processed, then low digestive efficiency translates into less matter and energy available for maintenance, growth, and reproduction.

1.2 The Importance of Size: Scaling of Physiological and Ecological Traits

There are at least ten million kinds of organisms on earth and most of these have not yet been named, let alone studied. It is impractical to study the biology of all these kinds of animals; a selective sample may (and perhaps must) suffice. Are there any features of organisms that allow us to generalize from a few to the many? Although the diversity of life varies along a very large number of axes, body size is particularly important. From bacteria ($\approx 10^{-13}$ g) to whales (10^{8} g), organisms vary in body weight by more than 21 orders of magnitude. This astounding variation led Brown and colleagues to assert that "biological diversity is largely a matter of size" (Brown et al. 2000). Body size influences virtually all aspects of an organism's structure and function. To a large extent, body size also shapes an organism's role in biological communities and ecosystems. The importance of body size for biology led Bartholomew (1981) to exclaim "the most important attribute of an animal, both physiologically and ecologically,

is its size." This section links body size with the budget framework that we outlined at the beginning of the chapter. We describe how many traits (including pool sizes and turnover or residence times) vary with body size in a predictable fashion both within and among species.

The predictability of the relationship between body size and an organism's traits is fundamentally useful because it allows us to summarize and compare data. It also permits us to make educated guesses about an organism's biology simply from its size. The term that refers to these patterns of change in some parameter with change in body size is allometry. In this section we use the metabolic rate as an example of one of the many important biological rates determined "allometrically" by body size. Researchers have made thousands of measurements of metabolic rates of animals under standardized conditions. For endotherms such as mammals and birds, for whom the measurement is often called the basal metabolic rate (BMR), those conditions include a resting, fasted state, and an air temperature in the so-called thermal neutral zone where metabolism is not increased for body temperature regulation (figure 1.2 and box 1.3 explain the terms used by physiologists to characterize the thermal biology of organisms). For ectotherms such as reptiles, amphibians, fish, and arthropods, the measurement is typically called the standard metabolic rate (SMR); the conditions also include a resting, fasted state, but the temperature of the measurement is specified (e.g., SMR at 30°C). Figure 1.2 should convince you why it is fundamentally important to report the temperature at which the metabolic rate was measured. Using mammals for our illustration, and ground squirrels particularly, the BMR of a marmot (1.546 L O_2/h, or 30.5 kJ/h) is greater than that of a least chipmunk (0.073 L O_2/h or 1.43 kJ/h) by 21 times, which is not as large a factor as their absolute difference in size (respectively, 4.3 kg versus 46 g, or 93 times).

If we plot whole-organism metabolic rate of mammals as a function of body mass on arithmetic axes we find that this relationship rises in a decelerating fashion. Actually, we might not see much of a relationship in certain data sets if there are many data in the small-size categories and few in the large-size category. Sometimes, physiologists "standardize" metabolic rate by body mass and call this measurement the mass-specific metabolic rate. If you plot mass-specific metabolic rate against body mass you will find a decreasing relationship. We will see why in a moment. When you plot whole-animal metabolism against body mass in a double-logarithmic plot the increasing trend is obvious and the relationship appears linear (figure 1.3). The relationship between metabolic rate (B) and body mass (m_b) appears to be well described by a power function of the form

$$B = a(m_b)^b \tag{1.3}$$

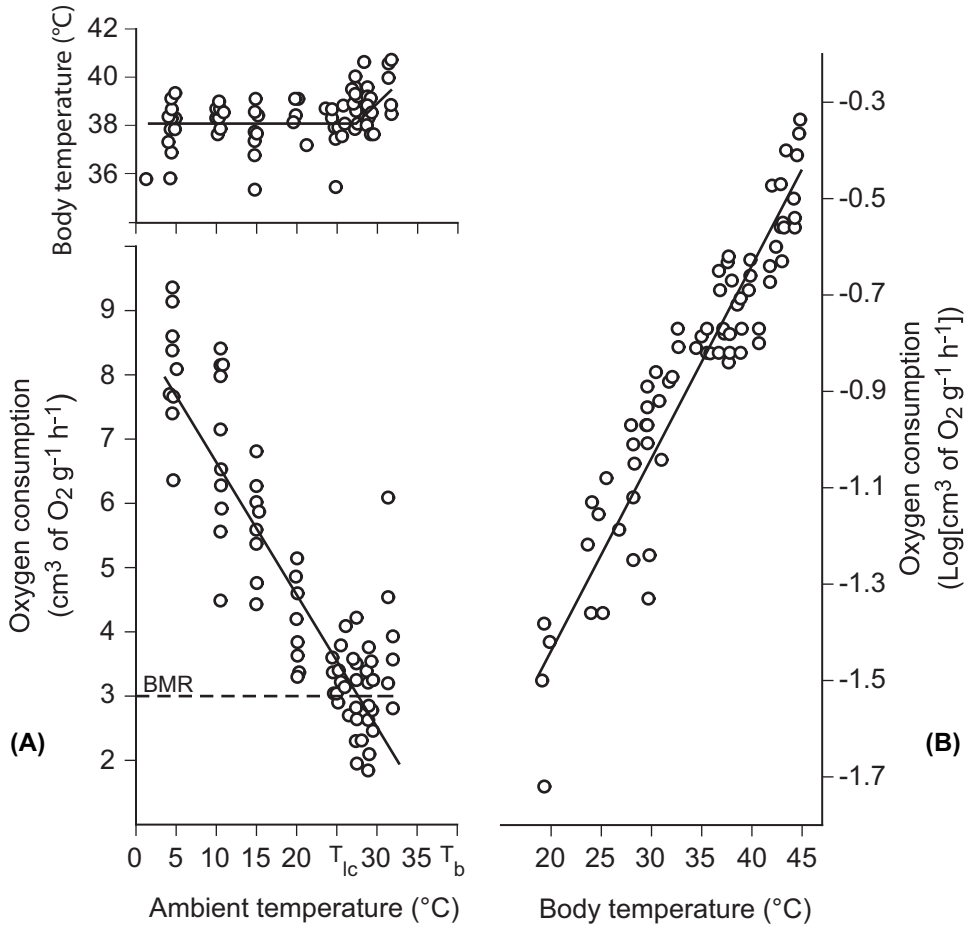

Figure 1.2. Endothermic homeotherms, like the heather vole (*Phenacomys intermedius*) maintain a constant body temperature by matching heat losses with metabolic heat production. The Scholander-Irving model shown in panel A describes the relationship between the metabolic energy production needed by an animal to maintain a constant core body temperature (T_b) and ambient temperature (T_a). Metabolic rate is measured by $\dot{V}O_2$, the rate of oxygen consumption. The slope in panel A, which has units of $cm^3\ g^{-1}\ h^{-1}\ {}^{o}C^{-1}$, is sometimes called "thermal conductance," and characterizes feature(s) of heat exchange between the animal and its simple environment in the metabolic chamber. In a subsequent chapter we will add biophysical complexity to this idea (box 13.4 in chapter 13). Note that the metabolic rate decreases linearly until $T_a = T_{lc}$ (lower critical temperature) and then remains relatively constant in the so-called thermal neutral zone (which our students often call the thermonuclear zone). The metabolic rate at the thermal neutral zone is called the "basal metabolic rate." (B) Resting metabolic rate increases roughly exponentially with body temperature. Because many ectothermic poikilotherms tend to have body temperatures dictated by ambient temperatures, metabolic rate often increases with ambient temperature. The data in panel B are for the desert iguana *Dipsosaurus dorsalis*. (Modified from McNab 2002.)

Box 1.3 Ectotherms, Endotherms, Homeotherms, and Poikilotherms

In the old days, animals were classified as warm blooded (birds and mammals) and cold blooded (all other animals). These terms are as well established as they are obsolete. They hide an astounding diversity in thermal biology. The thermal biology of animals can be classified by placing animals along two axes depending on the consistency in their body temperature, and on whether most of the energy used in the maintenance of their body temperature is derived from metabolism or from external heat sources. If an animal maintains a relatively constant body temperature, we call it a homeotherm (from the Greek adjective *homos* = same, uniform). If, in contrast, an animal has variable body temperature, we call it a poikilotherm (from the Greek adjective *poikilo* = varied). If an animal uses mostly energy from its own metabolism to keep its temperature high and above that of the ambient, the animal is an endotherm (from *endo* = within). If it uses primarily external heat sources, the animal is an ectotherm (*ecto* = outside).

Although it is often assumed that all homeotherms are endotherms, and that all poikilotherms are ectotherms, this is not necessarily true. An internal parasite of a bird maintains a very constant body temperature and hence it is a homeotherm. Yet, because its body temperature is maintained by the heat produced by its host, the parasite is an ectotherm. Conversely, many insects maintain a constantly high, and very tightly regulated, body temperature when they are active. These animals, however, do not regulate their body temperature when they are inactive (Heinrich 1993). At the scale of 24 hours, they are poikilotherms, but at the scale of the few hours during the active period of their daily cycle they regulate their body temperature by using metabolic heat production, and hence they are endotherms. Choosing the appropriate terminology is a matter of convenience, but terms must always be defined. Although the 2×2 possible combinations of the terms described here are often sufficient, in some cases it may be very difficult to find a good term to define the thermal biology of an animal.

where d and b are empirically derived parameters. Equation 1.3 is often referred to as the "allometric equation." Because metabolic rate is proportional to $(m_b)^b$, the mass-specific metabolic rate changes as $(m_b)^b/(m_b) = m_b^{b-1}$. The reason that mass-specific metabolic rate decreases with increasing body mass is that $b < 1$.

Both the pools of many materials in an animal's body and the rates of many physiological processes vary (or "scale") allometrically with body mass. Because

linear relations are much easier to manipulate than power ones, allometric equations are frequently converted to their logarithmic form (see box 1.4):

$$\log B = \log a + b \log M_b. \quad (1.4)$$

The benefits of presenting allometric data using log-log plots include a more even spread of data across the axes and the ability to plot a wide range of x and y values (or, respectively, M_b and B values in our case) in a relatively small space (figure 1.3). In spite of their usefulness, log-log transformations must be used judiciously. An important warning is that fairly large absolute differences can appear small on log-log scales. In addition, it is tempting to use log-log transformations to estimate the parameters a and b of the allometric equation from a data set. Although using normal least-squares regression on log-transformed data to estimate a and b is often done, it can sometimes yield results with strong statistical biases. Hence, fitting the parameters of power functions is *sometimes*

Box 1.4 Laws for Logarithms

Manipulating allometric laws requires remembering the four basic rules for logarithms and the seven algebraic laws for operating with expressions that contain powers and roots. If you ever feel self-conscious about having to refer to this box, your feelings may be assuaged by the following anecdote. When John T. Bonner, one of the most important biologists of the 20th century was compiling the data for his classic book *Size and cycle* (1965), he discovered that he could not remember the laws for logarithms. In a quandary, he crossed the hall to the office of Robert Macarthur, one of the founders of theoretical ecology. Macarthur devoted a few minutes to writing roughly the same rules that you see in this box. His handwritten page remained in Bonner's desk for many years.

