



TABLE CONTENTS

3. ALLOMETRIC EQUATIONS	3-1
3.1. FOOD INGESTION RATES	3-3
3.1.1. Birds	3-4
3.1.2. Mammals	3-5
3.1.3. Reptiles and Amphibians	3-6
3.2. WATER INTAKE RATES	3-7
3.2.1. Birds	3-8
3.2.2. Mammals	3-10
3.2.3. Reptiles and Amphibians	3-10
3.3. INHALATION RATES	3-11
3.3.1. Birds	3-11
3.3.2. Mammals	3-12
3.3.3. Reptiles and Amphibians	3-12
3.4. SURFACE AREAS	3-13
3.4.1. Birds	3-13
3.4.2. Mammals	3-14
3.4.3. Reptiles and Amphibians	3-14
3.5. ALLOMETRIC EQUATIONS FOR METABOLIC RATE	3-15
3.5.1. Birds	3-18
3.5.1.1 Basal Metabolic Rate	3-19
3.5.1.2 Existence Metabolic Rates	3-20
3.5.1.3 Free-Living Metabolic Rate	3-22
3.5.1.4 Temperature and Metabolic Rate	3-24
3.5.2. Mammals	3-26
3.5.2.1 Basal Metabolic Rate	3-26
3.5.2.2 Resting Metabolism	3-27
3.5.2.3 Field Metabolic Rate	3-27
3.5.2.4 Temperature and Metabolic Rate	3-28
3.5.3. Reptiles and Amphibians	3-29
3.5.3.1 Basal and Resting Metabolic Rates	3-29

TABLE CONTENTS

3.5.3.2.	Free-Living Metabolic Rates	3-30
3.6.	MATH PRIMER AND UNIT CONVERSIONS	3-32
3.6.1.	Summary of Operations Involving Logarithms	3-32
3.6.2.	Summary of Operations Involving Powers	3-32
3.6.3.	Unit Conversions	3-33
3.6.3.1.	Approximate Factors for Metabolic Equations	3-33
3.6.3.2.	Exact Conversions	3-33
3.7.	ESTIMATING CONFIDENCE INTERVALS	3-34
3.8.	REFERENCES	3-38

LIST OF TABLES

Table 3-1. Metabolizable Energy (ME) of Various Diets for Birds and Mammals	3-5
Table 3-2. Allometric Equations for Basal Metabolic Rate (BMR) in Birds	3-21
Table 3-3. Regression Statistics for Nagy's (1987) Allometric Equations for Food Ingestion Rates for Free-Living Animals	3-36
Table 3-4. Regression Statistics for Nagy's (1987) Allometric Equations for Free-Living (Field) Metabolic Rates	3-37

LIST OF FIGURES

Figure 3-1. Monthly Variation in Energy Budget Estimated for a House Sparrow	3-25
---	-------------

3. ALLOMETRIC EQUATIONS

Values for key contact rate factors such as food and water ingestion rates have been measured for few wildlife species. In this section, we describe allometric equations that can be used to estimate several exposure factors on the basis of animal body weight using models derived from taxonomically similar species. We emphasize, however, that measured values from well-conducted studies on the species of concern are likely to be more accurate and to have narrower confidence limits.

Allometry is defined as the study of the relationships between the growth and size of one body part to the growth and size of the whole organism; however, allometric relationships also exist between body size and other biological parameters (e.g., metabolic rate). The relationship between the physiological and physical parameters and body weight frequently can be expressed as:

$$Y = a Wt^b \pm \text{SE of } Y, \text{ or} \quad [3-1]$$

$$\log Y = \log a + b \log Wt \pm \text{SE of } \log Y \quad [3-2]$$

where Y is the biological characteristic to be predicted, Wt is the animal's body weight (mass), a and b are empirically derived constants, and SE is the standard error of the mean value of the parameter.

Equation 3-2 is the log transformation of Equation 3-1. Equation 3-2 represents a straight line, with b equal to the slope of the line and $\log a$ equal to the Y -intercept of the line. Values for a and b usually are determined empirically from measured values using linear regression analysis. Once values are determined for a and b , Equation 3-1 can be used to predict a value of Y from the body weight of the animal. The SE of Y is the standard error of the mean Y estimated for the mean of the Wt values; the SE of $\log Y$ is the standard error of the mean $\log Y$ estimated for the mean of the $\log Wt$ values.

Allometric equations can be used to estimate parameter values for species for which measured values are not available. The equations presented in this chapter, however, should not be used for taxonomic categories other than the category for which each was developed. For example, equations developed for iguanid lizards cannot be used for amphibians and should not be used for other groups of reptiles without careful evaluation of likely differences between the groups. It also is important to remember that the allometric equations presented in this chapter have been developed using mean values for a number of species within a taxonomic category. Individual species usually exhibit values somewhat different from those predicted by an allometric model based on several species. Furthermore, different-sized individuals within a species and individuals at varying stages of maturation are likely to exhibit a different allometric relationship between body weight and the dependent variable. For further discussion of within-species allometric equations related to growth and reproduction, see Reiss (1989).

In the next five sections, we describe empirically derived allometric equations that relate food ingestion rates (Section 3.1), water intake rates (Section 3.2), inhalation rates (Section 3.3), surface area (Section 3.4), and metabolic rate (Section 3.5) to body weight. As discussed above, most of the allometric models differ for birds, mammals, reptiles, and amphibians, and many also vary within these taxonomic groups. In Section 3.6, we provide a summary of operations involving logarithms and powers and unit conversion factors for those persons who may want to modify allometric equations found in the literature. Finally, in Section 3.7 we describe how to estimate 95-percent confidence intervals for food ingestion rates and free-living metabolic rates predicted on the basis of allometric equations presented in this chapter. We present most equations in the untransformed form only. For equations for which an investigator reported standard errors for the log transformation of the relationship, we present the equation both ways. For those persons interested in estimating confidence intervals for other allometric equations, Peters (1983) provides a simple review of how to estimate regression statistics for equations of the form of Equation 3-2. Section 3.8 contains the references for this chapter.

3.1. FOOD INGESTION RATES

Food ingestion rates vary with many factors, including metabolic rate, the energy devoted to growth and reproduction, and composition of the diet. The metabolic rate of free-ranging animals is a function of several factors, including ambient temperature, activity levels, and body weight. In birds and mammals, thermoregulation can considerably increase an animal's metabolic requirements during the winter, whereas reproductive efforts can replace thermoregulation as the predominant extra metabolic expenditure in the spring and summer. Many reptiles and amphibians, on the other hand, drop their activity levels and metabolic rates in the winter.

For homeotherms (i.e., animals that maintain a relatively constant body temperature such as most birds and mammals), metabolic rate generally decreases with increasing body mass (see Section 3.5). The smallest birds and mammals must consume quantities of food equal to their body weight or more daily; in contrast, the larger homeotherms may consume only a small fraction of their body weight in food daily. Herbivores tend to consume larger quantities of food than carnivores because of the lower energy content of their food. Ingestion rates, expressed in units of food energy normalized to body size (e.g., kcal/kg-day), are not significantly different for herbivores and carnivores (Peters, 1983). Four-legged poikilotherms (those animals whose usual body temperatures are the same as that of their environment, such as reptiles and amphibians) exhibit the same slope of decreasing ingestion rates per unit body weight with increasing body size but show a lower intercept (i.e., lower ingestion rate for a given body weight) than homeotherms (Nagy, 1987).

The rate of food consumption that an animal must achieve to meet its metabolic needs can be calculated by dividing its free-living (or field) metabolic rate (FMR) (see Section 3.5) by the metabolizable energy in its food (Nagy, 1987). Metabolizable energy (ME) is the gross energy (GE) in a unit of food consumed minus the energy lost in feces and urine. Assimilation efficiency (AE) equals the ratio ME/GE , or the fraction of GE that is metabolizable. AE is relatively constant among different groups of consumer species of mammals and birds that are all either carnivorous, insectivorous, herbivorous, or

granivorous (Hume, 1982; Peters, 1983; Nagy, 1987; Robbins, 1983). Nagy (1987) calculated the mean ME (i.e., kilojoules of ME per gram of dry matter) of various diets for birds and mammals from average values of AE for birds and mammals and typical GE contents of those diets as reported by Golley (1961) and Robbins (1983). These values are presented in Table 3-1. (For more information on ME and AE, see Section 4.1.2.) Using the values presented in Table 3-1, Nagy (1987) developed allometric equations for food ingestion (FI) rates as a function of body weight (Wt) for birds, mammals, and lizards using estimated FMRs and general dietary composition. In the remainder of this section, we present these equations for birds (Section 3.1.1) and mammals (Section 3.1.2). Section 3.1.3 summarizes Nagy's food ingestion allometric equations for iguanid lizards. We report this information even though no iguanid lizards were among our selected species because it is the only information of this type we identified for any amphibian or reptile.

Nagy's (1987) estimates of FMR are based on doubly labeled water measurements of CO₂ production in free-living animals. When performed correctly, this method is more accurate for estimating the metabolic rate of free-living animals than other methods commonly used (King, 1974). Other allometric equations for food ingestion rates that we identified in the open literature are based largely on captive animals without corrections for the additional energy requirements of free-living animals. For more accurate estimates of food ingestion rates by type of diet, we recommend following the procedures outlined in Section 4.1.2 instead of using these generic equations.

3.1.1. Birds

For birds, Nagy (1987) calculated FI rates (in grams dry matter per day) from ME and FMR and developed the following equations:

$$\text{FI (g/day)} = 0.648 \text{ Wt}^{0.651} \text{ (g), or} \qquad \text{all birds} \qquad [3-3]$$

$$\text{FI (kg/day)} = 0.0582 \text{ Wt}^{0.651} \text{ (kg)}$$

$$\text{FI (g/day)} = 0.398 \text{ Wt}^{0.850} \text{ (g)} \qquad \text{passerines} \qquad [3-4]$$

Table 3-1. Metabolizable Energy (ME) of Various Diets for Birds and Mammals

Diet	Metabolizable Energy		Animal Group
	(kJ/g) ^a	(kcal/g) ^a	
insects	18.7	= 4.47	mammals
	18.0	= 4.30	birds
fish	18.7	= 4.47	mammals
	16.2	= 3.87	birds
vegetation	10.3	= 2.26	mammals
seeds	18.4	= 4.92	mammals
nectar	20.6	= 4.92	hummingbirds
omnivory	14	= 3.35	mammals and birds

^ag = grams dry weight.
Source: Nagy, 1987.

$$FI \text{ (g/day)} = 0.301 Wt^{0.751} \text{ (g)} \quad \text{non-passerines} \quad [3-5]$$

$$FI \text{ (g/day)} = 0.495 Wt^{0.704} \text{ (g)} \quad \text{seabirds} \quad [3-6]$$

where *Wt* equals the body weight (wet) of the animal in grams (g) or kilograms (kg) as indicated. We provide the regression statistics for these equations (including sample size and regression coefficient) and information required to estimate a 95-percent confidence interval for an FI rate predicted for a specified body weight in Section 3.7. More accurate estimates of food requirements can be made from estimates of FMR (Section 3.5), dietary composition, and AE for the species of interest, as outlined in Section 4.1.2.

