

## 6

# Life-history strategies

- Diversity of life histories
- Power laws
- The metabolic theory of ecology
- The pioneering work of Cole and Lewontin
- The MacArthur and Wilson  $r$ - and  $K$ -selection theory
- Cost of reproduction, allocation of energy, and clutch sizes
- Predation and life histories
- The Grime model of life histories for plants

### 6.1 Introduction

To the uninitiated, nothing could be worse than accompanying a bunch of “birders” on a field trip. They keep stopping, peering through their binoculars, whispering to each other, and motioning you to keep quiet. Why are they so fascinated with birds? Aren’t they all pretty much the same?

Of course not. Even the most naive non-biologist knows that birds come in an amazing variety of colors and sizes; amateur birders are legion. What we are interested in exploring in this chapter, however, is the variety and potential adaptive value of life histories found in all groups of organisms. Since ornithologists such as David Lack have contributed so much to our understanding of life histories, we begin by using birds to illustrate the complexity and diversity of life histories. These accounts are mostly based on Janzen (1983).

- 1 The groove-billed ani (*Crotophaga sulcirostris*) is a common and conspicuous bird found in the lowlands and mid-elevations of Central America. Females are about 65 g in mass, but lay extremely large 11 g eggs. Since each female may deposit 4–8 eggs in the nest, the combined total mass of her eggs may exceed her body weight. What is more extraordinary, however, is that this species engages in a communal breeding system. The birds live and breed in a group ranging from two to eight adults, with an equal number of males and females. The group defends a common territory, year-round. A single nest is

constructed and all females deposit their eggs in it, forming a communal clutch. All members of the group contribute to incubation and feeding of the nestlings. Anis are highly social, roosting and sleeping in close contact with each other while engaging in mutual grooming. However, Vehrencamp (1977, 1978) found that there are specific costs and benefits to the individuals participating in this group endeavor. For example, there are individual differences in the number of eggs that get into the nest, in the amount of time and effort put into incubation, and in the care of the nestlings. Furthermore, the eggs and offspring of the dominant females and males benefit the most. Dominant females lay their eggs last and actually remove eggs laid by other females from the nest. These dominant females then behave like brood parasites in that they actually put less effort into incubation and feeding than do the subordinate females. On the other hand, so-called alpha males, who have the most eggs in the nest (and the most to lose), perform a large share of the incubation. What is the advantage of communal nesting, especially for the subordinate birds? How do the dominant females get away with dumping the subordinates' eggs while they do less of the work?

- 2 The northern jacana (*Jacana spinosa*) is found from Costa Rica northward in Central America wherever there is floating aquatic vegetation. Jacanas have reversed the usual roles of the genders. Males build the nests and incubate and care for the young. Females lay one egg a day for four days in a typical clutch. Females are able to lay a second clutch of eggs elsewhere within 7 to 10 days, if necessary. The eggs are quite small (7.9 g) as compared with the average weight of the females (160.9 g). Males are smaller (mean weight of 91.4 g) than females. The mating system is polyandrous. Each male defends a small territory while each female defends a territory containing one to four males. Once chicks reach 12–16 weeks of age the females often provide a second clutch for the males to care for. The ratio of males to females varies seasonally and from place to place, but is often skewed in favor of the males. For example, the long-term average at Turrialba, Costa Rica was 2.3 males per female (Jenni 1983). Jacanas have a very high reproductive potential, but the hatching and fledging survivorship rates are very low.
- 3 The frigatebird (*Fregata magnificens*) is a large (800–1700 g) seabird with a life history that is unusual because of its low reproductive potential. Both sexes do not become mature until 5–8 years of age. Females breed only every other year and lay one egg in a clutch. The egg takes 55 days for incubation and the nestlings grow very slowly. They are fed primarily by the females for as long as 14 months. Given a 50 : 50 sex ratio, a new female is produced, on average, only every four years! The potential  $r$ -value for this species is extremely low, but by contrast survivorship of adults is very high. The life span is 40 or more years. What selective pressures resulted in a life history so radically different from that of most bird species?
- 4 Brown pelicans (*Pelecanus occidentalis*) are one of the best-known birds in the western hemisphere. They are found on both the Atlantic and Pacific coasts from North Carolina to Brazil and from British Columbia to Chile. Breeding colonies may contain as many as 500 pairs. An adult brown pelican weighs between 2 and 5 kg; it takes 3–5 years to attain adult plumage. Males and females share chick-raising duties equally, and the normal clutch size is three eggs. Incubation takes 30 days and the nestlings need 10–12 weeks to fledge.