Logarithm rules

$\log(ab) = \log(a) + \log(b)$
$\log(1/a) = -\log(a)$
$\log(a/b) = \log(a) - \log(b)$
$\log(a^n) = n\log(a)$

Rules for powers and roots

$x^a x^b = x^{(a+b)}$
$x^{-a} = 1/x^a$
$x^a/x^b = x^{(a-b)}$
$(x^a)^b = x^{ab}$
$x^{1/a} = \sqrt[a]{x}$
$x^{a/b} = \sqrt[b]{x^a}$
$x^0 = 1$

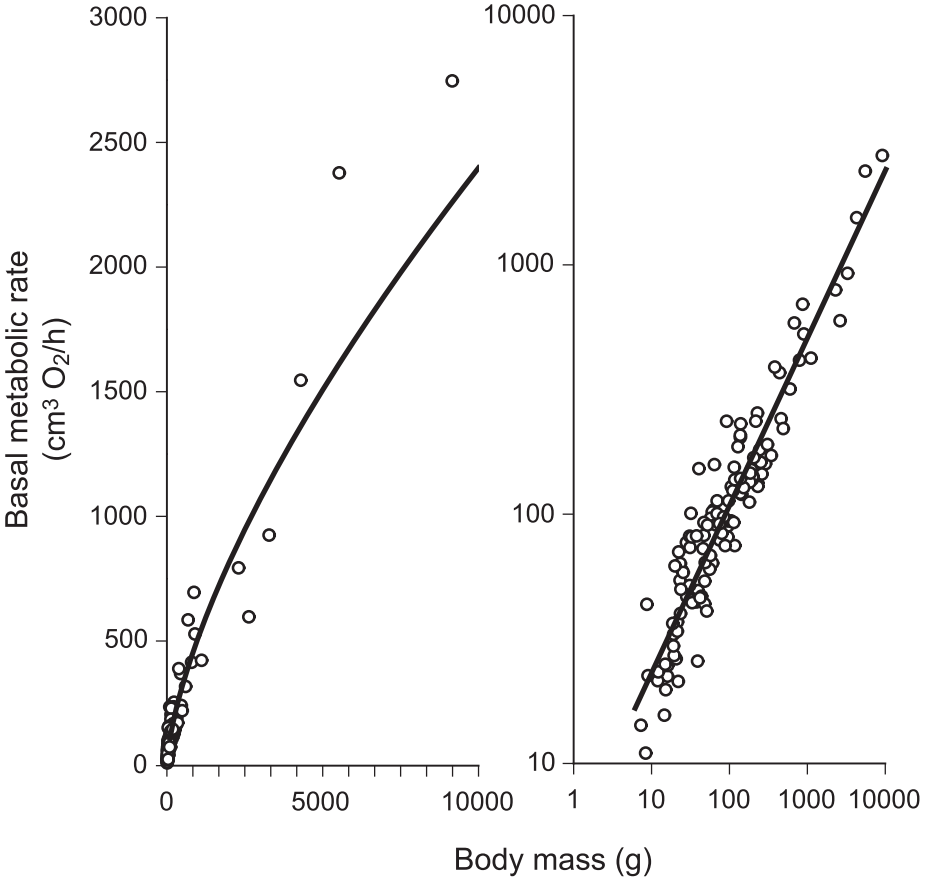

Figure 1.3. Basal metabolic rate is one of many variables that changes across body size in a nonlinear fashion but is linear when plotted on a log-log plot. Notice in the left-hand figure how the basal metabolic rate (BMR) increases in a sublinear fashion with increasing body size among 122 species of rodents (Hayssen and Lacy 1985). The same data appear linear in the right-hand log-log plot.

better done using nonlinear fitting procedures (see Motulsky and Ransnas 1987 for a friendly introduction).

Size has a pervasive role in determining the quantitative details of the distribution of materials within an organism, support against the force of gravity, and thermodynamics, and so size correlates with rates and capacities. Life history parameters such as developmental rate, reproductive rate, and lifespan are dependent in part on metabolic rate and tissue growth rate, each of which is size dependent, and so life history parameters also correlate to some extent with body size. Not only do variables such as metabolic rate, walking speed, and survival time during fasting scale with body mass, but also lifespan, age at first reproduction, gestation time, and birth rate.

The debate about the reasons for scaling laws started when Julian Huxley first formalized them in 1932 and has gone on for decades, but we can still apply them usefully even if we cannot explain them with complete assurance.

Allometric relationships have practical and theoretical importance for at least four reasons:

(1) Mountains of physiological, morphological, and ecological data can be summarized in them (e.g., Calder 1984; Peters 1983; Robbins 1993), thereby avoiding a sense of confusion from the quantity and complexity of raw data.
(2) We can use the allometric relationships in a predictive manner to make allometrically educated guesses. For example, suppose one wants to model the energetic needs of a population of endangered rodents for whom metabolism has not been measured. Why not use the value predicted by an allometric model as the first approximation? Because it is unethical to assess the safety and toxicity of new therapeutic drugs for the first time on humans, allometric scaling has an interesting application in pharmacology (Mahmood 1999). Pharmacologists rely on measurements on small laboratory animals such as mice, rats, rabbits, dogs, and monkeys to predict the properties of therapeutic agents in humans.
(3) We can use allometric relationships to derive new relationships, and sometimes they help us to formulate theoretical expectations. For example, knowing that the locomotory energetic cost to move 1 km scaled as $(m_b)^{3/4}$ allowed Tucker (1971) to predict that maximum migration distance of birds would increase as $(m_b)^{1/4}$. He arrived at this guess by reasoning that birds of all sizes could allocate a similar proportion of their body mass to fat (e.g., up to 50%), and that migration distance would be proportional to the ratio of energy stores (the kJ of energy in fat should be proportional to $(m_b)^{1.0}$) to the cost of transport (kJ/km, which should be proportional to $(m_b)^{3/4}$). To perform allometric manipulations such as these (migration distance is proportional to $(m_b)^{1.0}/(m_b)^{3/4} = (m_b)^{1/4}$) it is convenient to be familiar with the basic operations involving powers and logarithms (box 1.4). Juggling allometric equations is a sport favored by many theoretically inclined biologists. It is not only harmless fun, it can lead to remarkably interesting insights. Calder (1984) and Schmidt-Nielsen (1984), two distinguished comparative physiologists, have written useful manuals on this topic.
(4) Finally, the fact that so many physiological and life history variables can be described by allometric equations tells us that size alone accounts for a large proportion of the variance among species. Thus, one can argue that almost any comparative analysis of physiological or life history data should begin with a consideration of size. Allometric laws not only force us to consider body mass in comparative analyses, they allow us to compare among organisms of different sizes.

Because many biological rates scale as power functions of m_b (i.e., rate = $a(m_b)^b$), the confounding effect of mass can be removed by expressing rates relative to $(m_b)^b$. A comparison of the BMRs of the chipmunk and marmot described in our previous example using metabolic rates corrected by $(m_b)^{0.75}$ reveals differences of only about 40% (respectively, 10.2 versus 14.4 kJ d^{-1} $kg^{-3/4}$). In a subsequent section, we will justify why the b value for the metabolic rate is often assumed to be 0.75. Using the ratio of a trait to $(m_b)^b$ for comparative purposes is simple and appealing. However, it can be fraught with statistical problems (see Packard and Boardman 1999). Box 1.5 outlines one of the statistically correct ways in which body size can be accounted for in comparative analyses. Calder (1984) pointed out that "adaptation" can be conceived as "adaptive deviation" from the basic size-dependent allometric pattern. In a subsequent section (1.4 "Using Historical Data in Comparative Studies") we will describe how body size and phylogenetic data can be combined to test Calder's size-dependent definition of adaptation.

Box 1.5 How Can We Eliminate the Effect of Body Size in a Comparative Analysis?

One possible way is to use the residuals of the allometric relationship in question. Panel A of figure 1.4 shows the relationship between lipid content (y) and body length (x) in rainbow trout (*Oncorhynchus mykiss*) that have been fasted for up to 150 days. Note that this is a case of intraspecific allometry; most of the other examples in this chapter are interspecific allometric relationships. Clearly, lipid content increases as an allometric power function with length (indeed, lipid content is roughly proportional to $(\text{length})^3$). If we plot lipid content against time, we find no relationship (B). The effect of length overwhelms the effect of fasting time on lipid content. However if we plot the *residuals* of the expected relationship between length and lipid content (i.e., $y_{\text{observed}}(x_i) - y_{\text{expected}}(x_i)$) against days fasting, we find that lipid content decreases linearly with time (C). Residuals ($y_{\text{observed}}(x_i) - y_{\text{expected}}(x_i)$) are depicted as the dashed distance between a point and the curve in (A). Data are from Darin Simpkins (unpublished).

Because allometric relationships are often well described by power functions, researchers frequently work with log-transformed data. Hence residuals acquire the form

$$\log(y_{\text{observed}}) - \log(y_{\text{expected}}) = \log(y_{\text{observed}}/y_{\text{expected}}).$$

Because log-transforming data can lead to statistical biases, we often prefer to use the residuals of allometric curves fitted using nonlinear methods

continued

continued

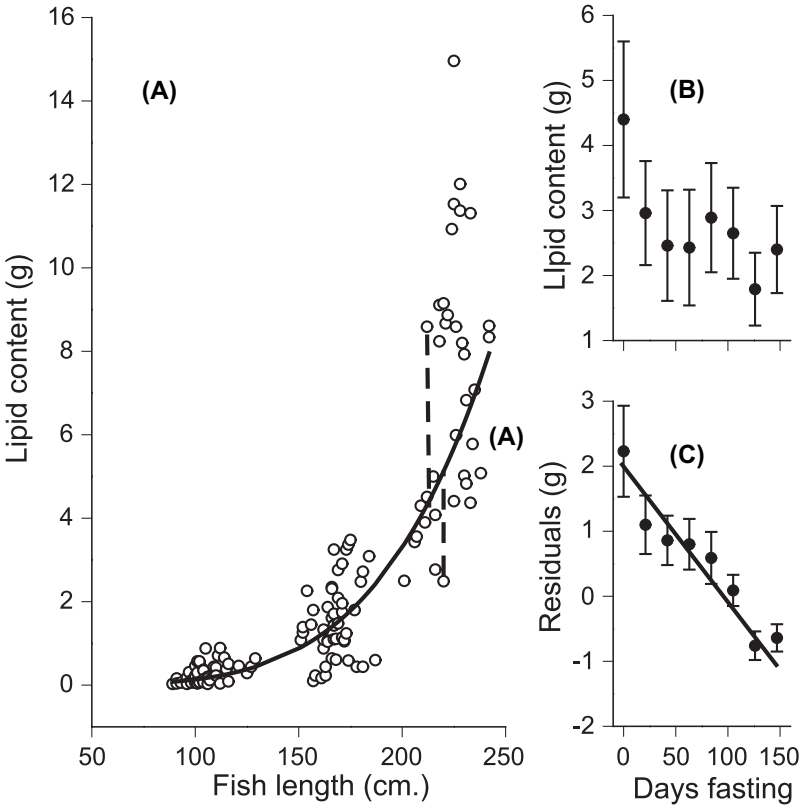

Figure 1.4. The relationship between body length and lipid content in trout that fasted for variable amounts of time is well described by a power function. Although lipid content is correlated with fasting time, the residuals of the relationship between lipid content and length clearly decrease with fasting time. To obtain a pattern, we must correct for the variation in the data set produced by differences in the body length of the fish.

