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Energetics of Free-Ranging Seabirds

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Energetics of Free-Ranging Seabirds

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11 Energetics of Free-Ranging Seabirds

Hugh I. Ellis and Geir W. Gabrielsen

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11.1 INTRODUCTION

Nearly 30 years ago, Calder and King (1974), noting that metabolic rates on 38 species of passerine and 34 species of nonpasserine birds had been measured since 1950 and recognizing the predictive power of allometric equations, asked whether it was better to add more birds to the list or to ask new questions. Of course, both happened. In fact, adding more species to the list in part led to new questions. Among these developments has been the ability to look at groups of birds in terms of both their phylogeny and their ecology. One such approach has been to single out seabirds as an ecological group (Ellis 1984, Nagy 1987). In the more than 15 years since a comprehensive review of seabird energetics has appeared (Ellis 1984), the information on basal metabolic rates (BMR) in this group has doubled and the reports on field metabolic rates (FMR, using doubly labeled water) have more than tripled. New analyses using both of these measurements have appeared during that time. It is the goal of this chapter to summarize our current knowledge of seabird energetics, provide a comprehensive review of BMR and FMR measurements, and examine many correlates of both. The relationships of BMR with color and activity pattern (Ellis 1984) need no further development. However, unlike the earlier review, we treat thermoregulation and provide information on thermal conductance and lower critical limits of thermoneutrality. For a comprehensive treatment of avian thermoregulation, refer to [Dawson and Whittow](#) (2000). Lustick (1984) remains the best source on seabird thermoregulation generally. Ellis (1984) demonstrated a latitudinal gradient for BMR in Charadriiformes. We reevaluate that gradient and consider whether such an analysis can be extended outside that order. We examine a variety of metabolic costs, including locomotion, and survey information on community energetics, critiquing old models and suggesting new ones.

In this chapter, we limit ourselves mainly to adults in the four orders of seabirds: Sphenisciformes, Procellariiformes, Pelecaniformes, and Charadriiformes. Where feasible, we also include available information on sea ducks (Anseriformes). References to shorebirds or other birds are made only when necessary. But because the energetics of seabird migration is so poorly known, we direct the reader to those publications, relevant for shorebirds, which may provide useful insights (e.g., Alerstam and Hedenström 1998).

11.2 BASAL METABOLIC RATE IN SEABIRDS

Basal metabolic rate is a unique parameter (McNab 1997). It represents a limit, the minimal rate of energy expenditure in an endotherm under prescribed conditions (see below) and otherwise subject only to variations in time of day or season. Because it is replicable under those conditions, comparisons across a variety of species are possible. McNab (1997) cites seven conditions for BMR, some of which we view as too restrictive. We believe that BMR should be defined as the rate found in a thermoregulating, postabsorptive, adult animal at rest in its thermoneutral zone. This is fairly close to the definition given by Bligh and Johnson (1973), except that it does not demand measurement in the dark (although in actual practice it is typically measured in the dark or in dim light), and, like McNab (1997), requires the measurement be of adults to remove potential costs of growth. However, we believe that BMR is a statistic, not a constant because of circadian and seasonal effects. For example, Aschoff and Pohl (1970) demonstrated that for many birds that period of activity affects BMR; namely, BMR may be lower in the inactive (ρ) period and higher in the active (α) period. BMR may also change with season as found for a gull (Davydov 1972), sea duck (Jenssen et al. 1989, Gabrielsen et al. 1991a), and shorebird (Piersma et al. 1995); this is also known in terrestrial birds (Gavrilov 1985) and mammals (Fuglei and Ørietsland 1999). Fyhn et al. (2001) have even shown in Black-legged Kittiwakes (*Rissa tridactyla*) that BMR may change from one stage of the breeding season to another (although different individuals were used in the two periods chosen). Consequently, it is essential to note the circumstances under which BMR was measured (i.e., time of day, season) in addition to the complete experimental protocols urged by McNab (1997). The repeatability of BMR measurements within individuals, sometimes assumed by researchers, has now been demonstrated in Black-legged Kittiwakes over relatively long periods of time (1 year; Bech et al. 1999).

There are areas where there is contention over whether measured metabolic rates can be considered basal. McNab (1997) warns against the measurement of endotherms in a reproductive condition; he includes incubating birds. Indeed, King (1973) and Walsberg and King (1978) report incubation metabolic rates (IMR) above BMR, although there may be no appreciable differences between IMR and BMR in other species (cf. Williams 1996). Values for IMR in seabirds are reported in this volume by Whittow (see Chapter 12), who discusses this problem. Whereas the effect of incubation on metabolism is varied, changes in body composition (e.g., liver mass) during chick-rearing can affect metabolic rate (Langseth et al. 2000). In fact, changes in body composition in a variety of contexts, such as migration (Weber and Piersma 1996), can affect metabolic rate. We are undecided on whether these metabolic rates should be considered BMR. Although body composition may change during long-term fasting, metabolic rate may drop in Phase I of the fast before those changes become apparent; Cherel et al. (1988) consider this to be a change in BMR. Long-term fasting is further discussed in Section 11.2.5 below. Is metabolism during sleep BMR? Most metabolic experiments are done in the dark or in dim light, but the bird is thought to be awake. That often is not verifiable. However, Stahel et al. (1984) argue that for Blue Penguins (*Eudyptula minor*) the reduction in BMR ($\leq 8\%$) due to sleep is minor.

The literature has many measurements reported as SMR (standard metabolic rate) or RMR (resting metabolic rate). Generally, SMR in endotherms can be considered equivalent to BMR. That is not necessarily the case with RMR. Resting rates may not be measured in the zone of thermoneutrality nor on birds that are postabsorptive. The RMR reported for Common (*Uria aalge*) and Thick-billed Murres (*U. lomvia*) were measured under the conditions specified for BMR (Croll and McLaren 1993). On the other hand, insufficient information exists to draw that conclusion in the case of Tufted Ducks (*Aythya fuligula*; Woakes and Butler 1983) used in comparisons with seabirds in Section 11.4.3.1 below. In fact, the ducks' RMRs were measured in water; in most cases RMR of a floating bird is higher than BMR (Prange and Schmidt-Nielsen 1970, Hui 1988a, Luna-Jorquera and Culik 2000, H. Ellis unpublished, in Eared Grebes, *Podiceps nigricollis*). Similar problems are reported in penguins by Culik and Wilson (1991a).

The use of BMR and other physiological parameters has recently come under scrutiny by those who argue that phylogenetic relationships must be considered in all such comparisons, especially across broad taxonomic groups (Garland and Carter 1994, Reynolds and Lee 1996). However, this presumes knowledge of phylogenetic relationships that may be unknown or disputed, and it is not without its detractors (Mangum and Hochachka 1998). In this paper, we have chosen to provide metabolic data in a straightforward manner. However, there are differences among the orders; for example, sphenisciform birds have generally a lower BMR (see Section 11.2.2).

Our allometric equations below are given both for seabirds as a group and for each of the four orders of seabirds. It is our intention to provide as much information as possible, but we recommend that workers interested in making seabird comparisons use the all-seabird equation unless they have specific reasons for doing otherwise. Other, more serious problems affect the validity of the data themselves. These occur during both the measurement of metabolism and the conversion of units in metabolic studies and are discussed below.

11.2.1 METHODS AND ERRORS IN METABOLIC MEASUREMENTS

Direct and indirect calorimetry are the two main methods used to determine BMR in birds. The origins of both go back to Lavoisier; they are compared in Brody (1945). The indirect method has been used in most metabolic studies, including all those cited in this chapter. It is based on determinations of the quantities of oxygen consumed or carbon dioxide produced or food assimilated. In fact, for reasons discussed in most introductory physiology texts, oxygen consumption is the primary means by which such information is obtained.

Two methods have been used to measure oxygen consumption in animals: closed- and open-circuit respirometry. In open-circuit respirometry, a constant flow of air goes to an animal and then

to some analytical device. In closed-circuit respirometry, gas pressure is measured as it decreases due to the consumption of oxygen; carbon dioxide production does not compensate for such reductions because it is absorbed by some chemical (NaOH, Ascarite®, soda lime, etc.). Although not essential, closed-circuit respirometry often reduces metabolic chamber size to increase the pressure change signal. These experiments typically have shorter equilibration times and are of shorter duration than open-circuit experiments. All of these introduce sources of error likely to raise metabolic rate. We think that is likely to be the case for the study by Ricklefs and White (1981) on Sooty Terns (*Sterna fuscata*). This study is cited in Table 11.1, which compares data collected in open circuitry with those collected in closed circuitry for the same species but in different studies.

An opposite problem that may occur in closed-circuit respirometry is an apparently reduced metabolic rate due to a buildup of carbon dioxide. This would occur if the CO₂ absorbent failed, was depleted, or was ineffective (this last may occur because, unlike open systems where the absorbent is in columns through which the air passes, in closed systems it is often on the bottom of the chamber providing limited surface area). This may have occurred in the studies by Cairns et al. (1990) on the Common Murre and Birt-Friesen et al. (1989) on the Northern Gannet (*Morus bassana*), as shown in Table 11.1. Not only may the buildup of CO₂ reduce apparent metabolic rate by giving false readings of pressure changes in a closed system, but it may, in extreme cases, actually reduce the metabolic rate of a bird directly. The situation is complicated in the Northern Gannets because while the closed system of Birt-Friesen et al. (1989) may have allowed a buildup of CO₂, the experiment by Bryant and Furness (1995) actually did result in CO₂ levels as high as 2.8%.

Although we tend to trust open-circuit respirometry over closed-circuit respirometry when the results are as different as they often are in Table 11.1, we recognize that other errors may make the results of open systems suspect. The study by Kooyman et al. (1976) on Adélie Penguins (*Pygoscelis adeliae*) probably gives an inflated value for BMR because the birds were restrained. This practice, almost entirely abandoned today, may be necessary in unusual cases; but its consequences are likely to compromise results.

Another problem that can create problems for open- as well as closed-circuit respirometry involves the respiratory quotient. Respiratory quotient (RQ) is the ratio of the volume of CO₂ produced to the volume of O₂ consumed. It varies with the food substrate being metabolized by the subject. A carbohydrate diet yields an RQ of 1.0; a diet based on lipids yields an RQ of 0.71; protein substrates (Elliott and Davison 1975) and mixed substrates are intermediate (Schmidt-Nielsen 1990). An animal that is postabsorptive, a condition of BMR, would typically be sustaining itself on stored fat. Consequently, RQs measured during studies of BMR should be around 0.71. In fact, reported RQs measured in fasting birds, usually during metabolic experiments, show values at or close to 0.71 (King 1957, Drent and Stonehouse 1971). This is equally true for seabirds (Pettit et al. 1985, Gabrielsen et al. 1988, Chappell et al. 1989). Higher values suggest that birds were not postabsorptive or that CO₂ built up during the experiment. This may be illustrated by Iversen and Krog (1972) whose open-circuit BMR for Leach's Storm-petrels (*Oceanodroma leucorhoa*) is about 30% higher than was found in two closed-circuit studies (Table 11.1). Iversen and Krog did not remove CO₂ before measuring oxygen and reported RQ = 0.83. The buildup of CO₂ explains the high RQ, although not the high BMR. That high value may be a function of the very small (0.5 L) chamber used. Small chambers, often used in closed systems (see above) may cause inflated levels of oxygen consumption (H. Ellis unpublished). Here, we prefer the comparable closed-circuit experiments which used much larger chambers. A high RQ may also reflect a nonpostabsorptive condition.