Schreiber and McCoy visited a pelican colony four times during the breeding season of 1979 on Isla Guayabo in Costa Rica. Of 430 nests surveyed, most had three eggs, but the average was 2.42. By their fourth visit the number of surviving fledglings was 506, which was an average 1.18 per nest. The brown pelican is much larger than the frigatebird, has a much higher reproductive potential, but also has a lower survival rate.

- 5 Oropendolas [*Zarhynchus wagleri*], which are related to blackbirds and orioles, nest in colonies. Males weigh twice as much as females (212 versus 110 g) and they have been shown to take twice the energy to fledge as opposed to a female. As a result, male mortality among chicks is much higher during times of food scarcity. The sex ratio at colonies is normally 5 : 1 in favor of females. In Costa Rica, nesting begins with the dry season (December) and three complete breeding cycles are possible before the beginning of the rainy season in May. The normal clutch size is two, but breeding success is very low. The average number of chicks fledged per nest is 0.40. On the other hand, survivorship of adults is very high. Adults have been recorded living beyond the age of 26 in the field. By contrast to frigatebirds, which also have very long adult life spans, this species has a much higher reproductive potential.

So what have we learned about life histories from these birds? Nesting ranges from communal to colonial to pair-wise. Breeding systems vary from communal to polyandrous to simple pair bonds. Fecundity varies from one egg every other year to as many as eight in one clutch. Survivorship of the chicks is as low as only 0.40 per nest, but adult survivorship is as high as 40 years. What accounts for all this variation in life histories? Under what conditions do we find high versus low fecundity and/or survivorship? These are questions we want to attack in this chapter.

Another set of questions we wish to address concerns the relationship between the body size of an organism and its reproductive potential. Although body mass does not determine all aspects of life history, it is a powerful influence. For example, Fig. 6.1 is based on data for 24 species of mammals found in Costa Rica. The log of the length of the pre-reproductive period was graphed against the log of adult body mass. The obvious conclusion is that there is a higher likelihood of delay in reproductive maturity in the larger animals. Similarly, Fig. 6.2 demonstrates that animals with larger mass also have a longer interval between births. Litter size and total reproductive output per year were negatively associated with body mass, though the relationships were weak in this set of data.

Basic life-history equations were available early in the twentieth century (Lotka 1925). But a serious comparison of life-history parameters across a large number of species did not begin until 1954. In that year Frederick Smith and L.C. Cole published important papers that have become the foundation of life-history analysis.

Smith (1954) surveyed the literature and published what was known about  $r$ ,  $R_0$ , and  $G$  (generation time) at that time. Using the well-known relationship:

$$N_t = N_0 e^{rt}$$

and setting  $t =$  the generation time,  $G$ , we have:

$$N_G = N_0 e^{rG} \quad \text{and} \quad \frac{N_G}{N_0} = e^{rG}$$

Taking an equation from Chapter 1 we have:

$$N_G = N_0 R_0 \quad \text{and} \quad \frac{N_G}{N_0} = R_0$$

The result is:

$$R_0 = e^{rG} \quad (6.1)$$

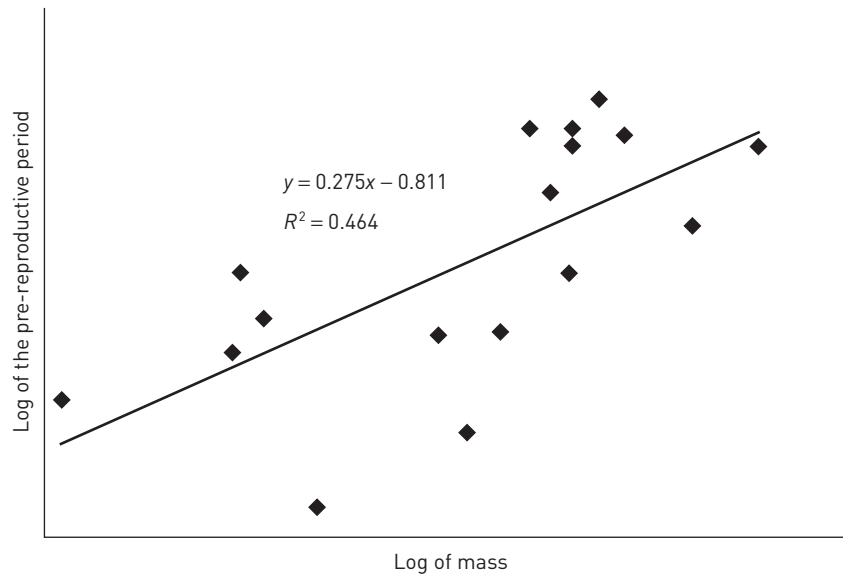
or

$$\ln R_0 = rG \quad (6.2)$$

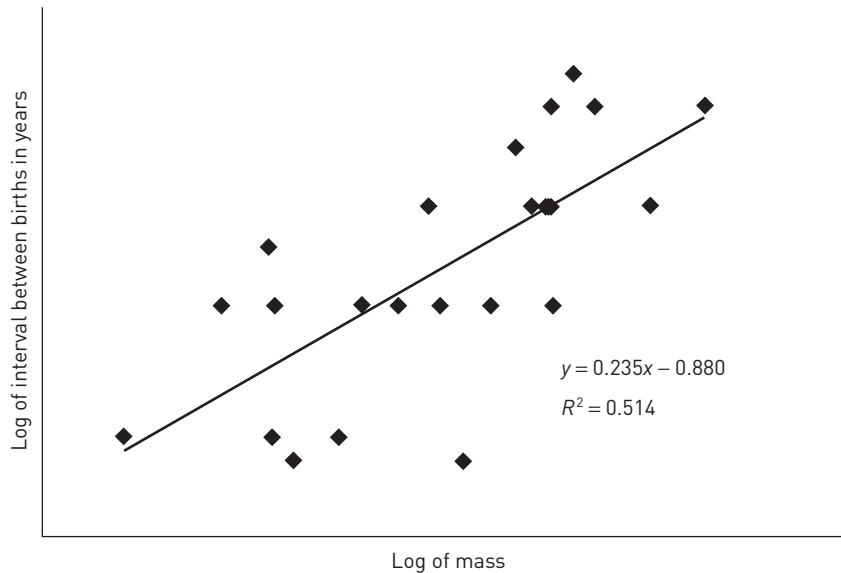
If two of these variables are known, the third can be determined, as least for a population with a stable age distribution. However, **there is no necessary relationship among all three of these variables.**

Smith (1954) and a number of more recent surveys of life histories have shown that:

- 1  $r$  is inversely related to generation time,  $G$ .  $r$ -values respond very strongly to generation time, as we will show later in this chapter.
- 2 Generation time is directly related to size. Since generation time is highly influenced by the length of the pre-reproductive period and by intervals between births, Figs 6.1 and 6.2 illustrate the relationship between these parameters and size (mass).



**Figure 6.1** Log length of the pre-reproductive period versus log of mass in 24 species of Costa Rican mammals. Data from Janzen (1983). Note that the slope is close to the predicted value of 0.25. Linear regression is significantly positive.



**Figure 6.2** Log interval between births in years as a function of the log of mass based on 24 species of Costa Rican mammals. Data from Janzen (1983). Note that the value of the slope is close to the predicted value of 0.25. Linear regression is significantly positive.

Points 1 and 2 lead to point 3:

- 3  $r$  is inversely related to size (mass);
- 4 life span and growth rate are negatively associated (Stearns 1992);
- 5 high individual growth rates are positively correlated with  $r$ ;
- 6 growth rate is inversely related to body mass.

In summary, small size is associated with fast growth rates, high  $r$ -values and short generation times, while organisms with large mass have slower growth rates, small  $r$ -values and long generation times (Smith 1954, Enquist *et al.* 1999).

Smith also speculated that  $r$  is related to the harshness of an animal's environment, and that large organisms live in a more benign world. That is, small environmental changes are less catastrophic for large organisms. This is a point made by Hanski (1999; see Chapter 5). He speculated that environmental stochasticity was reduced for larger organisms. By contrast, organisms with high  $r$ -values have the ability to recover more quickly from events that decimate their populations. Furthermore, over evolutionary time, the fossil record shows many lines of organisms continually increasing in size until they go extinct. This is known as "Cope's rule" (Southwood 1976).