(Motulsky and Rasnas 1987). However, not all researchers are as log-phobic as we are and there are situations in which it is more appropriate to log-transform data prior to analyses. Logarithmic-transformations can be absolutely essential when the variation along the allometric line increases with body size (as it often does).

1.2.1 Ontogenetic, Intraspecific, and Interspecific Allometry

As animals grow, their body mass changes. It is often useful to plot the change in a trait as a function of body mass throughout an animal's development. Huxley (1932) constructed a myriad of these ontogenetic allometric relationships. Ontogenetic allometry remains an essential tool in the analytical arsenal of developmental biologists (Stern and Emlen 1999). In a similar fashion, it is

often useful to analyze the allometric relationships among the traits of fully grown adults within a species. We can call this form of allometry intraspecific allometry (it is also called static allometry). The boundaries between ontogenetic and intraspecific allometry can become blurred in animals that continue growing throughout their lives ("indeterminate growers"; see chapter 13). Therefore, on occasion you will encounter allometric analyses that combine animals not only of different sizes, but also of different developmental stages. Finally, many allometric analyses use the average values for a species as data points. In ontogenetic and intraspecific allometric analyses data points represent individuals. In interspecific allometries (also called evolutionary allometries), data points represent species averages (Cheverud 1982). On occasion, you will find that an allometric plot is a mélange of ontogenetic and intra- and interspecific allometries.

Interspecific allometries are very useful, but one must deal with them carefully for a variety of reasons. The primary one is that species are not statistically independent data points. They are related by descent. We will discuss in some detail how to deal with this important detail in a subsequent section (1.4 "Using Historical Data in Comparative Studies"). Also, interspecific allometries do not often satisfy the assumption that the independent variable (which more often than not is body mass) is measured without error. Hence, using standard least-squares procedures to analyze them can be inappropriate and one must rely on other statistical estimation procedures (Sokal and Rohlf 1995). Chapter 6 in Harvey and Pagel's (1991) book on the comparative method in evolutionary biology gives more detailed descriptions of these approaches. With surprising frequency authors mix ontogenetic, intraspecific, and interspecific data in a single allometric analysis (we avoid giving examples to evade the wrath of colleagues). This practice is statistically incorrect and hides interesting biological information (Cheverud 1982). The final reason why interspecific allometries must be treated with caution is that they assume that we can characterize the magnitude of a trait by a single number. Many traits, however, are phenotypically plastic. Phenotypic plasticity and its sometimes confusing terminology is the theme that we deal with next.

1.2.2 Phenotypic Plasticity: Physiological Variation at a Variety of Time Scales

Comparative physiologists have spent an inordinate amount of time describing the allometric relationship between the basal metabolic rate (BMR) of birds and mammals and body mass (McNab 2002). The BMR was not chosen because it is particularly relevant ecologically—it is not. Recall that it is

measured on fasted animals at rest confined within dark boxes, which are not conditions that most animals experience naturally. Many factors (temperature, radiation, wind speed, activity, etc.) influence metabolic rate. The BMR provides a measurement done under controlled and standardized conditions that allows comparison without these confounding factors. The wide use of the BMR by comparative physiologists recognizes that the expression of physiological traits changes within an animal. But the BMR itself is variable; it changes when measured at different seasons in a single animal (reviewed by McNab 2002). The phenotypic variability that can be expressed by a single genotype is called phenotypic plasticity (Pigliucci 2001). Understanding how animals work and how their function influences their role in ecological systems demands that we recognize and investigate the phenotypic plasticity of physiological traits.

Comparative and ecological physiologists have investigated the phenotypic plasticity of animals for years. We will give many examples of ecologically relevant physiological phenotypic plasticity throughout this book. One of the confusing results of an otherwise wonderfully rich literature is a proliferation of terms. In this book we have adopted the terminology proposed by Piersma and Drent (2003; see table 1.2) to describe the different forms that phenotypic plasticity can take. We caution that this nomenclature has not been adopted widely, and that some biologists dislike it. We find it useful as an attempt to bring a semblance of order to a sometimes befuddling terminological tangle. According

TABLE 1.2
Phenotypic plasticity

Plasticity category	*Phenotypic change is reversible*	*Variability in phenotype occurs in a single individual*	*Phenotypic change is seasonally cyclic*
Developmental plasticity	No	No	No
Phenotypic flexibility	Yes	Yes	No
Life-cycle staging	Yes	Yes	Yes

Note: Often a single genotype can produce a variety of phenotypes if exposed to different environmental conditions (temperature, diet, presence of predators, , etc.). The phenotypic variability that can be expressed by a single genotype is called phenotypic plasticity. Piersma and Drent (2003) defined three mutually exclusive categories of phenotypic plasticity. These categories depend on whether the phenotypic change is reversible, whether it occurs in a single individual, and whether it is seasonal or cyclic. We include polyphenism as a subcategory of developmental plasticity.

to Piersma and Drent (2003), phenotypic plasticity can be divided into 3 more or less mutually exclusive categories: developmental plasticity, phenotypic flexibility, and life-stage cycling.

Developmental plasticity is defined as the ability of a single genome to produce two or more alternative morphologies in response to an environmental cue such as temperature, photoperiod, or nutrition. The term developmental plasticity contains "polyphenism" as a subcategory. The term polyphenism refers to the ability of many arthropods to produce a sequence of generations with discrete phenotypes to accommodate sometimes seasonal environmental changes (Shapiro 1976). A nice example of developmental plasticity is the phenomenon of predator-induced morphological changes in which prey change their morphology in response to predation risk (Tollrian and Harvell 1999). For example, the presence of fish predators induces the development of defensive spines in a variety of aquatic arthropods and crustaceans (e.g., Harvell 1990). Figure 1.5 illustrates the use of allometry to document predator-induced morphological changes.

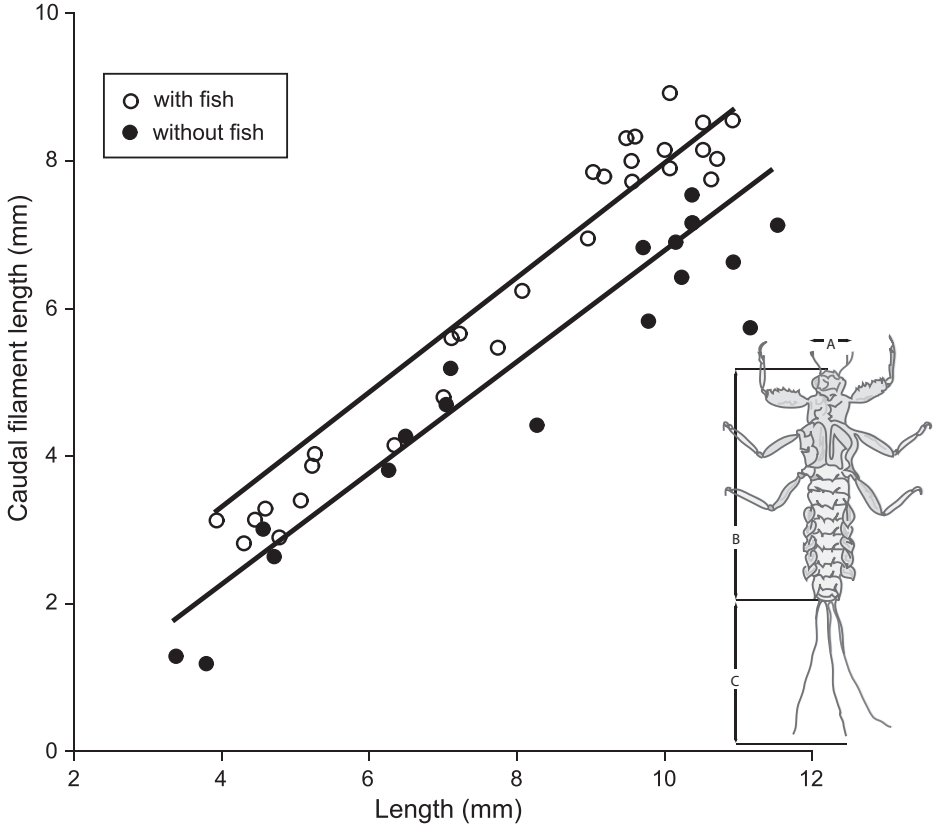

Figure 1.5. Dahl and Peckarsky (2002) discovered that when the larvae of the mayfly *Drunella coloradensis* grow exposed to predatory brook trout (*Salvelinus frontalis*), they develop longer caudal filaments (C in the image of the mayfly). Because caudal length increases with body length, the comparison between caudal filament lengths in streams with and without trout must be done allometrically. Long caudal filaments can be induced experimentally by dripping water from a container containing live trout into the water in which *D. coloradensis* are reared. Longer caudal filaments significantly reduce predation by brook trout on the mayfly larvae. (After Dahl and Peckarsky 2002.)

Developmental plasticity is irreversible. When environmental conditions change rapidly and over time scales that are shorter than a lifetime, animals can show reversible transformations in physiology and morphology. This phenotypic flexibility is widespread and ecologically very important. We will describe examples of it in many chapters of this book. In addition to changes in function that occur in direct response to a change in an environmental condition, many animals live in distinctly seasonal environments. In these, different activities tend to be predictably separated in time within individuals. Long-lived individuals must adjust their morphology, physiology, and behavior to fit the conditions of these seasonal changes. Piersma and Drent (2003) refer to these changes as life-cycle stages. They use the annual life cycle of the arctic rock ptarmigan *Lagopus mutus* as an example of such changes. These birds change plumage seasonally from white (which is cryptic in snow) to green and brown (which hides them in the brief summer of the tundra).

Although it is often assumed that phenotypic plasticity confers a selective advantage to individuals that have it, this assumption is better construed as a hypothesis that must be tested (Schmitt et al. 1999). It is called the adaptive plasticity hypothesis. Indeed, the intraindividual trait variation generated by different environmental conditions is ideally suited to test the criterion of "goodness of design" for phenotypic adaptation, which was proposed by the evolutionary biologist George C. Williams (1966). Intragenomic phenotypic variation is especially useful for testing the performance of alternative phenotypes when interspecific comparisons cannot be made.

Although we will not often use the terms acclimatization and acclimation in this book, you should be aware of them. Both terms are used frequently in the thermal biology literature to characterize the phenotypically flexible responses of animals to changes in their thermal environment. The term acclimatization refers to phenotypic responses in response to changes in the natural, and hence complex, thermal environment. The word acclimation refers to phenotypic changes in response to controlled changes in one or several thermal variables in the laboratory. You will also find the word adaptation used to refer to reversible phenotypic variation. In future chapters we will give examples of this misuse of the term adaptation, which are unfortunately in relatively common usage in some fields. In our view, the use of the term adaptation must be restricted to the Darwinian concept of adaptation as "an anatomical, physiological, or behavioral trait that contributes to an individual's ability to survive and reproduce ("fitness") in competition *and cooperation* with conspecifics in the environment in which it evolved" (Williams 1966) (emphasis added). Rose and Lauder's (1996) book gives more nuanced definitions of Darwinian adaptation and details about how we go about testing the hypothesis that a trait is adaptive.

