2.3.7. Green Frog (true frog family)

Order *Anura*, Family *Ranidae*. These are typical frogs with adults being truly amphibious, living at the edge of water bodies and entering the water to catch prey, flee danger, and spawn (Behler and King, 1979). This profile covers medium-sized ranids. The next profile (Section 2.3.8) covers large ranids.

Selected species

The green frog (*Rana clamitans*) is usually found near shallow fresh water throughout much of eastern North America. Two subspecies are recognized: *R. c. clamitans* (the bronze frog; ranges from the Carolinas to northern Florida, west to eastern Texas, and north along the Mississippi Valley to the mouth of the Ohio River) and *R. c. melanota* (the green frog; ranges from southeastern Canada to North Carolina, west to Minnesota and Oklahoma but rare in much of Illinois and Indiana, introduced into British Columbia, Washington, and Utah) (Conant and Collins, 1991).

***Body size*. The green frog is a medium-sized ranid usually between 5.7 and 8.9 cm snout-to-vent length (SVL) (Conant and Collins, 1991; Martof et al., 1980). Its growing period is primarily confined to the period between mid May and mid September (Martof, 1956b). Females are usually larger than males (Smith, 1961). Adults typically weigh between 30 and 70 g (Wells, 1978). Hutchinson et al. (1968) developed an allometric equation relating green frog surface area (SA in cm) to body weight (Wt in grams):**

$$SA = 0.997\ Wt^{0.712}.$$

This equation also is presented in Chapter 3 as Equation 3-25.

***Habitat*. Adult green frogs live at the margins of permanent or semipermanent shallow water, springs, swamps, streams, ponds, and lakes (Wells, 1977). Martof (1953b) found green frogs primarily to inhabitat the banks of streams. They also can be found among rotting debris of fallen trees (Behler and King, 1979; Conant and Collins, 1991). Juveniles prefer shallower aquatic habitats with denser vegetation than those preferred by adults (Martof, 1953b). McAlpine and Dilworth (1989) observed that green frogs inhabited aquatic habitats about two-thirds of the time and terrestrial habitats the remaining time. Similarly, Martof (1953b) found that the green frog relies on terrestrial habitats for feeding and aquatic habitats for refuge from desiccation, temperature extremes, and enemies. Ponds used by green frogs are usually more permanent than those used by other anuran species (Pough and Kamel, 1984).**

***Food habits*. Adult *R. clamitans* are terrestrial feeders among shoreline vegetation. They consume insects, worms, small fish, crayfish, other crustaceans, newts, spiders, small frogs, and molluscs. Stewart and Sandison (1973) found that terrestrial beetles often are their most important food item but noted that any locally abundant insect along the shoreline may be consumed in large numbers. There is a pronounced reduction in food consumption during the breeding period for both males and females (Mele, 1980). During the breeding season, males spend most of their energy defending breeding territories, and**

females expend their energy producing eggs (Wells, 1977). Fat reserves acquired during the prebreeding period compensate for reduced food intake during the breeding period (Mele, 1980). Jenssen and Klimstra (1966) found that green frogs consume most of their food in the spring and eat little during the winter. Food eaten in the spring, summer, and fall consists mostly of terrestrial prey, whereas winter food is composed mostly of aquatic prey (Jenssen and Klimstra, 1966). Juveniles (sexually immature frogs) eat about half the volume of food as do adults over the course of a year (Jenssen and Klimstra, 1966). Tadpoles are herbivorous (DeGraaf and Rudis, 1983). Green frogs eat their cast skins following molting; the casting of skin is frequent during midsummer (Hamilton, 1948).

***Temperature regulation and daily activities*. Martof (1953b) found that the green frog's activity period varies by frog size, with larger frogs being primarily nocturnal, small frogs being diurnal, and middle-sized frogs (5 to 7 cm SVL) being equally active during day and night.**

***Hibernation*. Adult green frogs overwinter by hibernating underground or underwater from fall to spring (Ryan, 1953). Martof (1956a) observed frogs hibernating in mud and debris at the bottom of streams approximately 1 m deep. Jenssen and Klimstra (1966) noted that adults usually hibernate in restricted chambers within rock piles or beneath plant debris, while juveniles are more often found in locations with access to passing prey. The frogs begin emerging when the mean daily temperature is about 4.4°C and the maximum temperature is about 15.6°C for 3 to 4 days (Martof, 1953b). Juvenile frogs enter and exit hibernation after adult frogs (Martof, 1956a).**

***Breeding activities and social organization*. Green frogs breed from spring through the summer, spawning at night (Smith, 1961; Wells, 1976). Female green frogs stay in nonbreeding habitat until it is time to spawn (Martof, 1956a). In preparation for breeding, males establish territories near shore that serve as areas for sexual display and as defended oviposition sites (Wells, 1977). Males establish calling sites within their territories where they attempt to attract females (Wells, 1977). Females visit male territories to mate and lay their egg masses. The masses are contained in films of jelly and are deposited in emergent, floating, or submerged vegetation; they hatch in about 3 to 6 days (Behler and King, 1979; Martof, 1956a; Ryan, 1953). Adults are solitary during non-breeding periods (Smith, 1956).**

***Tadpole and metamorphosis*. In the southern part of their range, green frog tadpoles metamorphose into frogs in the same season in which they hatched, while in the northern part, 1 or 2 years pass before metamorphosis (Martof, 1956b). Tadpoles that hatch from egg masses laid in the spring usually metamorphose that fall, while those hatching from summer-laid eggs typically overwinter as larvae and metamorphose the following spring (Pough and Kamel, 1984). Ryan (1953) found that most tadpoles are 2.6 to 3.8 cm SVL at the time of transformation. Those that transform in late June or early July grow rapidly, adding 1.4 to 2.0 cm SVL in the first 2 months and 0.4 to 0.7 cm SVL more before hibernation. Tadpoles that transform at approximately 3.1 cm SVL may reach between 5.0 and 5.8 cm SVL before hibernation (Ryan, 1953). Newly transformed frogs often move from lakes and ponds where they were tadpoles to shallow stream banks, usually during periods of rain (Martof, 1953b).**

***Home range and resources*.** **The species' home range includes its foraging and refuge areas in and around aquatic environments. During the breeding period, the male's home range also includes its breeding territory (Wells, 1976). Martof (1953b) found that roughly 80 percent of adult frogs captured in the spring and again in the fall occupied the same home ranges.**

***Population density*.** **During the breeding season, green frog densities at breeding ponds can exceed several hundred individuals per hectare (Wells, 1978). Adult male frogs space their breeding territories about 2 to 3 m apart (Martof, 1953a).**

***Population dynamics*.** **Sexual maturity is attained in 1 or 2 years after metamorphosis; individuals may reach maturity at the end of the first year but not attempt to breed until the next year (Martof, 1956a,b). Most females lay one clutch per year, although some may lay two clutches, about 3 to 4 weeks apart (Wells, 1976). In natural populations, green frogs can live to approximately 5 years of age (Martof, 1956b).**

Similar species (from general references)

- **The river frog (*Rana heckscheri*) is slightly larger than the green frog (8.0 to 12.0 cm SVL) and is found in swamps from southeast North Carolina to central Florida and southern Mississippi.**
- **The leopard and pickerel frogs (*Rana pipiens* and its relatives, and *Rana palustris*) are medium sized and strongly spotted. There are four leopard frogs whose ranges are mostly exclusive from each other, but overlap with the green frog. The pickerel frog has a similar range with gaps in the upper midwest and the southeast.**
- **The mink frog (*Rana septentrionalis*) is only slightly smaller (4.0 to 7.0 cm) and is found on the borders of ponds and lakes, especially near waterlilies. It ranges from Minnesota to New York, north to Labrador.**
- **The carpenter frog (*Rana virgatipes*) is about the same size as the green frog (4.1 to 6.7 cm) and is closely associated with sphagnum bogs and grasslands. It has a coastal plain range from New Jersey to Georgia and Florida.**

The bullfrog and pig frog are much larger ranid species and are covered in the next profile (Section 2.3.8).

General references

Behler and King (1979); Conant and Collins (1991); DeGraaf and Rudis (1983); Martof (1953a, b, 1956a, b); Smith (1956, 1961).

Green Frog (*Rana clamitans*)

Factors	Age/Sex/ Cond./Seas.	Mean	Range or (95% CI of mean)	Location (subspecies)	Reference	Note No.
Body Weight (g)	B B	49.1 ± 20.0 SD	25.5 - 103.5	New Brunswick, Canada	McAlpine & Dilworth, 1989	
	A M breeding	44.0 ± 10.0 SD	27.0 - 66.0	New York (*melanota*)	Wells, 1978	
	at metamorphosis	3		New York	Pough & Kamel, 1984	1
Length (mm SVL)	A	54 - 102		NS	Behler and King, 1979	
	A M	79.8 ± 8.5 SD	103 maximum	s Michigan	Martof, 1956b	
	A F	80.3 ± 8.9 SD	105 maximum			
	J B	32.6	28.4 - 36.3	s Michigan	Martof, 1956b	
Metabolic Rate (kcal/kg-d)	basal:					
	A	8.08			estimated	2
	at metamorphosis	15.8			estimated	3
Food Ingestion Rate (g/g-d)						4
Surface Area (cm^2)	A	17			estimated	5
	at metamorphosis	2			estimated	6

Dietary Composition	Spring	Summer	Fall	Winter	Location (subspecies)/Habitat (measure)	Reference	Note No.
adults:					New York/lake	Stewart & Sandison, 1973	7
plant material		10.8					
Araneae		12.1			(% total volume;		
Coleoptera		32.8			stomach contents)		
Hemiptera		12.9					
Hymenoptera		14.4					
Diptera		6.8					
Ephemeroptera		5.6					
Mollusca		5.4					
Lepidoptera		2.5					

Green Frog (*Rana clamitans*)

Dietary Composition	Spring	Summer	Fall	Winter	Location (subspecies)/Habitat (measure)	Reference	Note No.
adults:					s Illinois/swamp, stream	Jenssen & Klimstra, 1966	
mineral	-	-	-	2.6			
plant	5.7	8.3	4.2	0.5	(% wet volume; stomach contents)		
Pulmonata	15.7	18.3	6.4	11.0			
Oligochaeta	2.1	0.8	2.3	6.4			
Amphipoda	1.2	0.1	-	4.6			
Isopoda	5.6	1.4	-	4.6			
Decapoda	-	-	4.1	-			
Julioforma	7.5	0.3	1.7	-			
Araneida	2.8	3.4	6.6	7.4			
Odonata	1.6	12.4	5.9	-			
Orthoptera	0.9	3.0	1.5	-			
Hemiptera	1.0	7.0	6.1	2.2			
Coleoptera	9.6	19.6	15.9	9.1			
Lepidoptera	25.4	7.0	25.1	-			
Diptera	6.0	5.2	4.5	10.3			
Hymenoptera	9.9	6.0	13.5	-			
Salientia	-	-	3.9	-			

Population Dynamics	Age/Sex/ Cond./Seas.	Mean	Range or (95% CI of mean)	Location (subspecies)/ Habitat	Reference	Note No.
Home Range Size	A B nonbreeding	0.0065 ± 0.0036 SD ha	0.0020 - 0.020 ha	s Michigan (*melanota*)/ shallow water	Martof, 1953b	8
	A M breeding	meters shoreline: 4.0 - 6.0		New York (*melanota*)/ open nearshore areas of ponds	Wells, 1977	
	A M breeding	meters shoreline: 1.0 - 1.5		New York (*melanota*)/ densely vegetated nearshore areas of ponds	Wells, 1977	
Population Density (N/ha)	A M A F	476 567		New York (*melanota*)/ artificial pond	Wells, 1978	9

Green Frog (*Rana clamitans*)

Population Dynamics	Age/Sex/ Cond./Seas.	Mean	Range or (95% CI of mean)	Location (subspecies)/ Habitat	Reference	Note No.
Clutch Size		4,100	3,800 - 4,300	s Michigan (*melanota*)/ pond	Martof, 1956a	
			1,000 - 7,000	New York (*melanota*)/ shallow ponds	Wells, 1976	
			3,500 - 4,000	New York (*melanota*)/ shallow water	Wright, 1914	10
Clutches/Year			1 - 2	New York (*melanota*)/ shallow ponds	Wells, 1976	
Days Incubation (d)		3 - 6		Connecticut (*melanota*)/ shallow water	Babbit, 1937	10
		3 - 5		New York/ponds, pools	Ryan, 1953	
Age at Metamorphosis			1 - 2 yrs	New England (*melanota*)/ shallow water	DeGraaf & Rudis, 1983	
	early eggs	3 mo		Virginia, Carolinas/ shallow ponds	Martof et al., 1980	
	late eggs	10 - 12 mo				
	early eggs	2.5 - 3 mo		s Michigan (*melanota*)/ shallow ponds	Martof, 1956a, b	11
	late eggs	11 - 12 mo				
Age at Sexual Maturity (yr)	A M	1 - 2		s Michigan (*melanota*)/ shallow ponds	Martof, 1956a, b	
	A F	1 - 2				
	B	1		New York (*melanota*)/ pond	Wells, 1977	

Green Frog (*Rana clamitans*)

Seasonal Activity	Begin	Peak	End	Location (subspecies)	Reference	Note No.
Mating/Laying	May May early June	early June	mid-August September mid-August	s Michigan (*melanota*) Illinois (*melanota*) New York	Martof, 1956a Smith, 1961 Wells, 1976	
Meta-morphosis						
eggs laid early	early August		late September	s Michigan (*melanota*)	Martof, 1956b	12
		August, September		New York	Pough & Kamel, 1984	12
eggs laid late	early June		mid-July	s Michigan (*melanota*)	Martof, 1956b	13
		next spring		New York	Pough & Kamel, 1984	13
Hibernation	Oct. - Nov. Oct.		March - April late March	s Michigan (*melanota*) New York	Martof, 1956a Ryan, 1953	

1 Weight at metamorphosis can vary by two to four times between the smallest and largest individuals.
2 Estimated assuming temperature of 20°C using Equation 3-50 (Robinson et al., 1983) and body weights from McAlpine and Dilworth (1989).
3 Estimated assuming temperature of 20°C using Equation 3-50 (Robinson et al., 1983) and body weights from Pough and Kamel (1984).
4 See Chapters 3 and 4 for methods of estimating food ingestion rates from metabolic rate and diet.
5 Estimated using Equation 3-25 (Hutchinson et al., 1968) and body weights from McAlpine and Dilworth (1989).
6 Estimated using Equation 3-25 (Hutchinson et al., 1968) and body weights from Pough and Kamel (1984).
7 Season not specified.
8 Daily activity range of nonbreeding frogs.
9 Frogs were initially hand-captured and placed in pond; the numbers given are for those frogs that stayed.
10 Cited in DeGraaf and Rudis (1983).
11 Eggs laid before June.
12 Metamorphosed in the same year eggs were laid.
13 Metamorphosed the year following the season the eggs were laid.