The general questions are: Under what conditions is it advantageous to have a high  $r$ -value, combined with small size? Under what conditions will evolution select for large size, with its presumed lower  $r$ -value? Is it inevitable that large size must be combined with a low  $r$ -value?

## 6.2 Power laws

The relationship between size (mass) and a wide variety of metabolic, physiological, and ecological functions (everything from skeletal muscle contraction rate to incubation period to maximum life span) have been shown to follow general **power** or **scaling laws**:

$$Y = Y_0 M^b \quad (6.3a)$$

$M$  is mass;  $b$  is an allometric constant;  $Y$  is a physiological rate or some other variable dependent on mass; and  $Y_0$  is the normalization constant.

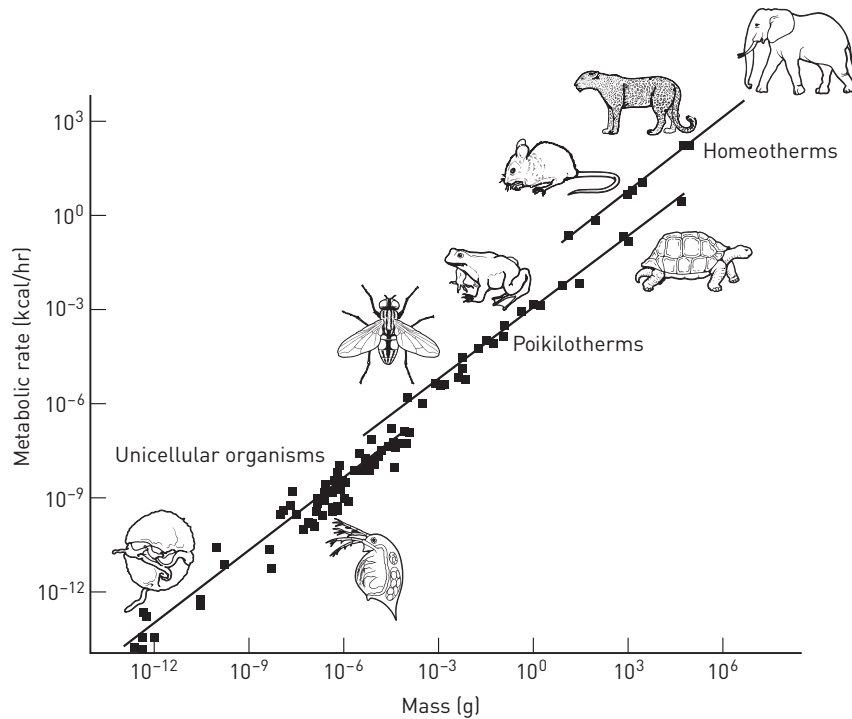
Taking the log of both sides of Equation 6.3a leads to Equation 6.3b, which shows us that on a log–log scale we can expect a linear relationship between mass and a dependent variable, with the slope equal to  $b$ .

$$\text{Log } Y = \log Y_0 + b \log M \quad (6.3b)$$

Amazingly, despite the fact that size ranges over 21 orders of magnitude (from bacteria to whales), these scaling laws consistently apply, and it has been asserted that  $b$  is a multiple of  $1/4$  (Brown *et al.* 2004). For example, heart rate versus mass scales as  $-0.25$ , life span versus mass as  $0.25$ , and the length of both mammalian aortas and tree trunks versus mass as  $0.25$  (West *et al.* 2000). These are known as allometric relationships because the scaling factor,  $b$ , is not equal to one. If  $b = 1$  the relationship would be isometric and plot as a straight line on both an arithmetic and a logarithmic axis. However, in these allometric relationships  $b$  is not equal to one. Kleiber (1932) showed long ago that the relationship between mass and basal metabolic rate followed an allometric relationship with  $b = 3/4$ . Figure 6.3 shows us that, in fact, the  $3/4$  relationship between metabolic rate and mass appears to apply to everything from unicellular organisms to both poikilothermic and homeothermic vertebrates. More recently West *et al.* (2000) claimed that  $M^{3/4}$  also “coincides with the respiratory rate . . . of mammalian mitochondria . . . [and] . . . even with that of the molecular respiratory complex and terminal oxidase molecular units within mitochondrial membranes!”