1.2.3 Why Is b ≈ n/4? The Enigma of Quarter Power Scaling

There is little disagreement about the generality and value of allometric equations as phenomenological descriptions of a variety of biological relationships (but see Kooijman 2000 for a lone dissenting view). However, the mechanisms that lead to these relationships and the factors that determine the values of their parameters are unclear and the subject of some controversy (and sometimes of acrimonious criticism; Kozlowski and Konarzewski 2004). A perplexing pattern is the seeming ubiquity of simple multiples of 1/4 in the estimated value of the exponent b of allometric equations. A few examples are heartbeat frequency ($b \approx -1/4$), lifespan ($b \approx 1/4$), and the radii of both mammalian aortas and tree trunks ($b \approx 3/8$; West et al. 2000). Perhaps the best-known allometric patterns in physiology are the relationships between metabolic rate and mass. In 1932, Max Kleiber proposed that in mammals metabolic rate scaled with body mass to the 0.75 (i.e., 3/4) power (Kleiber 1932). Kleiber's pattern has come to be used as a standard in studies of mammalian metabolism, and researchers frequently describe their results in relationship to expectations based on Kleiber's original data set. You will still encounter in the literature reference to values that are x% higher or lower than Kleiber (McNab 2002).

Kleiber's observation should bewilder you. At first glance, one may assume that metabolic rate should increase in proportion (i.e., "isometrically" using allometric terminology) to body mass. After all, mammalian cells are built more or less from the same substances and the number of cells should increase isometrically with body mass. Jonathan Swift (1735) made this assumption when he estimated the amount of food that Lilliputians fed Gulliver. The Lilliputians found that Gulliver's height

> exceeded theirs in proportion to twelve to one . . . they concluded from the similarity of their bodies that Gulliver's must contain at least 1728 of theirs [12^3 assuming that Gulliver was geometrically similar to his treacherous hosts] and consequently would require as much food as necessary to support that number of Lilliputians.

There is a mistake in this argument. Animals do not fuel their metabolism by eating in proportion to their body mass. Had the Lilliputians fed Gulliver as much as Swift describes, he would have become enormously fat. Metabolic rate does not scale in proportion to body mass. The approach of Rubner, a German physiologist, was closer to reality. In the late 19th century, he proposed that animals feed to replace the heat that is dissipated through their body surface, which scales with $(m_b)^{2/3}$. The notion that metabolic rate scales with $(\text{mass})^{2/3}$ is called "Rubner's surface law." Many, perhaps most, organisms, break Rubner's law. Their metabolism scales with mass to a value usually higher than 0.66.

Why should *b* equal 0.75 rather than 0.66? The 3/4 exponent seems to describe adequately the relationship between metabolic rate and body mass in animals ranging from protozoans to whales (figure 1.6). The value of *a*, the intercept of the log-log allometric relationship, varies significantly with the thermal biology of the beast—as we will discuss in a following section (1.3 "The Importance of Temperature"), and with other factors, but *b* remains remarkably constant and close to 0.75.

A veritable flock of theories have been proposed to explain why *b* should equal 3/4. Brown et al. (2000) review these theories in a historical context. We, very briefly, summarize the latest one, which can be called the fractal theory of quarter-power allometric laws (West et al. 1997). We must mention that West et al.'s theory has received significant challenges (see, e.g., Dodds et al. 2001; Darveau et al. 2002). West and his collaborators have addressed these criticisms in what has become a scientific ping-pong of ideas (Savage et al. 2004; Brown et al. 2005). Although we cannot guarantee that this theory will be accepted in the future, we present its foundations for three reasons: (1) We find its arguments compelling, (2) it has generated a significant amount of exciting novel research

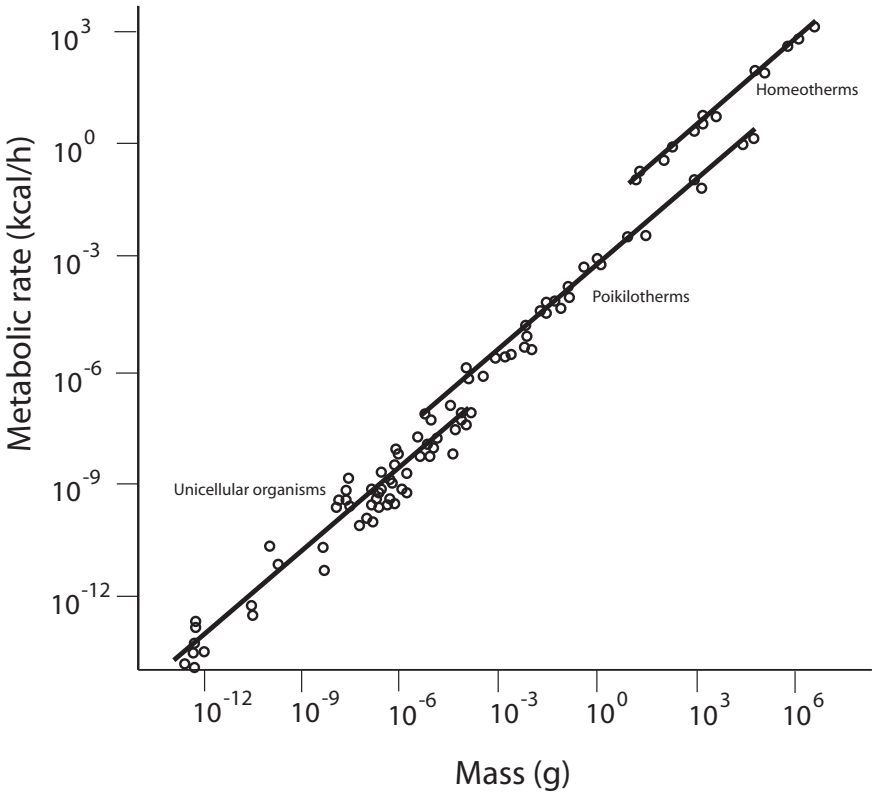

Figure 1.6. Hemmingsen (1960) compiled metabolic rate data for organisms ranging in size over 21 orders of magnitude. He standardized all the poikilothermic ectotherms to a temperature of 20°C and the endothermic homeotherms to one of 39°C. The relationship between metabolic rate and body mass is well described by a power function with exponent b = 3/4. The intercept of the log-log form of this relationship (log(a)), however, varies among groups in a seemingly predictable fashion. Homeotherms seem to have higher metabolic rates than poikilotherms, and poikilotherms appear to have higher rates than unicellular organisms.

that integrates physiology with ecology (Niklas and Enquist 2001; Gillooly et al. 2001; Carbone and Gittleman 2002), and (3) we will use some of its results in subsequent chapters. We again emphasize that West et al.'s hypothesis is one of many and that other competing hypotheses exist. Kozlowski and Weiner (1997) and Kooijman (2001) describe alternative mechanisms that can lead to the allometric scaling of metabolic rate and body mass. After consulting the literature and reflecting on what you have read, you may not find West et al.'s (1997) arguments convincing, and you may join the ranks of the 3/4-power-law skeptics. In that case, do not throw the allometry baby away with the 3/4-power-law water. Instead of using 3/4 (or multiples of 1/4) in your equations, use an empirically derived value for b. This value will almost certainly be between 0.6 and 1. Indeed, you may want to substitute in your mind an empirical value for 3/4 in many of our subsequent equations. Often, the conclusions of this substitution will not greatly change the conclusions of an analysis.

The derivation of West et al.'s model requires superficial acquaintance with fractal mathematics. Because in our experience this is not part of most biologists' backgrounds (although maybe it ought to be), we skip it. We simply list the model's assumptions and give a qualitative description. Interested readers may find West et al.'s (1999) general derivation of quarter power laws significantly more accessible than the original model published in 1997 (we do). West et al. (1997) base their fractal explanation of quarter power laws on the observation that biological structures and functions are determined by the rates at which resources (oxygen, nutrients, and water) can be delivered to them. Their main hypothesis is that to supply their metabolizing units (cells in organisms, respiratory molecules in mitochondria and cells) with resources, organisms use fractal-like, volume-filling, hierarchical transport systems (figure 1.7). West et al. (1997, 2000) make two additional assumptions: (1) The final branch of the transport network at the site where nutrients are exchanged is size invariant (i.e., the capillaries of elephants and those of shrews have the same radius), and (2) organisms have evolved so that the energy required to transport material through the network is minimized. These more or less reasonable premises lead to the 3/4 exponent in the relationship between metabolic rate and body mass and to its many 1/4-power-law corollaries.

One way to visualize what West and his collaborators suggest is the following: Organisms must exchange materials across surfaces. These surfaces must reach into all the corners of an organism's volume, and must have a system of delivery of materials that is efficient. To achieve these dual purposes, the circulatory system divides in a fractal-like fashion again and again so that its surfaces reach all the nooks and crannies of an animal's body. The circulatory system has a surface that "wants" to become a volume and that achieves volume-like characteristics by virtue

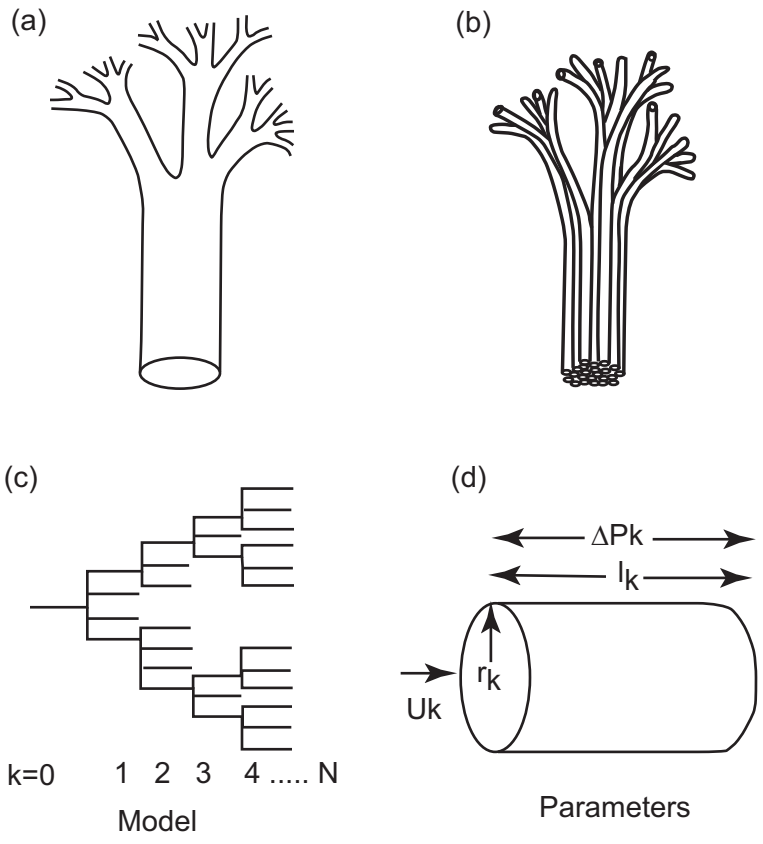

Figure 1.7. Many biological branching distribution networks show fractal-like structures. Common examples are vertebrate circulatory and respiratory systems (A) and plant vessel-bundle vascular systems (B). Diagram (C) shows the topological representation of these systems used by West et al. (1997) in their derivation of fractal theories for scaling laws. The parameter k specifies the order of the branching level. These levels in a vertebrate circulatory system would begin in the aorta ($k = 0$) and end in capillaries ($k = N$). The parameters used in West et al.'s (1997) model are summarized for a tube at level k in diagram (d) (l_k is the length of the tube, r_k is its radius, ΔP_k is the drop in pressure along its length, and U_k is the velocity of the material moved along the tube).

of its fractal-like structure (we apologize for the teleological language!). You can apply the same logic to a variety of "volume-filling" surfaces including the respiratory tree in mammals and the hydraulic system that conducts water from roots to leaves in plants.