3.1.2. Mammals

For placental mammals, Nagy (1987) calculated FI rates (in grams dry matter per day) from ME and FMR values and developed the following equations:

$FI \text{ (g/day)} = 0.235 Wt^{0.822} \text{ (g)}$, or	all mammals	[3-7]
$FI \text{ (kg/day)} = 0.0687 Wt^{0.822} \text{ (kg)}$		

$FI \text{ (g/day)} = 0.621 Wt^{0.564} \text{ (g)}$	rodents	[3-8]
---	---------	-------

$FI \text{ (g/day)} = 0.577 Wt^{0.727} \text{ (g)}$	herbivores	[3-9]
---	------------	-------

We provide the regression statistics for these equations (including sample size and regression coefficient) and information required to estimate a 95-percent confidence interval for an FI rate predicted for a specified body weight in Section 3.7. More accurate estimates of food requirements can be made from estimates of FMR (Section 3.5), dietary composition, and AE for the species of interest, as outlined in Section 4.1.2.

Herbivores tend to consume more food than carnivores or omnivores on a dry-weight basis because of the lower energy content of the herbivores' diets. On an energy basis (e.g., kilocalories), the ingestion rates of carnivores and herbivores are not significantly different (Farlow, 1976):

$FI \text{ (kjoule/day)} = 971 Wt^{0.73} \text{ (kg)}$ ($r^2 = 0.942$), or	herbivores	[3-10]
$FI \text{ (kcal/day)} = 1.518 Wt^{0.73} \text{ (g)}$		

$FI \text{ (kjoule/day)} = 975 Wt^{0.70} \text{ (kg)}$ ($r^2 = 0.968$), or	carnivores	[3-11]
$FI \text{ (kcal/day)} = 1.894 Wt^{0.70} \text{ (g)}$		

3.1.3. Reptiles and Amphibians

This section summarizes food ingestion allometric equations for iguanid lizards, which is the only information of this type we identified for any amphibian or reptile. Nagy (1987) calculated FI rates (in grams dry matter per day) from ME and FMR values on spring and summer days and developed the following equations:

$$\text{FI (g/day)} = 0.019 \text{ Wt}^{0.841} \text{ (g)} \quad \text{herbivores} \quad [3-12]$$

$$\text{FI (g/day)} = 0.013 \text{ Wt}^{0.773} \text{ (g)} \quad \text{insectivores} \quad [3-13]$$

Again, on an energy basis, carnivores and herbivores are not significantly different and can be represented by a single relationship:

$$\text{FI (kjoule/day)} = 0.224 \text{ Wt}^{0.799} \text{ (g)}, \text{ or} \quad \text{all iguanids} \quad [3-14]$$

$$\text{FI (kcal/day)} = 0.054 \text{ Wt}^{0.799} \text{ (g)}$$

We provide the regression statistics for these equations (including sample size and regression coefficient) and information required to estimate a 95-percent confidence interval for an FI rate predicted for a specified body weight in Section 3.7. More accurate estimates of food requirements for these and other groups of reptiles and amphibians can be made from estimates of FMR (Section 3.5), dietary composition, and AE for the species of interest, as outlined in Section 4.1.2.

Allometric equations for FI rates for other groups of reptiles and amphibians were not found. For other groups, we recommend estimating FI rates from FMR and diet, as described in Section 4.1.2.

3.2. WATER INTAKE RATES

Daily water requirements depend on the rate at which animals lose water to the environment due to evaporation and excretion. Loss rates depend on several factors, including body size, ambient temperature, and physiological adaptations for conserving water. Drinking water is only one way in which animals may meet their water requirements. All animals produce some water as a product of their metabolism. The degree to which metabolic water production and dietary water content can satisfy an animal's water requirements varies from species to species and with environmental conditions. Extensive literature describes the allometry of total water flux for various

groups of animals. Allometric models to predict drinking water intake, on the other hand, are limited.

3.2.1. Birds

Based on measured body weights and drinking water values from Calder (1981) and Skadhauge (1975), Calder and Braun (1983) developed an equation for drinking water ingestion (WI) for birds:

$$\text{WI (L/day)} = 0.059 \text{ Wt}^{0.67} \text{ (kg)} \qquad \text{all birds} \qquad [3-15]$$

where Wt equals the average body weight in kilograms (kg) of the bird species. This equation is based on data from 21 species of 11 to 3,150 g body weight. Total water turnover should be proportional to metabolic rate (body weight to the 3/4 power, see Section 3.5.2.1). The exponent for Equation 3-15 is not significantly different from 0.75 (Calder and Braun, 1983). Additional sources of water not accounted for in this equation (metabolic water and water contained in food) also help to balance the animals' daily water losses. For allometric equations for total water flux (including water obtained from food) for birds, see Nagy and Peterson (1988).

To estimate daily drinking water intake as a proportion of an animal's body weight (e.g., as g/g-day), the WI rate estimated above is divided by the animal's body weight in kg:

$$\begin{aligned} \text{WI (g/g-day)} &= \text{WI (kg/kg-day)}, \text{ or} && [3-16] \\ &= \text{WI (L/day)} / \text{Wt (kg)} \end{aligned}$$

In general, birds drink less water than do mammals of equivalent body weights. Because of their relatively high metabolic rates, the quantity of metabolic water produced by birds is greater in relationship to body size than that produced by other vertebrates (Bartholomew and Cade, 1963). In addition, birds are able to conserve water by excreting nitrogen as uric acid instead of urea (as excreted by mammals); uric acid can be excreted

in a semi-solid suspension, whereas urea must be excreted in aqueous solution. On the other hand, birds exhibit a high rate of water loss from the respiratory system and use panting and evaporative water loss to prevent overheating at high ambient temperatures. For example, Dawson (1954) found evaporative losses in two species of towhees to increase fourfold between 30 and 40°C.

Although birds may satisfy some of their water needs by oxidative food metabolism, it has not been demonstrated that any normally active bird can satisfy its water requirements with metabolic water alone (Bartholomew and Cade, 1963). The balance must be obtained from water contained in foods such as insects or succulent plant material and from drinking water.

As would be expected, birds drink more water at warmer temperatures to make up for evaporative losses. Seibert (1949) found that juncos (weighing 16 to 18 g) consumed an average of 11 percent of their body weight in water daily at an ambient temperature of 0°C, 16 percent at 23°C, and 21 percent at 37°C. The white-throated sparrow increased water consumption from 18 percent of its body weight at 0°C to 27 percent at 23°C and 44 percent at 37°C.

Water consumption rates per unit body weight also tend to decrease with increasing body weight within a species. For example, in white leghorn chickens, water intake per gram of body weight is highest in the youngest chicks (45 percent of the body weight at 1 week when chicks average 62 g) and decreases with age thereafter (13 percent of the body weight at 16 weeks when chicks average 2.0 kg) until egg-laying, when water consumption increases for the production of eggs (24 percent of the body weight for laying hens) (Medway and Kare, 1959).

Some species obtain more of their daily water needs from their diet and therefore drink less water than others; therefore, measured water ingestion values from well-conducted studies should be used when available. In the absence of measured values, Equation 3-15 should provide a reasonable central value. Additional information required to estimate a 95-percent confidence interval was not provided along with this equation.

3.2.2. Mammals

Based on measured body weights and drinking water values from Calder (1981) and Skadhauge (1975), Calder and Braun (1983) developed an allometric equation for drinking water ingestion (WI) for mammals:

$$WI \text{ (L/day)} = 0.099 Wt^{0.90} \text{ (kg)} \qquad \text{all mammals} \qquad [3-17]$$

where Wt equals the average body weight in kilograms (kg). Additional sources of water not accounted for in this equation (i.e., metabolic water and water contained in food) help to balance the animals' daily water losses. The empirically determined exponent of 0.90 does not suggest a simple physiological explanation. If total water turnover (metabolic water combined with water obtained from food) is proportional to metabolic rate (body weight to the 3/4 power, see Section 3.5.2.1), then drinking water ingestion would be expected to scale similarly, as was the case for birds (see Section 3.2.1). For allometric equations relating body weight to total water flux (including water obtained from food) for mammals, see Nagy and Peterson (1988).

To normalize drinking water intake to body weight (e.g., as g/g-day; see Chapter 4, Equation 4-4), the WI rate estimated above is divided by the animal's body weight in kg:

$$\begin{aligned} \text{NWI (g/g-day)} &= \text{WI (kg/kg-day)}, \text{ or} && [3-18] \\ &= \text{WI (L/day)} / \text{Wt (kg)} \end{aligned}$$

We present normalized drinking water intakes in the species profiles.

3.2.3. Reptiles and Amphibians

Allometric equations relating body weight to drinking water ingestion rates were not identified for reptiles and amphibians. The water balance of these groups is complex, in part because they can absorb water through their skin as well as drink water and extract water from their food (Duellman and Trueb, 1986; Minnich, 1982). The relative

contribution of these three routes of water intake depends on the species, habitat, temperature, and body surface area. In general, the skin of reptiles is less permeable than that of amphibians. Aquatic turtles (e.g., snapping turtle, painted turtle) also may ingest large amounts of water when feeding on aquatic plants and animals; however, the magnitude of such ingestion has not been quantified (Mahmoud and Klicka, 1979). For further discussion of water balance for these groups, see Duellman and Trueb (1986), Feder and Burggren (1992), Minnich (1982), and Nagy and Peterson (1988).

3.3. INHALATION RATES

Inhalation rate is one of the respiratory parameters needed to estimate potential exposure of wildlife to airborne contaminants. Inhalation rates vary with species, body size, body temperature, ambient temperature, and activity levels. When inhalation rate is increased, either because of increased activity levels or to promote evaporative cooling, exposure to airborne contaminants may be increased. As discussed in Section 4.1.4, an inhalation toxicologist should be consulted when assessing this pathway because additional respiratory parameters also must be considered (see U.S. EPA, 1990).