References (including Appendix)

Babbitt, L. H. (1937) The amphibia of Connecticut. Hartford, CT: State Geol. and Nat. Hist. Surv.; Bull. No. 57. 9-50

Behler, J. L.; King, F. W. (1979) The Audubon Society field guide to North American reptiles and amphibians. New York: Alfred A. Knopf, Inc.

Bush, F. M. (1959) Foods of some Kentucky herptiles. Herpetologica 15: 73-77.

Conant, R.; Collins, J. T. (1991) A field guide to reptiles and amphibians. Boston, MA: Houghton Mifflin Co.

DeGraaf, R. M.; Rudis, D.D. (1983) Green frog. Amphibians and reptiles of New England. Amherst, MA: University of Massachusetts Press.

Hamilton, W. J., Jr. (1948) The food and feeding behavior of the green frog, *Rana clamitans* (Latreille), in New York state. Copeia 1948: 203-207.

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.

Jenssen, T. A.; Klimstra, W. D. (1966) Food habits of the green frog, *Rana clamitans*, in southern Illinois. Amer. Midl. Nat. 76: 169-182.

Martof, B. S. (1953a) Territoriality in the green frog, *Rana clamitans*. Ecology 34: 165-174.

Martof, B. S. (1953b) Home range and movements of the green frog, *Rana clamitans*. Ecology 34: 529-543.

Martof, B. S. (1956a) Factors influencing size and composition of populations of *Rana clamitans*. Am. Midl. Nat. 56: 224-245.

Martof, B. S. (1956b) Growth and development of the green frog, *Rana clamitans*, under natural conditions. Am. Midl. Nat. 55: 101-117.

Martof, B. S.; Palmer, W. M.; Bailey, J. R.; et al. (1980). Amphibians and reptiles of the Carolinas and Virginia. Chapel Hill, NC: University of North Carolina Press.

McAlpine, D. F.; Dilworth, T. G. (1989) Microhabitat and prey size among three species of *Rana* (Anura: Ranidae) sympatric in eastern Canada. Can. J. Zool. 67: 2241-2252.

Mele, J. A. (1980) The role of lipids in storage and utilization of energy for reproduction and maintenance in the green frog, *Rana clamitans* [Ph.D. dissertation]. New Brunswick, NJ: Rutgers University.

Pope, C. H. (1947) Amphibians and reptiles of the Chicago area. Chicago, IL: Chicago Nat. Hist. Mus. Press.

Pough, F. H.; Kamel, S. (1984) Post-metamorphic physiological change in relation to anuran life histories. Oecologia 65: 138-144.

Robinson, F. 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.

Ryan, R. A. (1953) Growth rates of some ranids under natural conditions. Copeia 1953:73-80.

Smith, H. M. (1956) Handbook of amphibians and reptiles of Kansas. Univ. Kansas Mus. Nat. Hist. Misc. Publ. 9.

Smith, P. W. (1961) The amphibians and reptiles of Illinois. Ill. Nat. Hist. Surv. Bull. 28.

Stewart, M. M.; Sandison, P. (1973) Comparative food habits of sympatric mink frogs, bullfrogs, and green frogs. J. Herpetol. 6: 241-244.

Wells, K. D. (1976) Multiple egg clutches in the green frog (*Rana clamitans*). Herpetologica 32: 85-87.

Wells, K. D. (1977) Territoriality and male mating success in the green frog (*Rana clamitans*). Ecology 58: 750-762.

Wells, K. D. (1978) Territoriality in the green frog (*Rana clamitans*): vocalizations and agonistic behaviour. Anim. Behav. 26: 1051-1063.

Wright, A. H. (1914) North American anura: life histories of the anurans of Ithaca, New York. Washington, DC: Carnegie Institute; Publ. No. 197.

2.3.8. Bullfrog (true frog family)

Order *Anura*, Family *Ranidae*. These are typical frogs with adults being truly amphibious. They tend to live at the edge of water bodies and enter the water to catch prey, flee danger, and spawn (Behler and King, 1979). This profile covers large ranids. Medium-sized ranids are covered in the previous profile (Section 2.3.7).

Selected species

The bullfrog's (*Rana catesbeiana*) natural range includes the eastern and central United States and southeastern Canada; however, it has been introduced in many areas in the western United States and other parts of North America. It is continuing to expand its range, apparently at the expense of several native species in many locations (Bury and Whelan, 1984). There are no subspecies for the bullfrog.

***Body size*. The bullfrog is the largest North American ranid. Adults usually range between 9 and 15 cm in length from snout-to-vent length (SVL) and exceptional individuals can reach one half kilogram or more in weight (Conant and Collins, 1991; Durham and Bennett, 1963). Males are usually smaller than females (Smith, 1961). Frogs exhibit indeterminate growth, and bullfrogs continue to increase in size for at least 6 years after metamorphosis (Durham and Bennett, 1963; Howard, 1981a). Hutchinson et al. (1968) developed an allometric equation relating bullfrog surface area (SA in cm) to body weight (Wt in grams):**

$$SA = 0.953\ Wt^{0.725}.$$

This equation also is presented in Chapter 3 as Equation 3-24.

***Habitat*. Adult bullfrogs live at the edges of ponds, lakes, and slow-moving streams large enough to avoid crowding and with sufficient vegetation to provide easily accessible cover (Behler and King, 1979). Small streams are used when better habitat is lacking (Conant and Collins, 1991). Bullfrogs require permanent bodies of water, because the tadpoles generally require 1 or more years to develop prior to metamorphosis (Howard, 1981b). Small frogs favor areas of very shallow water where short grasses or other vegetation or debris offer cover (Durham and Bennett, 1963). Larger bullfrogs seem to avoid such areas (Durham and Bennett, 1963). Tadpoles tend to congregate around green plants (Jaeger and Hailman, 1976, cited in Bury and Whelan, 1984).**

***Food habits*. Adult *R. catesbeiana* are indiscriminate and aggressive predators, feeding at the edge of the water and among water weeds on any available small animals, including insects, crayfish, other frogs and tadpoles, minnows, snails, young turtles, and occasionally small birds, small mammals, and young snakes (Behler and King, 1979; DeGraaf and Rudis, 1983; Korschgen and Baskett, 1963). Bullfrogs often focus on locally abundant foods (e.g., cicadas, meadow voles) (Korschgen and Baskett, 1963). Crustaceans and insects probably make up the bulk of the diet in most areas (Carpenter and Morrison, 1973; Fulk and Whitaker, 1968; Smith, 1961; Tyler and Hoestenbach, 1979). Bullfrog tadpoles consume primarily aquatic plant material and some invertebrates,**

but also scavenge dead fish and eat live or dead tadpoles and eggs (Bury and Whelan, 1984; Ehrlich, 1979).

***Temperature regulation and daily activities*. Bullfrogs forage by day (Behler and King, 1979). They thermoregulate behaviorally by positioning themselves relative to the sun and by entering or leaving the water (Lillywhite, 1970). In one study, body temperatures measured in bullfrogs during their normal daily activities averaged 30°C and ranged from 26 to 33°C (Lillywhite, 1970). At night, their body temperatures were found to range between 14.4 and 24.9°C (Lillywhite, 1970). Tadpoles also select relatively warm areas, 24 to 30°C (Bury and Whelan, 1984). Despite this narrow range of temperatures in which bullfrogs normally maintain themselves, they are not immobilized by moderately lower temperatures (Lillywhite, 1970). The metabolic rate of bullfrogs increases with increasing body temperature. Between 15 and 25°C, the Q_{10} for oxygen consumption is 1.87; between 25 and 33°C, the Q_{10} is 2.41 (Burggren et al., 1983).**

***Hibernation*. Most bullfrogs hibernate in mud and leaves under water beginning in the fall, but some bullfrogs in the southern states may be active year round (Bury and Whelan, 1984). They emerge sometime in the spring, usually when air temperatures are about 19 to 24°C and water temperatures are at least 13 to 14°C (Wright, 1914; Willis et al., 1956). Bullfrogs emerge from hibernation later than other ranid species (Ryan, 1953).**

***Breeding activities* and *social organization*. Bullfrogs spawn at night close to shorelines in areas sheltered by shrubs (Raney, 1940, cited in DeGraaf and Rudis, 1983). The timing and duration of the breeding season varies depending on the location. In the southern states, the breeding season extends from spring to fall, whereas in the northern states, it is restricted to late spring and summer (Behler and King, 1979). Males tend to be territorial during the breeding season, defending their calling posts and oviposition sites (i.e., submerged vegetation near shore) (Howard, 1978b; Ryan, 1980). Female visits to the pond tend to be brief and sporadic (Emlen, 1976). Some males mate with several females whereas others, usually younger and smaller males, may not breed at all in a given year (DeGraaf and Rudis, 1983). Females attach their eggs, contained in floating films of jelly, to submerged vegetation (Behler and King, 1979). Adults are otherwise rather solitary occupying their own part of a stream or pond (Smith, 1961).**

***Tadpole and metamorphosis*. Eggs hatch in 3 to 5 days (Clarkson and DeVos, 1986; Smith, 1956). Temperatures above 32°C have been shown to cause abnormalities in tadpoles and above 35.9°C to kill embryos (Howard, 1978a). Tadpole growth rates increase with increasing oxygen levels, food availability, and water temperature (Bury and Whelan, 1984). Tadpole gill ventilation at 20°C can generate a branchial water flow of almost 0.3 ml/g-min (Burggren and West, 1982). Metamorphosis from a tadpole to a frog can occur as early as 4 to 6 months in the southern parts of its range; however, most tadpoles metamorphose from 1 to 3 years after hatching, depending on latitude and temperature (DeGraaf and Rudis, 1983; Martof et al., 1980).**

***Home range and resources*. The species' home range includes its foraging areas and refuges in and around aquatic environments. Home range size decreases with increasing bullfrog density, and males tend to use larger home ranges than females (Currie and Bellis, 1969). Bullfrogs tend to stay in the same pools throughout the summer months**

if the water level is stable (Raney, 1940, cited in DeGraaf and Rudis, 1983). During the breeding season, adult males establish territories that they defend against conspecific males (Emlen, 1968). During the non-breeding season, Currie and Bellis (1969) found no evidence of territorial defense. Males often do not return to the same pond the following spring (Durham and Bennett, 1963).

***Population density*. During the breeding season, each breeding male may defend a few meters of shoreline (Currie and Bellis, 1969; Emlen, 1968). The densities of females and non-breeding males vary with time of day and season and are difficult to estimate. Tadpoles can be present locally in extremely high densities (Cecil and Just, 1979).**

***Population dynamics*. Sexual maturity is attained in about 1 to 3 years after metamorphosis, depending on latitude (Howard, 1978a; Raney and Ingram, 1941, cited in Bury and Whelan, 1984). Only females that are at least 2 years past metamorphosis mate during the early breeding season; males and females 1 year past metamorphosis may breed during the later breeding periods (Howard, 1978a, 1981b). Also, some older females have been observed to mate and to lay a second clutch during the later breeding period (Howard, 1978a). Willis et al. (1956) estimated the minimum breeding length for females in Missouri to be 123 to 125 mm SVL. Mortality of tadpoles is high (Cecil and Just, 1979), and adult frogs are unlikely to live beyond 5 to 8 years postmetamorphosis (Howard, 1978b). In some areas, snapping turtles may be responsible for a large component of adult bullfrog mortality (Howard, 1981a).**

Similar species (from general references)

- **The pig frog (*Rana grylio*) is smaller than the bullfrog (8 to 14 cm) and is found in south South Carolina to south Florida and south Texas.**

The remaining ranid species are more similar in size to the green (or bronze) frog. See Section 2.3.7 for a description of these frogs.

General references

Behler and King (1979); Bury and Whelan (1984); Conant and Collins (1991); DeGraaf and Rudis (1983); Smith (1961).

Bullfrog (*Rana catesbeiana*)

Factors	Age/Sex/ Cond./Seas.	Mean	Range or (95% CI of mean)	Location	Reference	Note No.
Body Weight (g)	B B	142.8 ± 77.4 SD	9.5 - 274.0	New Brunswick, Canada	McAlpine & Dilworth, 1989	1
	A B	249		central Arkansas	McKamie & Heidt, 1974	
	young tadpole	2.0 ± 1.1 SD		Kentucky	Viparina & Just, 1975	
	1-yr tadpole	35.7 ± 5.2 SD				
	post-emergence:					
	1 month	18	13 - 42	Louisiana/lab	Modzelewski & Culley, 1974	2
	2 months	30	19 - 52			
	3 months	42	27 - 77			
	4 months	56	41 - 101			
			total length:			
	at metamorph.	9	(84 mm)	east central Illinois	Durham & Bennett, 1963	
	1 yr B	91	(240 mm)			
	2 yr B	210	(307 mm)			
	3 yr B	240	(320 mm)			
	4 yr B	260	(335 mm)			
	5 yr B	290	(348 mm)			
	6 yr B	360	(356 mm)			
Metabolic Rate (lO_2/kg-d)	tadpole, 25°C	2.6 ± 0.2 SE		NS/lab	Burggren et al., 1983	3
	adult resting, 5°C	1.0	0.31 - 2.3	NS/NS	Hutchinson et al., 1968	4
Metabolic Rate (kcal/kg-d)	basal:				estimated	5
	2 mo (30 g)	9.1				
	1 yr (91 g)	7.0				
	B B (143 g)	6.3				
	A B (249 g)	5.5				

Bullfrog (*Rana catesbeiana*)

Factors	Age/Sex/ Cond./Seas.	Mean	Range or (95% CI of mean)	Location	Reference	Note No.
Food Ingestion Rate (g/g-d)	(13 - 42 g) (18 - 52 g) (28 - 77 g) (40 - 100 g)	0.071 0.059 0.040 0.033		Louisiana (24 - 27°C)	Modzelewski & Culley, 1974	
Surface Area (cm^2)	2 mo (30 g) 1 yr (91 g) B B (143 g) A B (249 g)	11 25 35 52			estimated	6

Dietary Composition	Spring	Summer	Fall	Winter	Location/Habitat (measure)	Reference	Note No.
adults: Decapoda-Astacidae Lepidoptera Coleoptera (Lampryidae) (Chrysomelidae) (Carabidae) Pulmonata-Zonitidae Chilipoda sand, rock, gravel		 47.7 19.0 16.0 (5.8) (5.8) (4.1) 8.3 7.7 1.2			Kentucky/NS (% wet volume; stomach contents)	Bush, 1959	
adults: plant animal (Odonata) (Coleoptera) (Hemiptera) (Hymenoptera) (Amphibia) unaccounted		 19.7 65.2 (8.8) (15.8) (0.5) (2.2) (26.4) 15.1			New York/mountain lake (% volume; stomach contents)	Stewart & Sandison, 1973	