Why is the quarter power law important? We believe that it is important because it helps us to account for a very large range of life's variation. It suggests that similar, maybe universal, design principles apply to organisms and that these principles allow us to understand one of life's important axes. West et al. (2002) provide a remarkable example showing that the fractal explanation may be extended to organelles and even to the molecules of the respiratory complex inside mitochondria (figure 1.8). The explanatory value of allometric quarter power laws, however, should not blind us to their limitations. Allometric laws work very well if one views the world through log-log glasses, but these glasses provide a peculiar perspective. The beautifully tight relationships in allometric data summaries plotted on log-log axes hide enormous amounts of variation. If you were to amplify an allometric plot, focusing only on a narrow range of body masses, and retransform the data to arithmetic axes, the relationship would not

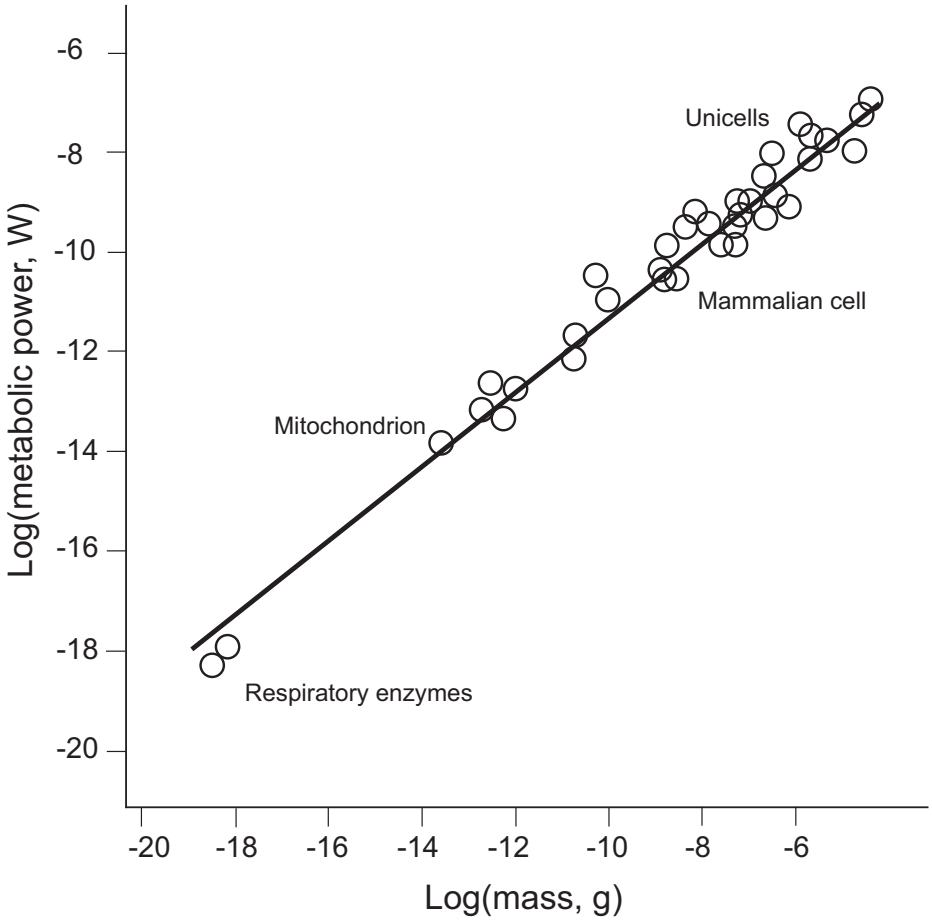

Figure 1.8. The metabolic power of isolated mammalian cells, mitochondria, respiratory complex, and cytochrome oxidase increases as a power function of mass with exponent equal to 3/4. The plot shows unicellular organisms for comparison. All data were adjusted to mammalian temperature using equation 1.12. (Data from West et al. 2002.)

look nearly as tight. For some body ranges there would still be severalfold variation remaining to be explained and predicted. Factors other than body mass still account for much of the functional variation that is of interest to physiological ecologists. One of these factors is, of course, temperature, but there are others. We will discuss the importance of temperature in a subsequent section, but before doing so, we illustrate the use of allometric laws in an area of ecology that has many of its foundations in physiological ecology: macroecology.

1.2.4 The Energetic Equivalence Principle: A Scaling Law for Macroecology

Macroecologists look for statistical patterns in the abundance, distribution, diversity, and biomass of individual organisms and species. They aim to understand why these patterns emerge, and to discover the processes that govern them

(Brown 1999). It is reasonable to conjecture that many of the patterns of abundance, distribution, and diversity of organisms over space and time can be attributed to resources (energy, nutrients, and water) and to the physiological mechanisms that shape how animals use them. Macroecology's wide-angle lens and physiological ecology's zoom are complementary. The processes studied by physiological ecologists should often reveal the mechanisms that underlie macroecological patterns. In this section we describe the energetic equivalence rule, a macroecological pattern that stems from physiological principles.

The energetic equivalence rule states that the total rate of energy use of a population per unit area (B_p) is invariant with respect to body size. In simpler terms, the energy used by all the herbivorous voles living in an island should not be very different from that of all the herbivorous deer that coexist with them. This surprising rule is a direct consequence of the dependence of the metabolic rate of an individual (B) on its body mass (m_b). The amount of energy used by a local population is its population density multiplied by the metabolic requirements of its individual members. Maximum population density for a given species (N_{max}) should be approximately equal to

$$N_{max} = \left(\frac{j}{B}\right) = \left(\frac{j}{a\,(m_b)^{3/4}}\right) \tag{1.5}$$

where j represents the rate at which resources become available to the population, B is the metabolic rate of each individual ($B = a(m_b)^{3/4}$), and a is a constant. This simple model predicts that population density should decrease with increasing species body mass to the –3/4 power. There is significant evidence for this pattern in creatures ranging from marine phytoplankton and terrestrial plants (Belgrano et al. 2002) to a variety of consumers (Damuth 1987). The energy used by a population (B_p) per unit time equals its density times the energy use of each of its members:

$$B_p \approx N_{max} B \approx \left(\frac{j}{a\,(m_b)^{3/4}}\right) a\,(m_b)^{3/4} = j. \tag{1.6}$$

Therefore, the amount of energy used by a population is independent of body mass but dependent on j, the ecosystem's productivity.

Although there is significant support for the energetic equivalence rule, there are also exceptions. Carbone and Gittelman (2002) used a remarkably complete data set to examine the dependence of mammalian carnivore densities on body

mass and productivity. They found that, as expected, population density decreased as a power function of body mass (figure 1.9). However, they found that the exponent of this function was not −0.75; it was roughly −1. Why? A possibl explanation may be that productivity j decreases with increasing body mass o the prey, which in turn is often (but not always) correlated with the mass of the carnivores (Carbone et al. 1999). The argument is as follows: Peters (1983 documented that productivity decreases as $(m_b)^{-1/4}$. Then, assume that the mass of the prey (m_{bp}) increases isometrically with the mass of the carnivore (m_{bc}), i.e., $m_{bp} \propto m_{bc}$, and hence $j = a' m_{bc}^{-1/4}$. Therefore,

$$N_{\max} \approx \left(\frac{j}{B_d}\right) \approx \left(\frac{a' m_{bc}^{-1/4}}{a m_{bc}^{3/4}}\right) = \frac{a'}{a}(m_{bc})^{-1} \qquad (1.7)$$

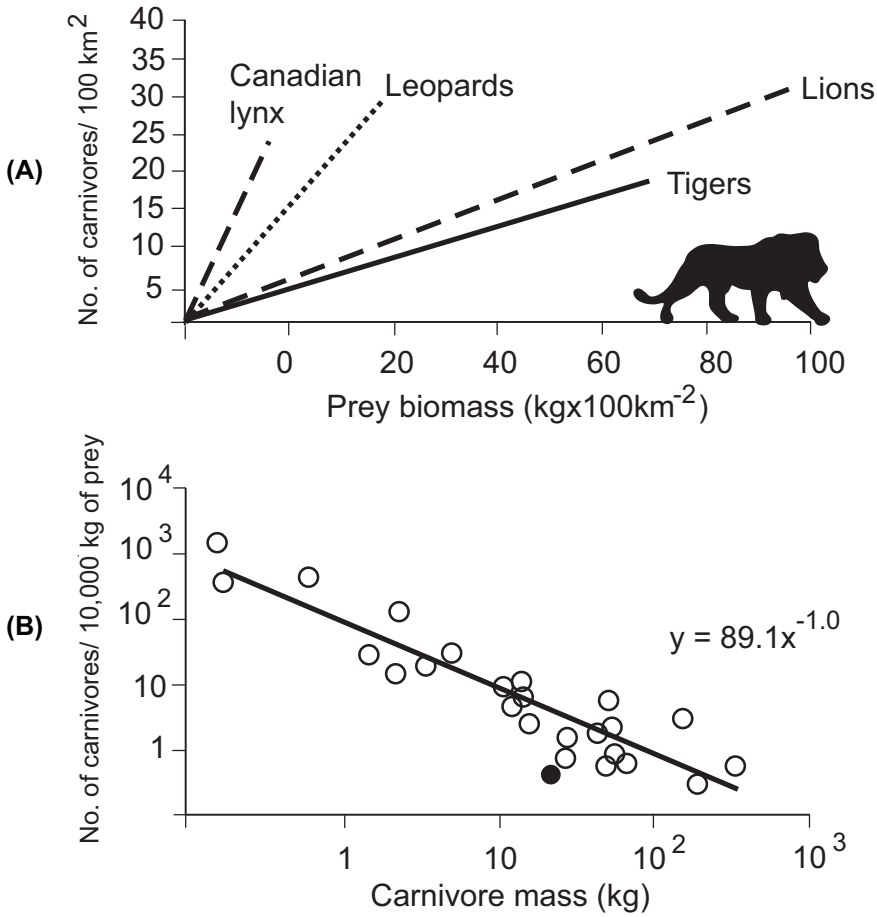

Figure 1.9. (A) The population density (numbers/km^2) of mammalian carnivores increases as a function of prey biomass (in 10,000 kg/km^2). Different lines represent different species The lines are regressions through the origin. Because carnivore population density depends strongly on prey biomass, panel B standardizes density by prey biomass and plots it against carnivore mass. The relationship between standardized density and carnivore mass is well described by a power function with exponent ≈ −1. The filled circle in panel is the Eurasian lynx (*Lynx lynx*). This population is subject to poaching, which may explain its relativel low density. (Modified from Carbone and Gittleman 2002.)