Open and closed systems, when used with care, can give similar results. The nearly identical results coming from the independent studies on Southern Giant Fulmars (*Macronectes giganteus*) by Ricklefs and Matthew (1983) using a closed system and Morgan et al. (1992) using an open one underscore that (see Table 11.1). Overall, while we recognize that a closed system is sometimes

TABLE 11.1
Open- vs. Closed-Circuit Respirometry in Independent Studies

Species	N ^a	Mass ^b	BMR: Open ^c	BMR: Closed ^c	% Open	Reference
Sooty Tern (<i>Sterna fuscata</i>)	4	150.4 ± 13.0	0.97 ± 0.14	—	—	MacMillen et al. 1977
	5	156.6 ± 8.4	0.93 ± 0.14	—	—	Ellis, Pettit, and Whittow unpublished in 1982
	4	170.4	—	1.75	80.4	Ricklefs and White 1981
Common Murre (<i>Uria aalge</i>)	11	913 ± 53	1.20 ± 0.03	—	—	Gabrielsen 1996
	3	972 ± 24	—	0.77 ± 0.15	-35.8	Cairns et al. 1990
Northern Gannet (<i>Morus bassana</i>)	4	2574 ± 289	0.89 ± 0.16	—	—	Bryant and Furness 1995
	4	3030 ± 140	—	0.48 ± 0.10	-46.1	Birt-Friesen et al. 1989
Southern Giant Fulmar (<i>Macronektes giganteus</i>)	6	3929	0.92	—	—	Morgan et al. 1992
	8	3460	—	0.89	-3.3	Ricklefs and Matthew 1983
Leach's Storm-petrel (<i>Oceanodroma leucorhoa</i>)	2	42	2.77 ^d	—	—	Iversen and Krog 1972
	4	47	—	1.92 ± 0.37	-30.7	Ricklefs et al. 1986
	7	46.6	—	2.02 ± 1.01	-27.1	Montevicchi et al. 1992
Adélie Penguin (<i>Pygoscelis adeliae</i>)	13	3970	1.20 ^e	—	—	Kooyman et al. 1976
	8	3500 ± 60	—	0.92 ± 0.06	-23.3	Ricklefs and Matthew 1983

^a Number of experimental birds.

^b Mass in g.

^c mL O₂ g⁻¹ h⁻¹.

^d RQ = 0.83.

^e Restrained animals.



FIGURE 11.1 Conducting physiological studies under field conditions is often difficult: catching and confining the animal, working without electricity, dealing with weather conditions. All of these can add error to measurements. (Photo by R. W. and E. A. Schreiber.)

the only practical method under often difficult field conditions, and that it can give reliable results, we think caution should be exercised in choosing it when both options are available (Figure 11.1).

The conversion of metabolic data from units actually measured (typically oxygen consumption) to derivative units of energy (kJ, W, or previously kcal), invariably used in allometric studies (Lasiewski and Dawson 1967, Aschoff and Pohl 1970, Ellis 1984), may also be a source of error. The conversion of oxygen consumption to energy is a function of RQ, for which caloric equivalents of oxygen are provided by Bartholomew (1982). Scattered throughout the metabolic literature is the equivalency of 20.8 kJ/L O₂. This is based on an RQ of 0.79. The more reasonable RQ of 0.71 for a postabsorptive bird gives an equivalency of 19.8 kJ/L O₂. So a common misunderstanding of RQ introduces a 5% overestimate in many metabolic papers. We suggest that authors provide measured data (e.g., mL O₂ h⁻¹) or conversion factors used.

Other problems may affect the data base for seabirds. For instance, it is possible that some values presented in this chapter do not represent true values of BMR because they were not measured within the thermoneutral zone (TNZ, that range of environmental temperatures across which resting metabolic rates are lowest and independent of temperature). McNab (1997) provides examples of this. We have found far fewer data in the seabird literature on thermal conductance and lower limits of thermoneutrality than BMR. This suggests that full metabolic profiles may not always have been done and that the actual TNZ may not always have been known (e.g., Roby and Ricklefs 1986, Bryant and Furness 1995).

Not all differences in BMR can be attributed to obvious sources of error, however. The BMR of Blue Penguins (*Eudyptula minor*) reported by Stahel and Nicol (1982) is 69% higher than the value reported by Baudinette et al. (1986). We cannot explain this difference but it can have implications beyond the BMR value itself, as noted in Section 11.4.2 below. Table 11.2 includes all the measurements of BMR we found in the literature.

11.2.2 ALLOMETRY OF BMR

King and Farner (1961) reviewed previous allometric analyses and provided the best equation then possible. But they noted an incongruity between small birds and those exceeding 125 g. In 1967, Lasiewski and Dawson argued that passerines and nonpasserines required separate allometric analyses. Their nonpasserine equation is given below:

$$\text{BMR} = 327.8 \text{ m}^{0.723} \quad (11.1)$$

TABLE 11.2
Body Mass, Basal Metabolic Rates (BMR; in kJ d^{-1} and $\text{kJ g}^{-1} \text{h}^{-1}$), and Breeding Region in Seabirds

Order/Species	Body Mass (g)	n	BMR		Latitude/Region (degree)	Source
			(kJ d^{-1})	($\text{kJ g}^{-1} \text{h}^{-1}$)		
Sphenisciformes						
Adelie Penguin	3970	14	1060	0.0111	64 S	Kooyman et al. 1976
<i>Pygoscelis adeliae</i>						
Adelie Penguin	3500	8	1552	0.0185	64 S	Ricklefs and Matthew 1983
<i>P. adeliae</i>						
Emperor Penguin	23370	5	3704	0.0066	78 S	Pinshow et al. 1976
<i>Aptenodytes forsteri</i>						
Emperor Penguin	24800	11	4239	0.0071	46 S	Le Maho et al. 1976
<i>A. forsteri</i>						
Fjordland Penguin	2600	4	599	0.0096	40 S	In Drent and Stonehouse 1971
<i>Eudyptes pachyrhynchus</i>						B. Stonehouse unpublished
Yellow-eyed Penguin	4800	1	996	0.0086	40 S	In Drent and Stonehouse 1971
<i>Megadyptes antipodes</i>						B. Stonehouse unpublished
Humboldt Penguin	3870	3	821	0.0088	49 N	Drent and Stonehouse 1971
<i>Spheniscus humboldti</i>						
Blue Penguin	900	6	384	0.0178	42 S	Stahel and Nicol 1982
<i>Eudyptula minor</i>						
Blue Penguin	1106	8	298	0.0112	36 S	Baudinette et al. 1986
<i>E. minor</i>						
Blue Penguin	1082	14	308	0.0119	42 S	Stahel and Nicol 1988
<i>E. minor</i>						
Procellariiformes						
Wandering Albatross	8130	4	1755	0.0090	47 S	Adams and Brown 1984
<i>Diomedea exulans</i>						
Laysan Albatross	3103	5	637	0.0086	24 N	Grant and Whittow 1983
<i>Phoebastria immutabilis</i>						
Grey-headed Albatross	3753	3	735	0.0082	47 S	Adams and Brown 1984
<i>Thalassarche chrysostoma</i>						
Sooty Albatross	2875	4	715	0.0104	47 S	Adams and Brown 1984
<i>Phoebastria fusca</i>						
Southern Giant Petrel	3460	8	1466	0.0177	64 S	Ricklefs and Matthew 1983
<i>M. giganteus</i>						
Southern Giant Petrel	4780	6	1154	0.0101	47 S	Adams and Brown 1984
<i>M. giganteus</i>						
Southern Giant Petrel	3929	6	1735	0.0184	64 S	Morgan et al. 1992
<i>Macronectes giganteus</i>						
Southern Fulmar	780	5	437	0.0233	69 S	Weathers et al. 2000
<i>Fulmarus glacialis</i>						
Northern Fulmar	651	16	314	0.0201	79 N	Gabrielsen et al. 1988
<i>F. glacialis</i>						
Northern Fulmar	728	4	330	0.0189	56 N	Bryant and Furness 1995
<i>F. glacialis</i>						
Antarctic Petrel	718	6	408	0.0237	69 S	Weathers et al. 2000
<i>Thalassoica antarctica</i>						
Cape Pigeon	420	7	317	0.0314	69 S	Weathers et al. 2000
<i>Daption capense</i>						
Snow Petrel	292	6	199	0.0284	69 S	Weathers et al. 2000
<i>Pagodroma nivea</i>						

TABLE 11.2 (Continued)
Body Mass, Basal Metabolic Rates (BMR; in kJ d^{-1} and $\text{kJ g}^{-1} \text{h}^{-1}$), and Breeding Region in Seabirds

Order/Species	Body Mass (g)	n	BMR		Latitude/Region (degree)	Source
			(kJ d^{-1})	($\text{kJ g}^{-1} \text{h}^{-1}$)		
Kerguelen Petrel	315	2	153	0.0202	47 S	Adams and Brown 1984
<i>Leugensa brevirostris</i>						
Soft-plumaged Petrel	274	2	151	0.0230	47 S	Adams and Brown 1984
<i>Pterodroma mollis</i>						
Bonin Petrel	180	2	89	0.0206	24 N	Grant and Whittow 1983
<i>Pterodroma hypoleuca</i>						
Bonin Petrel	167	7	72	0.0181	24 N	Pettit et al. 1985
<i>P. hypoleuca</i>						
Salvin's Prion	165	3	134	0.0338	47 S	Adams and Brown 1984
<i>Pachyptila salvini</i>						
Bulwer's Petrel	87	6	44	0.0211	24 N	Pettit et al. 1985
<i>Bulweria bulwerii</i>						
White-chinned Petrel	1287	3	545	0.0176	47 S	Adams and Brown 1984
<i>Procellaria aequinoctialis</i>						
Grey Petrel	1014	2	433	0.0178	47 S	Adams and Brown 1984
<i>P. cinerea</i>						
Wedge-tailed Shearwater	332	18	121	0.0152	24 N	Pettit et al. 1985
<i>Puffinus pacificus</i>						
Sooty Shearwater	740	3	249	0.0140	37 N	Krasnow 1979
<i>P. griseus</i>						
Christmas Shearwater	308	6	127	0.0172	24 N	Pettit et al. 1985
<i>P. nativitatis</i>						
Manx Shearwater	413	10	195	0.0197	62 N	Bech et al. 1982
<i>P. puffinus</i>						
Manx Shearwater	367	4	201	0.0228	57 N	Bryant and Furness 1995
<i>P. puffinus</i>						
Georgian Diving-petrel	127	2	85	0.0279	47 S	Adams and Brown 1984
<i>Pelecanoides georgicus</i>						
Georgian Diving-petrel	119	5	122	0.0427	54 S	Roby and Ricklefs 1986
<i>P. georgicus</i>						
Common Diving-petrel	132	4	126	0.0398	54 S	Roby and Ricklefs 1986
<i>P. urinatrix</i>						
Wilson's Storm-petrel	42	9	37	0.0367	64 S	Obst et al. 1987
<i>Oceanites oceanicus</i>						
Wilson's Storm-petrel	34	6	35	0.0429	64 S	Morgan et al. 1992
<i>O. oceanicus</i>						
Leach's Storm-petrel	47	7	45	0.0399	47 N	Montevecchi et al. 1991
<i>Oceanodroma leucorhoa</i>						
Leach's Storm-petrel	45	4	43	0.0402	45 N	Ricklefs et al. 1986
<i>O. leucorhoa</i>						
Leach's Storm-petrel	44	6	59	0.0565	48 N	Ricklefs et al. 1980
<i>O. leucorhoa</i>						
Leach's Storm-petrel	42	2	55	0.0548	54 N	Iversen and Krog 1972
<i>O. leucorhoa</i>						
Fork-tailed Storm-petrel	49	16	56	0.0476	54 N	Iversen and Krog 1972
<i>O. furcata</i>						
Fork-tailed Storm-petrel	45	1	39	0.0361	59 N	Vleck and Kenagy 1980
<i>O. furcata</i>						