The  $3/4$ -power scaling relationship for animals was, and still is, known as Kleiber’s law. But a different scaling power was rooted in the botanical literature based on geometric or Euclidian principles. The basic idea is that “resources are acquired by surfaces and used by volumes” (Horn 2004). For example, a cell acquires nutrients across a two-dimensional surface area, but must distribute those resources throughout its three-dimensional volume. For a forest, the area of ground that a tree covers scales as the square of the diameter of ground area covered or shaded (canopy “footprint”). The volume scales according to volume or the cube of this same diameter. The number of individuals that can fit into a given area is assumed to be the reciprocal of the area covered. Plant volume and biomass were therefore proposed to be proportional to negative  $3/2$  (Equation 6.4a) of population density.

This is the basis, for example, of the “geometric model” of self-thinning. Agronomists and plant ecologists had proposed that mortality during the intraspecific self-thinning process followed a  $-3/2$  power law (Yoda *et al.* 1963). This law asserted that the mean weight per plant increased faster than density decreased. During the thinning process, if density ( $N$ ) and mean weight per plant ( $\bar{w}$ ) are points on a graph, over time these points will



**Figure 6.3** Allometric scaling of metabolic rate for organisms ranging from unicellular Protista to homeothermic mammals. The regression lines all have a slope of 0.75. After Hemmingsen (1960); reprinted with permission from the Steno Diabetes Center.

produce a linear relationship in which the slope will be  $-3/2$  (Eqns 6.4a and 6.4b). Total mass continues to increase until the constant final yield ( $C$ ) is reached.

$$\bar{w} = CN^{-3/2} \quad (6.4a)$$

$$\text{Log } \bar{w} = \text{Log } C - (3/2) \text{Log } N \quad (6.4b)$$

The  $-3/2$  power law, however, began to be questioned late in the twentieth century (Lonsdale 1990), since thinning exponents were shown to be highly variable among species. In a recent series of papers (West *et al.* 1997, Enquist *et al.* 1998) a different model was proposed. This model assumes that growth continues until it is limited by a resource, and that resources are acquired through branching, linear, or “fractal” networks that distribute resources throughout the organism. In plants, Enquist *et al.* (1998) used whole-plant xylem transport as an estimate of resource use. They found that resource use scales as the  $3/4$  power of mass, the same exponent that Kleiber found. West *et al.* (1997) and Enquist *et al.* (1998) therefore asserted that the real exponent in Equations 6.4a and 6.4b should be  $-4/3$ , not  $-3/2$ .

Again, the quarter-scaling rule has many applications in both animal and plant populations. Calder (1984) showed that maximum life span, reproductive maturity, incubation

time for birds, and a large number of metabolic functions scaled to the  $1/4$  power against body mass on a log–log scale. For example a regression line through  $\ln(\text{density})$  versus  $\ln(\text{mass})$  in terrestrial mammals has a slope of  $-0.77$  ( $b \approx -3/4$ ) (see fig. 6 of Brown *et al.* 2004). Enquist *et al.* (1998) showed that the population densities of both plant and animal populations scale as  $M^{-0.75}$ . From such similarities, they suggested that plants and animals share a similar scaling law that “reflects how resource requirements of individual organisms affect competition and spacing among individuals within ecological communities.”

West *et al.* (1997) and Enquist *et al.* (1998, 2000) have proposed the existence of a common mechanism underlying the scaling or power laws in both plants and animals. They assert that living things are sustained by the transport of materials through linear networks that branch to supply all parts of the organism. These networks include mammalian blood vessels and bronchial trees, plant vascular systems (xylem and phloem), as well as tracheal tubes in insects. Most of these distribution systems can be described as a branching network in which the size of the tubes decreases. This “vessel-bundle” structure is characteristic not only of plant vascular systems but also of vertebrate and invertebrate circulatory systems. These networks vary in the properties of the tubes, in the type of fluid transported (liquid to gas), and in the nature of the pump. A pulsating compression pump is found in cardiovascular systems, a bellows in respiratory systems, diffusion in insect tracheae, and osmotic and vapor pressure in plant vascular systems. In spite of these differences, West *et al.* (1997) proposed that they all follow the same scaling laws. The scaling laws are based on the following principles, to which all biological networks should adhere. (i) The system must fill the volume of the organisms so as to distribute essential nutrients to all of its cells. (ii) The terminal branches of these networks should be roughly the same size, regardless of body size. Indeed, capillary size does not vary much among animals, and the same is true of petioles or terminal xylem in plants. (iii) Supply networks should be so efficient that fluids move through them with a minimal loss of energy. Models of fluids flowing through networks lead to the conclusion that the summed cross-sectional areas of the “daughter” branches at each level should be equal to that of the “parent” branch. Such an area-preserving pattern is found in trees and in artery–arteriole branches. Enquist *et al.* (2000) have modeled the physical structures of the networks and substituted them into equations describing fluid volume and rate of flow in a system. The end result is a formula for metabolic rate versus mass with a scaling exponent of 0.75. In other words, their model successfully confirms the  $3/4$ -power scaling law.