Bullfrog (*Rana catesbeiana*)

Dietary Composition	Spring	Summer	Fall	Winter	Location/Habitat (measure)	Reference	Note No.
adults:					Missouri/bait minnow pond	Corse & Metter, 1980	
frogs	35	33	39				
tadpoles	8	11	0		(number of items found;		
shiners	305	157	25		stomach contents)		
other fish	7	2	5				
Gastropoda	55	70	26				
crayfish	22	162	18				
other crustacea	71	42	47				
Arachnida	3	23	3				
Coleoptera (adult)	31	33	15				
Diptera (larvae)	2	7	0				
Hemiptera	41	43	16				

Population Dynamics	Age/Sex/ Cond./Seas.	Mean	Range or (95% CI of mean)	Location/Habitat	Reference	Note No.
Home Range Size (m radius)	A M nonbreed	2.9	0.76 - 11.3	Ontario, Canada/pond	Currie & Bellis, 1969	
	A F nonbreed	2.4	0.61 - 10.2			
	A M territory	2.7		Michigan/pond	Emlen, 1968	7
Population Density (N/ha)	B B (1960)	1,376		Ontario, Canada/pond	Currie & Bellis, 1969	
	B B (1961)	892				
	tadpoles:			Kentucky/pond	Cecil & Just, 1979	
	November	130,000				
	March	69,000				
	May	16,000				
Clutch Size		7,360 ± 741.7 SE	10,000 - 20,000	Kansas/NS New Jersey/pond	Smith, 1956 Ryan, 1980	
Clutches/Year	93% of F	1		Michigan/pond	Emlen, 1977	
	7% of F	2				
Days to Hatching		2 - 4		Arizona, California/river	Clarkson & DeVos, 1986	
		4 - 5		Kansas/NS	Smith, 1956	

Bullfrog (*Rana catesbeiana*)

Population Dynamics	Age/Sex/ Cond./Seas.	Mean	Range or (95% CI of mean)	Location/Habitat	Reference	Note No.
Age at Metamor-phosis	B B B B	1 yr 1 - 2 yr 2 - 3 yr 3 yr		Carolinas, Virginia/NS Michigan/pond New York/NS Nova Scotia, Canada/NS	Martof et al., 1980 Collins, 1979 Ryan, 1953 Bleakney, 1952	 8
Age at Sexual Maturity	M F B	1 yr after metam. 1 - 2 yr after metam. 1 - 2 yr after metam.		Michigan/pond New York/NS	Howard, 1978a Ryan, 1953	
Annual Mortality Rates (%) Mortality Rates (%)	A M 1 - 2 yr A M 2 - 3 yr A M 3 - 4 yr A M 4 - 5 yr tadpoles (to metamorph.)	58 58 48 77 85.5	 82.4 - 88.2	Michigan/pond Kentucky/shallow ponds	Howard, 1984 Cecil & Just, 1979	
Longevity (yr)	A B		up to 5 - 8	Michigan/ponds	Howard, 1978b	

Seasonal Activity	Begin	Peak	End	Location	Reference	Note No.
Mating/Laying	February April May late May	 May late June July	October late June August July	southern range in N America California, Arizona Missouri northern range in N America	Behler & King, 1979 Clarkson & DeVos, 1986 Willis et al., 1956 DeGraaf & Rudis, 1983; Behler & King, 1979	
Metamor-phosis	August March June July	(1st clutch) (2nd clutch) late June-Aug.	October April early October Sept., October	California, Arizona California, Arizona Missouri New York	Clarkson & DeVos, 1986 Clarkson & DeVos, 1986 Willis et al., 1956 Ryan, 1953	

Bullfrog (*Rana catesbeiana*)

Seasonal Activity	Begin	Peak	End	Location	Reference	Note No.
Hibernation	late October mid-October		late March March	east central Illinois Missouri	Durham & Bennett, 1963 Willis et al., 1956	

1 Mean snout-to-vent length (SVL) of frogs was 98 mm SVL and the range was 45 to 128 mm SVL.
2 Age postmetamorphosis; maintained at a temperature of 24 to 27 °C and fed mosquitofish, crickets, and earthworms.
3 Restrained, cannulated; weight 5.7 g.
4 Mean weight of frogs was 74.8 g.
5 Estimated assuming temperature of 20 °C using Equation 3-50 (Robinson et al., 1983). Body weights (1) for 2-month postmetamorphosis frog from Modzelewski and Culley (1974); (2) for a 1-year postmetamorphosis frog from Durham and Bennett (1963), Farrar and Dupre (1983); (3) for both juveniles and adults of both sexes, McAlpine and Dilworth (1989); and (4) for adults of both sexes, McKamie and Heidt (1974).
6 Estimated using Equation 3-24 (Hutchinson et al., 1968) and body weights as described in note 5.
7 Based on average distance between frogs.
8 Cited in Bury and Whelan (1984).

References (including Appendix)

Behler, J. L.; King, F. W. (1979) The Audubon Society field guide to North American reptiles and amphibians. New York, NY: Alfred A. Knopf, Inc.

Bleakney, J. S. (1952) The amphibians and reptiles of Nova Scotia. Can. Field-Nat. 66: 125-129.

Brooks, G. R., Jr. (1964) An analysis of the food habits of the bullfrog by body size, sex, month, and habitat. Va. J. Sci. 15: 173-186.

Bruneau, M.; Magnin, E. (1980) Croissance, nutrition, et reproduction des ouaouarons *Rana catesbeiana* Shaw (Amphibia Anura) des Laurentides au nord de Montreal. Can J. Zool. 58: 175-183.

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 larvae of *Rana berlandieri* and *Rana catesbeiana*. Physiol. Zool. 56: 263-273.

Bury, R. B.; Whelan, J. A. (1984) Ecology and management of the bullfrog. U.S. Fish Wildl. Serv. Resour. Publ. No. 155; 23 pp.

Bush, F. M. (1959) Foods of some Kentucky herptiles. Herpetologica 15: 73-77.

Carpenter, H. L.; Morrison, E. O. (1973) Feeding behavior of the bullfrog, *Rana catesbeiana*, in north central Texas. Bios 44: 188-193.

Cecil, S. G.; Just, J. J. (1979) Survival rate, population density and development of a naturally occurring anuran larvae (*Rana catesbeiana*). Copeia 1979: 447-453.

Clarkson, R. W.; DeVos, J. C., Jr. (1986) The bullfrog, *Rana catesbeiana* Shaw, in the lower Colorado River, Arizona-California. J. Herpetol. 20: 42-49.

Cohen, N. W.; Howard, W. E. (1958) Bullfrog food and growth at the San Joaquin Experimental Range, California. Copeia 1958: 223-225.

Collins, J. P. (1975) A comparative study of life history strategies in a community of frogs [Ph.D. dissertation]. Ann Arbor, MI: University of Michigan.

Collins, J. P. (1979) Intrapopulation variation in the body size at metamorphosis and timing of metamorphosis in the bullfrog. Ecology 60: 738-749.

Conant, R.; Collins, J. T. (1991) A field guide to reptiles and amphibians - eastern and central North America. Boston, MA: Houghton Mifflin Co.

Corse, W. A.; Metter, D. A. (1980) Economics, adult feeding and larval growth of *Rana catesbeiana* on a fish hatchery. J. Herpetol. 14: 231-238.

Currie, W.; Bellis, E. D. (1969) Home range and movements of the bullfrog, *Rana catesbeiana* (Shaw), in an Ontario pond. Copeia 1969: 688-692.

DeGraaf, R. M.; Rudis, D. D. (1983) Amphibians and reptiles of New England. Amherst, MA: University of Massachusetts Press.

Dowe, B. J. (1979) The effect of time of oviposition and microenvironment on growth of larval bullfrogs (*Rana catesbeiana*) in Arizona [master's thesis]. Tempe, AZ: Arizona State University.

Durham, L.; Bennett, G. W. (1963) Age, growth, and homing in the bullfrog. J. Wildl. Manage. 27: 107-123.

Ehrlich, D. (1979) Predation by bullfrog tadpoles (*Rana catesbeiana*) on eggs and newly hatched larvae of the plains leopard frog (*Rana blairi*). Bull. Md. Herpetol. Soc. 15: 25-26.

Emlen, S. T. (1968) Territoriality in the bullfrog, *Rana catesbeiana*. Copeia 1968: 240-243.

Emlen, S. T. (1976) Lek organization and mating strategies of the bullfrog. Behav. Ecol. Sociobiol. 1: 283-313.

Emlen, S. T. (1977) "Double clutching" and its possible significance in the bullfrog. Copeia 1977: 749-751.

Farrar, E. S.; Dupre, R. K. (1983) The role of diet in glycogen storage by juvenile bullfrogs prior to overwintering. Comp. Biochem. Physiol. A: Comp. Physiol. 75: 255-260.

Frost, S. W. (1935) The food of *Rana catesbeiana* Shaw. Copeia 1935: 15-18.

Fulk, F. D.; Whitaker, J. O., Jr. (1968) The food of *Rana catesbeiana* in three habitats in Owen County, Indiana. Indiana Acad. Sci. 78: 491-496.

George, I. D. (1940) A study of the bullfrog, *Rana catesbeiana* Shaw, at Baton Rouge, Louisiana [Ph.D. dissertation]. Ann Arbor, MI: University of Michigan.

Gibbons, J. W.; Semlitsch, R. D. (1991) Guide to the reptiles and amphibians of the Savannah River Site. Athens, GA: The University of Georgia Press.

Glass, M. L.; Burggren, W. W.; Johansen, K. (1981) Pulmonary diffusing capacity of the bullfrog (*Rana catesbeiana*). Acta Physiol. Scand. 113: 485-490.

Hammer, D. A.; Linder, R. L. (1971) Bullfrog food habits on a waterfowl production area in South Dakota. Proc. SD Acad. Sci. 50: 216-219.

Howard, R. D. (1978a) The influence of male-defended oviposition sites on early embryo mortality in bullfrogs. Ecology 59: 789-798.

Howard, R. D. (1978b) The evolution of mating strategies in bullfrogs, *Rana catesbeiana*. Evolution 32: 850-871.

Howard, R. D. (1981a) Sexual dimorphism in bullfrogs. Ecology 62: 303-310.

Howard, R. D. (1981b) Male age-size distribution and male mating success in bullfrogs. In: Alexander, R. D.; Tinkle, D. W., ed. Natural selection and social behavior: recent research and new theory; pp. 61-77.

Howard, R. D. (1984) Alternative mating behaviors of young male bullfrogs. Am. Zool. 24: 397-406.

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.

Jaeger, R. G.; Hailman, J. P. (1976) Ontogenetic shift of spectral phototactic preferences in anuran tadpoles. J. Comp. Physiol. Psychol. 90: 930-945.

Korschgen, L. J.; Baskett, T. S. (1963) Foods of impoundment and stream dwelling bullfrogs in Missouri. Herpetologica 19: 89-97.

Korschgen, L. J.; Moyle, D. L. (1955) Food habits of the bullfrog in central Missouri farm ponds. Amer. Midl. Nat. 54: 332-341.

Lillywhite, H. B. (1970) Behavioral temperature regulation in the bullfrog, *Rana catesbeiana*. Copeia 1970: 158-168.

Martof, B. S.; Palmer, W. M.; Bailey, J. R.; et al. (1980) Amphibians and reptiles of the Carolinas and Virginia. Chapel Hill, NC: University of North Carolina Press.

McAlpine, D. F.; Dilworth, T. G. (1989) Microhabitat and prey size among three species of *Rana* (Anura: Ranidae) sympatric in eastern Canada. Can. J. Zool. 67: 2241-2252.

McAuliffe, J. R. (1978) Biological survey and management of sport-hunted bullfrog populations in Nebraska. Lincoln, NE: Nebraska Game and Parks Commission; 78 pp.

McKamie, J. A.; Heidt, G. A. (1974) A comparison of spring food habits of the bullfrog, *Rana catesbeiana*, in three habitats of central Arkansas. Southwest. Nat. 19: 107-111.

Modzelewski, E. H., Jr.; Culley, D. D., Jr. (1974) Growth responses of the bullfrog, *Rana catesbeiana* fed various live foods. Herpetologica 30: 396-405.

Oliver, J. A. (1955) The natural history of North American amphibians and reptiles. Princeton, NJ: Van Nostrand Co.

Raney, E. C. (1940) Summer movements of the bullfrog, *Rana catesbeiana* (Shaw), as determined by the jaw-tag method. Am. Midl. Nat. 23: 733-745.

Raney, E. C.; Ingram, W. M. (1941) Growth of tagged frogs (*Rana catesbeiana* Shaw and *Rana clamitans* Daudin) under natural conditions. Am. Midl. Nat. 26: 201-206.

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.

Ryan, M. J. (1980) The reproductive behavior of the bullfrog (*Rana catesbeiana*). Copeia 1980: 108-114.

Ryan, R. A. (1953) Growth rates of some ranids under natural conditions. Copeia 1953: 73-80.

Smith, H. M. (1956) Handbook of amphibians and reptiles of Kansas. Univ. Kansas Mus. Nat. Hist. Misc. Publ. 9.

Smith, P. W. (1961) The amphibians and reptiles of Illinois. Ill. Nat. Hist. Surv. Bull. 28.

Stewart, M. M.; Sandison, P. (1973) Comparative food habits of sympatric mink frogs, bullfrogs, and green frogs. J. Herpetol. 6: 241-244.

Storer, T. I. (1922) The eastern bullfrog in California. Calif. Fish and Game 8: 219-224.

Treanor, R. R.; Nichola, S. J. (1972) A preliminary study of the commercial and sporting utilization of the bullfrog, *R. catesbeiana* Shaw in California. Calif. Dept. Fish and Game, Inland Fish. Admin. Rep. 72-4; 23 pp.

Turner, F. B. (1960) Postmetamorphic growth in anurans. Am. Midl. Nat. 64: 327-338.

Tyler, J. D.; Hoestenbach, R. D., Jr. (1979) Differences in food of bullfrogs (*Rana catesbeiana*) from pond and stream habitats in southwestern Oklahoma. Southwest. Nat. 24: 33-38.

Viparina, S.; Just, J. J. (1975) The life period, growth and differentiation of *Rana catesbeiana* larvae occurring in nature. Copeia 1975: 103-109.

Weathers, W. W. (1976) Influence of temperature acclimation on oxygen consumption, haemodynamics and oxygen transport in bullfrogs. Aust. J. Zool. 24: 321-330.

Willis, Y. L.; Moyle, D. L.; Baskett, T. S. (1956) Emergence, breeding, hibernation, movements and transformation of the bullfrog, *Rana catesbeiana*, in Missouri. Copeia 1956: 30-41.