3.3.1. Birds

Lasiewski and Calder (1971) developed an allometric relationship for inhalation rate (IR) associated with standard metabolism (i.e., post-digestive, at rest) for non-passerine birds (N = 6 species ranging in weight from 43 to 88,000 grams). They excluded passerines, which have a somewhat higher metabolic rate than non-passerines (see Section 3.5):

$$\begin{aligned} \text{IR (ml/min)} &= 284 \text{ Wt}^{0.77} \text{ (kg), or} && \text{all non-passerines} && \text{[3-19]} \\ \text{IR (m}^3\text{/day)} &= 0.4089 \text{ Wt}^{0.77} \text{ (kg), or} \\ \text{IR (m}^3\text{/day)} &= 0.002002 \text{ Wt}^{0.77} \text{ (g)} \end{aligned}$$

As noted above, these inhalation rates were associated with standard metabolic rates. Free-living metabolic rates are likely to be higher by a factor of at least 2 or 3 (see Section

3.5); therefore, IRs estimated from these equations should be adjusted accordingly (e.g., multiplied by 2 or 3) although IRs might not be directly proportional to metabolic rate.

3.3.2. Mammals

Using measured values from several reports of respiration rates in mammals (covering 691 data points), Stahl (1967) developed an allometric relationship for inhalation rate with body size for mammals (N = 691, r = 0.98, SE Y = 45):

$$\begin{aligned} \text{IR (ml/min)} &= 379 \text{ Wt}^{0.80} \text{ (kg), or} && \text{all mammals} && [3-20] \\ \text{IR (m}^3\text{/day)} &= 0.5458 \text{ Wt}^{0.80} \text{ (kg), or} \\ \text{IR (m}^3\text{/day)} &= 0.002173 \text{ Wt}^{0.80} \text{ (g)} \end{aligned}$$

As for the equations given for birds, these IRs were associated with standard metabolic rates. Field metabolic rates are likely to be higher by a factor of at least 2 or 3 (see Section 3.5); therefore, IRs determined from these equations should be adjusted accordingly (e.g., multiplied by 2 or 3, although IRs may not be directly proportional to metabolic rate).

3.3.3. Reptiles and Amphibians

In contrast to the fairly regular breathing patterns of most birds and mammals, most reptiles breath air in distinct episodes. They may take single breaths, or exhibit an episode of several breaths, and then hold their breath for varying lengths of time (Milsom and Chan, 1986). Inhalation rate varies for reptiles and amphibians not only with body size and activity level, as for birds and mammals, but also with body temperature. Some gas exchange occurs normally through the integument of both reptiles and amphibians (Duellman and Trueb, 1986; Lillywhite and Maderson, 1982). Moreover, for semiaquatic species, a significant proportion of gas exchange can occur underwater through the skin, reducing the need to inspire air (Seymour, 1982). For example, in adult bullfrogs, gas exchange through the skin can account for 18 percent of total oxygen uptake (Burggren and West, 1982). Given the complexity of the subject, we refer those interested in

inhalation exposures for reptiles or amphibians to more specific treatments of these topics (e.g., Duellman and Trueb, 1986; Feder and Burggren, 1992; Gans and Dawson, 1976; Jackson, 1979; Hutchinson et al., 1968; Lillywhite and Maderson, 1982).

3.4. SURFACE AREAS

The degree to which an animal may absorb contaminants through direct contact with its skin depends on many factors, including the surface area of the skin available for contact. Summarizing measured surface areas for more than 100 animals reported by Hemmingsen (1960), Schmidt-Nielsen (1970, 1972) determined that animals have surface areas that usually are approximately twice that of a sphere of the same weight (assuming a specific gravity of 1 for both the sphere and the animal). The permeability of an animal's skin to contaminants, however, depends on characteristics of the skin (e.g., presence of keratinized scales) as well as the contaminant (e.g., molecule size, lipophilicity). This section presents allometric equations for estimating skin surface area; characteristics affecting skin permeability are not discussed.

3.4.1. Birds

In studies of avian thermal biology, skin surface area is commonly estimated using Meeh's (1879, cited in Walsberg and King, 1978) formula with Rubner's (1883, cited in Walsberg and King, 1978) constant of 10:

$$SA_{\text{skin}} (\text{cm}^2) = 10 Wt^{0.667} (\text{g}) \quad \text{all birds} \quad [3-21]$$

where SA_{skin} is the skin surface area beneath the feathers and Wt is body weight (Walsberg and King, 1978). Although Rubner's constant of 10 was derived originally from domestic fowl, Drent and Stonehouse (1971) have verified the formula for birds in a variety of taxa and of weights spanning three orders of magnitude. For passerines, beak surface area tends to be about 1 percent (range 0.7 percent to 1.6 percent of 10 passerine species) of skin surface area, and leg surface area about 7 percent (range 5.9 percent to

7.9 percent of 10 passerine species) (Walsberg and King, 1978). These ratios would be expected to vary for many non-passerines (e.g., herons, woodcock).

3.4.2. Mammals

Summarizing data from more than 100 mammals, Stahl (1967) developed a relationship between surface and body weight:

$$SA_{\text{skin}} (\text{m}^2) = 0.11 Wt^{0.65} (\text{kg}), \text{ or} \quad \text{all mammals} \quad [3-22]$$

$$SA_{\text{skin}} (\text{cm}^2) = 12.3 Wt^{0.65} (\text{g})$$

This relationship is very similar to that developed for birds (Equation 3-21).

3.4.3. Reptiles and Amphibians

Surface area has been found to be a different function of body weight for adult amphibians than for birds or mammals (Hutchinson et al., 1968; Whitford and Hutchinson, 1967):

$$SA_{\text{skin}} (\text{cm}^2) = 1.131 Wt^{0.579} (\text{g}) \quad \text{all frogs} \quad [3-23]$$

$$SA_{\text{skin}} (\text{cm}^2) = 0.953 Wt^{0.725} (\text{g}) \quad \text{bullfrog} \quad [3-24]$$

$$SA_{\text{skin}} (\text{cm}^2) = 0.997 Wt^{0.712} (\text{g}) \quad \text{green frog} \quad [3-25]$$

$$SA_{\text{skin}} (\text{cm}^2) = 8.42 Wt^{0.694} (\text{g}) \quad \text{salamanders} \quad [3-26]$$

Models by which to estimate surface areas for turtles (exclusive of the shell and plastron) and snakes were not found. The general formula for the surface area of a cylinder can be used to approximate the surface area of a snake if the length and girth are known or estimated.

3.5. ALLOMETRIC EQUATIONS FOR METABOLIC RATE

The allometric equations for estimating food ingestion rates provided in Section 3.1 were derived using very simple assumptions about the energetic content and digestibility of the diet for the species included in the regression equations. Consequently, the equations will provide only very rough estimates of food ingestion rates for any given species. For a site-specific exposure assessment, it may be more appropriate to evaluate ingestion rates for a diet that is likely to represent the species and study area. The caloric content and percent water, fat, and protein of wildlife diets vary not only among species, but also among individuals within the same species depending on factors such as location, time of year, age, and sex. If one can estimate the energetic requirements of the animal in the field and its dietary composition for a specified situation, one can estimate food ingestion rates for that diet and situation. In the remainder of this section, we discuss metabolic rate and provide allometric equations to estimate field free-living metabolic rates (FMRs) for wildlife species. Chapter 4 describes how to use FMR estimates and information about the energy content of specific diets to estimate food ingestion rates.

Several factors influence metabolic rates of free-ranging animals, including body size, body temperature, and type and level of activity. For homeotherms, metabolic energy must be expended to keep core body temperature within relatively narrow limits. At moderate ambient temperatures, homeotherms lose heat to the surrounding environment as rapidly as they gain it and therefore need not expend extra metabolic energy to maintain core body temperature. That range of ambient temperatures over which an animal's metabolic rate is at a minimum and constant level is called the thermoneutral zone. Below the thermoneutral zone, the organism loses heat to the environment and must increase its metabolic activity to compensate. Above the thermoneutral zone, the organism gains heat from its environment and must increase its metabolic rate to use evaporation to cool its body.

Thermoneutral zones vary somewhat among species depending upon the insulating properties and color of the fur or feathers, surface-to-volume ratios, and other factors. The degree to which metabolic rate increases with changes in ambient temperature outside of

the thermoneutral zone is referred to as the temperature coefficient (TC). Temperature coefficients also vary with body size, insulation, and other factors.^a

There are several ways to measure and express metabolic rate, including basal metabolic rate (BMR), resting metabolic rate (RMR), existence metabolic rate (EMR), average daily metabolic rate (ADM), and free-living or field metabolic rate (FMR). The different measures are distinguished by the range of animal activities included in the measure:

- Basal metabolic rate (BMR), also sometimes labeled standard metabolic rate (SMR), represents the minimal value of heat production for homeotherms. BMR must be measured within the thermoneutral zone of ambient temperatures when the animal is at rest and in a post-absorptive state (i.e., all food has been digested) (Gessaman, 1973).
- Standard metabolic rate (SMR) has been used in the literature in more than one way. Many authors define SMR as BMR (see above). Others use SMR if the thermoneutral zone has not been defined so that some cost of thermoregulation may be included (Bennett and Harvey, 1987).
- Resting metabolic rate (RMR) is usually measured at temperatures below the thermoneutral zone when the animal is at rest, but *not* post-absorptive (i.e., the animal is eating regularly and may be expending energy to digest its food). The RMR exceeds the BMR by the heat liberated in the digestion of food (i.e., the specific dynamic action, or SDA) and by some cost of thermoregulation. RMR and BMR are usually measured using indirect calorimetry (i.e., oxygen consumption and carbon dioxide production) over a period of 1 to 3 hours.

^aWater has a much higher heat conductance than air. When submerged or swimming, the degree to which metabolic rate increases with decreasing water temperature depends on the animal's insulation (e.g., whether the fur traps an air layer next to the skin over part or all of the body or whether there is an insulative layer of blubber), duration of submergence, and body size.