Unlike what seems to be the case in many other taxa (see Damuth 1987), the energy fluxes of mammalian carnivore populations seem to decrease with increasing body mass:

$$B_P \approx N_{\max} B \approx \left(\frac{a'}{a}\right) a\,(m_b)^{3/4} = a'(m_b)^{-1/4} \quad (1.8)$$

1.3 The Importance of Temperature

The effect of temperature on biochemical reactions has been known for over a century and is summarized in the Arrhenius equation:

$$K = Ae^{-E_i/kT}, \quad (1.9)$$

in which K is the rate constant of a reaction, A is a constant relating to molecular collision frequency, E_i is the activation energy, k is Boltzmann's constant, and T is absolute temperature (in °K). Because enzymatic processes mediate most biological processes, the importance of temperature as a determinant of biological rates should not be surprising. Within the range of temperatures at which most biological processes take place (0 to about 40°C) the Arrhenius equatio behaves very roughly as an exponential. Thus, biologists often assume an exponential relationship and use the ratio of two biological rates 10°C apart ($Q_{10} = (K_{T+10})/K_T$) as an index of the thermal sensitivity of a process. Q_{10} is some times called the temperature coefficient and is related to the Arrhenius equation by

$$Q_{10} = \frac{K_{T+10}}{K_T} = e^{E_i/k(10)(T)(T+10)}) \quad (1.10)$$

Although Q_{10} is often assumed to be constant and approximately equal to 2 equation 1.10 emphasizes that it is not. It varies with T among other factors. Like most physiologists, we have often used Q_{10} in back-of-the envelope calculations. However, we recognize that its use can be problematic.

The importance of body temperature for biological processes is well illustrated by an allometric application. Gillooly and colleagues (2001) used the following reasoning to incorporate temperature into the allometric equation relatin metabolic rate (B) and body mass (m_b): Metabolic rate is the consequence of many biological reactions (B_i). Using the simplest possible assumption, we

can postulate that the mass-specific metabolic rate is the sum of all the energy-consuming reactions taking place in the organism:

$$B = \sum_{i} B_i . \tag{1.11}$$

Each B_i depends on three major variables:

$B_i \propto$ (density of reactants)(fluxes of reactants)(kinetic energy of the system).

The first term of this product is mass independent, whereas the second scales with $(m_b)^{3/4}$. The third term is governed by the Arrhenius relationship. Hence equation 1.11 can be rewritten as

$$B(T, M) \propto (m_b)^{3/4} e^{-E_i/kT} \tag{1.12}$$

where E_i is the average activation energy for the reactions that govern metabolism. To compare among organisms of varying body masses, Gillooly et al (2001) standardized equation 1.12 to $(m_b)^{3/4}$ as

$$\frac{B(T)}{(m_b)^{3/4}} = B_0 e^{-E_i/kT} . \tag{1.13}$$

Equation 1.13 makes two predictions. The first one is that plotting the logarithm of the mass-corrected metabolic rate ($\ln(B(T)/m_b^{3/4})$) against $1/T$ should yield a straight line with slope equal to $-E_i/k$:

$$\ln\left(\frac{B(T)}{(m_b)^{3/4}}\right) = \ln(B_0) - \left(\frac{E_i}{k}\right)\frac{1}{T}. \tag{1.14}$$

The graph of the logarithm of a rate constant against $1/T$ is called an Arrhenius plot. Arrhenius plots are used frequently in physical chemistry to estimat the values of energies of activation. Therefore, this first prediction states that the response of whole organisms to temperature should follow the same principles as enzymatic reactions. Gillooly and colleagues made a second, more precise prediction: Because E_i has an average value of about 0.65 eV ($\approx 1.12 \times 10^{-19}$ J) in biochemical reactions, and the Boltzmann factor k is 8.62×10^{-5} eV (°K)$^{-1}$, they predicted that the slope of the plot of $\ln(B(T)/(m_b)^{3/4})$ against $1000/T$ (i.e., $E_i/k1000$) should equal approximately –7.5 °K. Figure 1.10 shows only one example of the many plots made by Gillooly et al. (2001) for a variety of organisms. All these plots were linear, which we do not find terribly surprising. However, their slopes ranged from –5.02 to –9.15 °K, which is a relatively narrow range and includes the value that Gillooly et al. (2001) had predicted.

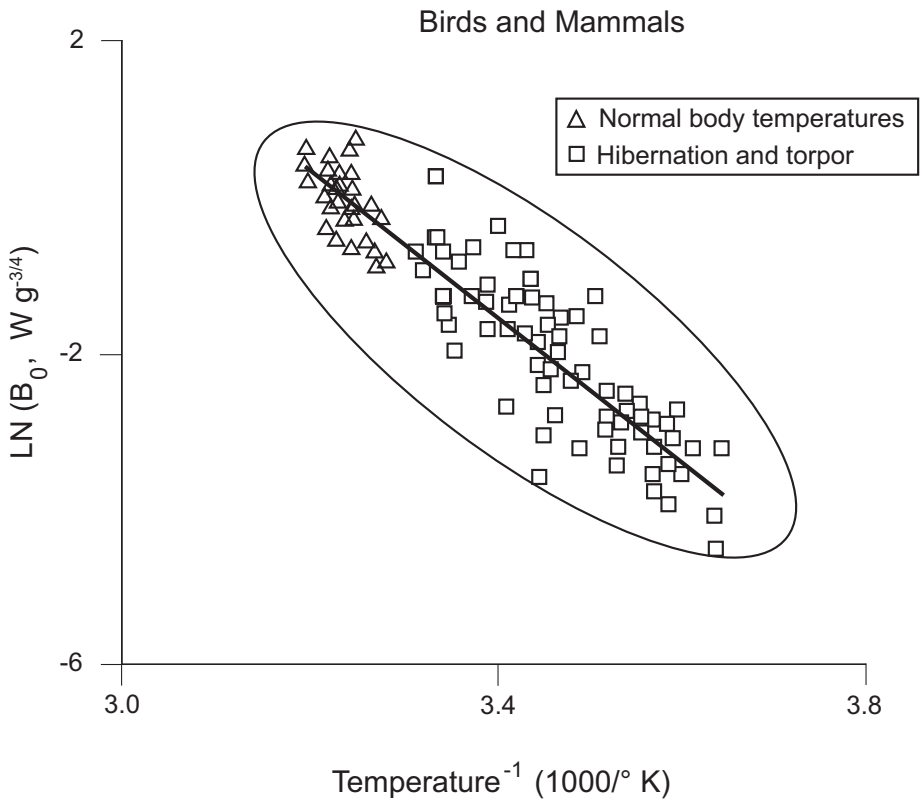

Figure 1.10. An Arrhenius plot demonstrates that metabolic power (in watts = Joules/second) standardized by (body mass)$^{3/4}$ depends on temperature in the same fashion as biochemical reactions. The data set includes only birds and mammals, but data from unicellular organisms, plants, fish, amphibians, and reptiles show similar relationships. The relationship between metabolism and temperature indicates that a significant fraction of the reduction in metabolic rate experienced by animals in torpor or hibernation is simply the result of lowered body temperature.

Figure 1.6 depicts the relationship between metabolic rate and body mass for animals ranging from unicells to whales. When Hemmingsen constructed this plot in 1960, he standardized the resting metabolic rates of all the poikilotherms to 20°C and those of endotherms to 39°C. Sensibly, Gillooly and collaborators (2001) standardized all metabolic rates to a common temperature (20°C). This standardization reduced the variation in metabolic rate enormously (figure 1.11). Temperature-standardized metabolic rates for unicells, invertebrates, and plants fell along a common line. The metabolic rates of fishes, amphibians, and reptiles were only slightly higher, and those for birds and mammals were still higher. In contrast with Hemmingsen's (1960) figure, which showed no overlap among groups, figure 1.11 shows a lot of overlap. Hemmingsen (1960) calculated a 225-fold range in mass-standardized metabolic rates. When temperature differences are accounted for, the range is reduced to a 20-fold range. The extraordinarily simple model summarized by equation 1.13 suggests that, as a first approximation, the metabolic rate can be estimated as the product of an allometric (quarter power) function of body mass and the Arrhenius relationship. A vast amount of variation in one of life's central traits seems to be accounted for by body mass and temperature.

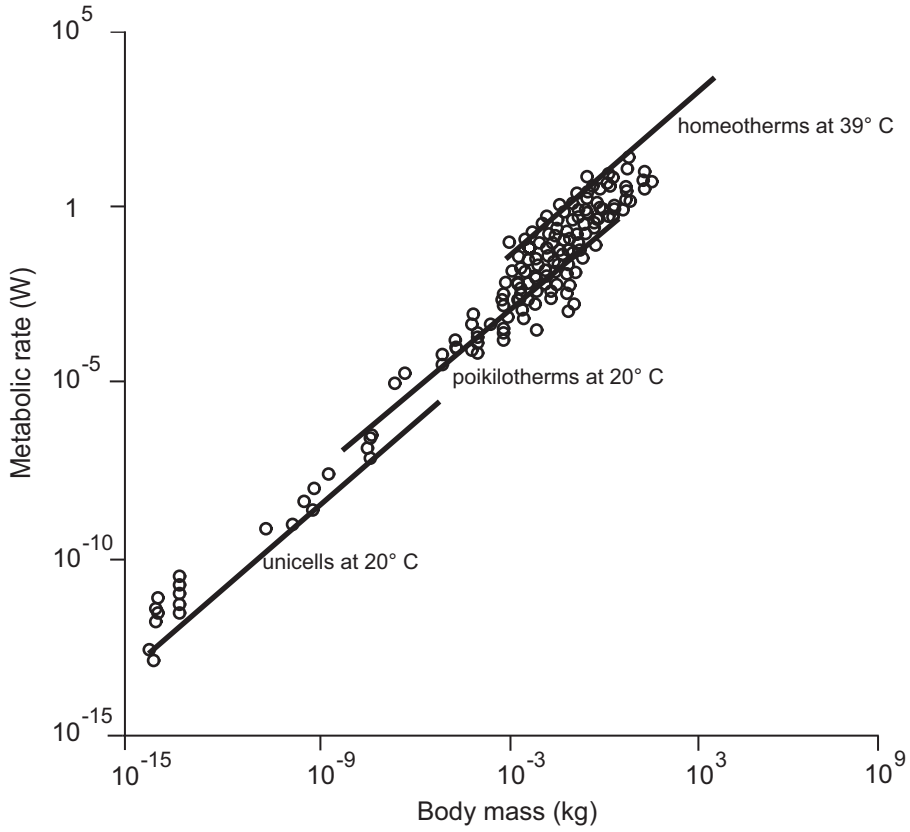

Figure 1.11. When all measurements are standardized to 20°C, differences in metabolic rate are reduced. The regression lines are the same lines shown in figure 1.5 and derived by Hemmingsen (1960). Birds and mammals have temperature-corrected metabolic rates that are higher than those of reptiles and amphibians, but the overlap in values between the two groups is extensive. The difference between unicellular organisms and ectothermic poikilotherms is very small. A significant fraction—albeit not all—of the variation in mass-corrected metabolic rate is explained by variation in body temperature.