Wright, A. H. (1914) North American Anura: life histories of the Anurans of Ithaca, New York. Washington, DC: Carnegie Institute; Publ. No. 197.

Wright, A. H.; Wright, A. A. (1949) Handbook of frogs and toads of the United States and Canada. Ithaca, New York: Comstock Publishing Co.

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:

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

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

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 CO_2 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:

$FI\ (g/day) = 0.648\ Wt^{0.651}\ (g)$, or $FI\ (kg/day) = 0.0582\ Wt^{0.651}\ (kg)$	all birds	[3-3]
$FI\ (g/day) = 0.398\ Wt^{0.850}\ (g)$	passerines	[3-4]

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

Diet	Metabolizable Energy (kJ/g)[a]	(kcal/g)[a]	Animal Group
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

[a]g = grams dry weight.
Source: Nagy, 1987.

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

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

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 (g/day) = 0.235 $Wt^{0.822}$ (g), or **FI (kg/day) = 0.0687 $Wt^{0.822}$ (kg)**	**all mammals**	**[3-7]**
FI (g/day) = 0.621 $Wt^{0.564}$ (g)	**rodents**	**[3-8]**
FI (g/day) = 0.577 $Wt^{0.727}$ (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 (kjoule/day) = 971 $Wt^{0.73}$ (kg) (r^2 = 0.942), or **FI (kcal/day) = 1.518 $Wt^{0.73}$ (g)**	**herbivores**	**[3-10]**
FI (kjoule/day) = 975 $Wt^{0.70}$ (kg) (r^2 = 0.968), or **FI (kcal/day) = 1.894 $Wt^{0.70}$ (g)**	**carnivores**	**[3-11]**

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:

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

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

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

$$FI\ (kjoule/day) = 0.224\ Wt^{0.799}\ (g),\ \text{or} \qquad \text{all iguanids} \qquad [3\text{-}14]$$
$$FI\ (kcal/day) = 0.054\ Wt^{0.799}\ (g)$$

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:

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

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:

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

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:

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

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:

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

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):

$IR\ (ml/min) = 284\ Wt^{0.77}\ (kg)$, or — all non-passerines — [3-19]

$IR\ (m^3/day) = 0.4089\ Wt^{0.77}\ (kg)$, or

$IR\ (m^3/day) = 0.002002\ Wt^{0.77}\ (g)$

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):

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

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:

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

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:

$$SA_{skin}\ (m^2) = 0.11\ Wt^{0.65}\ (kg), \text{ or} \qquad \text{all mammals} \qquad [3\text{-}22]$$
$$SA_{skin}\ (cm^2) = 12.3\ Wt^{0.65}\ (g)$$

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):

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

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

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

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

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 (ADMR), 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.**

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[a]Water 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; Koplin 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

$$\log BMR\ (kcal/day) = 2.11 + 0.724 \log Wt\ (kg) \pm 0.113, \text{ or} \quad [3\text{-}27]$$

$$BMR\ (kcal/day) = 128\ Wt^{0.724}\ (kg)$$

Non-passerines

$$\log BMR\ (kcal/day) = 1.89 + 0.723 \log Wt\ (kg) \pm 0.068, \text{ or} \quad [3\text{-}28]$$

$$BMR\ (kcal/day) = 77.6\ Wt^{0.723}\ (kg)$$

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):

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[b] **Seabirds included penguins, albatross, petrels, shearwaters, pelicans, skuas, gulls, terns, noddys, murres, cormorants, and frigatebirds.**

Seabirds

log BMR (kcal/day) = 1.96 + 0.721 log Wt (kg) (no SE provided), or [3-29]

BMR (kcal/day) = 91.2 $Wt^{0.721}$ (kg)

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)

log EMR (kcal/day) = 0.1965 + 0.6210 log Wt (g) ± 0.0633, or [3-30]

EMR (kcal/day) = 1.572 $Wt^{0.6210}$ (g), or

log EMR (kcal/day) = 2.060 + 0.6210 log Wt (kg), or

EMR (kcal/day) = 114.8 $Wt^{0.6210}$ (kg)

Non-passerines (N = 9 species)

log EMR (kcal/day) = -0.2673 + 0.7545 log Wt (g) ± 0.0630, or [3-31]

EMR (kcal/day) = 0.5404 $Wt^{0.7545}$ (g), or

log EMR (kcal/day) = 1.996 + 0.7545 log Wt (kg), or

EMR (kcal/day) = 99.03 $Wt^{0.7545}$ (kg), or

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
Ploeceidae	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

[a]Values for the equation relating BMR to body weight (Wt): log BMR (kcal/day) = log a + b log Wt (kg).
[b]Estimated 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:

<u>All birds (24 species)</u>

$$\log \text{EMR (kcal/day)} = 0.6372 + 0.5300 \log \text{Wt (g)} \pm 0.0613, \text{ or} \quad [3\text{-}32]$$

$$\text{EMR (kcal/day)} = 4.337\ \text{Wt}^{0.5300}\ \text{(g)}$$

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:

NEMR (kcal/kg-day) = EMR (kcal/day) / Wt (kg) [3-33]

3.5.1.3. Free-Living Metabolic Rate

FMRs have been measured using doubly-labeled water (DLW) to measure CO_2 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:

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

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):

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

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).

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[c]All 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.

[d]Insufficient 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:

NFMR (kcal/kg-day) = FMR (kcal/day) / Wt (kg) [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).**

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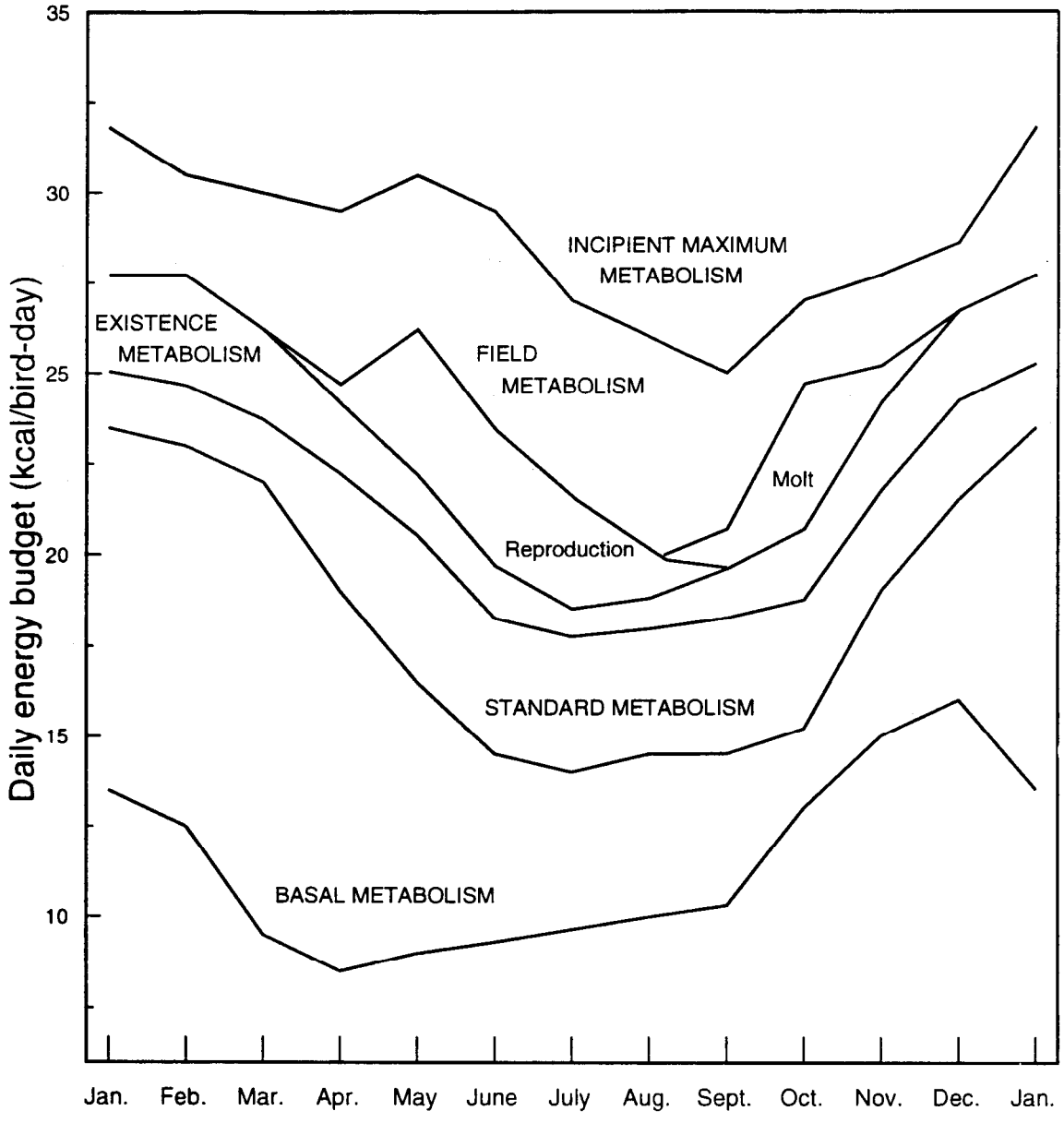
[e]**This is because conductance and heat loss for a given thermal gradient between body temperature and ambient temperature rise more slowly with body size than do basal metabolic rates.**

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) meatbolic 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:

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

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:

BMR (kcal/day) = 70 $Wt^{0.75}$ (kg) ± 0.004 **[3-42]**

Boddington's (1978) analysis produced similar results:

BMR (kcal/day) = 75 $Wt^{0.73}$ (kg) ± 0.013 **[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):

RMR (kcal/day) = 80 $Wt^{0.76}$ (kg) **[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:

FMR (kjoules/day) = 3.35 $Wt^{0.813}$ (g), or **placental mammals** **[3-45]**
FMR (kcal/day) = 0.800 $Wt^{0.813}$ (g)

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:

FMR (kjoules/day) = 5.943 $Wt^{0.727}$ (g), or **herbivores** **[3-46]**
FMR (kcal/day) = 1.419 $Wt^{0.727}$ (g)

FMR (kjoules/day) = 2.582 $Wt^{0.862}$ (g), or non-herbivores [3-47]

FMR (kcal/day) = 0.6167 $Wt^{0.862}$ (g)

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

FMR (kjoules/day) = 10.51 $Wt^{0.507}$ (g), or rodents [3-48]

FMR (kcal/day) = 2.514 $Wt^{0.507}$ (g)

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).**

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[f]This 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:

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

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:

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

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:

$$\text{MR (ml } O_2\text{/hr)} = 0.013\ Wt^{0.80}\ \text{(g)} \times 10^{0.038\ \text{temperature (°C)}} \times 10^{0.14\ \text{metabolic state}} \quad \text{[3-51]}$$

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 Q_{10} 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:

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[g]Measured for fasting individuals during the period of normal inactivity (at night for most species).
[h]Measured for fasting individuals during the period of normal activity (daytime for most species).

FMR (kjoules/day) = 0.224 $Wt^{0.799}$ (g), or **[3-52]**

FMR (kcal/day) = 0.0535 $Wt^{0.799}$ (g)

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:

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

and

FMR (µlO_2/hr) = 2.5 (dry mass)$^{0.878}$ (mg), or **[3-54]**

FMR (mlO_2/day) = 0.06 (dry mass)$^{0.878}$ (mg)

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

FMR (cal/day) = 0.288 (dry mass)$^{0.878}$ (mg) **[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 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 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)

1 joule (J)	=	1 kg-m^2/s^2
	=	0.239 calories (cal)

Power (energy per unit time)

1 watt (W)	=	1 kg-m^2/s^3
	=	1 joule/s
	=	20.64 kcal/day
1 ml O_2/s	=	0.0446 mMol O_2/s
	=	1.43 mg O_2/s

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:

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

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:

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

where y is FMR in kilojoules/day or FI in grams (dry weight)/day. Log Wt is the log of the body weight in grams of the species for which y is being estimated. Log Wt bar is the mean log Wt of the species used to develop the allometric equation. Values for *c*, *d*, *e*, and log Wt bar 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).

$$95\%\ CI_{\log FI(\text{species s})} = \log FI_{(\text{species s})} \pm c\,[d + e\,(\log Wt_{(\text{species s})} - \overline{\log Wt})^2]^{0.5}$$

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).

$$95\%\ CI_{\log FMR(species\ s)} = \log FMR_{(species\ s)} \pm c\,[d + e\,(\log Wt_{(species\ s)} - \log \overline{Wt})^2]^{0.5}$$

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: Petrusewicz, 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: Nuttal Ornithological Club; Publication no. 15.

Drent, R. H.; Stonehouse, B. (1971) Thermoregulatory responses of the Peruvian penguin *Spheniscus humbolti*. 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: Nuttal 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) Oberflachenmessungen des mensclichen Korpers. 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) Uber den Einfluss der Korpergrosse auf Stoff- und Kraftweschsel. 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:

$$D_{pot} = \int_{t1}^{t2} C(t)\ IR(t)\ dt \qquad [4\text{-}1]$$

where D_{pot} is the total potential dose over time (e.g., total mg contaminant intake between t1 and t2), C(t) is the contaminant concentration in the contacted medium at time t (e.g., mg contaminant/kg medium), and IR(t) is the intake rate of the contaminated medium at time t measured as mass ingested or inhaled by an animal per unit time (e.g., kg medium/day). If C and IR are constant over time, then the total potential dose can be estimated as:

$$D_{pot} = C \times IR \times ED \qquad [4\text{-}2]$$

where ED is the exposure duration and equals t2 - t1.

Therefore, if C and IR are constant, the potential average daily dose (ADD_{pot}) for the duration of the exposure, normalized to the animal's body weight (e.g., mg/kg-day), is estimated by dividing total potential dose by ED and by body weight (BW):

$$ADD_{pot} = (C \times IR \times ED) / (BW \times ED), \text{ or} \qquad [4\text{-}3]$$
$$ADD_{pot} = (C \times IR) / BW$$

If C or IR vary over time, they may be averaged over ED. However, it is not always appropriate to average intake over the entire exposure duration: For example, a given quantity of a chemical might acutely poison an animal if ingested in a single event, but if that amount is averaged over a longer period, effects might not be expected at all. Similarly, developmental effects occur only during specific periods of gestation or development. A toxicologist should be consulted to determine which effects may be of concern given the exposure pattern and chemicals of interest. For carcinogenic compounds, it may be more appropriate to average exposure over the animal's lifetime. Again, address any questions to a toxicologist.

In addition, IR and BW can be combined into a normalized ingestion or inhalation rate (NIR) (e.g., kg medium/kg body weight - day):

$$NIR = IR / BW \qquad [4\text{-}4]$$

Therefore,

$$ADD_{pot} = C \times NIR \qquad [4\text{-}5]$$

It is important to remember that NIR can vary with changes in age, size, and reproductive status of an animal.