- **Existence metabolic rate (EMR)** is the metabolic rate necessary for an animal to maintain itself in captivity without a change in body weight. EMR is greater than RMR due to the cost of locomotor and other activities required for self-maintenance. Most researchers measure EMR on the basis of food consumption and energy excretion at a constant weight over the period of several days or weeks (Kendeigh, 1969).
- **Average daily metabolic rate (ADMR)** is usually measured over 24 hours at a temperature similar to the animal's natural environment and with food and water available *ad libitum*. ADMR is the sum of BMR and the metabolic costs of thermoregulation, digestion, and daily activities.
- **Free-living or field metabolic rate (FMR)** can be measured using doubly-labeled water, and it represents the total daily energy requirement for an animal in the wild. FMR includes the costs of BMR, SDA, thermoregulation, locomotion, feeding, predator avoidance, alertness, posture, and other energy expenditures. Various models and measures have indicated that a constant value of approximately three times BMR is a reasonable estimate of FMR for birds and mammals (Lamprey, 1964; Buechner and Golley, 1967; Koplín et al., 1980), although more precise estimates also have been developed (see Sections 3.5.1.3, 3.5.2.3, and 3.5.3.2).

FMR also has been used in the literature to represent fasting metabolic rate (e.g., Gessaman, 1973), but we do not discuss fasting metabolic rate estimates in this Handbook.

The relationships between metabolic rate and body weight fall into two broad categories: those for homeothermic animals (i.e., most birds and mammals), and those for poikilothermic animals (i.e., most reptiles and amphibians). For poikilotherms, metabolic rate must be related to body temperature. It also is important to remember that poikilotherms can adjust their body temperatures relative to ambient temperatures

somewhat by modifying their behavior (e.g., basking in the sun, adopting postures to minimize or maximize absorption of solar radiation).

Allometric models relating metabolic rate to body size for birds and mammals are described in Sections 3.5.1 and 3.5.2, respectively. Allometric models for reptiles and amphibians are described in Section 3.5.3. We have attempted to identify the most accurate allometric equations currently available for estimating free-living metabolic rates. We also present allometric equations for basal and existence metabolism, which in combination with appropriate information on activity budgets and energy costs can be used to estimate field metabolic rates. Furthermore, measures of basal and existence metabolism are available for considerably more species than are measures (or estimates) of free-living metabolic rates. Consequently, more allometric models have been developed that distinguish the metabolic rate-weight relationship among taxonomic groups using measures of basal and existence metabolism than using measures of field metabolic rates. We caution users to pay close attention to the units for the parameters in the allometric equations. For most equations, energy is expressed as kcal (with the exception of some equations for reptiles and amphibians). Mass may be expressed either in g or kg, depending on how the equation was reported.

We emphasize that the literature on allometric relationships and metabolic rate is extensive and complex. We provide a very simplified overview that should be of assistance for screening-level exposure assessments only. For additional information on methods of estimating metabolic costs of free-ranging animals, please consult expert reviews on the subject (e.g., Bennett and Dawson, 1976; Bennett and Harvey, 1987; Ellis, 1984; Gans and Dawson, 1976; Gessaman, 1973; Kendeigh et al., 1977; King, 1974; Peters, 1983; Robinson et al., 1983; Wiens, 1984).

3.5.1. Birds

In birds, metabolic rate generally decreases with increasing body mass. Several authors have found passerine birds to have higher metabolic rates overall for their body size than non-passerines (Lasiewski and Dawson, 1967; Nagy, 1987; Kendeigh, 1970;

Zar, 1968). In this section, we present allometric models for three measures of metabolic rate on the basis of body size in birds: basal metabolic rate (BMR), existence metabolic rate (EMR), and field metabolic rate (FMR). All equations take the general form of $Y = aWt^b$, but can also be represented in their log-transformed form (the equation of a straight line). We conclude this section by discussing the influence of ambient temperature on avian metabolic rates. Additional information required to estimate a 95-percent confidence interval (CI) for a predicted FMR (the expression of metabolic rate that is generally most appropriate for wildlife exposure assessments) is provided in Section 3.7.

3.5.1.1. Basal Metabolic Rate

Several investigators have derived values for the constants a and b for the equation relating BMR to body weight (Wt) from empirical data on birds. Lasiewski and Dawson (1967) compiled body weight and BMR for almost 100 species of birds. They found BMR for passerines to be higher than BMR for non-passerines (i.e., the Y-intercept for passerines is higher than the Y-intercept for non-passerines):

Passerines

$$\begin{aligned} \log \text{BMR (kcal/day)} &= 2.11 + 0.724 \log \text{Wt (kg)} \pm 0.113, \text{ or} & [3-27] \\ \text{BMR (kcal/day)} &= 128 \text{Wt}^{0.724} \text{ (kg)} \end{aligned}$$

Non-passerines

$$\begin{aligned} \log \text{BMR (kcal/day)} &= 1.89 + 0.723 \log \text{Wt (kg)} \pm 0.068, \text{ or} & [3-28] \\ \text{BMR (kcal/day)} &= 77.6 \text{Wt}^{0.723} \text{ (kg)} \end{aligned}$$

Ellis (1984) found the Y-intercept for seabirds^b to be somewhat higher than the Y-intercept for non-passerines determined by Lasiewski and Dawson (1967):

^bSeabirds included penguins, albatross, petrels, shearwaters, pelicans, skuas, gulls, terns, noddys, murre, cormorants, and frigatebirds.

Seabirds

$$\begin{aligned}\log \text{BMR (kcal/day)} &= 1.96 + 0.721 \log \text{Wt (kg)} \text{ (no SE provided), or} && [3-29] \\ \text{BMR (kcal/day)} &= 91.2 \text{Wt}^{0.721} \text{ (kg)}\end{aligned}$$

Zar (1968) reexamined the data compiled by Lasiewski and Dawson (1967) and developed models for relating BMR to body weight (kg) for several orders and families of birds (Table 3-2). These may be used to estimate whether the FMR for a species of interest is likely to fall above or below that predicted on the basis of the allometric equations derived for "all birds."

3.5.1.2. Existence Metabolic Rates

Kendeigh (1970) developed allometric equations for EMRs as a function of weight (Wt) at 30°C separately for passerines and for non-passerines. As was the case for BMRs, passerines showed higher EMRs than did non-passerines:

Passerines (N = 15 species)

$$\begin{aligned}\log \text{EMR (kcal/day)} &= 0.1965 + 0.6210 \log \text{Wt (g)} \pm 0.0633, \text{ or} && [3-30] \\ \text{EMR (kcal/day)} &= 1.572 \text{Wt}^{0.6210} \text{ (g), or} \\ \log \text{EMR (kcal/day)} &= 2.060 + 0.6210 \log \text{Wt (kg), or} \\ \text{EMR (kcal/day)} &= 114.8 \text{Wt}^{0.6210} \text{ (kg)}\end{aligned}$$

Non-passerines (N = 9 species)

$$\begin{aligned}\log \text{EMR (kcal/day)} &= -0.2673 + 0.7545 \log \text{Wt (g)} \pm 0.0630, \text{ or} && [3-31] \\ \text{EMR (kcal/day)} &= 0.5404 \text{Wt}^{0.7545} \text{ (g), or} \\ \log \text{EMR (kcal/day)} &= 1.996 + 0.7545 \log \text{Wt (kg), or} \\ \text{EMR (kcal/day)} &= 99.03 \text{Wt}^{0.7545} \text{ (kg), or}\end{aligned}$$

The average increase of EMR at 30°C over BMR is 31 and 26 percent in passerine and non-passerine species, respectively (Kendeigh, 1970). At 0°C, on the other hand, EMR of passerine and non-passerine species is similar, indicating that non-passerines are affected

Table 3-2. Allometric Equations for Basal Metabolic Rate (BMR) in Birds^a

Avian group	Number of data points	a	log a	b	SE ^b of mean BMR	SE ^b of mean log BMR
Apodiformes	9	114	2.06	0.769	0.201	0.0558
Strigiformes	7	66.4	1.82	0.69	11.1	0.0989
Columbiformes	10	92.1	1.96	0.858	2.68	0.0491
Galliformes	13	72.6	1.86	0.698	15.3	0.0904
Falconiformes	5	65.3	1.82	0.648	45.3	0.108
Anseriformes	9	95.8	1.98	0.634	23.4	0.0524
Ciconiiformes	7	86.9	1.94	0.737	22.0	0.0464
Passeriformes	48	129	2.11	0.724	8.71	0.0806
Corvidae	8	126	2.10	0.709	23.3	0.147
Ploceidae	17	164	2.21	0.794	1.40	0.0808
Fringillidae	19	125	2.10	0.714	1.02	0.0473
All Nonpasserines	72	78.5	1.90	0.723	42.8	0.111
All Species	120	86.3	1.94	0.668	52.8	0.133

^aValues for the equation relating BMR to body weight (Wt): $\log \text{BMR (kcal/day)} = \log a + b \log \text{Wt (kg)}$.

^bEstimated from the mean log Wt used to develop the allometric equation.

Source: Zar, 1968.

more by cold than passerines. Kendeigh (1970) estimated the equation for all bird species (N = 24) at 0 °C to equal:

All birds (24 species)

$$\begin{aligned} \log \text{EMR (kcal/day)} &= 0.6372 + 0.5300 \log \text{Wt (g)} \pm 0.0613, \text{ or} && [3-32] \\ \text{EMR (kcal/day)} &= 4.337 \text{Wt}^{0.5300} \text{ (g)} \end{aligned}$$

The equations also indicate that smaller species are affected more by cold than are larger species. The slopes of the regression lines for EMR on body weight is less steep at 0°C than at 30°C, indicating that small birds must increase heat production more than large birds to regulate body temperature during cold weather.

To normalize EMR to body weight, divide the daily EMR by body weight:

$$\text{NEMR (kcal/kg-day)} = \text{EMR (kcal/day)} / \text{Wt (kg)} \quad [3-33]$$

3.5.1.3. Free-Living Metabolic Rate

FMRs have been measured using doubly-labeled water (DLW) to measure CO₂ production in animals in the field. Based on DLW measurements with 25 species of birds, Nagy (1987) developed an equation relating FMR for birds to body weight:

$$\begin{aligned} \text{FMR (kjoules/day)} &= 10.89 \text{ Wt}^{0.640} \text{ (g), or} && \text{all birds} && [3-34] \\ \text{FMR (kcal/day)} &= 2.601 \text{ Wt}^{0.640} \text{ (g)} \end{aligned}$$

In birds, the slope of FMR (i.e., 0.640) does not differ significantly from the BMR slope of 0.668 (see Table 3-2). This indicates that FMR may be a relatively constant multiple of BMR in birds over a large range of body mass.