TABLE 11.2 (Continued)

Body Mass, Basal Metabolic Rates (BMR; in kJ d^{-1} and $\text{kJ g}^{-1} \text{h}^{-1}$), and Breeding Region in Seabirds

Order/Species	Body Mass (g)	n	BMR		Latitude/Region (degree)	Source
			(kJ d^{-1})	($\text{kJ g}^{-1} \text{h}^{-1}$)		
<i>Pelecaniformes</i>						
Red-tailed Tropicbird	593	5	288	0.0202	24 N	Pettit et al. 1985
<i>Phaethon rubricauda</i>						
Australian Pelican	5090	1	1566	0.0128	41 N	Benedict and Fox 1927
<i>Pelecanus conspicillatus</i>						
Brown Pelican	3510	1	1105	0.0131	41 N	Benedict and Fox 1927
<i>P. occidentalis</i>						
Brown Pelican	3038	3	896	0.0123	29 N	H. Ellis and W. Hennemann unpublished data
<i>P. occidentalis</i>						
Magnificent Frigatebird	1078	4	240	0.0093	9 N	Enger 1957
<i>Fregata magnificens</i>						
Cape Gannet	2660	5	856	0.0134	32 S	Adams et al. 1991
<i>Morus capensis</i>						
Northern Gannet	3030	4	701	0.0096	47 N	Birt-Friesen et al. 1989
<i>M. bassanus</i>						
Northern Gannet	2574	4	1079	0.0175	55 N	Bryant and Furness 1995
<i>M. bassanus</i>						
Masked Booby	1289	1	476	0.0154	28 N	H. Ellis unpublished data
<i>Sula dactylatra</i>						
Red-footed Booby	1017	8	376	0.0154	21 N	Ellis et al. 1982a
<i>S. sula</i>						
Double-crested Cormorant	1330	5	537	0.0168	28 N	Hennemann 1983a
<i>Hypoleucos auritus</i>						
Great Cormorant	1950	3	721	0.0154	35 N	Sato et al. 1988
<i>Phalacrocorax carbo</i>						
Imperial Shag	2660	6	1317	0.0206	64 S	Ricklefs and Matthew 1983
<i>Notocarbo atriceps</i>						
European Shag	1619	4	739	0.0190	56 N	Bryant and Furness 1995
<i>Stictocarbo arstotelis</i>						
<i>Charadriiformes</i>						
Parasitic Jaeger	351	4	199	0.0236	60 N	Bryant and Furness 1995
<i>Stercorarius parasiticus</i>						
Great Skua	970	1	410	0.0176	41 N	Benedict and Fox 1927
<i>S. skua</i>						
Great Skua	1159	4	538	0.0193	60 N	Bryant and Furness 1995
<i>S. skua</i>						
South Polar Skua	1130	9	705	0.0260	64 S	Ricklefs and Matthew 1983
<i>Catharcta maccormicki</i>						
South Polar Skua	1250	6	708	0.0236	64 S	Morgan et al. 1992
<i>C. maccormicki</i>						
Pacific Gull	1210	1	532	0.0183	41 N	Benedict and Fox 1927
<i>Larus pacificus</i>						
Common Gull	428	1	201	0.0196	55 N	Gavrilov 1985
<i>L. canus</i>						
Ring-billed Gull	439	3	250	0.0237	29 N	Ellis 1980a
<i>L. delawarensis</i>						
Kelp Gull	980	4	610	0.0259	64 S	Morgan et al. 1992
<i>L. dominicanus</i>						

TABLE 11.2 (Continued)
Body Mass, Basal Metabolic Rates (BMR; in kJ d^{-1} and $\text{kJ g}^{-1} \text{h}^{-1}$), and Breeding Region in Seabirds

Order/Species	Body Mass (g)	n	BMR		Latitude/Region (degree)	Source
			(kJ d^{-1})	($\text{kJ g}^{-1} \text{h}^{-1}$)		
Western Gull <i>L. occidentalis</i>	761	7	294	0.0161	34 N	Obst unpublished data
Glaucous Gull <i>L. hyperboreus</i>	1210	2	754	0.0260	71 N	Scholander et al. 1950b
Glaucous Gull <i>L. hyperboreus</i>	1326	9	562	0.0177	79 N	Gabrielsen and Mehlum 1989
Herring Gull <i>L. argentatus</i>	1000	6	415	0.0173	45 N	Lustick et al. 1978
Herring Gull <i>L. argentatus</i>	924	6	428	0.0193	56 N	Bryant and Furness 1995
Common Black-headed Gull <i>L. ridibundus</i>	285	1	173	0.0253	55 N	Gavrilov 1985
Common Black-headed Gull <i>L. ridibundus</i>	252	10	188	0.0311	60 N	Davydov 1972
Laughing Gull <i>L. atricilla</i>	276	4	162	0.0250	29 N	Ellis 1980a
Black-legged Kittiwake <i>Rissa tridactyla</i>	407	11	242	0.0248	57 N	Gabrielsen et al. submitted
Black-legged Kittiwake <i>R. tridactyla</i>	420	17	304	0.0302	70 N	G. Gabrielsen unpublished
Black-legged Kittiwake <i>R. tridactyla</i>	365	16	289	0.0330	79 N	Gabrielsen et al. 1988
Black-legged Kittiwake <i>R. tridactyla</i>	305	4	237	0.0324	56 N	Bryant and Furness 1995
Red-legged Kittiwake <i>R. brevirostris</i>	333	7	230	0.0288	57 N	Gabrielsen et al. submitted
Ivory Gull <i>Pagophila eburnea</i>	508	2	443	0.0363	79 N	Gabrielsen and Mehlum 1989
Royal Tern <i>Sterna maxima</i>	373	3	217	0.0242	29 N	Ellis 1980a
Arctic Tern <i>S. paradisaea</i>	85	3	79	0.0386	79 N	Klaassen et al. 1989
Grey-backed Tern <i>S. lunata</i>	131	2	61	0.0192	24 N	Pettit et al. 1985
Sooty Tern <i>S. fuscata</i>	148	6	69	0.0194	21 N	MacMillen et al. 1977
Brown Noddy <i>Anous stolidus</i>	139	16	67	0.0201	21 N	Ellis et al. 1995
Black Noddy <i>A. tenuirostris</i>	90	4	55	0.0260	24 N	Pettit et al. 1985
White Tern <i>Gygis alba</i>	98	6	70	0.0299	24 N	Pettit et al. 1985
Dovekie <i>Alle alle</i>	153	23	178	0.0490	79 N	Gabrielsen et al. 1991b
Razor-billed Auk <i>Alca torda</i>	589	2	311	0.0220	56 N	Bryant and Furness 1995
Common Murre <i>Uria aalge</i>	836	8	517	0.0258	57 N	Croll and McLaren 1993
Common Murre <i>U. aalge</i>	803	10	461	0.0239	57 N	Gabrielsen et al. submitted

TABLE 11.2 (Continued)

Body Mass, Basal Metabolic Rates (BMR; in kJ d^{-1} and $\text{kJ g}^{-1} \text{h}^{-1}$), and Breeding Region in Seabirds

Order/Species	Body Mass (g)	n	BMR		Latitude/Region (degree)	Source
			(kJ d^{-1})	($\text{kJ g}^{-1} \text{h}^{-1}$)		
Common Murre <i>U. aalge</i>	956	4	588	0.0256	65 N	Johnson and West 1975
Common Murre <i>U. aalge</i>	913	11	580	0.0270	70 N	Gabrielsen 1996
Common Murre <i>U. aalge</i>	771	4	390	0.0211	56 N	Bryant and Furness 1995
Thick-billed Murre <i>U. lomvia</i>	803	6	595	0.0309	57 N	Croll and McLaren 1993
Thick-billed Murre <i>U. lomvia</i>	1094	11	619	0.0236	57 N	Gabrielsen et al. submitted
Thick-billed Murre <i>U. lomvia</i>	989	5	588	0.0248	65 N	Johnson and West 1975
Thick-billed Murre <i>U. lomvia</i>	819	11	438	0.0223	79 N	Gabrielsen et al. 1988
Black Guillemot <i>Cepphus grylle</i>	342	13	262	0.0319	79 N	Gabrielsen et al. 1988
Parakeet Auklet <i>Cyclorhynchus psittacula</i>	243	3	172	0.0300	57 N	Gabrielsen et al. submitted
Least Auklet <i>Aethia pusilla</i>	83	5	116	0.0582	56 N	Roby and Ricklefs 1986
Atlantic Puffin <i>Fratercula arctica</i>	329	4	313	0.0396	56 N	Bryant and Furness 1995
Atlantic Puffin <i>F. arctica</i>	470	22	335	0.0300	70 N	Barrett et al. 1995
Horned Puffin <i>F. corniculata</i>	452	5	296	0.0273	57 N	Gabrielsen et al. submitted
Anseriformes						
Common Eider <i>Somateria mollissima</i>	1600	12	649	0.0169	79 N	Gabrielsen et al. 1991a
Oldsquaw <i>Clangula hyemalis</i>	490	5	237	0.0202	63 N	Jenssen and Ekker 1989

where BMR is in kJ d^{-1} and m is mass in kg. Unfortunately, Lasiewski and Dawson (1967) assumed a caloric equivalency of 4.8 kcal/L O_2 , which represents an RQ of about 0.79, for all data given in original gaseous units. Aschoff and Pohl (1970) proposed separate allometric relationships for passerines and nonpasserines based on activity pattern (anticipated earlier by King and Farner 1961). Their equations were used for most studies that thereafter noted the time that experiments were done, and most experiments were conducted at night from that time on. Their equations for nonpasserines are

$$\text{BMR}_\alpha = 381.0 m^{0.729} \quad (11.2)$$

$$\text{BMR}_\rho = 307.7 m^{0.734} \quad (11.3)$$

where α refers to the active phase and ρ the resting phase; the units are as in Equation 11.1. None of these studies included many seabirds. Ellis (1984) provided a comparison of seabird BMR with Aschoff and Pohl (1970) predictions where possible, but relied on the Lasiewski and Dawson (1967) model, which used data collected both in the day and at night, for several reasons: (1) some of the

older literature did not give the time of the experiment; (2) it was unclear at very high latitudes, where summers lacked nights and winters days, that the α/ρ differences of Aschoff and Pohl (1970) would hold; and (3) it seemed that not all seabirds followed those activity differences. Ellis (1984) then constructed an allometric relationship exclusively for seabirds:

$$\text{BMR} = 381.8 \text{ m}^{0.721} \quad (11.4)$$

where the units are the same as in Equations 11.1 to 11.3. Ellis' equation is very close to the α Equation 11.2 of Aschoff and Pohl (1970), but because he did not distinguish between active and resting phases, it is probably not directly comparable. Ellis meant for the equation to be descriptive only, but in fact it has been used in a predictive manner as well.