Two other variables often are used in calculations of average daily dose. A frequency term (FR) is used to denote the fraction of the time that an animal is exposed to contaminated media. In ecological exposure assessments, this term often is used when the foraging range of an animal is larger than the area of contamination.[a] An absorption factor (ABS) is used when an estimate of absorbed dose rather than potential dose is desired. It is commonly assumed that absorption in the species of concern in the field is the same as in the test organism, so no absorption factor is needed. However, if absorption is expected to differ, a ratio of the absorption factors would be used in the exposure equation.

4.1.1. Drinking Water

Figure 4-1 presents two wildlife oral exposure equations corresponding to two patterns of contamination of water:

(1) the animal obtains some of its drinking water from a contaminated source and the remainder from uncontaminated sources; and

(2) the animal consumes drinking water from several sources contaminated at different levels.

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[a]The frequency term should be estimated with care. For example, if a feature attractive to wildlife is contaminated, an animal may spend a proportionally longer time in the contaminated area. Similarly, if only part of an animal's theoretical foraging range has suitable habitat, the animal may spend more time feeding in that habitat. Finally, animals may avoid areas or media with contamination they can detect.

Figure 4-1. Wildlife Dose Equations for Drinking Water Exposures

One Source of Contamination

$$ADD_{pot} = C \times FR \times NIR \qquad [4\text{-}6]$$

Different Sources With Varying Levels of Contamination

$$ADD_{pot} = \sum_{i=1}^{n} (C_i \times FR_i) \times NIR \qquad [4\text{-}7]$$

ADD_{pot} = Potential average daily dose (e.g., in mg/kg-day).

C = Average contaminant concentration in a single water source (e.g., in mg/L or in mg/kg, because 1 liter of water weighs 1 kg).

FR = Fraction of total water ingestion from the contaminated water source (unitless).

NIR = Normalized water ingestion rate (i.e., fraction of body weight consumed as water per unit time; e.g., in g/g-day)

and

C_i = Average contaminant concentration in the i^{th} water source (e.g., in mg/L).

FR_i = Fraction of water consumed from the i^{th} water source (unitless).

n = Number of contaminated water sources.

In the first case, the distribution and mean value of the contaminant concentration in the one source could be determined. In the second case, the different water sources are likely to be characterized by different mean levels of contamination, and consumption from these sources would be weighted by the fraction (FR_i) of the animal's total daily water ingestion obtained from each source. FR (or FR_i) in Figure 4-1 is a function of the degree of overlap of the contaminated water source(s) and the animal's home range. If the area of the contaminated water source is larger than the typical home range for the species, FR could

equal one for many individuals. The number of individuals for which FR equals one could be estimated from information on population density, distribution, and social structure. For large, mobile animals, the area of contamination may be smaller than the area over which a single animal is likely to move. In these cases, FR for an animal with the contaminated area entirely within its home range can be estimated using information on the home range, attributes of the contaminated area, and drinking behavior of the animal. Home range estimates should be used with care because (1) the area in which an animal moves varies with several factors, including reproductive status, season, and habitat quality; (2) most animals do not drink or feed randomly within their home range; (3) the term home range has been used inconsistently in the literature; and (4) estimates of home range can vary substantially with the measurement technique used. In this Handbook and accompanying Appendix, we have tried to identify clearly which estimates of home range correspond to a daily activity and foraging home range.

When using home range data, we recommend that users consult the Appendix tables for the species of interest to become familiar with how estimates of home range size vary with geographic area, season, type of habitat, animal reproductive status, and measurement technique. The Appendix tables provide both the sample size and a brief description of the method used to estimate home range size, which can help indicate the robustness of an estimate and whether it is likely to over- or underestimate home range size. For mark-and-recapture studies, the number of recaptures per animal is provided when possible to assist the user in determining the degree to which the reported values may underestimate true home range size. If a study indicated that the home range estimate is likely to include areas outside of the animals' usual activity range (e.g., distant egg-laying sites used only once per season), this would be noted in the Appendix tables, and the value would not be included in Chapter 2. Some animals use a fixed "home base" some distance from feeding grounds such as a rookery. For these animals, we have reported foraging radius (the distance they will travel to a feeding area). Foraging radius can be used to determine whether the animal might feed or drink in a given contaminated area.

4.1.2. Diet

Wildlife can be exposed to contaminants in one or more components of their diet, and different components can be contaminated at different levels. In this section, we outline methods of estimating food ingestion rates that allow total doses to be estimated when different components of the diet are contaminated, either at similar or different levels (Section 4.1.2.1). We also provide data on caloric content of foods and assimilation efficiencies that can be used in the dose equations provided (Section 4.1.2.2).

4.1.2.1. Dose Equations

Figure 4-2 presents a generic equation for estimating oral doses of contaminants in food for wildlife species. FR_k is a function of the degree of overlap of the k^{th} type of simplest case, the normalized ingestion rate for each food type, NIR_k, is known on a wet-

Figure 4-2. Wildlife Dose Equations for Dietary Exposures

$$ADD_{pot} = \sum_{k=1}^{m} (C_k \times FR_k \times NIR_k) \qquad [4\text{-}8]$$

ADD_{pot}	=	Potential average daily dose (e.g., in mg/kg-day).
C_k	=	Average contaminant concentration in the k^{th} type of food (e.g., in mg/kg wet weight).
FR_k	=	Fraction of intake of the k^{th} food type that is contaminated (unitless). For example, if the k^{th} component of an animal's diet were salmon, FR_k for salmon would equal the fraction of the salmon consumed that is contaminated at level C_k. If all of the salmon consumed were contaminated at level C_k, then FR_k would equal one.
NIR_k	=	Normalized ingestion rate of the k^{th} food type on a wet-weight basis (e.g., in g/g-day).
m	=	Number of contaminated food types.

contaminated forage or prey and the animal's home range (see Section 4.1.1). In the weight basis, and Equation 4-8 can be used directly. In many cases, however, NIR_k is unknown or has been determined for laboratory diets that differ significantly from natural diets in terms of caloric value per unit wet weight. Ingestion rates based on relatively dry laboratory diets might underestimate the amount of food a free-living animal consumes.

There are several ways to estimate NIR_k, depending on the type of information that is available. If dietary composition is expressed as the number of each prey type captured on a daily basis (N_k), estimating the normalized ingestion rate for each prey type (NIR_k) requires only one step:

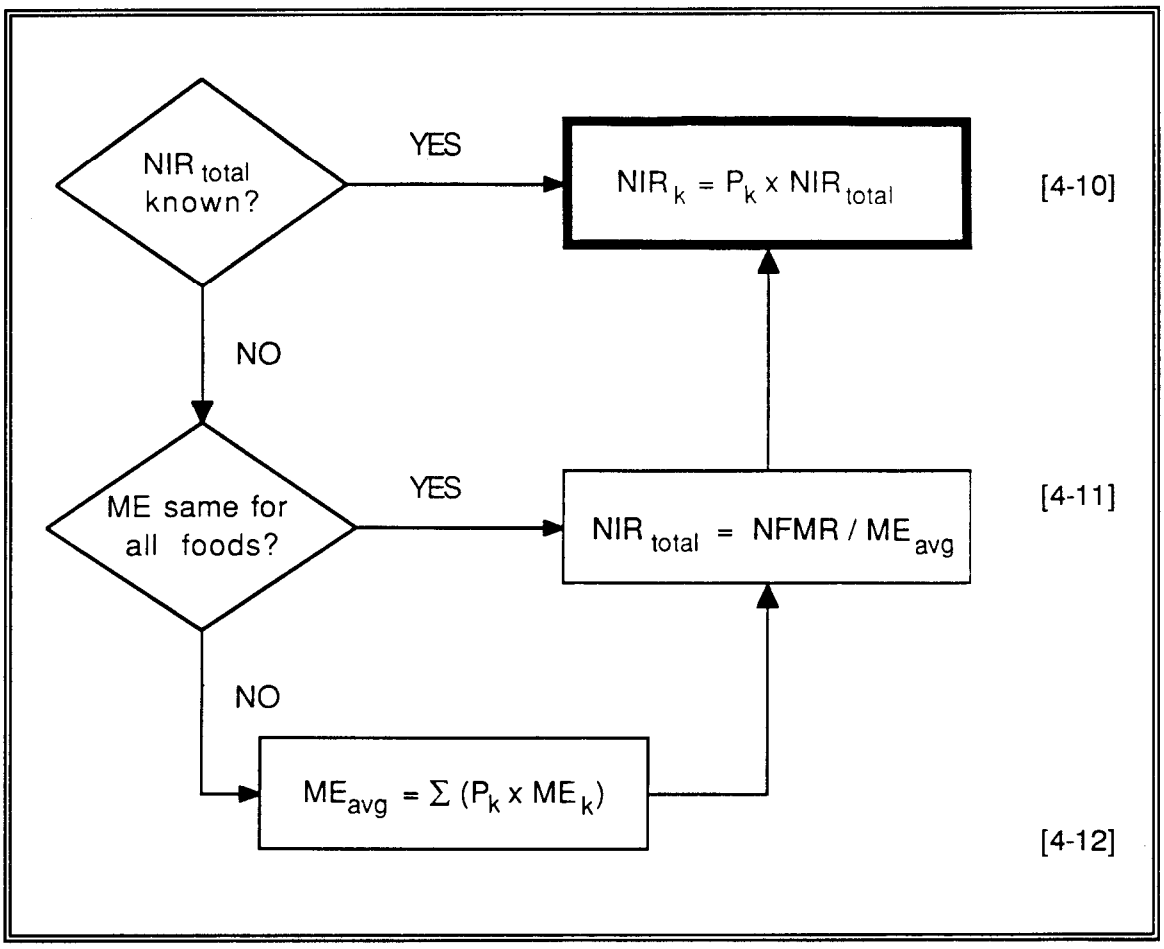
$$NIR_k = (N_k \times Wt_k) / BW \qquad [4\text{-}9]$$

where Wt_k is the body weight of the k^{th} prey type and BW is the body weight of the predator.

Figure 4-3 presents a flow chart depicting equations that can be used if the proportion of the diet for a given food type has been measured or estimated on a wet-weight basis. These equations may require estimates of the free-living metabolic rate (FMR) of the organism and the metabolizable energy (ME) of the organism's forage or prey. Estimated FMRs can be found in the species profiles in Chapter 2, and allometric equations for estimating FMR on the basis of body weight are provided in Chapter 3 (Section 3.5). ME should be averaged over the food types when ME on a wet-weight basis (e.g., cal/g wet weight) differs substantially among the different foods. Section 4.1.2.2 describes how to estimate ME.

A common situation facing someone conducting a wildlife exposure assessment for predators is that in a key study, dietary composition is expressed as a percentage of the total number of prey captured over a period of time instead of as a percentage of the total wet weight of food ingested daily. Because some prey can be substantially larger than others (e.g., rabbits compared with voles), and because ME of different types of prey may

Figure 4-3. Estimating NIR_k When Dietary Composition Is Known on a Wet-Weight Basis



NIR_{total} = Total normalized ingestion rate (e.g., in g/g-day).
NIR_k = Normalized ingestion rate of the k^{th} food type (e.g., in g/g-day).
P_k = Proportion of diet consisting of the k^{th} food type on a wet-weight basis (unitless).
ME_{avg} = Average metabolizable energy of the total diet on a wet-weight basis (e.g., in kcal/g wet weight).
ME_k = Metabolizable energy of the k^{th} food type on a wet-weight basis (e.g., in kcal/g wet weight).
NFMR = Free-living metabolic rate normalized to body weight (e.g., in kcal/g-day).

differ, the steps outlined in Figure 4-4 may be needed to estimate prey-specific ingestion rates. First, one calculates the ME of each prey type. Then, one determines the average number of prey (N_{avg}) captured daily on the basis of the metabolic needs of the predator

Figure 4-4. Estimating NIR_k Based on Different ME Values When Dietary Composition Is Expressed as Percentage of Total Prey Captured

Step 1: Calculate the metabolizable energy (ME) content of each prey or food type on a wet-weight basis:

$$ME(\text{wet wt})_k = GE(\text{wet wt})_k \times AE_k \quad [4\text{-}13]$$

Step 2: Estimate the average number of prey (or other food items) consumed each day:

$$N_{avg} = FMR / (\text{weighted average prey ME})$$

$$N_{avg} = FMR / \left(\sum_{k=1}^{m} PN_k \times Wt_k \times ME(\text{wet wt})_k\right) \quad [4\text{-}14]$$

Step 3: Calculate IR_k:

$$IR_k = N_{tot} \times PN_k \times Wt_k \quad [4\text{-}15]$$

Step 4: Normalize to body weight:

$$NIR_k = IR_k / BW \quad [4\text{-}16]$$

$ME(\text{wet wt})_k$	=	Metabolizable energy in the k^{th} prey or food type (e.g., in kcal/g wet weight).
$GE(\text{wet wt})_k$	=	Gross energy content of the k^{th} food type (e.g., in kcal/g wet weight).
AE_k	=	Assimilation efficiency for the species for the k^{th} food type (unitless).
N_{avg}	=	Average number of prey (or other food items) eaten each day.
FMR	=	Free-living metabolic rate (e.g., in kcal/day).
m	=	Number of different types of prey or other foods.
PN_k	=	Proportion of the total number of prey that is composed of the k^{th} prey type (unitless). It often is the case that larger numbers of relatively small prey and smaller numbers of relatively large prey are captured. (If the total number of prey of each type captured each day are reported in the literature, calculations of IR_k are very simple [i.e., $N_k \times Wt_k$] and steps 1 and 2 are unnecessary.)
Wt_k	=	Body weight of an individual of the k^{th} food type (e.g., in g).
IR_k	=	Ingestion rate of the k^{th} food type (e.g., in g/day).

and the weighted average ME of the prey. Given N_{avg} , the ingestion rate for each prey type (IR_k) can be computed on a wet-weight basis and normalized to body weight (NIR_k). Because N_{avg} is estimated using prey weight, different sizes of the same prey species (e.g., smaller and larger fish) should be separated into appropriate size intervals to reduce uncertainty in the estimate.

4.1.2.2. Energy Content and Assimilation Efficiencies

The total or gross energy (GE) content of a food type is a function only of characteristics of the food. On the other hand, metabolizable energy (ME) depends on characteristics of both the food and the organism eating it. To clarify the meaning of ME, Figure 4-5 presents a flow chart of energy utilization by animals. Digestible energy in a diet is GE consumed minus the energy lost as feces; digestible energy efficiency (DE) is digestible energy divided by GE. ME is GE consumed minus the energy lost as both feces and urine. Assimilation efficiency (AE, also called metabolizable energy efficiency) is ME divided by GE. Rearranging this relationship, ME is equal to GE of the diet multiplied by the animal's AE for the diet as shown in Figure 4-6, Equation 4-17. General ME values can be found in Table 3-1 or more specific ones calculated from GE content of the food and the AE of the animal eating that food, as discussed below.