Using estimates of FMR determined for 42 species by a variety of methods, Walsberg (1983) found a similar relationship ($r^2 = 0.98$, SE Y = 0.415, SE b = 0.012):

$$\begin{aligned} \text{FMR (kjoules/day)} &= 13.05 \text{ Wt}^{0.605} \text{ (g), or} && \text{all birds} && [3-35] \\ \text{FMR (kcal/day)} &= 3.12 \text{ Wt}^{0.605} \text{ (g)} \end{aligned}$$

Separating the passerine from the non-passerine species, Nagy (1987) found a higher FMR among passerines than non-passerines of comparable weight (i.e., the Y-intercept for passerines is higher than the Y-intercept for non-passerines), as expected on the basis of basal metabolic rate:

FMR (kjoules/day)	= 8.892 Wt ^{0.749} (g), or	passerines	[3-36]
FMR (kcal/day)	= 2.123 Wt ^{0.749} (g)		

FMR (kjoules/day)	= 4.797 Wt ^{0.749} (g), or	non-passerines	[3-37]
FMR (kcal/day)	= 1.146 Wt ^{0.749} (g)		

FMR (kjoules/day)	= 8.017 Wt ^{0.704} (g), or	seabirds	[3-38]
FMR (kcal/day)	= 1.916 Wt ^{0.704} (g)		

FMR (kjoules/day)	= 21.13 Wt ^{0.440} (g), or	non-seabirds ^c	[3-39]
FMR (kcal/day)	= 5.051 Wt ^{0.440} (g)		

We provide the regression statistics for Nagy's (1987) equations (including sample size and the regression coefficient) and information required to estimate a 95-percent confidence interval for an FMR in Section 3.7.^d

Nagy (1987) estimated the accuracy of the doubly-labeled water method to be ± 8 percent or better. Because of difficulties in recapturing birds during the nonbreeding season, most of the measured FMRs were for breeding birds (Nagy, 1987).

King (1974) estimated that FMR exceeds BMR by a factor of 3.5 on average (based on a sample of 18 measures for species ranging from 4 to 400 g in weight). Gessaman (1973) summarized data on mockingbirds and purple martins from Utter (1971) that indicated an FMR equal to 1.6 to 2.4 times the predicted BMR for adults not actively feeding nestlings. Feeding nestlings increased the ratio of FMR to BMR from 2.7 to 3.4 in purple martins (Utter, 1971, cited in Gessaman, 1973).

^cAll of the large birds included in the database were seabirds such as noddy, kittiwake, shearwater, albatross, tern, and petrel (Nagy, 1987). Other large birds, such as herons, hawks, and owls, were not included. Accordingly, non-passerine and non-seabird equations should be used with caution.

^dInsufficient information is provided in Walsberg (1983) to estimate confidence intervals for a predicted FMR for species with body weights above or below the mean log body weight value of his data set.

To normalize FMR to body weight, divide the daily FMR by body weight:

$$\text{NFMR (kcal/kg-day)} = \text{FMR (kcal/day)} / \text{Wt (kg)} \quad [3-40]$$

Figure 3-1 illustrates approximate monthly variations in the total energy budget of an adult house sparrow in Illinois throughout the year and the relationship between BMR and FMR (adapted from Kendeigh et al., 1977). For this bird, FMR varies seasonally, with a maximum value in midwinter (28 kcal/day) and a minimum in August prior to molting (20 kcal/day). Other species, however (e.g., willow ptarmigan), show no significant variation in FMR with season (King, 1974). For examples of nestling energy budgets, see Kendeigh et al. (1977) and Dunn (1980). For a discussion of modeling energy budgets for birds in general and for seabirds in particular, see Wiens (1984).

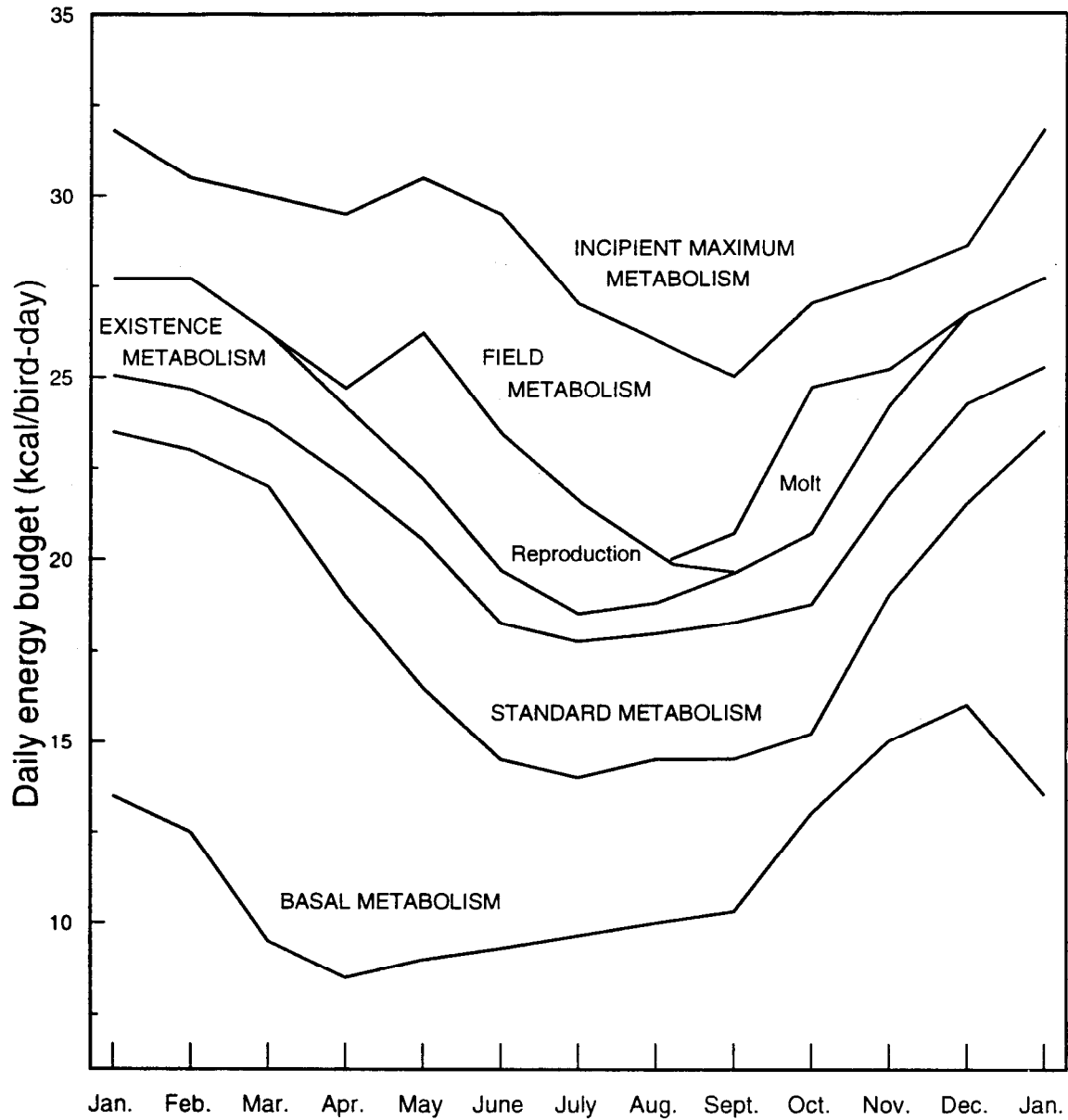
3.5.1.4. Temperature and Metabolic Rate

Below an animal's thermoneutral zone, metabolism increases with decreasing ambient temperature. Section 3.5.1.2 presented equations for EMR at 30°C and at 0°C, but these are not particularly helpful for estimating EMR at other temperatures. Although few researchers have attempted general multiple regressions of metabolic rate on both body size and temperature for birds, some relationships have been investigated in general terms (Peters, 1983):

- Low temperatures induce a greater proportional rise in metabolic rate relative to basal metabolic rate in smaller birds than in larger ones.^e
- At high temperatures, metabolic rate increases to increase blood flow and evaporative cooling (via panting).

^eThis is because conductance and heat loss for a given thermal gradient between body temperature and ambient temperature rise more slowly with body size than do basal metabolic rates.

Figure 3-1. Monthly Variation in Energy Budget Estimated for a House Sparrow



Note: In this figure, the incipient maximum metabolism is the maximum metabolic rate that a bird can maintain in times of stress (e.g., lower than usual temperatures) on a sustained basis. The difference between this value and the field (or free-living) metabolic rate represents energy that might be available during times of need.

Source: Adapted from Kendeigh et al., 1977.

Peters (1983) developed an equation relating the ratio of SMR to BMR to thermal gradient (i.e., the difference between ambient temperature and body temperature) for birds:

$$\text{SMR/BMR} = 0.029 (\text{thermal gradient in } ^\circ\text{C}) \text{Wt}^{-0.249} (\text{kg}) \quad [3-41]$$

Thus, standard metabolic costs increase relative to basal metabolism at lower temperatures, but less so for larger birds than for smaller birds. Despite the strong dependence of metabolic rate on ambient temperature, for screening-level risk assessments, it should not be necessary to adjust estimates of FMR for seasonal temperature changes. As Figure 3-1 illustrates, high metabolic demands of thermoregulation in the winter can be replaced by those of reproduction and molting during spring, summer, and fall.

3.5.2. Mammals

As for birds, metabolic rate in mammals generally decreases with increasing body size. The metabolic rates of herbivorous and carnivorous mammals are similar for similarly sized species. In this section, we present allometric models for three measures of metabolic rate on the basis of body size in mammals: basal metabolic rate (BMR), resting metabolic rate (RMR), and free-living metabolic rate (FMR). All equations take the general form of $Y = aWt^b$, but also can be represented in their log-transformed form (the equation of a straight line). We conclude this section by discussing the influence of ambient temperature on mammalian metabolic rates. Additional information that allows one to estimate a 95-percent confidence interval for a predicted FMR, the expression of metabolic rate that is generally most appropriate for wildlife exposure assessments, is provided in Section 3.7.