1.3.1 Gillooly's Equation and the Metabolic Theory of Ecology

Equation 1.12 is very important because it summarizes the combined effect of body size and temperature on metabolic rate. We call it "Gillooly's equation" to recognize James Gillooly's insight about the multiplicative effect of allometry and temperature on metabolism. Gillooly's equation summarizes a fundamental property of organisms. It tells us that the rate at which energy flows through an organism depends on how big and how hot the organism is. Recall from box 1.2 that we can estimate the fractional rate of energy input into the energy pool of an organism as the ratio of the energy flux and the energy pool contained in the organism, which is proportional to body mass. Thus, the fractional rate of metabolism (or "mass-specific metabolism", $b = B/m_b$) can be expressed as

$$b \propto (m_b)^{-1/4} e^{-E_i/kT}. \quad (1.15)$$

Again, recall from box 1.2 that the residence time is the reciprocal of a fractional rate. Thus, the residence, or turnover, time of metabolic substrates (t_b) should be proportional to the reciprocal of equation 1.15:

$$t_b \propto (m_b)^{1/4} e^{E_a/kT} \quad (1.16)$$

These equations summarize relationships that have been studied for a very long time. We know that large organisms require more resources, but use them (or "flux" them) on a mass-specific basis more slowly than smaller organisms, and that both resource requirements and flux rates are higher at higher body temperatures (Brown et al. 2004). These observations are not front-page news to most physiological ecologists. However, Gillooly's equation combines the effect of size and temperature in a single simple mathematical expression, which is useful. This expression allows us to compare across organisms that differ in size and temperature using an equation that is grounded on first principles of chemistry and physics.

Arguably, the rate at which organisms use energy (i.e., the metabolic rate) is at the heart of the processes in which they participate. Thus, Brown et al. (2004) have extended the metabolic framework embodied in equation 1.12 to document remarkable patterns in populations, communities, and even ecosystems. Let us look at one example at two of these levels: populations and interacting populations.

(1) Maximal population growth depends predictably on body mass and temperature. Although populations vary in number in complicated ways, one of the indisputable rules of population biology is that populations at low density and with large amounts of resources grow exponentially, with growth dictated by maximal intrinsic growth rates (r_{max}). Brown et al. (2004) found that, as predicted by equation 1.14, r_{max} scales with body mass to the –1/4 power, and depends on temperature with an energy of activation E_a equal to 0.68 eV. The populations of smaller and hotter organisms have the potential of growing faster than those of larger and cooler ones.

(2) The characteristics of interspecific interactions depend on temperature. Brown et al. (2004) compiled all the studies in which components of competitive or predator-prey interactions have been measured at several temperatures. They found that the rate of attack by predators and parasites, the feeding rate of herbivores, and the time that it takes for a species to exclude another one competitively all depend on temperature. Furthermore, the "energy of activation" of the temperature dependency of these components ranged from 0.56 to 0.81 eV. Brown et al. (2004) give more examples of the plethora of potential ecological applications of Gillooly's equation.

Equation 1.12 and the formulas that spin from it are the foundation of what Brown and his colleagues have called the "metabolic theory of ecology" or MTE. The MTE is a mechanistic synthetic framework that (1) characterizes the effects of body mass and temperature on metabolism, and (2) describes how metabolism dictates the effects of individuals on the pools, fluxes, and turnover of energy and materials in populations, communities, and ecosystems (Brown et al. 2004). Although we are enthusiastic about the MTE, we hasten to add two caveats. First, the MTE is a log-log theory that leaves a lot of residual variation unexplained. Most ecologists and physiologists are interested in understanding the factors that explain this residual variation. Second, the MTE concerns variation in pools, rates/fluxes, and times. We have argued in this chapter that these are important unifying themes in biology, but they are not the only themes. The MTE is not a theory of "everything" (Brown et al. 2004).

1.4 Using Historical Data in Comparative Studies

Previous sections emphasized that almost any prediction or comparison of physiological or life history data should begin with a consideration of the size and body temperature of the animal. There is another major factor that must be taken in consideration when comparing and even predicting traits among animals: we must have some information about the evolutionary history of the species under consideration. The use of phylogenetic information in comparative physiological studies is one of the main thrusts of evolutionary physiology, a vibrant, rapidly growing field that touches many, maybe most, of the topics included in this book. Because we emphasize ecology, our treatment of the importance of phylogenetics and evolution in ecological physiology will be cursory. We will not ignore evolution, but we will emphasize ecological applications of physiology. Readers must consult Feder et al.'s (2000) excellent review as a guide to evolutionary physiology. Because we will rely on phylogenetic data at several points in this book, a brief introduction to the tools that we will use is merited.

To motivate the use of phylogenetics in physiological ecology we will remind you of Calder's hypothesis (1984). He suggested that we could perceive adaptation in a trait as a deviation from the basic size-dependent allometric pattern resulting from selection. Calder suggested that animals may be similar because they are of the same size, but differ because they live in contrasting environments, feed on different foods, and so on. We often hypothesize that animals are similar because similar selective pressures have made them converge, and different because dissimilar selective pressures have made them diverge. How do we go about testing this hypothesis? In the old days (some say "good old days"), we

would have simply chosen two species (preferably related and of roughly the same size) but with different ecological habits. We would have made a directional prediction about differences in the magnitude of a physiological trait, and then examined in the laboratory or the field whether this prediction was correct. An enormous amount of extraordinarily important research was done in this way for many years.

But times change and so do research approaches. As pointed out by Garland and Adolph (1994) the "two-species comparison" approach is limiting and plagued with difficulties of all sorts. Briefly, there are many possible reasons why two species could show a statistically significant difference in a physiological trait: First, the process of speciation by itself may lead to differences; second, genetic drift and founder effects may also lead to nonadaptive divergence between species that experience little or no genetic exchange; and third, adaptive change will lead to divergence. Although it is only the third of these reasons that we are testing, the other two can lead to differences as well. For any two species, comparison of any physiological trait is likely to reveal a difference, given that the researcher has chosen a sufficient large sample of individuals. The solution, then, is to conduct a multispecies comparative study. If we fail to account for phylogenetic relationships, a multispecies comparison is flawed as well (figure 1.12). The problem with two-species comparisons and naive phylogeny-free multispecies comparisons is that they assume that species are statistically independent data points, when they are not (figure 1.12). Species are related by descent in a hierarchical fashion and hence, when one uses them as independent data points in statistical comparisons, one commits phylogenetic pseudoreplication (figure 1.11). The term pseudoreplication was coined by Hurlbert (1984) and refers to a statistical mistake that is committed all too often. This mistake consists in assuming that data are statistically independent when they are not. Hurlbert (1984) illustrates pseudoreplication with the following example: Imagine taking many subsamples within a lake and treating them as replicates from all lakes. A similar logic applies to comparative studies. The different species within a genus (or any monophyletic lineage) are not proper independent replicates.

Testing the hypothesis that there is an evolutionary correlation between a potential selective pressure (an environment or a diet) and a trait is tricky. It requires that we identify the number of evolutionary transitions in which a change in the selective pressure was accompanied by a change in the trait that we have chosen as a response variable. This comparison requires recognizing the phylogenetic relationships among the species in our comparison. Box 1.6 describes what we believe is the most commonly used method to test for evolutionary correlations: Felsenstein's phylogenetically independent contrasts (or PICs; Felsenstein 1985). This is one of a growing number of statistical methods used to

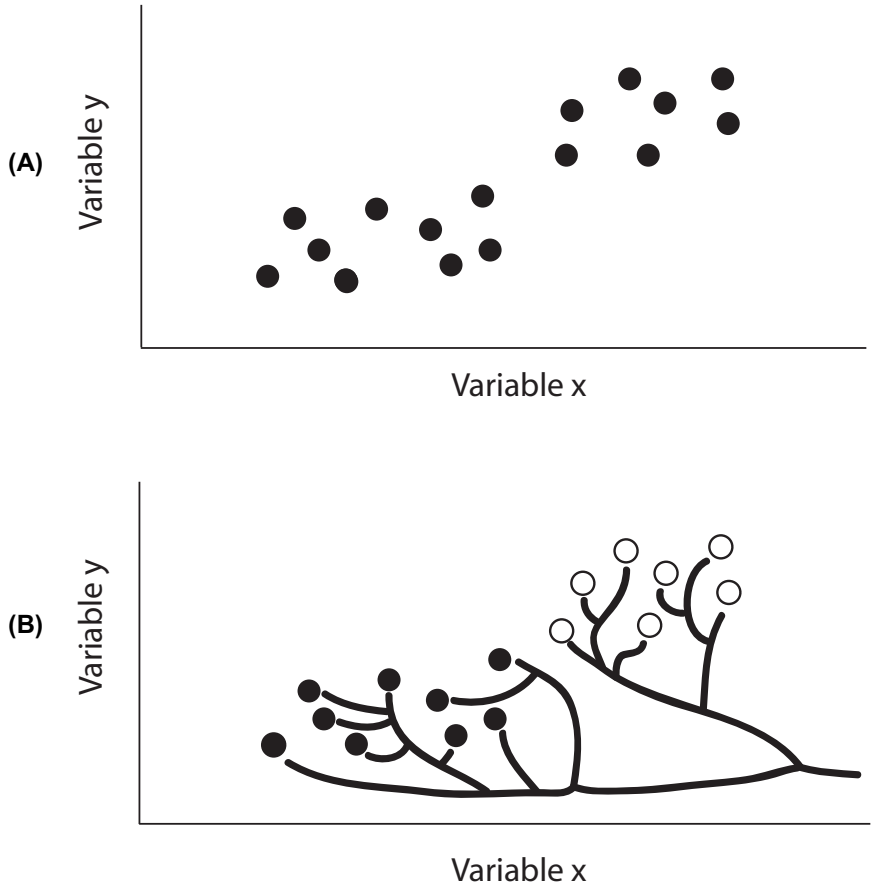

Figure 1.12. Imagine that you have hypothesized that when the diet (or any trait *x*) of an organism changes, then natural selection should favor a change in the expression of digestive enzymes (or any other relevant trait *y*). Thus, you predict that an interspecific comparison will reveal that *x* and *y* will be correlated across species. You assemble a sample of 15 species and plot *y* against *x*. When you perform a statistical test, you find that there is a highly significant correlation (panel A). You submit the result to a prestigious journal and one of the reviewers replies that your correlation is spurious, that the 15 species in your sample can be neatly divided into two monophyletic clades (i.e., two genera), and that hence your statistical test has inflated degrees of freedom. Your sample represents a single evolutionary divergence (panel B), and hence your sample size is reduced to $N = 2$. The reviewer is, of course, strictly right. Addressing her comment requires that you use the method described in box 1.6 (or one of its many alternatives; see Martins 2000). (Redrawn from Madison and Madison 1992.)

incorporate phylogenetic information in comparative studies. This book is not the place to review these methods. We suggest Martins' (2000) review and the references in it as a guide to the maze of phylogenetic comparative methods.