While we acknowledged above that BMR may vary with activity phase (Aschoff and Pohl 1970), we suspect that activity phase may not be as important as is often considered. Differences due to activity phase were not found in several high-latitude seabirds (Gabrielsen et al. 1988, Bryant and Furness 1995) or in three tropical or temperate seabirds (H. Ellis unpublished). Brown (1984) found no activity phase difference in either Macaroni Penguins (*Eudyptes chrysolophus*) or Rockhopper Penguins (*E. chrysocome*), and although Baudinette et al. (1986) did find one in Blue (= Little) Penguins, it was not significant. Because of the difficulty in ascertaining a metabolic difference between activity phases in some seabirds and because not all studies report the time at which measurements were made, our allometric equation for BMR in seabirds includes all measurements without respect to phase. For ease of comparison, our equation, like Equations 11.1 to 11.4 above, employs units of kJ d^{-1} . However, if there are circadian differences, those units are inappropriate; so Table 11.2 also provides units of $\text{kJ g}^{-1} \text{ h}^{-1}$. But in many instances these mass-specific units are inferred from an average body mass and an average BMR. Readers should consult original papers where possible. Finally, several species in Table 11.2 are represented by multiple studies. We averaged multiple studies, weighting them with the number of individuals (n) used in each.

Our overall equation for BMR in all seabirds of the four main orders, based on 110 studies on 77 species (Table 11.2) and irrespective of any possible circadian influence, is

$$\text{BMR} = 3.201 \text{ m}^{0.719} \quad (11.5)$$

with mass in g (intercept s.e. = 1.143; exponent s.e. = 0.021; $R^2 = 0.919$). The exponent is close to that of Ellis (1984; Equation 11.4 above).

Table 11.3 provides the BMR equations for each order. Based on our analysis, Sphenisciformes and all but the largest Pelecaniformes have the lowest BMRs. The lower body temperatures, longer incubation times, and longer times to raise chicks in procellariiform birds generally are not reflected

TABLE 11.3
Comparison of Allometric Equations for BMR in All Seabirds, including Two Sea Ducks, and by Order

Taxon	Total	N	R ²	s.e. intercept	s.e. exponent
All Seabirds	$\text{BMR} = 3.201 \text{ m}^{0.719}$	77	0.919	1.143	0.021
Charadriiformes	$\text{BMR} = 2.149 \text{ m}^{0.804}$	31	0.842	1.374	0.052
Pelecaniformes	$\text{BMR} = 1.392 \text{ m}^{0.823}$	12	0.756	2.729	0.135
Procellariiformes	$\text{BMR} = 2.763 \text{ m}^{0.726}$	26	0.954	1.176	0.027
Sphenisciformes	$\text{BMR} = 1.775 \text{ m}^{0.768}$	6	0.944	1.721	0.066

Note: BMR is in units of kJ d^{-1} and mass (m) is in g. N refers to number of species; for the number of studies, see Table 11.2. N for all the seabird equations includes two sea ducks, which explains the apparent discrepancy between the values in the table.

in a lower BMR except when compared to charadriiform species. However, at larger body sizes (>1 kg), pelecaniiform BMR exceeds that of the procellariiforms. The number of pelecaniiform species in our analysis is relatively small (12) and there is a greater variance in both the intercept and the exponent of that equation (reflected also in the low R^2 value). More data on a variety of pelecaniiform birds would be useful.

Finally, we would like to address the predictive value of allometric equations. We feel that enough birds fall away from allometric predictions that allometric equations must be used with care. Using an equation to predict BMR and then treating it as fact remains risky, a point also noted by Bryant and Furness (1995). In spite of our hesitancy about using allometric equations for prediction, we know they will inevitably be used that way (e.g., Ellis 1984). If that be the case, we urge readers to pay close attention to the standard errors and R^2 values we provide; only Equation 11.5 and the procellariiform equation (Table 11.3) should even be considered for such use. Given that caveat, we present in Table 11.2 every value for BMR that we know.

11.2.3 ANTICIPATED CORRELATES OF BMR

We tested BMR as a function of: (1) taxonomic order, (2) latitude/region, (3) ocean regime, (4) season, (5) activity mode, and (6) body mass. Of these parameters, only order and latitude increase the ability of body mass to predict BMR. Of those two, latitude was the more important. Using $N = 107$ studies on 76 species, we found

$$\text{BMR} = 1.865 (\text{mass}^{0.712})[\exp_{10}(\text{latitude})]^{0.0047} \quad (11.6)$$

where BMR remains in kJ d^{-1} , mass in g, and latitude in degrees (intercept s.e. = 1.120; body mass s.e. = 0.015; and latitude exponent s.e. = 0.001; $R^2 = 0.958$). The inclusion of order does not increase the predictive value much ($R^2 = 0.966$). This confirms the importance of latitude in seabird BMR first noted by Ellis (1984) for charadriiforms and extended to other seabird taxa by Bryant and Furness (1995).

A correlate of BMR found in birds (McNab 1988) and mammals (McNab 1986a, b) is food habits. We failed to find such a relationship among seabirds, probably owing to the lack of variety in diet among these carnivores. Whether some relationship may eventually be found that allows, for example, filter-feeders (of plankton) to be separated from feeders of whole fish or squid by BMR awaits a more comprehensive data set.

Ellis (1984) suggested a correlation between activity mode, in terms of flight or feeding, and BMR. That was not verified statistically in this study, when looking at all seabirds as a group. Whether it exists within specific taxa is currently unknown and may also, for some taxa, require a larger data set.

11.2.4 UNUSUAL CORRELATES OF BMR

Basal metabolic rate can be invoked as a correlate of several characters in the life histories and demographics of birds. One of these is life span, since life span in birds scales positively with body size (Lindstedt and Calder 1976), which is the major predictor of BMR as noted above (Figure 11.2; see Chapters 5 and 8). Similarly, mass-specific BMR can be inferred to vary inversely with life span. For example, long-lived Laysan Albatrosses (*Phoebastria immutabilis*) have a low BMR (Grant and Whittow 1983) based on the predictions of Equation 11.5 or even the procellariiform equation (Table 11.3). However, there has not yet been a systematic study of the relationship of BMR and life span in seabirds or any other birds in spite of Calder's (1985) hypothesis. A particularly interesting correlate of BMR is the intrinsic rate of reproduction (r). McNab (1980a, 1987) and Hennemann (1983b) suggested a positive correlation between BMR and r , both factors under the control of natural selection. Though Hennemann's formulation has been challenged

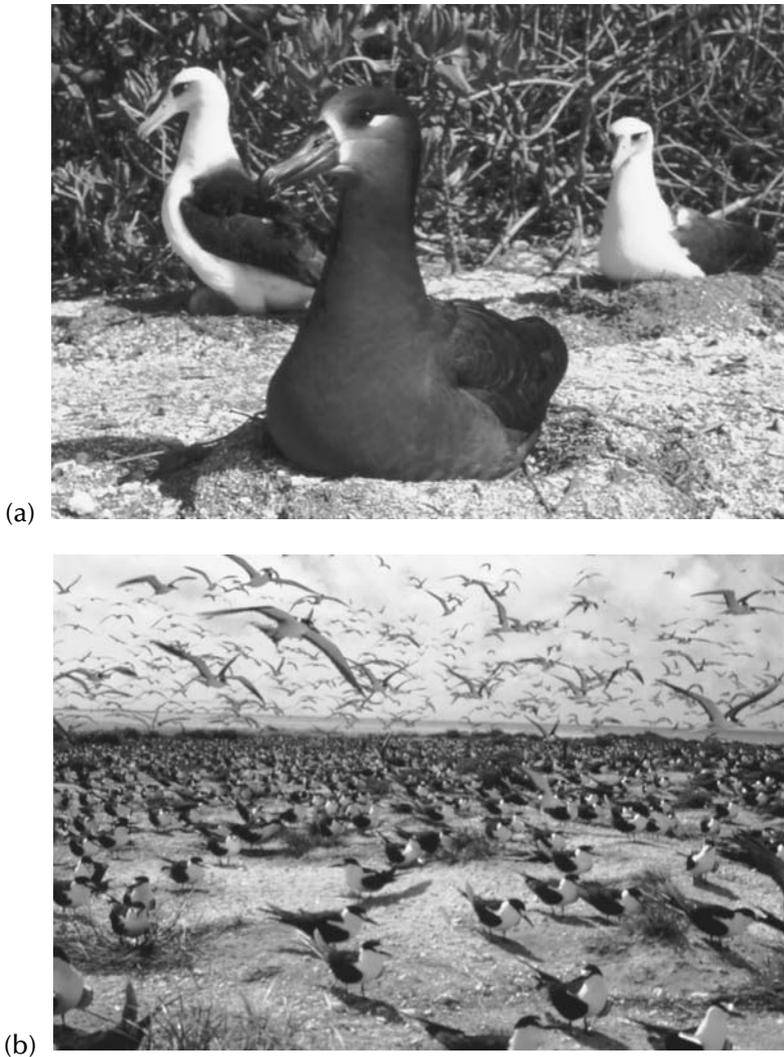


FIGURE 11.2 Body size scales directly with BMR: (a) BMR in albatrosses ranges from 637 to 1755 kJ d⁻¹, here Laysan and Black-footed Albatrosses weighing 3000 g; (b) BMR of Sooty Terns is 69 kJ d⁻¹, body mass 150 g. (Photos by R. W. and E. A. Schreiber.)

(Hayssen 1984), testing this imputed association may be of great value to seabird biologists looking for relationships between reproductive effort and energy costs.

Another interesting correlate of BMR is the cost of feather production. Lindström et al. (1993) demonstrated that the cost of feather production (C_f in kJ g⁻¹ of dry feathers) is a function of mass-specific BMR. They found

$$C_f = 270 \text{ BMR m}^{-1} \quad (11.7)$$

where BMR is in units of kJ g⁻¹ d⁻¹. They further inferred an inverse relationship between body mass and molt efficiency. Recent work on penguin molting (Cherel et al. 1994) seems to confirm this relationship and therefore suggests confirmation of Equation 11.7 for seabirds as well (see Section 11.4.2).

Once it was recognized that different taxa have different evolutionary molecular clocks (see Nunn and Stanley 1998), efforts were made to determine the factor or factors that set that rate.

Martin and Palumbi (1993) suggested that metabolic rate was the key determinant because it was related to higher mutation rates. Nunn and Stanley (1998), recognizing the close correspondence of FMR and especially BMR with body mass, used body mass as a surrogate in their analysis of 85 species of procellariiform seabirds. They concluded that in these seabirds, metabolic rate was the most likely factor setting the rate of change in the mitochondrial gene for cytochrome b. Stanley and Harrison (1999) subsequently explained why molecular clocks in birds were slower than those of mammals, despite higher metabolic rates in birds, by reconciling the avian constraint hypothesis, which argues that increased functional constraint in birds limits substitutions of mutations, with the metabolic rate hypothesis. This work is likely to stimulate new areas of research for birds generally and may lead to the justification of many more BMR measurements. One question that might be addressed is how very different metabolic rates in closely related birds (e.g., *Egretta*; see Ellis 1980b) may affect this analysis.

11.2.5 LONG-TERM FASTING METABOLISM

While the measurement of BMR is dependent upon the animal being postabsorptive, this involves a fast of only 8 to 14 h. However, several seabirds are deprived of food for longer periods during incubation. The best known of these are the penguins, albatrosses, and eiders which can go from several days to weeks without food (e.g., Croxall 1982, Gabrielsen et al. 1991a). During these long-term fasts, the metabolic substrates can change from a largely lipid form to include more protein (Groscolas 1990), which may be reflected in an increase in the RQ of the animal. A description of the physiology and biochemistry of this kind of fast may be found in Le Maho (1993) and Cherel et al. (1988) who describe the three phases of fasting. Briefly, Phase I is a period of adaptation and lipid mobilization; body mass decreases with BMR decreasing even faster. Phase II is a period of reduced activity and slow loss of body mass; mass-specific BMR reaches an equilibrium, and 90% or more of the metabolic substrate is lipids. It is in Phase III that proteins may be mobilized; daily body mass loss increases rapidly, and various behaviors, including locomotor activity, return, perhaps as a hormonal “refeeding signal” to improve the bird’s chances of survival (Robin et al. 1998). These changes in metabolic activity should be noted, because many studies on the costs of molt (Section 11.4.2) and incubation (see Chapter 12 and Section 11.5.1.1 below) have been done on birds during long-term fasting.