3.5.2.1. Basal Metabolic Rate

On the basis of BMR measurements for 26 species weighing 3.5 to 600 kg, Kleiber (1961) estimated that BMR was related to body weight in mammals according to the 3/4 power:

$$\text{BMR (kcal/day)} = 70 \text{ Wt}^{0.75} \text{ (kg)} \pm 0.004 \quad [3-42]$$

Boddington's (1978) analysis produced similar results:

$$\text{BMR (kcal/day)} = 75 \text{ Wt}^{0.73} \text{ (kg)} \pm 0.013 \quad [3-43]$$

3.5.2.2. *Resting Metabolism*

Stahl (1967) used an extensive database (349 species) to determine slightly higher values for RMR than had been determined for BMR (Section 2.5.2.1):

$$\text{RMR (kcal/day)} = 80 \text{ Wt}^{0.76} \text{ (kg)} \quad [3-44]$$

3.5.2.3. *Field Metabolic Rate*

Based on doubly-labeled water measurements with 23 species of placental mammals, Nagy (1987) developed an equation relating FMR to body weight:

$$\begin{aligned} \text{FMR (kjoules/day)} &= 3.35 \text{ Wt}^{0.813} \text{ (g), or} && \text{placental mammals} && [3-45] \\ \text{FMR (kcal/day)} &= 0.800 \text{ Wt}^{0.813} \text{ (g)} \end{aligned}$$

The slope of 0.813 is significantly higher than the BMR slopes of 0.73 to 0.76 reported above. Thus, the FMR does not appear to be a constant multiple of BMR over a range of body sizes as was the case in birds. However, no FMR measurements have yet been made on shrews or other very active small mammals, and whales were included in the FMR data set (Nagy, 1987).

Separating the herbivores from non-herbivores, Nagy (1987) developed two additional equations:

$$\begin{aligned} \text{FMR (kjoules/day)} &= 5.943 \text{ Wt}^{0.727} \text{ (g), or} && \text{herbivores} && [3-46] \\ \text{FMR (kcal/day)} &= 1.419 \text{ Wt}^{0.727} \text{ (g)} \end{aligned}$$

$$\begin{aligned} \text{FMR (kjoules/day)} &= 2.582 \text{ Wt}^{0.862} \text{ (g), or} && \text{non-herbivores} && [3-47] \\ \text{FMR (kcal/day)} &= 0.6167 \text{ Wt}^{0.862} \text{ (g)} \end{aligned}$$

Separating rodents from other animals, Nagy (1987) found:

$$\begin{aligned} \text{FMR (kjoules/day)} &= 10.51 \text{ Wt}^{0.507} \text{ (g), or} && \text{rodents} && [3-48] \\ \text{FMR (kcal/day)} &= 2.514 \text{ Wt}^{0.507} \text{ (g)} \end{aligned}$$

Nagy (1987) estimated the accuracy of the doubly-labeled water method to be ± 8 percent or better.

To normalize FMR to body weight (e.g., kcal/kg-day), divide the daily FMR by body weight. In Section 3.7, we provide the regression statistics for Nagy's (1987) equations (including sample size and the regression coefficient) and information that allows one to estimate a 95-percent confidence interval for an FMR value predicted for a specified body weight.

3.5.2.4. *Temperature and Metabolic Rate*

Few researchers have attempted general multiple regressions of metabolic rate with both body mass and temperature for mammals. However, several relationships have been investigated qualitatively (Peters, 1983):

- Low temperatures induce a greater proportional rise in metabolic rate relative to basal metabolic rate in smaller mammals than in larger ones.^f
- At high temperatures, metabolic rate increases to increase blood flow and evaporative cooling (e.g., panting).

^fThis is because conductance and heat loss for a given thermal gradient between body temperature and ambient temperature rise more slowly with body size than do basal metabolic rates (Peters, 1983).

Peters (1983) developed an equation relating the ratio of SMR to BMR to thermal gradient for mammals:

$$\text{SMR/BMR} = 0.068 (\text{thermal gradient in } ^\circ\text{C}) \text{ Wt}^{-0.182} (\text{kg}) \quad [3-49]$$

Thus, standard metabolic costs increase relative to basal metabolism at lower temperatures, but less so for larger than for smaller mammals.

3.5.3. Reptiles and Amphibians

Most reptiles and amphibians tend to have much lower metabolic rates than birds or mammals because they are poikilothermic. For example, at temperatures similar to normal body temperatures of birds and mammals (around 37 to 39 °C), resting metabolic rates of reptiles and amphibians tend to be only 10 to 20 percent of those of birds and mammals of similar body weight (Bennett and Dawson, 1976). In this section, we provide some examples of allometric equations for metabolic rate. Because metabolic rate depends on body temperature, which in poikilotherms can vary substantially over time, we recommend that those persons interested in estimating metabolic rates consult more complete treatments of the subject, including thermoregulation in poikilotherms (e.g., Bennett and Dawson, 1976; Congdon et al., 1982; Duellman and Trueb, 1986; Feder and Burggren, 1992; Harless and Morlock, 1979; Hutchinson, 1979).

3.5.3.1. Basal and Resting Metabolic Rates

Robinson et al. (1983) developed an equation for the relationship between BMR and body mass for reptiles and amphibians at 20 °C:

$$\begin{aligned} \text{BMR (Watts)} &= 0.19 \text{ Wt}^{0.76} (\text{kg}), \text{ or} & [3-50] \\ \text{BMR (kcal/day)} &= 3.92 \text{ Wt}^{0.76} (\text{kg}) \end{aligned}$$

Thus, the BMR of homeotherms (Sections 3.5.1 and 3.5.2) is approximately 30 times the BMR of poikilotherms at this ambient temperature (Peters, 1983). The difference in

metabolic rates between homeotherms and poikilotherms is lessened when poikilotherms modify their body temperatures by behavioral adjustments (such as basking in the sun).

Andrews and Pough (1985) used multiple regression analysis to evaluate the relationship between metabolic rate and three variables—mass, temperature, and standard or resting metabolic state—for snakes and lizards. From a total of 226 observations on 107 species (between 20 and 30 °C for most observations), they developed the following equation:

$$\text{MR (ml O}_2\text{/hr)} = 0.013 \text{ Wt}^{0.80} \text{ (g)} \times 10^{0.038 \text{ temperature (}^\circ\text{C)}} \times 10^{0.14 \text{ metabolic state}} \quad [3-51]$$

where MR equals either SMR or RMR and metabolic state equals zero (0) for standard metabolism^g and equals 1 for resting metabolism.^h The Q₁₀ values for the influence of temperature on metabolic rate (i.e., quotient of the rate measured at one temperature divided by the rate measured at a temperature 10 °C lower) were 2.4 for resting metabolism and 1.4 for standard metabolism. Thus SMR depended less on ambient temperature than did RMR.

Equation 3-51 is based on adult animals and should not be used to estimate metabolic rates of juvenile snakes and lizards. Andrews and Pough (1985) reviewed allometric equations relating resting metabolic rate to body weight within species and found that the exponents were significantly lower than the value of 0.80 in Equation 3-51. See Andrews and Pough (1985) for intraspecific allometric models for this group.

3.5.3.2. *Free-Living Metabolic Rates*

Nagy (1987) developed an equation for the relationship between FMR and body size in iguanid lizards:

^gMeasured for fasting individuals during the period of normal inactivity (at night for most species).

^hMeasured for fasting individuals during the period of normal activity (daytime for most species).

$$\begin{aligned} \text{FMR (kjoules/day)} &= 0.224 \text{ Wt}^{0.799} \text{ (g)}, \text{ or} & [3-52] \\ \text{FMR (kcal/day)} &= 0.0535 \text{ Wt}^{0.799} \text{ (g)} \end{aligned}$$

Bennett and Nagy (1977) estimated that the ratio of FMR to EMR for lizards is 2.0. Robinson et al. (1983) estimated the value to be 2.9, assuming that lizards rest at maintenance levels for 8 hours per day at 35°C.

Feder (1981, 1982) presented equations relating FMR to body size of unrestrained ranid (frog) tadpoles at 25°C:

$$\text{dry mass (mg)} = 0.047 \text{ (wet mass)}^{1.06} \text{ (mg)} \quad [3-53]$$

and

$$\text{FMR } (\mu\text{I}\text{O}_2/\text{hr}) = 2.5 \text{ (dry mass)}^{0.878} \text{ (mg)}, \text{ or} \quad [3-54]$$

$$\text{FMR (mlO}_2/\text{day)} = 0.06 \text{ (dry mass)}^{0.878} \text{ (mg)}$$

Assuming 1 milliliter of oxygen is metabolically equivalent to approximately 4.80 calories (Dawson, 1974):

$$\text{FMR (cal/day)} = 0.288 \text{ (dry mass)}^{0.878} \text{ (mg)} \quad [3-55]$$

Burggren et al. (1983) estimated Q_{10} values for metabolic rates for bullfrog larvae of 1.87 between temperatures of 15 and 25°C and of 2.41 between temperatures of 25 and 33°C. Q_{10} values for a second ranid species (*Rana berlandieri*) were similar (1.97 and 1.76, respectively). Thus, the metabolic rate for ranid frogs approximately doubles with each 10-degree rise in temperature over this range of temperatures.

The equations presented in this section show that poikilotherm metabolic rate depends strongly on temperature. The available literature on the subject is extensive and complex, and again, interested readers are encouraged to consult substantive treatments of the subject (see references cited in the introduction to Section 3.5.3).

3.6. MATH PRIMER AND UNIT CONVERSIONS

To assist readers in using or modifying allometric equations presented in this Handbook or in using allometric equations presented in the open literature, we provide a brief summary of logarithm and power functions in Sections 3.6.1 and 3.6.2. Section 3.6.3 contains frequently used unit conversion factors.