The GE content of food typically is reported using one (or more) of three measures: (1) energy per unit total dry weight, (2) energy per unit ash-free dry weight, or (3) energy per unit fresh biomass (i.e., per unit wet weight) (Górecki, 1975). Caloric content per unit total dry weight is obtained directly from the combustion of dried material in a calorimeter. Ash-free dry weight is the dry weight after subtracting the ash content.[b] The ash-free dry-weight caloric value exceeds the total dry-weight caloric value by the ratio of the total dry weight to the ash-free dry weight. Typically, animal (exclusive of thick shells) and plant materials are 1 to 10 percent ash on a wet-weight basis and 5 to 30 percent ash on a dry-weight basis (Ashwell-Erickson and Elsner, 1981; Cummins and Wuycheck, 1971;

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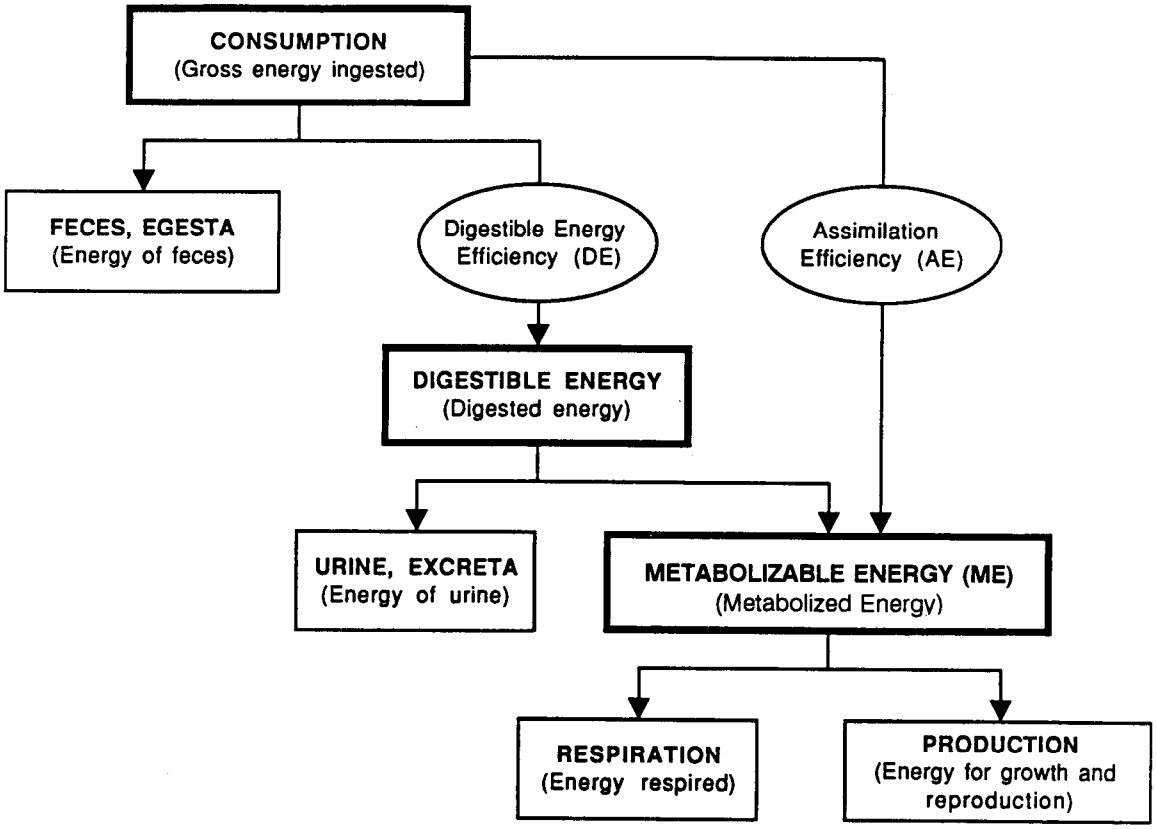
[b] **Ash constituents typically include calcium carbonate (e.g., shell), calcium phosphate (vertebrate bone), and hydrated silica salts.**

Figure 4-5. Utilization of Food Energy by Animals



Source: Adapted from Grodzinski and Wunder, 1975.

Figure 4-6. Metabolizable Energy (ME) Equation

$$ME = GE \times AE \quad [4\text{-}17]$$

where:

ME = Metabolizable energy (e.g., in kcal/g)

GE = Gross energy (e.g., in kcal/g)

AE = Assimilation efficiency (unitless)

This Handbook assumes ME and GE are estimated on a wet-weight basis. To estimate ME or GE of the k^{th} food type on a wet-weight basis from dry-weight measurements, the following equations can be used:

$$GE(\text{wet wt})_k = GE(\text{dry wt})_k \times (1 - \text{proportion water}_k) \quad \text{or} \quad [4\text{-}18]$$

$$GE(\text{wet wt})_k = GE(\text{dry wt})_k \times (\text{dry weight}_k / \text{wet weight}_k) \quad [4\text{-}19]$$

and

$$ME(\text{wet wt})_k = ME(\text{dry wt})_k \times (1 - \text{proportion water}_k) \quad \text{or} \quad [4\text{-}20]$$

$$ME(\text{wet wt})_k = ME(\text{dry wt})_k \times (\text{dry weight}_k / \text{wet weight}_k) \quad [4\text{-}21]$$

Hunt, 1972). The ash content of the diet is not metabolized and thus does not provide energy to the animal. Figure 4-6 (Equations 4-18 through 4-21) illustrates how the caloric content per unit of fresh biomass can be obtained by adjusting the dry-weight value based on the water content of the biomass. A summary of GE contents of many wildlife food types are presented in Tables 4-1 a given species on a wet-weight basis tends to be more variable than caloric content on a dry-weight basis because plants, and to a lesser degree animals, vary in their water content depending on environmental conditions. Ash-free dry-weight caloric values are not presented because it is not appropriate to use them with the equations and AEs in this chapter. Ash contents are accounted for in the AEs presented in Table 4-3.

Table 4-1. Gross Energy and Water Composition of Wildlife Foods: Animal Prey (values expressed as mean [standard deviation]^n where n = number of studies)

Type of food	kcal/g wet wt	% H_20	kcal/g dry wt	References
Aquatic				
invertebrates				
bivalves (without shell)	0.80	82 (4.5)[3]	4.6 (0.35)[4]	1,2,3,4,5,6
crabs (with shell)	1.0 (0.21)[5]	74 (6.1)[5]	2.7 (0.45)[4]	1,2,3,7
shrimp	1.1 (0.24)[4]	78 (3.3)[7]	4.8 (0.31)[6]	1,3,4,6,7
isopods, amphipods	1.1	71-80	3.6 (0.78)[3]	4,6,7
cladocerans	0.74	79-87	4.8 (0.62)[14]	2,4
insect larvae			5.3 (0.37)[8]	1,4
vertebrates				
bony fishes	1.2 (0.24)[18]	75 (5.1)[18]	4.9 (0.38)[18]	7
Pacific herring	2.0 (0.43)[3]	68 (3.9)[3]	6.1 (0.50)[4]	8,9
small fish (e.g., bluegill)			4.1 (0.47)[3]	1,7
Terrestrial				
invertebrates				
earthworms[a]	0.78-0.83	84 (1.7)[3]	4.6 (0.36)[4]	1,7
grasshoppers, crickets	1.7 (0.26)[3]	69 (5.6)[11]	5.4 (0.16)[4]	1,10,11
beetles (adult)	1.5	61 (9.8)[5]	5.7-5.9	1,10,11
mammals				
mice, voles, rabbits	1.7 (0.28)[14]	68 (1.6)[4]	5.0 (1.3)[17]	12,13,14
birds				
passerines				
with peak fat reserves[b]			7.8 (0.18)[10]	15
with typical fat reserves	1.9 (0.07)[3]	68	5.6 (0.34)[13]	10,14,15,16
mallard (flesh only)	2.0	67	5.9	10
gulls, terns	1.9		4.4	1
reptiles and amphibians				
snake, lizards	1.4	66	4.5 (0.28)[5]	14,17
frogs, toads	1.2	85 (4.7)[3]	4.6 (0.45)[3]	12,14

Note: For Tables 4-1 and 4-2, a single value represents the results of a single study on one species, and should not be interpreted as a mean value or a value indicating no variation in the category. Two values separated by a hyphen indicate that values were obtained from only two studies.

[a]Not including soil in gut, which can constitute one-third of the wet weight of an earthworm.
[b]Peak fat reserves occur just prior to migration. Typical fat reserves are for resident passerines or migratory species during nonmigratory seasons.

References: (1) Cummins and Wuycheck, 1971; (2) Golley, 1961; (3) Tyler, 1973; (4) Jorgensen et al., 1991; (5) Pierotti and Annett, 1987; (6) Minnich, 1982; (7) Thayer et al., 1973; (8) Ashwell-Erickson and Elsner, 1981; (9) Miller, 1978; (10) Collopy, 1975; (11) Bell, 1990; (12) Górecki, 1975; (13) Golley, 1960; (14) Koplin et al., 1980; (15) Odum et al., 1965; (16) Duke et al., 1987; (17) Congdon et al., 1982.

Table 4-2 Energy and Water Composition of Wildlife Foods: Plants (values expressed as mean [standard deviation]^n where n = number of studies)

Type of food	kcal/g wet wt[a]	% H_20	kcal/g dry wt	References
Aquatic				
algae	0.41-0.61	84 (4.7)[3]	2.36 (0.64)[4]	1,2,3
aquatic macrophytes		87 (3.1)[3]	4.0 (0.31)[12]	1,2,4
emergent vegetation		[45-80][b]	4.3 (0.13)[3]	1,2,4
Terrestrial				
monocots				
young grasses	1.3	70-88	4.2	5,6
mature dry grasses		7-10	4.3 (0.33)[5]	1,5,7,8
dicots				
leaves		85 (3.5)[3]	4.2 (0.49)[57]	9
roots			4.7 (0.43)[52]	9
bulbs, rhizomes			3.6 (0.68)[3]	2,7,10
stems, branches			4.3 (0.34)[51]	9
seeds		9.3 (3.1)[12]	5.1 (1.1)[57]	6,9,11,12
fruit				
pulp, skin	1.1 (0.30)[3]	77 (3.6)[3]	2.0 (3.4)[28]	10,13
pulp, skin, seeds			2.2 (1.6)[10]	10

Note: For Tables 4-1 and 4-2, a single value represents the results of a single study on one species, and should not be interpreted as a mean value or a value indicating no variation in the category. Two values separated by a hyphen indicate that values were obtained from only two studies.

[a] **Few determinations of the energy content of plants have been made on a wet-weight basis because plants fluctuate widely in water content depending on environmental conditions.**

[b] **Values in brackets represent total range of field measurements, instead of values from only two studies, as for the remainder of the table. Buchsbaum and Valiela (1987) found the water content of the emergent marsh vegetation *Spartina alterniflora*, *S. patens*, and *Juncus gerardi* to decrease over a summer from 80 to 60 percent, 70 to 45 percent, and 78 to 61 percent, respectively, as the marsh dried. In contrast, they found a submerged macrophyte to maintain water content within a few percent throughout the season.**

References: (1) Cummins and Wuycheck, 1971; (2) Jorgensen et al., 1991; (3) Minnich, 1982; (4) Boyd and Goodyear, 1971; (5) Davis and Golley, 1963; (6) Drozdz, 1968; (7) Golley, 1960; (8) Kendeigh and West, 1965; (9) Golley, 1961; (10) Karasov, 1990; (11) Dice, 1922; (12) Robel et al., 1979; (13) Levey and Karasov, 1989.

Table 4-3. General Assimilation Efficiency (AE) Values (values expressed as mean [standard deviation]^n where n = number of studies)

Group	Prey/Forage	AE %	Reference
Birds			
	animals		
birds of prey	**birds, small mammals**	**78 (5.2)[16]**	**1,2,3,4**
eagles, seabirds	**fish**	**79 (4.5)[9]**	**1,2,4,5**
waterfowl	**aquatic invertebrates**	**77 (8.4)[3]**	**1**
birds	**terrestrial insects**	**72 (5.1)[16]**	**1,5,6**
	plants		
passerines	**wild seeds**	**75 (9)[11]**	**1**
non-passerines	**wild seeds**	**59 (13)[25]**	**1**
birds	**cultivated seeds**	**80 (8)[17]**	**1**
birds	**fruit pulp, skin**	**64 (15)[31]**	**1**
birds	**fruit pulp, skin, seeds**	**51 (15)[22]**	**1**
birds	**grasses, leaves**	**47 (9.6)[3]**	**1***
grouse, ptarmigans	**stems, twigs, pine needles**	**34 (5.3)[8]**	**1,1**
geese	**emergents (e.g., spartina)**	**39 (9.1)[4]**	**1***
ducks	**aquatic vegetation**	**23 (5.3)[5]**	**1***
geese, grouse	**bulbs, rhizomes**	**56 (18)[4]**	**1**
Mammals			
	animals		
pinnipeds	**fish**	**88 (1.1)[5]**	**7,8**
mammals	**small birds, mammals**	**84 (6.5)[4]**	**9,10,11**
mammals	**fish**	**91**	**12**
small mammals	**insects**	**87 (4.9)[6]**	**11,13**
	plants		
voles, mice	**seeds, nuts**	**85 (7.3)[8]**	**11,14**
lemmings, voles	**mature grasses**	**41 (9.1)[5]**	**15**
rabbits, voles, mice	**green forbs**	**73 (7.6)[8]**	**11,14,15**
rabbits, voles, rats	**"herbivory"**	**76 (7.6)[5]**	**11,14,16**

References: (1) Karasov, 1990; (1*) calculated from data presented in Appendix I of Karasov, 1990; (2) Stalmaster and Gessaman, 1982; (3) Koplin et al., 1980; (4) Castro et al., 1989; (5) Ricklefs, 1974; (6) Bryant and Bryant, 1988; (7) Ashwell-Erickson and Elsner, 1981; (8) Miller, 1978; (9) Litvaitis and Mautz, 1976; (10) Vogtsberger and Barrett, 1973; (11) Grodzinski and Wunder, 1975; (12) estimated by dividing 4.9 kcal/g gross energy for bony fishes (Table 4-1) by metabolizable energy of 4.47 reported for fish consumed by mammals (Nagy, 1987); (13) Barrett and Stueck, 1976; (14) Drozdz, 1968; (15) Batzli and Cole, 1979; (16) Drozdz et al., 1971.