11.3 SEABIRD THERMOREGULATION

When physiological studies of thermoregulation were still relatively new, Scholander et al. (1950a, b, c) argued that birds and mammals in cold climates could evolve higher metabolic rates (BMR) or lower thermal conductance (that is, better insulation). They demonstrated the latter, but not the former. However, Weathers (1979) and Hails (1983) showed some effect of climate on BMR in birds. Ellis (1984), using latitude as a general proxy for climate, also demonstrated a BMR correlation for charadriiform seabirds. Reducing thermal conductance would reduce the lower critical limit of an endotherm’s thermoneutral zone (TNZ), thus effectively extending downward the range of temperatures at which its metabolism could remain basal. In this section, we address both thermal conductance and the lower critical temperature.

Seabirds have metabolic rates that are somewhat higher than would be expected from an analysis of all nonpasserine birds. Climate might be one reason for this. Due to sea-surface temperatures (SST), tropical seabirds often have cooler environments than their terrestrial counterparts. Polar seabirds may actually benefit in winter from the moderating temperatures of the sea when compared to their terrestrial counterparts. Unlike the majority of polar land birds, many seabird species do not migrate to warmer climates during winter. Whether higher metabolic rates are accompanied by increases in insulation or reductions in the lower critical limit of the thermoneutral zone has not been analyzed in a comprehensive way for seabirds. We present a preliminary

analysis here but studies of the thermal biology of seabirds at different latitudes and under different conditions are needed. Aside from a study on the influence of wind speed on thermal conductance in Adélie Penguins and Imperial Shags (*Notocarbo atriceps*) by Chappell et al. (1989), these are not yet available.

11.3.1 THERMAL CONDUCTANCE

Thermal conductance (C) is a coefficient of heat transfer (Calder and King 1974) and is inversely related to insulation. It is the sum of many processes, including radiation, conduction, and convection. Whether it should also include the evaporative process is the subject of some debate. McNab (1980b) distinguishes between “wet” conductance, which includes the evaporative factor, and “dry” conductance, which does not. Drent and Stonehouse (1971) compared the wet and dry thermal conductances of many species, and the difference decreased with increasing size. Of the 16 species in their study exceeding 100 g, wet conductance averaged 15.5% higher than dry. In the only two seabirds in that analysis, the Common (Mew or Short-billed) Gull (*Larus canus*) and Humboldt Penguin (*Spheniscus humboldti*) both showed a difference of 11%. The difference between wet and dry thermal conductance in Double-crested Cormorants (*Hypoleucos auritus*) was also small (13%, which was not significant), though in the same study (Mahoney 1979) a large and significant difference of 31.5% was found in Anhingas (*Anhinga anhinga*).

We have found 37 values for C in seabirds (see Table 11.4), a mix of wet and dry values. Because the differences are likely to be small ($\leq 15\%$), we do not distinguish between them in our analysis. Most are “wet.” It should be noted, however, that these differences often become exacerbated when the correction of Dawson and Whittow (1994) is applied to one set of the data. Using the same data set, Ellis et al. (1982b) referred to a wet thermal conductance 25% higher than the dry, “corrected” values later reported for Brown Noddies (*Anous stolidus*) by Ellis et al. (1995) and cited in Table 11.4.

A more fundamental difference involves the nature of the measurement. Originally, thermal conductance was measured as a function of body surface area. This made sense, since heat exchange is across the surface; it also conforms to the definition provided by Bligh and Johnson (1973). But beginning with Morrison and Ryser (1951), McNab and Morrison (1963), and Lasiewski et al. (1967), conductance was reported as a function of body mass. In our review, we favor the use of body mass since surface area is not measurable, varies with posture, erection of feathers, etc., and is approximated by (Meeh’s) equation. Prosser (1973) viewed this approximation as a source of error. McNab (1980b) also noted that having surface area in the units for thermal conductance makes them inconsistent with the units typically reported for metabolism. Luna-Jorquera et al. (1997), analyzing the use of Meeh’s equation in penguins, argued that surface area is too problematic a measure and urged the use of body mass in the reporting of thermal conductance. Consequently, we use a modified Meeh’s equation to back calculate all values of thermal conductance in surface area units to body mass units ($\text{kJ g}^{-1} \text{h}^{-1} \text{ }^\circ\text{C}^{-1}$ rather than $\text{kJ cm}^{-2} \text{h}^{-1} \text{ }^\circ\text{C}^{-1}$). As with BMR, these are derived units, so wherever possible we began with the original units for oxygen consumption, and converted assuming $\text{RQ} = 0.71$ and a conversion of 19.8 kJ/L O_2 . Where the original data were already in heat or caloric equivalents, there exists the possibility of a 5% overestimate, as noted above. Finally, because avian conductance often drops with decreasing ambient temperatures (Drent and Stonehouse 1971), wherever possible we follow the convention of McNab (1980b) in using the lowest values of C at which the birds are still thermoregulating. This is the minimal thermal conductance.

Allometric relationships for thermal conductance in birds have been reported by Herreid and Kessel (1967) using cooling curves, Lasiewski et al. (1967) using metabolic data, Calder and King (1974) combining both 1967 data sets, and Aschoff (1981) who distinguished between active and resting phases. Seabirds barely contributed to any of those curves. Weathers et al. (2000) presented thermal conductances for 17 species of seabirds, but all were from high latitudes. The data set

TABLE 11.4
Body Mass, Thermal Conductance (C), and Lower Critical Temperatures (LCT) in Seabirds, by Breeding Region

Order/Species	Body Mass (g)	n	C (mL O ₂ g ⁻¹ h ⁻¹ °C ⁻¹)	LCT (°C)	Latitude/Region (degree)	Source
Sphenisciformes						
Gentoo Penguin	5850		0.0222			Scholander et al. 1940
<i>Pygoscelis papua</i>						
Adelie Penguin	3980	5	0.0132	10	65 S	Chappell et al. 1989
<i>P. adeliae</i>						
Emperor Penguin	23370	5	0.007	-7	78 S	Pinshow et al. 1977
<i>Aptenodytes forsteri</i>						
Blue Penguin	900	6	0.0346	10	41 S	Stahel and Nicol 1982
<i>Eudyptula minor</i>						
Procellariiformes						
Southern Fulmar	780	5	0.036	5.6	69 S	Weathers et al. 2000
<i>Fulmarus glacialisoides</i>						
Northern Fulmar	651	16	0.0336	9	79 N	Gabrielsen et al. 1988
<i>F. glacialis</i>						
Antarctic Petrel	718	6	0.037	6.4	69 S	Weathers et al. 2000
<i>Thalassoica antarctica</i>						
Cape Pigeon	420	7	0.058	10.8	69 S	Weathers et al. 2000
<i>Daption capense</i>						
Snow Petrel	292	6	0.058	13.6	69 S	Weathers et al. 2000
<i>Pagodroma nivea</i>						
Wedge-tailed Shearwater	321		0.0625	22.5	20 N	Whittow et al. 1987
<i>Puffinus pacificus</i>						
Manx Shearwater	413	8	0.0513		62 N	Bech et al. 1982
<i>P. puffinus</i>						
Georgian Diving-petrel	119	5	0.070	20	54 S	Roby and Ricklefs 1986
<i>Pelecanoides georgicus</i>						
Common Diving-petrel	132	4	0.070	20	54 S	Roby and Ricklefs 1986
<i>P. urinatrix</i>						
Wilson's Storm-petrel	36		0.117	16	64 S	Obst 1986
<i>Oceanites oceanicus</i>						
Leach's Storm-petrel	45	4	0.0318	14	45 N	Ricklefs et al. 1986
<i>Oceanodroma leucorhoa</i>						
Leach's Storm-petrel	47	7	0.0222		47 N	Montevicchi et al. 1991
<i>O. leucorhoa</i>						
Pelecaniformes						
Magnificent Frigatebird	1100	4	0.023	20	9 N	Enger 1957
<i>Fregata magnificens</i>						
Red-footed Booby	994	4	0.0394	19	21 N	H. Ellis unpublished
<i>Sula sula</i>						
Double-crested Cormorant	1500	12	0.0492		26 N	Mahoney 1979
<i>Hypoleucos aristotolis</i>						
Imperial Shag	2630	6	0.0278	0	65 S	Chappell et al. 1989
<i>Notocarbo atriceps</i>						
Charadriiformes						
Heerman's Gull	383	5	0.0506	23	32 N	H. Ellis unpublished
<i>Larus heermanni</i>						

TABLE 11.4 (Continued)
Body Mass, Thermal Conductance (C), and Lower Critical Temperatures (LCT) in Seabirds, by Breeding Region

Order/Species	Body Mass (g)	n	C (mL O ₂ g ⁻¹ h ⁻¹ °C ⁻¹)	LCT (°C)	Latitude/Region (degree)	Source
Ring-billed Gull	470	2	0.0443	16	29 N	Ellis 1980a
<i>L. delawarensis</i>						
California Gull	565	5	0.0412	20	38 N	H. Ellis unpublished
<i>L. californicus</i>						
Glaucous Gull	1326	9	0.0248	2	79 N	Gabrielsen and Mehlum 1989
<i>L. hyperboreus</i>						
Herring Gull	1000	6	0.0385	10	45 N	Lustick et al. 1978
<i>L. argentatus</i>						
Laughing Gull	278	4	0.0559	22	29 N	Ellis 1980a
<i>L. atricilla</i>						
Black-legged Kittiwake	365	16	0.0466	4.5	79 N	Gabrielsen et al. 1988
<i>Rissa tridactyla</i>						
Ivory Gull	508	2	0.0488	0.5	79 N	Gabrielsen and Mehlum 1989
<i>Pagophila eburnea</i>						
Royal Tern	386	3	0.0612	23	29 N	Ellis 1980a
<i>S. maxima</i>						
Sooty Tern	150	4	0.084	30	21 N	MacMillen et al. 1977
<i>Sterna fuscata</i>						
Brown Noddy	140	15	0.0513	20	21 N	Ellis et al. 1995
<i>Anous stolidus</i>						
Dovekie	153	23	0.063	4.5	79 N	Gabrielsen et al. 1991b
<i>Alle alle</i>						
Common Murre	956	4	0.0492	5	65 N	Johnson and West 1975
<i>U. aalge</i>						
Thick-billed Murre	819	11	0.0282	2	79 N	Gabrielsen et al. 1988
<i>Uria lomvia</i>						
Black Guillemot	342	13	0.0475	7	79 N	Gabrielsen et al. 1988
<i>Cephus grylle</i>						
Least Auklet	83	5	0.084	15	56 N	Roby and Ricklefs 1986
<i>Aethia pusilla</i>						
Anseriformes						
Common Eider	1661	12	0.024	7	79 N	Gabrielsen et al. 1991a
<i>Somateria mollissima</i>						

provided in Table 11.4 is the first comprehensive compilation of thermal conductances for seabirds from a variety of latitudes. It includes 37 measurements on 35 species. Unlike Aschoff (1981) or the restricted set of thermal conductances presented by Weathers et al. (2000), it does not separate these values into active and passive activity categories. This is because that information was not always available in the studies we cited and because of the absence of a clear activity dichotomy in the BMR data of many birds (see Section 11.2 above). Two of these measurements, both for Leach's Storm-petrel, represent significant outliers. Without them, we found the following relationship for all seabirds:

$$C = 0.435 m^{-0.374} \quad (11.8)$$

where m is mass in g and C in $\text{mL O}_2 \text{ g}^{-1} \text{ h}^{-1} \text{ }^\circ\text{C}^{-1}$ ($N = 35$; intercept s.e. = 1.225; exponent s.e. = 0.032; $R^2 = 0.806$). If the outliers were included, R^2 would drop dramatically to 0.511 and the equation would become $0.231 m^{-0.281}$ ($N = 37$ measurements on 36 species; intercept s.e. = 1.337; exponent s.e. = 0.046). Equation 11.8 differs considerably from earlier equations. Compared to the equation of Lasiewski et al. (1967), which like ours also avoids circadian phase, our equation predicts higher values of thermal conductance at all body masses above 150 g.