In plants, Enquist *et al.* (1998, 2000) predicted that if the log of average mass per plant is graphed against density, the slope would be  $-0.75$ . However, since the independent variable is density, and mass is the dependent variable, the expected slope is the inverse of  $-3/4$ , or  $-4/3$ . Enquist *et al.* (1998) then gathered data on plants ranging from *Lemma* to *Sequoia* and showed that the slope is as predicted,  $-4/3$  with an  $R^2 = 0.963$  on the regression model. The slope of  $-3/2$ , predicted by the geometric model, was not found.

Enquist *et al.* (1998) concluded that both animals and plants share a common set of allometric relationships involving body mass, growth rates, life spans, and densities. Like all grand theories, there are likely to be complications and exceptions. Darveau *et al.* (2002) raised doubts about any “single cause” explanation for scaling of basal metabolic rates, since metabolic rates are controlled by a number of steps and not by any single rate-controlling factor. They believe that the scaling constant  $b$  in Equations 6.3a and 6.3b is based on the sum of multiple metabolic factors, not on a limit based on any one



metabolic rate. As Agutter and Wheatley (2004) point out, not everyone is convinced that a uniform scaling constant exists, and many other models of metabolic scaling have been proposed. Nevertheless, the group lead by Brown, Enquist, and West have gone so far as to propose a “metabolic theory of ecology.”

### 6.3 The metabolic theory of ecology

The metabolic theory is based on the 1/4-power law. Brown *et al.* (2004) begin by linking basic metabolic processes to body mass and temperature. Since metabolism determines the rate of acquisition of energy and nutrients by organisms, it determines the rate of resource use and sets constraints on the allocation of resources to growth, reproduction, and other components of fitness.

Given Kleiber's finding that metabolic rate scales according to  $b = 3/4$ , we can write an equation for whole-organism metabolic rate ( $I$ ) as a function of mass ( $M$ ) and a normalization constant,  $I_0$ . Again, the justification for the 1/4-power scaling is based on West *et al.* (1997, 1999a, 1999b), in which “whole-organism metabolic rate is limited by rates of uptake of resources across surfaces and rates of distribution of materials through branching networks. The fractal-like designs of these surfaces and networks cause their properties to scale as 1/4 powers of body mass or volume, rather than 1/3 powers that would be expected from Euclidean geometric scaling” (Brown *et al.* 2004).

$$I = I_0 M^{3/4} \quad (6.5)$$

Next, Brown *et al.* (2004) introduce the effect of temperature on biological processes. Biological activity increases exponentially with temperature, and a general equation for the kinetics of this process is described in Equation 6.6. In this equation  $E$  is the activation energy,  $k$  is the Boltzmann constant, and  $T$  is absolute temperature in degrees Kelvin. The Boltzmann factor describes how temperature affects reaction rate by changing the proportion of molecules with sufficient kinetic energy.

$$e^{-E/kT} \quad (6.6)$$

What interests us here is that nearly all biological rates are temperature-dependent, including population growth rates, development time, and life span (Brown *et al.* 2004).

The effect of mass and temperature on metabolic rates can be combined into one equation as shown below (Eqn. 6.7a), where  $i_0$  is a normalization constant independent of both body size and temperature. After taking the natural log of both sides of Equation 6.7a we have 6.7b:

$$I = i_0 M^{3/4} e^{-E/kT} \quad (6.7a)$$

$$\ln(IM^{-3/4}) = -E(1/kT) + \ln(i_0) \quad (6.7b)$$

Equations 6.7a and 6.7b essentially predict that mass-corrected whole-organism metabolic rate is a linear function of the inverse of absolute temperature ( $1/kT$ ). Metabolic rate, in turn, determines the rate of resource acquisition from the environment. Brown *et al.*