Table 4-3 summarizes AEs for several different types of foods and species. Assimilation efficiency is a function of both the consumer species' physiology and the type of diet. Factors that reduce many species' ability to assimilate the energy contained in food include the ash content of the diet and the percentage of relatively indigestible organic materials such as chitin (arthropods) or cellulose (plants). The higher the ash content, the lower the AE, all else being equal.

Fat content also influences GE. For example, carbohydrates (approximately 4.3 kcal/g) and proteins (approximately 5.7 kcal/g) typically provide about half as many calories per gram as fat (approximately 9.5 kcal/g) (Peters, 1983). Thus, small changes in fat content of animal tissues or plant seeds cause significant changes in their caloric value. For example, just prior to fall migration, passerine birds have achieved peak fat deposition and average 7.8 kcal/g dry weight. Non-migrating passerines (i.e., permanent residents or migratory species during nonmigrating seasons) average only 5.6 kcal/g dry weight. Two references with substantial compilation of data on caloric content of biological materials are Jorgensen et al. (1991) and Cummins and Wuycheck (1971). The latter includes extensive data on invertebrates.

Figure 4-7 provides a sample calculation of food ingestion rates using the methodology outlined above.

4.1.3. Soil and Sediment Ingestion

In this section, we review information on the ingestion of soil and sediment for the species included in this Handbook (and similar species). Despite the potential importance of soil and sediment ingestion as a route of exposure of wildlife to environmental contaminants, data to quantify these ingestion rates are limited at this time.

Figure 4-7. Example of Estimating Food Ingestion Rates for Wildlife Species From Free-Living Metabolic Rate and Dietary Composition: Male Mink

1. **Estimate Field Metabolic Rate (FMR) [Equation 3-47]**

$$FMR\ (kcal/day) = 0.6167\ (g\ Wt)^{0.862}$$
$$= 0.6167\ (1{,}040)^{0.862}$$
$$= 246\ (kcal/day)$$

2. **Normalize to Body Weight (Wt) [Equation 3-40]**

$$NFMR\ (kcal/g\text{-}day) = 246\ (kcal/day)/1{,}040\ (g\ Wt)^{a}$$
$$= 0.24\ (kcal/g\text{-}day)$$

3. **Estimate Average Metabolizable Energy (ME_{avg}) of Diet [Equation 4-12]**

Dietary Item (k=5)	Proportion of Diet (P_k)[b]	Gross Energy (GE_k)[c] (kcal/g wet wt)	Assimilation Efficiency (AE_k)[d]	Metabolizable Energy (ME_k) (kcal/g wet wt) ($ME_k = GE_k \times AE_k$)	($P_k \times ME_k$)
Fish	0.85	1.2	0.91	1.1	0.93
Crustacea	0.04	1.1	0.87	0.96	0.038
Amphibia	0.03	1.2	0.91	1.1	0.033
Birds/ Mammals	0.06	1.8	0.84	1.5	0.090
Vegetation	0.02	1.3	0.73	0.95	0.019
ME_{avg} (kcal/g wet wt) = $\sum(P_k \times ME_k)$ = 1.1[e]					

4. **Estimate Total Normalized Ingestion Rate (NIR_{total}) [Equation 4-11]**

$$NIR_{total}\ (g/g\text{-}day) = \frac{0.24\ (kcal/g\text{-}day)}{1.1\ (kcal/g\ wet\ wt)\ (i.e.,\ ME_{avg})}$$
$$= 0.22\ (g/g\text{-}day)$$

5. **Estimate Prey-specific Normalized Ingestion Rates (e.g., NIR_{fish}) [Equation 4-10]**

$$NIR_{fish}\ (g/g\text{-}day) = 0.85\ (P_{fish}) \times 0.22\ (g/g\text{-}day)$$
$$= 0.19\ (g/g\text{-}day)$$

---

[a] Body weight for Montana population in the summer (Mitchell, 1961).
[b] Dietary composition based on Alexander (1977).
[c] Values from Tables 4-1 and 4-2 (for vegetation, assuming value for young grasses).
[d] Values from Table 4-3 (for vegetation, assuming green forbs; for crustacea, assuming equivalent AE for insects; for amphibia, assuming equivalent to mammals consuming fish).
[e] In this example, ME_{avg} is the same as the ME value for fish, which comprises 85 percent of the diet.

4.1.3.1. Background

Soil is ingested both intentionally and incidentally by many species of wildlife and can be a significant exposure pathway for some contaminants (Arthur and Alldredge, 1979; Garten, 1980). Many ungulates deliberately eat soil to obtain nutrients; some may travel a considerable distance to reach certain areas (salt licks) that are used by many animals. Some birds gather mud in their beaks for nest-building, and others consume it for calcium (Kreulen and Jager, 1984). Many animals can incidentally ingest soil while grooming, digging, grazing close to the soil, or feeding on items that are covered with soil (such as roots and tubers) or contain sediment (such as molluscs). Earthworms ingest soil directly; the soil in their guts may be an important exposure medium for animals that eat these organisms (Beyer et al., 1993).[c]

Soil ingestion rates have been estimated for only a few wildlife species and were not available in the published literature for most of the animals in this Handbook. The percentage of soil ingested is often estimated from the acid-insoluble ash content of wildlife scats or digestive tract contents. Scat analysis on small animals is often difficult because scat are small. Soil ingestion by large mammals also has been estimated using insoluble chemical tracers (Mayland et al., 1977) and using standard x-ray diffraction analysis (Garten, 1980).

4.1.3.2. Methods

Garten (1980) estimated the amount of soil in the gastrointestinal (GI) tract of a small mammal (the hispid cotton rat) using the following equation:

$$I = (S - F)W \qquad [4\text{-}22]$$

---

[c]**Seed-eating birds often consume "grit" to aid in digestion, which makes them vulnerable to poisoning by granular formulations of pesticides and fertilizers. In this section, however, we restrict our discussion to soils and sediments, which are composed of much smaller particle sizes.**

where I equals the amount of soil in the GI tract, S equals the ratio of insoluble ash to dry contents in the GI tract, F equals the ratio of insoluble ash to dry contents in fescue (the dominant vegetation in the rat's habitat), and W equals the dry weight of GI-tract contents.

It is also possible to estimate soil ingestion rates from the acid-insoluble ash content of the animal's scat because the percentage of acid-insoluble ash in mineral soil is much higher (usually at least 90 percent) than in plant or animal tissue (usually no more than a few percent). Beyer et al. (in press) used scat samples to estimate the fraction of soil in the diet for several species. The equation for this estimation approach is slightly more complicated than Equation 4-22, because it accounts for digestibility and the mineral content of the soil. They found a significant correlation between the measured and predicted relationships of the ratio of acid-insoluble ash to dry weight of scat and the percentage of soil in the diet.

4.1.3.3. Results

Percent soil in the diet for some of the selected and similar species included in Chapter 2 are included in Tables 4-4 and 4-5. Of the species studied, the sandpiper group, which feeds on mud-dwelling invertebrates, was found to have the highest rates of soil/sediment ingestion (30, 18, 17, and 7.3 percent of diet, respectively, for semipalmated, western, stilt, and least sandpipers, although only a single sample was analyzed for each species). Wood ducks also can ingest a high proportion of sediment (24 percent) with their food. Relatively high soil intakes were estimated for the raccoon (9.4 percent), an omnivore, and the woodcock (10.4 percent), which feeds extensively on earthworms. Other species that eat earthworms might be expected to exhibit similarly high soil intakes. The Canada goose, which browses on grasses, also exhibited a high percentage of soil in its diet (8.2 percent). Soil ingestion was lowest for the white-footed mouse, meadow vole, fox, and box turtle (<2, 2.4, 2.8, and 4.5 percent, respectively). Box turtles, tortoises, and other reptiles, however, have been known to intentionally ingest soil, perhaps for its nutrient content (Kramer, 1973; Sokal, 1971). Beyer et al.'s (in press) data should be used with caution, because error was introduced by estimating variables in

Table 4-4. Percent Soil or Sediment in Diet Estimated From Acid-Insoluble Ash of Scat

Species	Scat Samples[a]	% Insoluble Ash Mean (SE)	Range	Estimated % Digestibility of Diet	Estimated Percent Soil in Diet (dry weight)
Birds					
Canada goose	23	12 (1.5)	3.9 - 38	25	8.2
Mallard	88	6.9 (1.1)	0.36 - 47	30	<2
Wood duck	7	24 (13)	0 - 75	60	11
Blue-winged teal	12	2.3 (0.36)	0.72 - 5.1	60	<2
Ring-necked duck	6	0.72 (5.5)	0.50 - 1.2	60	<2
American woodcock	7	22 (5.5)	6.3 - 40	55	10.4
Semipalmated sandpiper	1	56		70	30
Western sandpiper	1	42		70	18
Stilt sandpiper	1	40		70	17
Least sandpiper	1	24		70	7.3
Mammals					
Red fox	7	14 (2.6)	4.8 - 25	70	2.8
Raccoon	4	28 (8.9)	13 - 50	70	9.4
White-footed mouse	9	8.5 (0.71)	5.7 - 11	65	<2
Meadow vole	7	8.9 (1.2)	4.2 - 14	55	2.4
Reptiles and Amphibians					
Eastern painted turtle	9	21 (2.9)	11 - 41	70	5.9
Box turtle	8	18 (6.5)	3.6 - 49	70	4.5

[a]For the sandpipers, the white-footed mouse, and the meadow vole, scat samples from more than one animal had to be combined into one sample to provide sufficient quantity for chemical analysis.

Source: Adapted from Beyer et al. (in press).

Table 4-5. Other Estimates of Percent Soil or Sediment in Diet

Species	Estimated % soil in diet (dry weight)	Reference
Jackrabbit	6.3	Arthur and Gates 1988
Hispid cotton rats	2.8	Garten 1980
Shorebirds	10-60	Reeder 1951

the equation (e.g., digestibility) and by the small samples they obtained from some of the smaller animals.

Other studies of soil ingestion by species similar to those presented in this Handbook are summarized in Table 4-5. Sediment has been found in the stomachs of white-footed mice (Garten, 1980) and ruddy ducks and shovelers (Goodman and Fisher, 1962). Sediment in the gut of tadpoles inhabiting highway drainages may be responsible for high concentrations of lead detected in these organisms (Birdsall et al., 1986).

4.1.3.4. Dose Equations

To estimate exposures to contaminants in soils or sediments from the data provided in Tables 4-4 and 4-5, Equation 4-23 (Figure 4-8) can be used. If the percent soil in the diet is measured on a dry-weight basis, as it usually is, total dietary intake should also be expressed on a dry-weight basis.

4.1.4. Air

Inhalation toxicity values and exposure estimates are usually expressed in units of concentration in air (e.g., mg/m^3) rather than as average daily doses. Assessment of the inhalation pathway becomes complicated if the toxicity values must be extrapolated from a test species (e.g., rat) to a different species (e.g., shrew). Inhalation toxicologists extrapolate toxicity values from species to species on the basis of the dose deposited and retained in the respiratory tract (the dose that is available for absorption, distribution,

Figure 4-8. Wildlife Oral Dose Equation for Soil or Sediment Ingestion Exposures

$$ADD_{pot} = \left(\sum_{k=1}^{m} (C_k \times FS \times IR_{total}(\text{dry weight}) \times FR_k)\right)/BW \qquad [4\text{-}23]$$

ADD_{pot} = Potential average daily dose (e.g., in mg/kg-day).

C_k = Average contaminant concentration in soils in the k^{th} foraging area (e.g., in mg/kg dry weight).

FS = Fraction of soil in diet (as percentage of diet on a dry-weight basis divided by 100; unitless).

IR_{total} = Food ingestion rate on a dry-weight basis (e.g., in kg/day). Nagy's (1987) equations for estimating FI rates on a dry-weight basis (presented in Section 3.1) can be used to estimate a value for this factor. If the equations for estimating FI rates on a wet-weight basis presented in Section 4.2 are used, conversion to ingestion rates on a dry-weight basis would be necessary.

FR_k = Fraction of total food intake from the k^{th} foraging area (unitless).

BW = Body weight (e.g., in kg).

m = Total number of foraging areas.

metabolism, and elimination). Once the appropriate toxicity benchmark (in terms of dose) has been estimated for the species of concern (e.g., shrew), the corresponding air concentration is estimated based on the respiratory physiology of that species. EPA uses this approach because it can account for nonlinear relationships between exposure concentrations, inhaled dose, and dose to the target organ(s). Because of the complexities associated with the extrapolations, an inhalation toxicologist should be consulted when assessing this pathway.

The dose deposited, retained, and absorbed in the respiratory tract is a function of species anatomy and physiology as well as physicochemical properties of the contaminant. The assessor will need to consider factors such as the target species' airway

size, branching pattern, breathing rate (volume and frequency), and clearance mechanisms, as well as whether the contaminant is a gas or aerosol and whether its effects are systemic or confined to the respiratory tract. Key information on the contaminant includes particle size distribution (for aerosols), temperature and vapor pressure (for gaseous agents), and pharmacokinetic data (e.g., air/blood partition coefficients, metabolic parameters). While physiologically based pharmacokinetic models have been useful for these calculations, they are available for only a few laboratory species. These issues are discussed in detail in *Interim Methods for Development of Inhalation Reference Concentrations* (U.S. EPA, 1990). Although the document specifically describes how to calculate inhalation reference concentrations for humans, the principles are useful for any air-breathing species.

4.1.5. Dermal Exposure

Dermal toxicity values and exposure estimates are usually expressed as an absorbed dose resulting from skin contact with a contaminated medium. This exposure pathway can be of great importance to wildlife, particularly when an animal is directly sprayed (Driver et al., 1991). Dermal exposures may also be a concern for wildlife that swim or burrow. Dermal absorption of contaminants is a function of chemical properties of the contaminated medium, the permeability of the animals' integument, the area of integument in contact with the contaminated medium, and the duration and pattern of contact. A full discussion of quantifying absorbed dose through the skin is beyond the scope of this document, and many of the required parameters have not been measured for wildlife species. Readers interested in pursuing this exposure pathway may find useful information in *Dermal Exposure Assessment: Principles and Applications* (U.S. EPA, 1992c).

4.2. ANALYSIS OF UNCERTAINTY

In the risk assessment process, several sources of uncertainty should be evaluated, including the uncertainties associated with the exposure assessment and the toxicity

assessment. The following sections discuss three sources of uncertainty related to the exposure assessment: (1) natural variability in the population in question, (2) uncertainty about population parameters as a consequence of limits on sampling the population (i.e., sampling uncertainty), and (3) uncertainty about models used to estimate values. There are other categories of uncertainties associated with site-specific risk assessments that also need to be considered (e.g., selection of substances of concern, data gaps, toxicity assessments). Additional discussion of sources and treatment of uncertainty is available in *Framework for Ecological Risk Assessment* (U.S. EPA, 1992a) and *Guidelines for Exposure Assessment* (U.S. EPA, 1992b). For treatment of site-specific uncertainties in particular, see the *Risk Assessment Guidance for Superfund, Volume I; Human Health Evaluation Manual (Part A) Interim Final* (U.S. EPA, 1989).