Thermal conductance varies among seabirds. In accordance with the analysis of Scholander et al. (1950a, c), low thermal conductance (i.e., good insulation) is one adaptation which might be expected in cold climates. On the other hand, high values of C (i.e., poor insulation) would promote convective heat loss and might be expected in warm climates (Yarborough 1971). In a hot climate, forced convection (wind) might be advantageous to a bird, but in a cold climate it represents a real threat, lowering effective operative temperatures (T_e). This must be the case for seabirds nesting in polar areas where a combination of wind and cold temperatures leads to substantial increases in metabolic rates, especially in adults (Chappell et al. 1989).

Avian insulation can derive from either the tissues or the feathers. Drent and Stonehouse (1971) reported that about 20% of the total insulation of the Humboldt Penguin comes from body tissues, including subcutaneous fat, the remainder being from the feathers. That being the case, it is likely that molt should be important in certain seasonal adjustments. The winter acclimatized Common Eider (*Somateria mollissima*) has a C which is 25% lower than the summer acclimatized eider (Jenssen et al. 1989, Gabrielsen et al. 1991a). This is also seen in land birds in the Arctic and sub-Arctic (West 1972, Bech 1980, Rintamäki et al. 1983, Barre 1984, Mortensen and Blix 1986). Mortensen and Blix found that ptarmigans (*Lagopus* spp.) reduced C in the winter by 8 to 32% by increasing subcutaneous fat and plumage thickness. Common Eiders probably reduce insulation in the summer by molting their down (which is then used as nest material) and producing naked brood patches (Gabrielsen et al. 1991a). Females also reduce insulation by losing fat during incubation (Korschgen 1977, Parker and Holm 1990, Gabrielsen et al. 1991a).

Thermal conductance does not seem to vary in a predictable way with latitude (Gabrielsen et al. 1988, 1991a, b). This may be because evolution may modify metabolic rate as well as thermal conductance in cold climates (Scholander et al. 1950a, c). But comparing seabirds as a group with land birds does indicate some connection between thermal conductance and climate. As was noted above, polar seabirds may actually be at a thermal advantage compared to polar land birds because of the high heat capacity of water and its moderating effect on climate. In fact, many land birds have a better insulation. Both arctic-breeding ravens (Schwann and Williams 1978) and ptarmigan (West 1972, Mortensen and Blix 1986) have lower values of C than do seabirds, indicating that these permanent residents may be better cold adapted than seabirds.

11.3.2 LOWER LIMIT OF THERMONEUTRALITY

The lower critical temperature (LCT) or lower limit of thermoneutrality is an indicator of thermoregulatory ability since below that level metabolism must increase. Scholander et al. (1950b) demonstrated the value of a reduced LCT in the metabolic economy of endotherms. Table 11.4 shows that, as expected, seabirds show an inverse relationship between size and LCT. We also find that there is an influence between LCT and latitude, with Arctic and Antarctic birds having a lower LCT than birds of similar mass from warmer climates. These relationships can be expressed by the equation

$$\text{LCT} = 43.15 - 6.58 \log \text{mass} - 0.26 \text{ latitude} \quad (11.9)$$

where LCT is in degrees Celsius; mass is in g; latitude in degrees ($N = 33$; intercept s.e. = 3.94; log mass coefficient s.e. = 1.43; latitude coefficient s.e. = 0.03; $R^2 = 0.779$).

11.3.3 BODY TEMPERATURE

Deep body temperature (T_b) is dependent on metabolic rate and insulation (Irving 1972). There is no evidence that body temperature varies with climate or latitude across a range from the Arctic through temperate and tropical to Antarctic regimes (Scholander et al. 1950c, Irving and Krog 1954, Drent 1965, Irving 1972, Barrett 1978, Prinzinger et al. 1991, Morgan et al. 1992). Body temperatures in seabirds are typical of birds generally, though Prinzinger et al. (1991) found T_b to be lower in Procellariiformes and Sphenisciformes than the average for all birds. The earliest measurements were by Eydoux and Souleyet (1838; cited in Warham 1996) on procellariiforms and Martins (1845) who measured T_b at 40.6°C in ten species of “webfooted” birds during summer expeditions to Svalbard in 1838 and 1840. We do not know the species in the Martins study, but they probably included Common Eider, Glaucous Gull (*Larus hyperboreus*), kittiwakes, and alcids. His value is very close to those presented in later studies of Arctic and sub-Arctic seabirds (Irving 1972). In the Antarctic, body temperature remains at expected avian levels (Chappell et al. 1989, Weathers et al. 2000). On the other hand, some tropical species allow T_b to show some lability under different conditions and even fall somewhat (Red-footed Boobies, *Sula sula* [Shallenberger et al. 1974]; Great Frigatebirds, *Fregata minor* [Whittow et al. 1978]).

While T_b is resistant to climate, it is linked tightly to metabolic rate. If metabolism drops for any reason, T_b may drop as well. This is the case with the Atlantic Puffin (*Fratercula arctica*) which can lower its RMR while incubating to conserve its energy reserves. Consequently, T_b drops and incubation times are lengthened (Barrett et al. 1995). There seems to be some linkage to BMR as well: procellariiform birds as a group have somewhat lower BMR than other seabirds (see Section 11.2.2) and their body temperatures are also lower (Warham 1971, 1996).

Body temperature may vary as a function of activity phase. Typically, birds that show a reduction in metabolic rate during the ρ -phase also show a depression in T_b (cf. Warham 1996). Great Frigatebirds drop T_b by 3 to 4°C during the night (Whittow et al. 1978). The linkage between T_b and metabolism is not dependent only on activity phase. Regel and Pütz (1997) found that Emperor Penguins (*Aptenodytes forsteri*) showed increases in body temperature as a function of human disturbance as mediated by metabolic rate.

Body temperature may also be affected by the water which, because of its high heat capacity, can represent an enormous heat sink when cold. Dumonteil et al. (1994) found T_b to remain very constant in water, although it was slightly (0.3°C) depressed below measurements in air. Bank Cormorants (*Compsahalieu neglectus*) show a more pronounced T_b depression in the water, either because of poor insulation or insufficient heat production from swimming activity. These birds may allow T_b to drop as much as 5°C while diving to save energy (Wilson and Grémillet 1996), regaining it quickly through sunning behavior out of the water (Grémillet 1995). On the other hand, Great Cormorants (*Phalacrocorax carbo*), which do not experience as much solar radiation as Bank Cormorants, show smaller depressions of T_b and have better insulation (Grémillet et al. 1998). Imperial Shags (Bevan et al. 1995a, Grémillet et al. 1998) and South Georgia Shags (*Notocarbo georgianus*, Bevan et al. 1997) in Antarctic seas face such cold waters and dive so deeply they cannot prevent T_b from dropping. The T_b of South Georgia Shags may drop by 5°C or more during diving. Abdominal temperature in King Penguins (*Aptenodytes patagonicus*) may fall to as low as 11°C, 10 to 20° below the normal stomach temperature. A slowing of metabolism in certain anatomical areas when diving may help explain why penguins can dive for such long durations (Handrich et al. 1997). Similar studies on diving birds in warm water do not exist.

Deep core temperatures monitored by implants in or near the stomach are likely to be distorted by feeding in free-ranging birds. The ingestion of food in petrels (Obst et al. 1987), boobies (Shallenberger et al. 1974), and cormorants (Ancel et al. 1997) is known to drop stomach temperature by 5°C or more. While there are obvious advantages to knowing when a diving bird ingests prey, the effect that event has on T_b needs to be understood better. Handrich et al. (1997) reported that low abdominal temperatures may preserve food until the bird reaches its chicks in the colony.

11.4 OTHER COSTS

BMR is defined for very specific sets of conditions, as noted above. If any of the restrictions are violated, metabolism is not basal. However, the metabolic rates then measured may convey additional information. Metabolism in nonpostabsorptive birds, for example, may provide information on the costs of digestion. Similarly, the costs of molt and locomotion have been quantified. Croll and McLaren (1993) provided one such measure which is otherwise rare in the seabird literature. They found the cost of preening in murres to be 2.5 to $3 \times$ RMR which was the most expensive activity these birds engaged in. Earlier Butler and Woakes (1984) had reported a preening cost in Humboldt Penguins of just over twice resting rates. Croll and McLaren (1993) suggested that the high increase in metabolic rate in preening murres might be linked to producing more heat for thermoregulation in cold water.

11.4.1 DIGESTION

The cost of digestion is often referred to as specific dynamic action (SDA) in the older literature, and today is more often referred to as the heat increment of feeding (HIF). The heat produced by digestion is transient, but it may aid thermoregulation (Hawkins et al. 1997), though Dawson and O'Connor (1996) did not find such a connection for most birds in their review. Baudinette et al. (1986) found metabolic rate in Blue Penguins increased by 87% as a result of feeding. The increment is smaller, though still appreciable (36 to 49%) in Common and Thick-billed Murres according to two studies (Croll and McLaren 1993, Hawkins et al. 1997). Hawkins et al. suggested that this increment could be responsible for nearly 6% of the daily energy expenditure of either murre species. However, caution is urged because Wilson and Culik (1991) found the increase in metabolic rate associated with feeding in Adélie Penguins to result from heating cold food to body temperature rather than actual SDA. Weathers et al. (2000) discussed the effect of HIF on nestling metabolic rates in four Antarctic fulmarine petrels. They do not attribute a thermoregulatory role to HIF in these birds.

11.4.2 MOLT

The metabolic cost of molt in birds was not known in any detail until late in the 20th century (King 1974, 1981). Murphy (1996) provides an excellent summary of the energetics of molt, but provides no information about seabirds. Among seabirds, molt has been best studied in penguins and was reviewed by Adams and Brown (1990). This section supplements that work with some more recent information and some slightly different perspectives. Readers concerned with the mechanisms of molt in penguins are referred to Groscolas (1990).