3.6.1. Summary of Operations Involving Logarithms

$$\log 1 = 0$$

$$\log (N_1 N_2) = \log N_1 + \log N_2$$

$$\log (N_1 / N_2) = \log N_1 - \log N_2$$

$$\log (1 / N_1) = -\log N_1$$

$$\log (N_1^c) = c \log N_1$$

$$\log c \text{ root of } N_1 = \log (N_1^{1/c}) = (1/c) \log N_1$$

3.6.2. Summary of Operations Involving Powers

$$W^a W^b = W^{a+b}$$

$$(W^a)^b = W^{ab}$$

$$(W_1 W_2)^a = W_1^a W_2^a$$

$$W^a / W^b = W^{a-b}$$

$$W^a / W = W^{a-1}$$

$$1/W^b = W^{-b}$$

$$W^0 = 1$$

$$(W_1 / W_2)^a = W_1^a / W_2^a$$

$$c \text{ root of } W^a = (W^a)^{1/c} = W^{a/c}$$

3.6.3. Unit Conversions

3.6.3.1. Approximate Factors for Metabolic Equations

1 kg dry mass	= 3 to 10 kg wet mass	(Peters, 1983)
1 kg dry mass	= 22×10^6 joules	(Peters, 1983)
1 kg wet mass	= 2 to 7×10^6 joules	(Peters, 1983)
1 kg fat	= 40×10^6 joules	(Peters, 1983)
tissue density	= 1 kg/liter	(Peters, 1983)
1 kg wet mass	= 1×10^{15} μm^3	(Peters, 1983)
1 kg dry mass	= 0.4 kg carbon	(Peters, 1983)
1 ml O ₂	= 20.1 joules	(Peters, 1983)
	= 4.8 calories	(Dawson, 1974)

3.6.3.2. Exact Conversions

Area

1 acre	=	0.4047 hectares (ha)
1 square mile (mi ²)	=	259 ha
1 square meter (m ²)	=	1×10^{-4} ha
1 square kilometer (km ²)	=	100 ha

Length

1 inch	=	2.54 centimeters (cm)
1 foot =	0.3 meters (m)	
	=	30.48 cm
1 mile (mi)	=	1.61 kilometers (km)

Volume

1 m ³	=	1×10^3 liters (L)
	=	1×10^6 cm ³

Mass

1 ounce (oz)	=	28.35 grams (g)
1 pound (lb)	=	453.6 g
1 lb	=	0.4536 kilograms (kg)

Work and energy (force × distance)

$$\begin{aligned} 1 \text{ joule (J)} &= 1 \text{ kg}\cdot\text{m}^2/\text{s}^2 \\ &= 0.239 \text{ calories (cal)} \end{aligned}$$

Power (energy per unit time)

$$\begin{aligned} 1 \text{ watt (W)} &= 1 \text{ kg}\cdot\text{m}^2/\text{s}^3 \\ &= 1 \text{ joule/s} \\ &= 20.64 \text{ kcal/day} \end{aligned}$$

$$\begin{aligned} 1 \text{ ml O}_2/\text{s} &= 0.0446 \text{ mMol O}_2/\text{s} \\ &= 1.43 \text{ mg O}_2/\text{s} \end{aligned}$$

3.7. ESTIMATING CONFIDENCE INTERVALS

A commonly reported measure of the precision of estimating log Y from log Wt (or Y from Wt) for allometric equations is the standard error (SE) of log Y:

$$\log Y = \log a + b \log Wt \pm \text{SE of log Y} \quad [3-2]$$

The SE of log Y is the standard error of the estimate of log Y from log Wt at a value of log Wt that represents the mean of the log Wt values used to estimate the allometric relationship. This value *cannot* be used to estimate a confidence interval (CI) for a log Y value predicted from log Wt values other than the mean log Wt value. The CI of a predicted log Y value is smallest at the mean log Y and mean log Wt values and increases as log Wt for the species of interest deviates from mean log Wt. Thus, to estimate the CI for a single predicted value of Y, one also must know the sample size and the mean of the log Wt values used in developing the allometric equation, which many investigators do not report.

Nagy (1987), however, did provide sufficient statistical information to estimate a 95-percent CI for a predicted value of Y given any value of Wt for his free-living (field) metabolic rate (FMR) and food ingestion (FI) rate equations. In this section, we outline Nagy's short-cut for estimating this CI and provide the statistical values required for each of Nagy's equations presented in this Handbook.

To estimate 95-percent CIs for the predicted FMR and FI rate, use the values from Table 3-3 (for FI rate equations) or 3-4 (for FMR equations) in the following formula:

$$95\% \text{ CI}_{\log y} = \log y \pm c [d + e (\log \text{Wt} - \overline{\log \text{Wt}})^2]^{0.5}$$

where y is FMR in kilojoules/day or FI in grams (dry weight)/day. $\log \text{Wt}$ is the log of the body weight in grams of the species for which y is being estimated. $\overline{\log \text{Wt}}$ is the mean $\log \text{Wt}$ of the species used to develop the allometric equation. Values for c , d , e , and $\overline{\log \text{Wt}}$ are provided in Tables 3-3 and 3-4. Tables 3-3 and 3-4 also provide sample sizes (N), regression coefficients (r^2), and SE estimates for b and $\log a$ in the applicable equations.

Table 3-3. Regression Statistics for Nagy's (1987) Allometric Equations for Food Ingestion Rates for Free-Living Animals

Regression Statistics for Allometric Equations for Food Ingestion (FI) Rates (Dry Matter Ingestion) Rates of Free-Living Mammals, Birds, and Lizards. Equations are in the form $Y = aWt^b$ where Y is Food Ingestion Rate (in grams dry weight/day) and Wt is body weight of species s (grams wet weight).										
95% CI _{log FI(species s)} = log FI _(species s) ± c [d + e (log Wt _(species s) - log Wt) ²] ^{0.5}										
Group subgroup	Equation	a	log a (SE log a)	b (SE b)	N	r ²	log Wt	c	d	e
Birds	3-3	0.64	-0.188 (0.060)	0.651 (0.028)	50	0.919	1.983	0.347	1.020	0.026
passerines	3-4	0.40	-0.400 (0.075)	0.850 (0.053)	26	0.915	1.378	0.158	1.038	0.480
non-passerines	3-5	0.30	-0.521 (0.132)	0.751 (0.048)	24	0.919	2.638	0.401	1.042	0.061
seabirds	3-6	0.49	-0.306 (0.187)	0.704 (0.061)	15	0.911	2.958	0.399	1.067	0.109
Eutherian Mammals (i.e., placental)	3-7	0.23	-0.629 (0.065)	0.822 (0.026)	46	0.958	2.196	0.425	1.022	0.015
rodents	3-8	0.62	-0.207 (0.194)	0.564 (0.119)	33	0.421	1.598	0.434	1.030	0.313
herbivores	3-9	0.58	-0.239 (0.109)	0.727 (0.039)	17	0.960	2.566	0.405	1.059	0.041
Iguanids										
herbivores	3-12	0.019	-1.713 (0.123)	0.841 (0.059)	5	0.985	1.896	0.358	1.200	0.278
insectivores	3-13	0.012	-1.890 (0.037)	0.773 (0.038)	20	0.958	0.870	0.151	1.050	0.279

Source: Nagy, 1987.

Table 3-4. Regression Statistics for Nagy's (1987) Allometric Equations for Free-Living (Field) Metabolic Rates

Regression Statistics for Allometric Equations for Free-Living Metabolic Rates (FMR) of Free-Living Mammals, Birds, and Lizards. Equations are in the form $Y = aWt^b$ where Y is FMR (in kilojoules/day) and Wt is body weight of species s (grams wet weight).										
95% CI _{log FMR(species s)} = log FMR _(species s) ± c [d + e (log Wt _(species s) - log Wt) ²] ^{0.5}										
Group subgroup	Equation	a	log a (SE log a)	b (SE b)	N	r ²	log Wt	c	d	e
Birds	3-34	10.9	1.037 (0.064)	0.640 (0.030)	50	0.907	1.983	0.368	1.020	0.026
passerines	3-36	8.89	0.949 (0.059)	0.749 (0.037)	26	0.899	1.378	2.014	0.026	0.0014
non-passerines	3-37	4.79	0.681 (0.102)	0.749 (0.037)	24	0.899	2.638	2.014	0.026	0.0014
seabirds	3-38	8.02	0.904 (0.187)	0.704 (0.061)	15	0.911	2.958	0.399	1.067	0.109
non-seabirds	3-39	21.1	1.325 (0.081)	0.440 (0.049)	35	0.709	1.565	0.297	1.029	0.113
Eutherian Mammals (i.e., placental)	3-45	3.35	0.525 (0.057)	0.813 (0.023)	46	0.967	2.196	0.371	1.022	0.015
rodents	3-48	10.5	1.022 (0.141)	0.507 (0.087)	33	0.524	1.598	0.316	1.030	0.313
herbivores	3-46	5.94	0.774 (0.109)	0.727 (0.039)	17	0.959	2.566	0.406	1.059	0.041
non-herbivores	3-47	2.58	0.412 (0.058)	0.862 (0.026)	29	0.977	1.980	0.321	1.035	0.027
Iguanids	3-52	0.224	-0.650 (0.029)	0.799 (0.023)	25	0.981	1.075	0.161	1.040	0.088

Source: Nagy, 1987.

3.8. REFERENCES

- Andrews, R. M.; Pough, F. H. (1985) Metabolism of squamate reptiles: allometric and ecological relationships. *Physiol. Zool.* 58: 214-231.
- Bartholomew, G. A.; Cade, T. J. (1963) The water economy of land birds. *Auk* 80: 504-539.
- Bennett, A. F.; Dawson, W. R. (1976) Metabolism. In: Gans, C.; Dawson, W. R., eds. *The biology of reptilia: v. 5, Physiology A*. New York, NY: Academic Press; pp. 127-223.
- Bennett, P. M.; Harvey, P. H. (1987) Active and resting metabolism in birds: allometry, phylogeny and ecology. *J. Zool. Lond.* 213: 327-363.
- Bennett, A. F.; Nagy, K. A. (1977) Energy expenditure in free-ranging lizards. *Ecology* 58: 697-700.
- Boddington, M. J. (1978) An absolute metabolic scope for activity. *J. Theor. Biol.* 75: 443-449.
- Buechner, H. K.; Golley, F. B. (1967) Preliminary estimation of energy flow in Uganda kob (*Adenota kob thomasi* Neumann). In: Petruszewicz, L., ed. *Secondary productivity of terrestrial ecosystems*. Warszawa-Krakow; pp. 243-254.
- Burggren, W. W.; West, N. H. (1982) Changing respiratory importance of gills, lungs and skin during metamorphosis in the bullfrog *Rana catesbeiana*. *Physiol. Zool.* 56: 263-273.
- Burggren, W. W.; Feder, M. E.; Pinder, A. W. (1983) Temperature and the balance between aerial and aquatic respiration in the larvae of *Rana berlandieri* and *Rana catesbeiana*. *Physiol. Zool.* 56: 263-273.
- Calder, W. A. (1981) Scaling of physiological processes in homeothermic animals. *Ann. Rev. Physiol.* 43: 301-322.
- Calder, W. A.; Braun, E. J. (1983) Scaling of osmotic regulation in mammals and birds. *Am. J. Physiol.* 244: R601-R606.
- Congdon, J. D.; Dunham, A. E.; Tinkle, D. W. (1982) Energy budgets and life histories of reptiles. In: Gans, C.; Pough, F. H., eds. *Biology of the reptilia, physiology D; physiological ecology: v. 13*. New York, NY: Academic Press; pp. 233-271.
- Dawson, W. R. (1954) Temperature regulation and water requirements of the brown and abert towhees, *Pipilo fuscus* and *Pipilo aberti*. *Univ. California Publ. Zool.* 59: 81-124.