4.2.1. Natural Variation

As a review of the data provided in this Handbook makes clear, there is natural variation in the values exhibited by populations for all exposure factors. Population values for some parameters (e.g., body weight) can assume a normal distribution that can be characterized by a mean and variance. We have provided the standard deviation (SD) as the measure of population variance whenever possible. If a risk assessor is concerned with exposures that might be experienced by animals exhibiting characteristics near the extremes of the population's distribution, the SD can be used with the mean value for a normally distributed population to estimate the parameter value for animals with characteristics at specified points in the distribution (e.g., 95th percentile). We also have provided the total range of values reported for each of the exposure factors whenever possible. The ranges can be particularly helpful for parameters that are not normally distributed, such as home-range size.

Another aspect of natural variation, however, is that different populations or the same population at different times or locations can exhibit different mean values for any parameter (e.g., body weight) and even different variances. We have tried to present enough data to give users of the Handbook a feel for the range of values that different populations can assume depending on geographic location, season, and other factors

(e.g., habitat quality). We recommend that risk assessors review the data presented in the Appendix to appreciate the potential for variation in the parameters of interest.

Dietary composition, in particular, can vary markedly with season, location, and availability of prey or forage. The latter factor varies with local conditions and usually is not available for risk assessments. Thus, it can be one of the larger sources of uncertainty in wildlife exposure assessments. State and local wildlife experts might be able to help specify the local dietary habits of a species of concern and should be consulted if screening analyses suggest that exposure at levels of concern is a possibility.

4.2.2. Sampling Uncertainty

Another source of uncertainty in exposure estimates results from limited sampling of populations. Estimates of a population mean and variance become more accurate as the number of samples taken from the population increases. With only a few samples from a population, our confidence that the true population mean is near the estimated mean is low; as the number of samples increases, our confidence increases. The standard error (SE) of the mean is equal to the variance of the population (σ) divided by the square root of the sample size (n). SE can be estimated from the standard deviation of the population divided by the square root of n. SE can be used to calculate confidence limits on an estimate of the mean value for a population. For a normally distributed population, the 95-percent confidence limit of the mean is the estimated mean plus or minus approximately 2 SEs for reasonable sample sizes (e.g., n = at least 20).

Sampling uncertainty occurs in many areas of exposure assessment. Contaminant concentration is one key parameter subject to sampling error. For site-specific risk assessments, as the number of environmental samples increases, the uncertainty about the true distribution of values decreases. Even with large sample sizes, however, this uncertainty can dominate the total uncertainty in the exposure assessment. Other parameters subject to sampling error are the exposure factors presented in this Handbook. One of our criteria for selecting values from the Appendix to include in Chapter 2 was a sample size large enough to ensure that SE was only a few percent of the mean value.

4.2.3. Model Uncertainty

Two main types of models are likely to be used in wildlife exposure assessments: (1) allometric models to predict contact-rate parameters (e.g., food ingestion rates) and (2) fate and transport models to predict contaminant concentrations to which wildlife are exposed.

In this Handbook, we have tried to present statistical confidence limits associated with allometric equations whenever possible. To reduce the confidence limits associated with allometric models, it is important to use a model derived from the smallest and most similar taxonomic/dietary group appropriate for the extrapolation. For example, to estimate a metabolic rate for a red-winged blackbird, it is preferable to use a metabolic rate model derived from data on passerines rather than a model derived from data on many different groups of birds (e.g., raptors, seabirds, geese), and best to use a model for Icterids (the subfamily to which the red-winged blackbird belongs) rather than a model derived from data on passerines.

Uncertainties in exposure models can include how well the exposure model or its mathematical expression approximates the true relationships in the field as well as how realistic the exposure model assumptions are for the situation at hand. Judicious field sampling (e.g., of contaminant concentrations in certain prey species) can help calibrate or confirm estimates in the exposure model (e.g., food-chain exposures). Often a sensitivity analysis can help a risk assessor identify which model parameters and assumptions are most important in determining risk so that attention can be focused on reducing uncertainty in these elements.

4.3. REFERENCES

Alexander, G. (1977) Food of vertebrate predators on trout waters in north central lower Michigan. Michigan Acad. 10: 181-195.

Arthur, W. J., III; Alldredge, A. W. (1979) Soil ingestion by mule deer in north central Colorado. J. Range Manage. 32: 67-70.

Arthur W. J., III; Gates, R. J. (1988) Trace element intake via soil ingestion in pronghorns and in black-tailed jackrabbits. J. Range Manage. 41: 162-166.

Ashwell-Erickson, S.; Elsner, R. (1981) The energy cost of free existence for Bering Sea harbor and spotted seals. In: Hood, D. W.; Calder, J. A., eds. The Eastern Bering Sea shelf: oceanography and resources: v. 2, Washington, DC: Department of Commerce; pp. 869-899.

Barrett, G. W.; Stueck, K. L. (1976) Caloric ingestion rate and assimilation efficiency of the short-tailed shrew, *Blarina brevicauda*. Ohio J. Sci. 76: 25-26.

Batzli, G. O.; Cole, F. R. (1979) Nutritional ecology of microtine rodents: digestibility of forage. J. Mammal. 60: 740-750.

Bell, G. P. (1990) Birds and mammals on an insect diet: a primer on diet composition analysis in relation to ecological energetics. Studies Avian Biol. 13: 391-415.

Beyer, N.; Connor, E.; Gerould, S. (In press) Estimates of soil ingestion by wildlife. J. Wildl. Manage. 1993.

Beyer, W. N.; Stafford, C.; Best, D. (1993) Survey and evaluation of contaminants in earthworms from confined disposal facilities for dredged material in the Great Lakes. Environ. Monit. Assess. 24: 151-165.

Birdsall, C. W.; Grue, C. E.; Anderson, A. (1986) Lead concentrations in bullfrog *Rana catesbeiana* and green frog *R. clamitans* inhabiting highway drainages. Environ. Poll. (Series A) 40: 233-247.

Boyd, C. E.; Goodyear, C. P. (1971) Nutritive quality of food in ecological systems. Arch. Hydrobiol. 69: 256-270.

Bryant, D. M.; Bryant, V. M. (1988) Assimilation efficiency and growth of nestling insectivores. Ibis 130: 268-274.

Buchsbaum, R.; Valiela, I. (1987) Variability in the chemistry of estuarine plants and its effect on feeding by Canada geese. Oecologia (Berl.) 73: 146-153.

Buchsbaum, R.; Wilson, J.; Valiela, I. (1986) Digestibility of plant constituents by Canada geese and Atlantic brant. Ecology 67: 386-393.

Castro, G.; Stoyan, N.; Myers, J. P. (1989) Assimilation efficiency in birds: a function of taxon or food type? Comp. Biochem. Physiol. A. Comp. Physiol. 92: 271-278.

Collopy, M. W. (1975) Behavioral and predatory dynamics of kestrels wintering in the Arcata Bottoms [master's thesis]. Arcata, CA: Humboldt State University.

Congdon, J. D.; Dunham, A. E.; Tinkle, D. W. (1982) Energy budgets and life histories of reptiles. In: Gans, C., ed. Biology of the reptilia: v. 13. New York, NY: Academic

Press; pp. 233-271.

Cummins, K. W.; Wuycheck, J. C. (1971) Caloric equivalents for investigations in ecological energetics. Stuttgart, West Germany: International Association of Theoretical and Applied Limnology.

Davis, D. E.; Golley, F. B. (1963) Principles in mammalogy. New York, NY: Van Nostrand Rheinhold.

Dice, L. R. (1922) Some factors affecting the distribution of the prairie vole, forest deer mouse, and prairie deer mouse. Ecology 3: 29-47.

Driver, C. J.; Ligotke, M. W.; Van Voris, P., et al. (1991) Routes of uptake and their relative contribution to the toxicological response of northern bobwhite (*Colinus virginianus*) to an organophosphate pesticide. Environ. Toxicol. Chem. 10: 21-33.

Drozdz, A. (1968) Digestibility and assimilation of natural foods in small rodents. Acta Theriol. 13: 367-389.

Drozdz, A.; Górecki, A.; Grodzinski, W.; et al. (1971) Bioenergetics of water voles (*Arvicola terrestris* L.) from southern Moravia. Ann. Zool. Fennici 8: 97-103.

Duke, G. E.; Mauro, L.; Bird, D. M. (1987) Physiology. In: Pendleton, B. A.; Millsap, B. A.; Cline, K. W.; et al., eds. Raptor management techniques manual. Washington, DC: Institute for Wildlife Research, National Wildlife Federation. Sci. Tech. Ser. No. 10; pp. 262-267.

Garten, C. T. (1980) Ingestion of soil by hispid cotton rats, white-footed mice, and eastern chipmunks. J. Mammal. 61: 136-137.

Golley, F. B. (1960) Energy dynamics of a food chain of an old-field community. Ecol. Monogr. 30: 187-206.

Golley, F. B. (1961) Energy values of ecological materials. Ecology 42: 581-584.

Goodman, D. C.; Fisher, H. I. (1962) Functional anatomy of the feeding apparatus in waterfowl (Aves: Anatidae). Carbondale, IL: Southern Illinois University Press; 193 pp.

Górecki, A. (1975) Calorimetry in ecological studies. In: Grodzinski, W.; Klekowski, R. Z.; Duncan, A., eds. IPB handbook no. 24: methods for ecological energetics. Oxford, London, Edinburgh, Melbourne: Blackwell Scientific Publications; pp. 275-281.

Grodzinski, W.; Wunder, B. A. (1975) Ecological energetics of small mammals. In: Golley, F. B.; Petrusewicz, K.; Ryszkowski, L., eds. Small mammals: their productivity and population dynamics. Cambridge, MA: Cambridge University Press; pp. 173-204.

Hunt, G. L., Jr. (1972) Influence of food distribution and human disturbance on the

reproductive success of herring gulls. Ecology 53: 1051-1061.

Jorgensen, S. E.; Nielsen, S. N.; Jorgensen, L. A. (1991) Handbook of ecological parameters and ecotoxicology. Amsterdam, The Netherlands: Elsevier Science Publishers.

Karasov, W. H. (1990) Digestion in birds: chemical and physiological determinants and ecological implications. Studies in Avian Biology 13: 391-415.

Kendeigh, S. C.; West, G. C. (1965) Caloric values of plant seeds eaten by birds. Ecology 46: 553-555.

Koplin, J. R.; Collopy, M. W.; Bammann, A. R.; et al. (1980) Energetics of two wintering raptors. Auk 97: 795-806.

Kramer, D. C. (1973) Geophagy in *Terrepene ornata ornata* Agassiz. J. Herpetol. 7: 138-139.

Kreulen, D. A.; Jager, T. (1984) The significance of soil ingestion in the utilization of arid rangelands by large herbivores, with special reference to natural licks on the Kalahari pans. In: International symposium on herbivore nutrition in the subtropics and tropics (1983: Pretoria, South Africa). Draignall, South Africa: Science Press; pp. 204-221.

Levey, D. J.; Karasov, W. H. (1989) Digestive responses of temperate birds switched to fruit or insect diets. Auk 106: 675-686.

Litvaitis, J. A.; Mautz, W. W. (1976) Energy utilization of three diets fed to a captive red fox. J. Wildl. Manage. 40: 365-368.

Mayland, H. F.; Shewmaker, G. E.; Bull, R. C. (1977) Soil ingestion by cattle grazing crested wheatgrass. J. Range Manage. 30: 264-265.

Miller, L. K. (1978) Energetics of the northern fur seal in relation to climate and food resources of the Bering Sea. Nat. Tech. Inf. Serv. P. B. 275-96.

Mitchell, J. L. (1961) Mink movements and populations on a Montana river. J. Wildl. Manage. 25: 48-54.

Minnich, J. E. (1982) The use of water. In: Gans, C.; Pough, F. H., eds. Biology of the reptilia, physiology C; physiological ecology: v. 12. 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.

Odum, E. P.; Marshall, S. G.; Marples, T. G. (1965) The caloric content of migrating birds. Ecology 46: 901-904.

Peters, R. H. (1983) The ecological implications of body size. Cambridge, England: Cambridge University Press.

Pierotti, R.; Annett, C. (1987) Reproductive consequences of dietary specialization and switching in an ecological generalist. In: Kamil, A. C.; Krebs, J.; H. R. Pulliam, eds. Foraging behavior. New York, NY: Plenum Press; pp. 417-442.

Reeder, W. G. (1951) Stomach analysis of a group of shorebirds. Condor 53: 43-45.

Ricklefs, R. E. (1974) Energetics of reproduction in birds. In: Paynter, R. A., ed. Avian energetics. Cambridge, MA: Nuttall Ornithological Club.

Robel, R. J.; Bisset, A. R.; Dayton, A. D.; et al. (1979) Comparative energetics of bobwhites on six different foods. J. Wildl. Manage. 43: 987-992.

Sokal, O. M. (1971) Lithophagy and geophagy in reptiles. J. Herpetol. 5: 69-71.

Stalmaster, M. V.; Gessaman, J. A. (1982) Food consumption and energy requirements of captive bald eagles. J. Wildl. Manage. 46: 646-654.

Thayer, G. W.; Schaaf, W. E.; Angelovic, J. W.; et al. (1973) Caloric measurements of some estuarine organisms. Fishery Bull. 71: 289-296.

Tyler, A. V. (1973) Caloric values of some North Atlantic invertebrates. Mar. Biol. 19: 258-261.

U. S. Environmental Protection Agency. (1989) Risk assessment guidance for Superfund: volume I - human health evaluation manual, interim final. Washington, DC: Office of Solid Waste, Office of Emergency and Remedial Response; EPA report no. EPA/540/1-89/002.

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.

U. S. Environmental Protection Agency. (1992a) Framework for ecological risk assessment. Washington, DC: Risk Assessment Forum; EPA report no. EPA/630/R-92/001.

U. S. Environmental Protection Agency. (1992b) Guidelines for exposure assessment. Washington, DC: Science Advisory Board; EPA report no. EPA/600/Z-92/001.

U. S. Environmental Protection Agency. (1992c) Dermal exposure assessment: principles and applications, interim report. Washington, DC: Office of Research and Development; EPA report no. EPA/600/8-91/001B.

Vogtsberger, L. M.; Barrett, G. W. (1973) Bioenergetics of captive red foxes. J. Wildl. Manage. 37: 495-500.