Adams and Brown (1990) evaluate the use of mass loss in estimating the energetic cost of molt in penguins. Based on mass loss, Williams et al. (1977) estimated the cost of molt to be 1.6 and $2.1 \times$ BMR for Macaroni Penguins and Rockhopper Penguins, respectively. However, these multiples were based on predictions from the Lasiewski-Dawson (1967) allometric equation, and the mass losses assumed a large component of fat during molt. Relying primarily on studies using mass loss, Croxall (1982) estimated the cost of molt at twice BMR and established that only about half the material lost was fat, which had clear energy implications. Brown (1985) underscored this by comparing the cost of molt in Macaroni and Rockhopper Penguins using both mass loss and oxygen consumption. Using mass loss, he estimated the cost to be 1.96 and $1.79 \times$ IMR (incubation metabolic rate, a value Brown felt was close to BMR; see Whittow on IMR, [Chapter 12](#)), respectively; but with oxygen consumption the multiples were 1.81 and 1.50. These two sets of figures could be partially reconciled by reducing the proportion of fat in the mass loss below the level assumed by Williams et al. (1977). Groscolas and Cherel (1992) reported the daily rate of mass specific weight loss to double in King Penguins and increase fivefold in Emperor Penguins during molt compared to breeding, suggesting a high associated cost of molt. Cherel et al. (1994) used



FIGURE 11.3 In King Penguins (Crozet Island), adults during the breeding season (here incubating eggs on their feet) have a significantly lower metabolic rate of fasting than when fasting during molt, implying a high cost of molt. (Photo by H. Weimerskirch.)

mass loss to estimate the cost of molt in King Penguins; it agreed with a value determined by indirect calorimetry. They found the metabolic rate of fasting King Penguins in molt to be 21% higher than in birds that were fasting during the breeding season (Figure 11.3). Their value for cost of molt as a multiple of BMR depends on the value for BMR used. It is $1.30 \times \text{BMR}$ as determined by Le Maho and Despin (1976) but $1.67 \times \text{BMR}$ (Adams and Brown 1990). These values bracket the 50% increase in Blue Penguins (Baudinette et al. 1986, Gales et al. 1988). Both Baudinette et al. (1986), using oxygen consumption in confined birds, and Gales et al. (1988), using doubly labeled water in free-ranging penguins, found the cost of molt to be $1.5 \times \text{BMR}$. However, they used different values for BMR (see Section 11.2.1). If Gales et al. had used the average value reported by Baudinette et al. (1986), or Stahel and Nicol (1988) instead of Stahel and Nicol (1982), their multiple would have been $2.6 \times \text{BMR}$.

Murphy (1996) reported that the energy content of feathers and other associated keratinous structures is 22 kJ g^{-1} of dry mass and argued that the cost of depositing these structures should be minimal, perhaps $<6\%$ of BMR. However, the actual energy costs of molt are higher because of associated costs including the processing and utilizing of nutrients for feather growth, specific nutritional costs associated with molt, etc. (King 1981, Lindström et al. 1993, Murphy 1996). These associated costs may not include additional thermogenesis, which Murphy (1996) discounted as a problem in most birds (but see Groscolas and Cherel 1992 for a different view regarding penguins). She cites a total cost of molt between 109 and 211% of nonmolt (BMR?) levels. Values for penguins, which have a more intense molt than most other birds, tend toward the upper end of that range. Lindström et al. (1993) looked at energetic efficiencies (energy deposited as feathers and associated structures divided by the feather mass specific cost of molt) of several avian species (none seabirds). They found efficiencies to increase with increasing body mass because the cost of feather production was inversely related to mass. This is validated by Cherel et al. (1994) who found the lowest cost of feather production (85 kJ g^{-1}) and one of the highest efficiencies (25%) in King Penguins, which began their molting fasts at 18 kg and ended them at a still quite large 10 kg.

11.4.3 LOCOMOTION

Seabirds move by flight, swimming, and walking, though several species are incapable of at least one such form (e.g., some of the better diving birds such as tropicbirds, loons, and grebes have legs so far back that they cannot walk; penguins cannot fly; frigatebirds and skimmers do not swim).

The energetics of flight in birds generally was reviewed recently (Norberg 1996, Butler and Bishop 2000). Two papers (Pennycuick 1987a, b) missed in those reviews add to our understanding of flight in seabirds. Pennycuick (1987b) noted that in spite of the great variety of feeding methods and provisioning frequencies found in seabirds, the only factor that has had a “drastic” effect on flight adaptations is the use of wings under water. That is obvious in penguins and will be noted below for alcids. Those interested in the full range of physiological trade-offs between flight and diving should consult Lavvorn and Jones (1994).

The costs of flight in particular species of seabirds was noted in Ellis (1984). Wind seems to be a major environmental factor. Sooty Terns have a low cost of flight due to their partial reliance on soaring (Flint and Nagy 1984). Red-footed Boobies also take advantage of the wind during flight and show considerably lower costs than would otherwise be expected (Ballance 1995). This was also inferred for Gray-headed Albatrosses (*Thalassarche chrysostoma*); the indirect measure of their flight costs was compared also to those of other seabirds known at that time (Costa and Prince 1987). The geographic distribution of the Wandering Albatross (*Diomedea exulans*; Jouventin and Weimerskirch 1990) and Northern Fulmar (*Fulmarus glacialis*; Furness and Bryant 1996) may be limited by the absence of wind. Boobies and frigatebirds roost in greater numbers during low or no-wind days implying a greater cost of flight on those days (Schreiber and Chovan 1986, Schreiber 1999). On the other hand, wind has been reported to increase the cost of flight (Black-legged Kittiwakes and Dovekies, *Alle alle*; Gabrielsen et al. 1987, 1991b).

11.4.3.1 Swimming

Large numbers of species of seabirds swim on the surface of the water; fewer swim under the surface. Of those that do, penguins, alcids (auks and their relatives), sulids (gannets and boobies), and some shearwaters propel themselves under water with their wings, whereas tropicbirds, diving petrels, and cormorants use their feet, as do the seasonally marine grebes and loons. Some of the larger procellariiforms (albatrosses and shearwaters) use both modes. The fact that many albatrosses dive at all was not well known until recently (Prince et al. 1994). In this section, the terms *diving* and *subsurface* or *underwater swimming* are used synonymously.

The earliest examination of the energetics of surface swimming was on ducks (Prange and Schmidt-Nielsen 1970). Most of the information developed recently on the energetics of diving has been for the wing-propelled groups. Baudinette and Gill (1985) compared surface and underwater swimming in Blue Penguins and found a 40% reduction in the cost of a penguin swimming below the surface compared to one swimming at the surface. Several studies have shown that as speed increases, birds that have a choice switch from surface to underwater swimming which can be accomplished more cheaply at higher speeds (Baudinette and Gill 1985, Hui 1988a). The greater efficiency of penguins may be gauged in a comparison of the metabolic costs of wing-propelled Humboldt Penguins at $1.26 \times \text{RMR}$ (Butler and Woakes 1984) with wing-propelled Common Murres at $1.8 \times \text{RMR}$ and Thick-billed Murres at $2.4 \times \text{RMR}$ (Croll and McLaren 1993) and foot-propelled divers (Tufted Ducks at $3.5 \times \text{RMR}$; Woakes and Butler 1983). Schmid et al. (1995) reported a multiple nearly $12 \times \text{BMR}$ (daytime) and $2.6 \times \text{RMR}$ (in water) in the Great Cormorant (foot-propelled). Given the paucity of data in foot-propelled divers, this very high value cannot be easily evaluated.

Cormorant feathers are more wettable than other diving birds, so buoyancy is a relatively small problem for them (Schmid et al. 1995, Grémillet et al. 1998). That suggests that one reason given for the poorer performance of ducks and alcids (greater costs of overcoming buoyancy; Woakes and Butler 1983, Croll and McLaren 1993) may not be as important as previously thought (but see Ancel et al. 2000). However, thermoregulatory costs may add to the high expense of diving in cormorants (Schmid et al. 1995, Grémillet and Wilson 1999, Ancel et al. 2000; but see also [Section 11.3.3](#) above). Potential thermoregulatory costs may be countered by more fat insulation, but that may confer additional costs for flight (Butler 2000). A more fundamental difference may be that

wing-propelled diving is cheaper than foot-propelled diving, and that wings uncompromised by the demands of flight confer an additional advantage.

Total efficiency of swimming is the ratio of power input (the product of drag and speed) to metabolic power output. In surface swimming, the efficiencies of Mallards (*Anas platyrhynchos*; Prange and Schmidt-Nielsen 1970), Black Ducks (*A. superciliosa*; Baudinette and Gill 1985), Blue Penguins (Baudinette and Gill 1985), and Humboldt Penguins (Hui 1988a) are remarkably similar: 4 to 5%. However, maximal efficiency for Humboldt Penguins is achieved when swimming under water; it is 19.2% (Hui 1988a). Hui attributes the increased efficiency to the greater proportion of wing muscles to body mass in penguins compared to the proportion of leg muscles in ducks. Efficiencies can often be reflected in the cost of transport (COT), which is the metabolic expenditure needed to move a unit of mass a unit distance (usually oxygen consumption or SI units of energy times $\text{kg}^{-1} \text{m}^{-1}$). Typically, it is the minimal COT which is reported. Blue Penguins swimming underwater have lower costs of transport than surface-swimming birds (Baudinette and Gill 1985); their costs are comparable to those found for Humboldt Penguins (Hui 1988a) and Jackass Penguins (*Spheniscus demersus*; Nagy et al. 1984), 13.5 to 15.5 $\text{J kg}^{-1} \text{m}^{-1}$. More recent studies that use birds that dive voluntarily and do not carry external devices indicate that COT values may be much lower in diving penguins. Culik et al. (1994) report values of 7.1, 6.3, and 8.9 $\text{J kg}^{-1} \text{m}^{-1}$ for Adélie, Chinstrap (*Pygoscelis antarctica*), and Gentoo (*P. papua*) Penguins, respectively. Using a similar analysis, Luna-Jorquera and Culik (2000) found a comparably low cost of transport, 6.8 $\text{J kg}^{-1} \text{m}^{-1}$ in Humboldt Penguins. A still lower value of 4.7 $\text{J kg}^{-1} \text{m}^{-1}$ has been reported for King Penguins (Culik et al. 1996). This lower COT increases still further the difference between surface and underwater swimming. By contrast, minimal COT = 19 $\text{J kg}^{-1} \text{m}^{-1}$ in foot-propelled Great Cormorants (Schmid et al. 1995) and Brandt's Cormorants (*Compsahalius penicillatus*; Ancel et al. 2000).

The effect of using external devices on birds for which either swimming metabolism or dive performance is measured has been questioned. In a swim channel, Adélie Penguins (Culik and Wilson 1991b) and Great Cormorants (Schmid et al. 1995) carrying external packs had higher costs of transport largely due to increases in drag; the penguins even had higher RMR values than controls. Culik and Wilson (1991b) predicted that penguins and alcids so instrumented would show reduced speeds, smaller foraging ranges, and lower food acquisition. Ropert-Coudert et al. (2000), using free-ranging animals, confirmed this with King Penguins carrying external packs. Their proportion of consecutive deep dives was reduced compared to birds with internal instrumentation. Ropert-Coudert et al. join Culik and Wilson (1991b) in recommending internal instrumentation in studies of free-living diving birds. However, the implanting of such devices requires a level of surgical skill not necessary with external devices.