- Dawson, W. R. (1974) Appendix: conversion factors for units used in the symposium. In: Paynter, R. A., ed. Avian energetics. Cambridge, MA: Nuttall Ornithological Club; Publication no. 15.
- Drent, R. H.; Stonehouse, B. (1971) Thermoregulatory responses of the Peruvian penguin *Spheniscus humboldti*. *Comp. Biochem. Physiol. A: Comp. Physiol.* 40: 689-710.
- Duellman, W. E.; Trueb, L. (1986) Biology of amphibians. New York, NY: McGraw-Hill Book Company.
- Dunn, E. H. (1980) On the variability in energy allocation of nestling birds. *Auk* 97: 19-27.
- Ellis, H. I. (1984) Energetics of free-ranging seabirds. In: Whittow, G. C.; Rahn, H., ed. Seabird energetics. New York, NY: Plenum Press; pp. 203-234.
- Farlow, J. O. (1976) A consideration of the trophic dynamics of a late Cretaceous large-dinosaur community (Oldman Formation). *Ecology* 57: 841-857.
- Feder, M. E. (1981) Effect of body size, trophic state, time of day, and experimental stress on oxygen consumption of anuran larvae: an experimental assessment and evaluation of the literature. *Comp. Biochem. Physiol. A*: 70: 497-508.
- Feder, M. E. (1982) Effect of developmental stage and body size on oxygen consumption of anuran larvae: a reappraisal. *J. Exp. Zool.* 220: 33-42.
- Feder, M. E.; Burggren, W. W., eds. (1992) Environmental physiology of the amphibia. Chicago, IL: University of Chicago Press.
- Gans, C.; Dawson, W. R., eds. (1976) Biology of the reptilia: v. 5, physiology A. New York, NY: Academic Press.
- Gessaman, J. A. (1973) Methods of estimating the energy cost of free existence. In: Gessaman, J. A., ed. Ecological energetics of homeotherms. Monogr. Ser. 20 ed. Logan, UT: Utah State University Press; pp. 3-31.
- Golley, F. B. (1961) Energy values of ecological materials. *Ecology* 42: 581-584.
- Harless, M.; Morlock, H., eds. (1979) Turtles: perspectives and research. Toronto, Canada: John Wiley and Sons, Inc.
- Hemmingsen, A. M. (1960) Energy metabolism as related to body size and respiratory surfaces, and its evolution. Rept. Steno Mem. Hosp. Nord. Insulin Lab., Part II 9: 1-95.
- Hume, I. D. (1982) Digestive physiology and nutrition of marsupials. Cambridge, England: Cambridge University Press.

- Hutchinson, V. H. (1979) Thermoregulation. In: Harless, M.; Morlock, H., ed. *Turtles: perspectives and research*. Toronto, Canada: John Wiley and Sons, Inc.; pp. 207-227.
- Hutchinson, V. H.; Whitford, W. G.; Kohl, M. (1968) Relation of body size and surface area to gas exchange in anurans. *Physiol. Zool.* 41: 65-85.
- Jackson, D. C. (1979) Respiration. In: Harless, M.; Morlock, H., ed. *Turtles: perspectives and research*. Toronto, Canada: John Wiley and Sons, Inc.; pp. 165-191.
- Kendeigh, S. C. (1969) Energy responses of birds to their thermal environments. *Wilson Bull.* 81: 441-449.
- Kendeigh, S. C. (1970) Energy requirements for existence in relation to size of bird. *Condor* 72: 60-65.
- Kendeigh, S. C.; Dol'nik, V. R.; Govrilov, V. M. (1977) Avian energetics. In: Pinowski, J.; Kendeigh, S. C., eds. *Granivorous birds in ecosystems*. Cambridge, MA: Cambridge University Press.
- King, J. R. (1974) Seasonal allocation of time and energy resources in birds. In: Paynter, R. A. Jr., ed. *Avian energetics*. Cambridge, MA: Nuttall Ornithological Club; Publication no. 15; pp. 4-85.
- Kleiber, M. (1961) *The fire of life*. New York, NY: John Wiley.
- Koplin, J. R.; Collopy, M. W.; Bammann, A. R.; et al. (1980) Energetics of two wintering raptors. *Auk* 97: 795-806.
- Lamprey, H. F. (1964) Estimation of the large mammal densities, biomass and energy exchange in the Tarangire Game Reserve and the Masai Steppe in Tanganyika. *E. Afr. Wild. J.* 2: 1-46.
- Lasiewski, R. C.; Calder, W. A. (1971) A preliminary allometric analysis of respiratory variables in resting birds. *Resp. Phys.* 11: 152-166.
- Lasiewski, R. C.; Dawson, W. R. (1967) A reexamination of the relation between standard metabolic rate and body weight in birds. *Condor* 69: 12-23.
- Lillywhite, H. B.; Maderson, P. F. (1982) Skin structure and permeability. In: Gans, C.; Pough, F. H., eds. *Biology of the reptilia: v. 12, physiology C; physiological ecology*. New York, NY: Academic Press; pp. 397-442.
- Mahmoud, I. Y.; Klicka, J. (1979) Feeding, drinking, and excretion. In: Harless, M.; Morlock, H., ed. *Turtles: perspectives and research*. Toronto, Canada: John Wiley and Sons, Inc.; pp. 229-243.

- Medway, W.; Kare, M. R. (1959) Water metabolism of the growing domestic fowl with specific reference to water balance. *Poultry Sci.* 38: 631-637.
- Meeh, K. (1879) Oberflächenmessungen des menschlichen Körpers. *Z. Biol.* 15: 426-458.
- Milsom, W. K.; Chan, P. (1986) The relationship between lung volume, respiratory drive and breathing pattern in the turtle *Chrysemys picta*. *J. Exp. Biol.* 120: 233-247.
- Minnich, J. E. (1982) The use of water. In: Gans, C.; Pough, F. H., eds. *Biology of the reptilia: v. 12, physiology C; physiological ecology*. New York, NY: Academic Press; pp. 325-395.
- Nagy, K. A. (1987) Field metabolic rate and food requirement scaling in mammals and birds. *Ecol. Monogr.* 57: 111-128.
- Nagy, K. A.; Peterson, C. C. (1988) *Scaling of water flux rate in animals*. Berkeley, CA: University of California Press.
- Peters, R. H. (1983) *The ecological implications of body size*. Cambridge, England: Cambridge University Press.
- Reiss, M. J. (1989) *The allometry of growth and reproduction*. Cambridge, United Kingdom: Cambridge University Press.
- Robbins, C. T. (1983) *Wildlife feeding and nutrition*. New York, NY: Academic Press.
- Robinson, R. W.; Peters, R. H.; Zimmermann, J. (1983) The effects of body size and temperature on metabolic rate of organisms. *Can. J. Zool.* 61: 281-288.
- Rubner, M. (1883) Über den Einfluss der Körpergröße auf Stoff- und Kraftwechsel. *Z. Biol.* 19: 535-562.
- Schmidt-Nielsen, K. (1970) Energy metabolism, body size and problems of scaling. *Fed. Proc. Am. Soc. Exp. Biol.* 29: 1524-1532.
- Schmidt-Nielsen, K. (1972) *How animals work*. Cambridge, MA: Cambridge University Press.
- Seibert, H. C. (1949) Differences between migrant and non-migrant birds in food and water intake at various temperatures and photoperiods. *Auk* 66: 128-153.
- Seymour, R. S. (1982) Physiological adaptations to aquatic life. In: Gans, C.; Pough, F. H., eds. *Biology of the reptilia: v. 13, physiology D; physiological ecology*. New York, NY: Academic Press; pp. 1-51.
- Skadhauge, R. (1975) Renal and cloacal transport of salt and water. *Symp. Zool. Soc. London* 35: 97-106.

- Stahl, W. R. (1967) Scaling of respiratory variables in mammals. *J. Appl. Physiol.* 22: 453-460.
- U. S. Environmental Protection Agency. (1990) Interim methods for development of inhalation reference concentrations, review draft. Washington, DC: Office of Research and Development; EPA report no. EPA/600/8-90/066A.
- Utter, J. M. (1971) Daily energy expenditures of free-living purple martins (*Progne subis*) and mockingbirds (*Mimus polyglottos*) with a comparison of two northern populations of mockingbirds [Ph.D. dissertation]. Rutgers, NJ: Rutgers University; 173 pp.
- Walsberg, G. E. (1983) Avian ecological energetics. In: Farner, D. S.; King, J. R.; Parkes, K. C., eds. *Avian biology*, v. 7. New York, NY: Academic Press; pp. 161-220.
- Walsberg, G. E.; King, J. R. (1978) The relationship of the external surface area of birds to skin surface area and body mass. *J. Exp. Biol.* 76: 185-189.
- Whitford, W. G.; Hutchinson, V. H. (1967) Body size and metabolic rate in salamanders. *Physiol. Zool.* 40: 127-133.
- Wiens, J. A. (1984) Modelling the energy requirements of seabird populations. In: Whittow, G. C.; Rahn, H., eds. *Seabird energetics*. New York, NY: Plenum Press; pp. 284.
- Zar, J. H. (1968) Standard metabolism comparisons between orders of birds. *Condor* 10: 278.

4. EXPOSURE ESTIMATES

This section provides equations to estimate oral doses of chemical contaminants for wildlife, along with a discussion of dose estimates for other exposure routes. Section 4.1 provides general dose equations. Equations for drinking water exposures are presented in Section 4.1.1, followed by equations for dietary exposures in Section 4.1.2. In the dietary exposure section, data on the caloric and water content of various food types and diet assimilation efficiencies are also provided. An equation and data to facilitate estimating doses received through soil or sediment ingestion are discussed in Section 4.1.3. Sections 4.1.4 and 4.1.5 provide a qualitative discussion of inhalation and dermal dose estimates. Section 4.2 describes considerations for analyses of uncertainty in exposure assessments. References are provided in Section 4.3.

4.1. GENERAL DOSE EQUATIONS

EPA's (1992a) *Framework for Ecological Risk Assessment* defines exposure as the co-occurrence of or contact between a stressor and an ecological component. When assessing risks of exposure to chemical contaminants, potential dose is often the metric used to quantify exposure. Potential dose is defined as the amount of chemical present in food or water ingested, air inhaled, or material applied to the skin (U.S. EPA, 1992b). Potential dose is analogous to the administered dose in a toxicity test. Because exposure to chemicals in the environment is generally inadvertent, rather than administered, EPA's (1992b) *Guidelines for Exposure Assessment* use the term potential dose rather than administered dose.

A general equation for estimating dose for intake processes is:

$$D_{\text{pot}} = \int_{t_1}^{t_2} C(t) IR(t) dt \quad [4-1]$$