1.4.1 Limitations of Phylogenetic Analyses

Phylogenetic approaches to multispecies comparisons are not without drawbacks: They require physiological data on many species, and they require at least some phylogenetic information. Furthermore, the conclusions of phylogenetic comparative studies depend on the assumption that the phylogenetic tree is accurate and that the model of evolution assumed by the statistical method is correct. These are not minor considerations, and we have often worried that many of the methods available are too conservative (i.e., lack statistical power)

Box 1.6

Phylogenetically Independent Contrasts

Although the values of traits *x* and *y* in phylogenetically related species are not independent statistically, we can transform them into independent rates of evolutionary change between sister species or nodes. We will use the hypothetical phylogeny in panel A of figure 1.13 to describe the method developed by Felsenstein (1985) to estimate phylogenetically independent contrasts (PICs). We follow Felsenstein's (1985) explanation very closely. Step 1 is to choose two species at the tip that share a common ancestor (say 1 and 2), and to compute the contrast $X_1 - X_2$. Assuming that evolution proceeds by Brownian motion (in our view a fairly iffy assumption for traits of physiological and ecological significance), this contrast has an expected value of 0 and a variance proportional to $v_1 + v_2$ (v_1 and v_2 are branch lengths proportional to time since divergence). Step 2 is to remove these two tips, leaving behind ancestor 7, which now becomes a tip. In step 3, we assign this ancestor a value equal to the average of X_1 and X_2 weighted by the lengths of the branches, v_1 and v_2 (i.e., we place less value on tips with longer branches):

$$X_7 = \frac{[(1/v_1)X_1 + (1/v_2)X_2]}{(1/v_1 + 1/v_2)} \qquad (1.6.1)$$

Finally, in step 4 we lengthen the branch below node 7 by increasing its length from v_7 to $v_7 + v_1v_2/(v_1 + v_2)$. This lengthening occurs because X_7 is estimated with error. After doing this, we have constructed one contrast and reduced the number of tips by one. Then we continue to repeat these steps until we have only one tip left in the tree. If there were *n* species, this procedure would produce $n - 1$ contrasts (panel A of figure 1.13). To bring all the contrasts to a common variance, each contrast can be divided by the square root of its variance (i.e., contrast 1 can be divided by $(v_1 + v_2)^{1/2}$). Then you have to do it all over again for trait *Y* and correlate the contrasts in *X* with those in *Y*. For allometric relationships the value of a trait is log transformed before constructing contrasts. Because no evolutionary change in *X* should lead to no change in *Y*, the regression between contrasts is constructed through the origin.

The method described here is probably the most widely used of all comparative approaches. Therefore it is wise to lists some of its assumptions and the consequences that these can have. The most important assumption is that traits evolve by Brownian motion, that is, that traits (which are assumed to be continuous) diverge as a result of random wanderings through time. Panel B of figure 1.13 (after Harvey and Pagel 1991)

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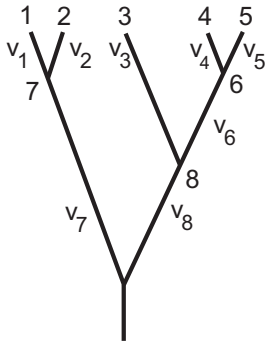


Contrast	Variance
$X_1 - X_2$	$v_1 + v_2$
$X_4 - X_5$	$v_4 + v_5$
$X_3 - X_6$	$v_3 + v'_6$
$X_7 - X_8$	$v'_7 + v'_8$

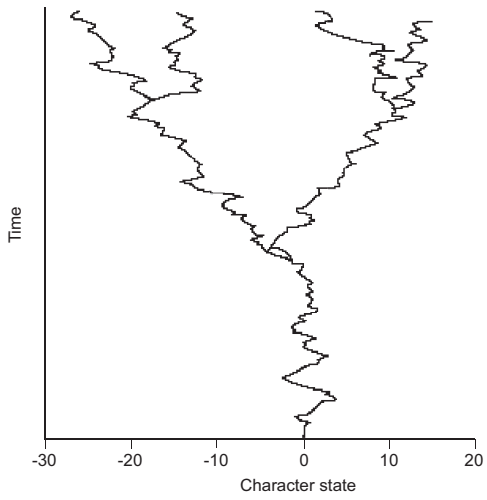
(A)

Where:

$$X_6 = \frac{v_4 X_5 + v_5 X_4}{v_4 + v_5} \qquad v'_6 = v_6 + v_4 v_5 / (v_4 + v_5)$$

$$X_7 = \frac{v_2 X_1 + v_1 X_2}{v_1 + v_2} \qquad v'_7 = v_7 + v_1 v_2 / (v_1 + v_2)$$

$$X_7 = \frac{v'_6 X_3 + v_3 X_6}{v_3 + v'_6} \qquad v'_8 = v'_7 + v_3 v'_6 / (v_3 + v'_6)$$



(B)

Figure 1.13. (panel A) Constructing phylogenetically 4 independent contrasts (PICs) in a phylogenetic tree with 5 species requires reconstructing 3 ancestors (nodes 6, 7, and 8). The table under the phylogeny demonstrates the calculations needed to estimate each contrast and its variance. (Panel B) Using PICs to establish an evolutionary correlation assumes that the traits under study evolve by Brownian motion. (Panel C) Using PICs to determine whether desert ringtails have lower basal metabolic rates (BMR) than expected from their body mass.

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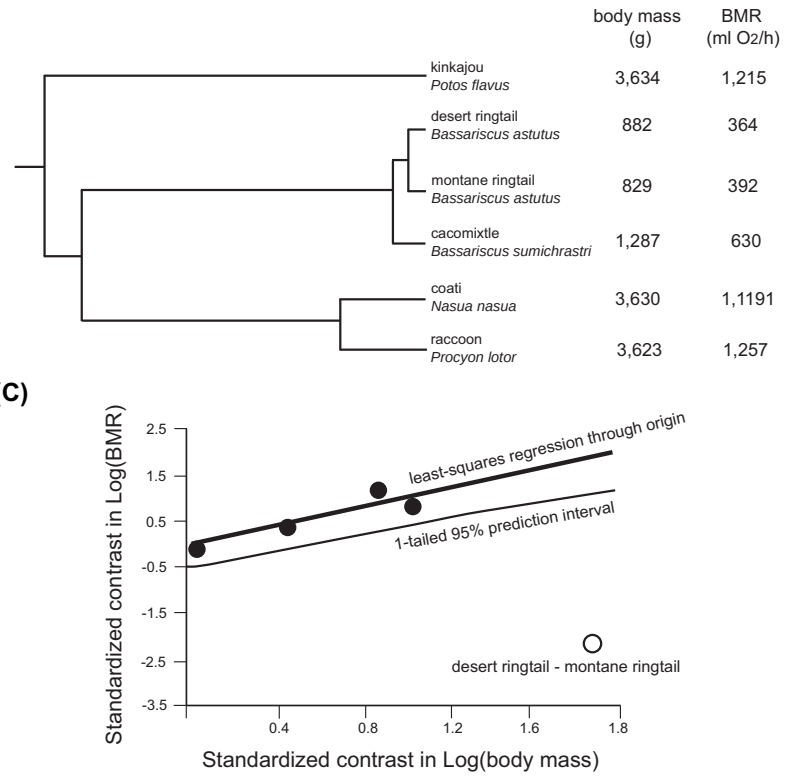

depicts the change in a trait in four lineages that follow random walks after splitting from a common ancestor at time 0. There is a lineage split at *n*2 and two more splits at *n*4 and *n*5. There are many reasons to be skeptical about using a random walk as a model for the evolution of traits. For example, there may be persistent selective pressures over time due to common selective regimes. This persistent selection may lead to trait conservatism and "clumping" in the values of the traits in some of the clades of the phylogeny. Cruz-Neto et al. (2001 and references there) discuss some of the problems that the potential collinearity between phylogeny and function has for a comparative analysis that relies on PICs. Briefly, under these conditions all the large evolutionary changes occur in deep nodes. This is problematic, because, as we have seen, contrasts that involved reconstructed ancestors tend to be small and hence close to the origin of a regression line. Collinearity between phylogeny and the traits reduces the power of comparative analyses. Garland et al. (1993) and Vanhoodydonck and van Damme (1999) discuss in some detail the issue of power in comparative analyses.

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Panel C of figure 1.13 presents an example of the use of PICs developed by Garland and Adolph (1994) using data from Chevalier (1991). The question is whether desert ringtails (*Bassariscus astutus*) have evolved lower metabolic rate than would be expected for a procyonid mammal of their size. To answer this question, Garland and Adolph (1994) compiled a phylogenetic tree for a group of closely related procyonids. They then conducted all the steps described above to construct a regression line between the contrast in the logarithm of body mass and the contrast in the logarithm of basal metabolic rate. However, they left out the contrast between montane and desert ringtails. Because Chevalier had expected desert ringtails to have lower than expected metabolic rates, they constructed a one-tailed confidence interval for this regression line. In a final step, they plotted the contrast that includes the desert ringtail. This contrast was, as expected, lower than the 95% confidence interval. This result is the consequence of 3 possible processes: (1) the desert ringtail evolved low metabolic rates, (2) the montane ringtail evolved high ones, or (3) both groups diverged up and down from the average value of their common ancestor. Standardized phylogenetic contrasts are nondirectional and do not allow differentiating among these options. To answer which one of these options is the correct one, we require supplementary paleontological and/or biogeographical knowledge. Chevalier (1991) used this type of additional evidence to propose that desert ringtail lineage evolved lower metabolism. We encourage readers to use the method described in the first paragraph of this box to reconstruct the results of Garland and Adolph's (1994) analyses. If the idea of spending 30 minutes with a calculator is unappealing, we suggest using one of the many free computer programs available to conduct PICs analyses. We recommend PDAP (Phenotypic Diversity Analysis Programs, v. 5; Garland et al. (1993, 1999), CAIC (developed by Purvis and Rambaut 1995, http://www.bio.ic.ac.uk/evolve/software/caic), and COMPARE 4.4 (developed by Martins 2001, http://compare.bio.indiana.edu).

and assume an unrealistic model of evolution (see Schondube et al. 2001, for example). We fear that an undue emphasis on "phylogenetical correctness" will impede and stifle comparative studies. Many interesting groups lack adequate phylogenetic information and it would be folly to shun their study. It will be a sad day when all ecological and evolutionary physiologists limit their attention to a few well-studied model organisms and taxa. Our domain of study is life's functional diversity and hence we advocate an opportunistic approach: If a phylogenetic approach is possible, use it. If it is not because a phylogenetic tree is not available or because the phylogenetic structure of the group that you are

interested in does not satisfy the assumptions of a comparative method, conduct the study anyway. Your study may inspire a systematist to study the phylogenetic relationships of your group or an evolutionary statistician to develop a method to test the hypotheses generated by your investigation. Phylogenetically informed comparative analyses are a central element of physiological ecology, but they should not be automatic or obligatory.

Having made a plea for phylogenetic tolerance, we emphasize the importance of considering all the phylogenetic data available when conducting a comparative study. Phylogenetic information does a lot more than allowing comparative physiologists the use of statistically rigorous methods. Perhaps more importantly, phylogenetics provides us with a map to the history of the traits that we study. David Winkler (2000) divides phylogenetically informed comparative approaches into two broad categories: the convergence approach (also called the "functional" approach), and the homology approach. The method of PICs is an example of the convergence approach that aims to look *across* phylogenetic lineages at repeated changes in traits and correlates these changes with changes in ecological circumstances or with changes in other traits. The homology approach explores unique events *within* lineages. The convergence approach strives to solve the problem of phylogenetic pseudoreplication. The homology approach recognizes that life's history has been punctuated by many important single events. Dealing with rare, or single, events precludes statistics and hence the homology approach has no pretense of statistical rigor. It simply attempts to map the evolutionary transitions that have occurred along the history of a lineage. Although the approach is descriptive, it causes us to focus carefully on the traits that we are interested in and to think about the kinds of forces that may have produced the observed changes in a lineage. We will provide many examples of the use of "homology thinking" throughout this book.

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