The multiples of BMR or RMR noted above are all low, with the possible exception of the Great Cormorant, compared to the maximum multiples we see in birds for aerial or cursorial locomotion. It is reasonable to infer that maximal metabolic rates were never achieved in these studies. In the case of the surface swimmers, the reason was first proposed by Prange and Schmidt-Nielsen (1970), later confirmed by Baudinette and Gill (1985): surface-swimming birds cannot exceed a particular "hull speed" dictated by forces of drag even if they have more metabolic capacity available. In the case of diving birds, it is likely that maximal speeds and thus power output were not achieved under experimental conditions. However, Kooyman and Ponganis (1994) attempted to achieve such a power output by attaching loads to swimming Emperor Penguins. Although they did not find a maximum metabolic rate, they felt that the $7.8 \times \text{RMR}$ was close to it. Because they were hesitant to accept RMR as true BMR (for reasons noted also above; Kooyman personal communication), they also provide a multiple of $9.1 \times$ the value predicted by Aschoff and Pohl (1970) for a 20.8-kg bird. Either multiple is smaller than found in running or flying birds, which Kooyman and Ponganis (1994) attribute to a higher anaerobic capacity of (Emperor) penguin muscles and the ability to conserve oxygen for longer periods while diving (see also Kooyman et al. 1992a). It is widely thought that diving birds, especially penguins, will attempt to remain within their aerobic dive limit (ADL), which is the dive duration that produces no increased lactate levels after a dive. Since ADL is rarely

measured, a calculated version (cADL) is often used. Analyzing these data for three penguin species, Butler (2000) concluded that the cost of normal dives may be very close to RMR values in the water. This surely is not true for cormorants (Ancel et al. 2000) and warrants additional testing.

The energetics of swimming in penguins is treated in several reviews (Oehme and Bannasch 1989, Croxall and Davis 1990, Kooyman and Ponganis 1990). Croxall and Davis (1990) also presented a valuable analysis and critique of methods used. One concern raised by Butler and Woakes (1984) was that attempts to quantify swimming costs using isotopes (doubly labeled or tritiated water; Kooyman et al. 1982) might confound the costs associated with locomotion and those reflecting thermoregulation. This is only a problem where water temperatures are considerably below the TNZ. An attempt to model the metabolic costs of (underwater) swimming in marine homeotherms, based on pinnipeds, but purportedly applicable to birds as well, is presented by Hind and Gurney (1997). Although it is ancillary to a discussion on metabolic costs, the mechanics of swimming in penguins (Hui 1988b, Oehme and Bannasch 1989) and in foot-propelled swimmers (Lavvorn 1991, Lavvorn et al. 1991) is available. A general review of the hydrodynamics and power requirements of all divers is provided by Kooyman (1989), and Butler and Jones (1997) reviews of the physiology of diving.

11.4.3.2 Walking

LeMaho and Dewasmes (1984) reviewed walking in penguins. In fact, all the work on seabird walking continues exclusively in this group. Although the cost of transport for walking has long been known to be higher than for other modes of locomotion (Baudinette and Gill 1985), the multiple of active metabolic rate to BMR in an extremely cursorial species (Rheas, *Rhea americana*; $35 \times$ BMR) may be the highest locomotion multiple reported in vertebrates (Bundle et al. 1998). To the extent that walking represents a major part of a species' time-activity budget, its energetics is of some importance. The Emperor Penguin has been documented to walk as far as 300 km to get to foraging areas (Ancel et al. 1992).

Pinshow et al. (1977) compared the metabolic rates and costs of transport of Emperor, Adélie, and White-flipped Penguins (*Eudyptula minor albosignata*) with those of other walking birds. They found penguin COT values to be quite high. But Wilson et al. (1999), observing that Magellanic Penguins (*Spheniscus magellanicus*) walked up the slope of a shore from the water's edge at a 39° angle, instead of the shorter 90° angle, concluded that COT in walking penguins may have been overestimated by as much as two times and that waddling walk might not be so expensive as suggested by Pinshow et al. (1977). Griffen and Kram (2000) concluded that the high cost of walking in Emperor Penguins is not due to waddling, which they found actually to conserve energy, but to their short legs which require them to generate muscular force more rapidly. Wilson et al. (1991) showed that tobogganing in Adélie Penguins was less expensive than walking under most conditions, but the savings were countered by feather wear, consequential reduced diving performance, and the added costs of feather maintenance.

11.5 DAILY ENERGY EXPENDITURE AND FIELD METABOLIC RATE IN SEABIRDS

Daily energy expenditure (DEE) is the energetic cost for an animal to live throughout a day during its normal routine. DEE may vary somewhat from day to day and more across seasons. It includes all those general maintenance functions necessary to stay alive and included in measurements of BMR; also included are the cost of thermoregulation and all other activities from feeding to locomotion to reproduction appropriate to the particular part of the annual cycle being studied.

11.5.1 TYPES OF DEE MEASUREMENTS

The development of a daily energy budget was long a goal of those working in the field of energetics. King (1974) explained several ways to estimate energy budgets: extrapolating

laboratory measurements of metabolism with or without time-activity budgets, often with activities reported as multiples of BMR; estimating energy consumption by changes in body mass or composition or by feeding activity; comparing activity to heart rate in telemetered birds; and use of doubly labeled water. He considered but rejected use of existence metabolism (see [Section 11.5.1.3](#)). Most of these methods have been used with seabirds since that time. Nagy (1989) evaluated some of those methods in a general way. Below, we briefly critique most of the methods commonly found in the seabird literature and then discuss in more detail one of the most direct measures, the field metabolic rate (FMR).

11.5.1.1 BMR Multiples and Mass Loss

Ellis (1984) analyzed the use of time-activity budgets with multiples of BMR in Lesser Sheathbills (*Chionis minor*; Burger 1981). In this study both BMR and individual activities were based on unmeasured estimates — a dangerous decision. Even when BMR and the cost of individual activities are based on actual measurements, there is enormous reliance on the accuracy of the time-activity budgets. For species that stay within sight and whose activities can thus be determined, this may be acceptable. This is rarely the case. Bernstein and Maxson (1985) estimated a DEE for Imperial Shags based on the metabolic measurements of Ricklefs and Matthew (1983), multiples of BMR found in the literature for numerous activities, and time-activity budgets. They reported a DEE/SMR ratio of less than two for both sexes in all phases of the breeding cycle; this is among the lowest ratios in the literature (see [Section 11.5.2.3](#)). Variations of this method have been proposed by Blake (1985) whose model included flight parameters for Black Skimmers (*Rynchops niger*) and by Carter and Morrison (1997) whose model for sandpipers was based in part on weather data.

The use of mass loss to estimate DEE, or some component of DEE, was pioneered in the Antarctic on fasting, usually incubating seabirds. It has been used in procellariiform birds (Prince et al. 1981, Croxall and Ricketts 1983, Grant and Whittow 1983, Mougín 1989) and Common Eiders (Gabrielsen et al. 1991a) to measure the costs of incubation; in penguins (Williams et al. 1977, Brown 1985, Adams and Brown 1990, Cherel et al. 1994) and petrels (Croxall 1982) to study the costs of molt. Several studies have noted that substrate use during fasting can vary across species and time (Croxall 1982, Gales et al. 1988, Groscolas 1990); the implication is that assumptions about substrate use in fasting birds can greatly affect the outcome of mass loss studies. This may be illustrated by studies on incubation costs in Wandering Albatrosses (Brown and Adams 1984) and Common Eiders (Gabrielsen et al. 1991a), as well as molt costs in Macaroni and Rockhopper Penguins (Brown 1985) where estimates from mass loss were lower than estimates from oxygen consumption in the first case and higher in the second. These studies cited possible errors in the proportion of fat oxidized during fasting as one possible reason for the discrepancy. The use of mass loss studies in long-term fasting birds may yield different results during different phases of the fast (see [Section 11.2.5](#) above). The use of the correct energy equivalents for fat and proteins is critical when making calculations of the energy cost for incubation and molt in seabirds.

11.5.1.2 Heart Rate

Heart rate (f_H) is known to increase with exercise in birds (cf. Bevan et al. 1994). So if heart rate can somehow be calibrated to metabolic rate, implantable data loggers (Woakes et al. 1995) could provide illuminating data about the cost of particular activities simply by monitoring heart rate. That is exactly the contention of recent studies on Black-browed Albatrosses (*Thalassarche melanophris*; Bevan et al. 1994) and Gentoo Penguins (Bevan et al. 1995b). In these studies, f_H was calibrated to oxygen consumption in treadmill and, in the latter case, swimming channel experiments. In both instances, heart rate was found to be an excellent predictor of metabolism, both in resting and active birds. The advantage of this method is that the cost of individual activities can be monitored in free-ranging birds and that DEE could be partitioned by activity. In addition, the

studies can be of longer duration than those using other methods, such as isotopic water. However, this method requires very careful calibration for each species, which may limit its usefulness. In addition, if heart rate is affected by the classic diving bradycardia, as Bevan et al. (1997) found in South Georgia Shags, it may not reflect actual oxygen consumption under certain circumstances. This needs to be tested, especially given the assertion of Kanwisher et al. (1981) that bradycardia is not found in nonstressed diving Double-crested Cormorants. In any event, while f_H allows estimation of metabolic rate during dive bouts (periods under water and at the surface), it cannot measure the cost of diving alone (Butler 2000). At the moment, this method is not yet widely accepted, but its potential, especially for annual energy budgets and when combined with other measures of DEE, is enormous.

11.5.1.3 Existence Metabolism and Metabolizable Energy

Existence metabolism (EM) is the metabolic rate of birds confined to small cages. It includes those costs that go into BMR, as well as the costs of thermoregulation, specific dynamic action, and a small amount of caged activity (Kendeigh 1970). It is typically estimated by measuring the amount of food ingested, the changes in body mass, and the eliminated products of digestion and metabolism. King (1974) discussed some of the problems of estimating the caloric equivalent of weight change; they are similar to the discussion in Sections 11.2.5 and 11.5.1.1 above. Estimations of EM often involve use of metabolizable energy (ME) coefficients that relate ingested food to energy budgets. An equation for the calculation of ME coefficients is provided by Davis et al. (1989). Problems with making certain assumptions about ME are addressed by Miller and Reinecke (1984). Related issues concerning methods using feces production or ecological assimilation are assessed by Nagy (1989).

Allometric predictions of EM exist for passerines and nonpasserines in summer (long photoperiod) and winter (short photoperiod) and at various temperatures (Kendeigh et al. 1977). In spite of the fact that the nonpasserine equations were not based on seabirds, they were often used to predict DEE in seabirds or to model population or community energetics in seabirds; Ellis (1984) reviewed some of the EM equations most often found in the seabird literature. One of the problems with EM, however, is that unlike BMR, it does not represent a limit, so is not easily replicable. Even if temperature were always held constant to control for thermoregulatory variation, the limited locomotion allowed is very difficult to regularize. Especially in seabirds, where swimming or flight may be the normal mode of locomotion, caged activity is often meaningless. We believe King (1974) was correct to avoid the use of EM in estimating DEE. It is an indirect estimate that presumes that all seabirds will follow a model based on very few ecologically equivalent or phylogenetically related species. In spite of its occasional appearance still in the literature (e.g., Gavrilov 1999), and given the direct measurements now available (doubly labeled water, oxygen consumption, perhaps heart rate), its use should be abandoned.

11.5.1.4 FMR and DEE

Field metabolic rate (FMR) has become the expression signifying DEE measurements based on doubly labeled water. First demonstrated by LeFebvre (1964) for pigeons, it has become the most common method for measuring DEE. The method utilizes the turnover of isotopes of hydrogen (either ^2H or more often ^3H) and oxygen (^{18}O) to determine CO_2 production. Its theory was described by Lifson and McClintock (1966) and has been assessed by Nagy (1980, 1989) and Nagy and Costa (1980).

11.5.2 FIELD METABOLIC RATE

Without question, the method most commonly used today in the acquisition of DEE is the field metabolic rate. Nagy and his collaborators have used FMR to partition a variety of components of

the DEE (e.g., swimming, brooding, foraging, Nagy et al. 1984; and flight, Flint and Nagy 1984) and even to extrapolate to food requirements (e.g., Nagy et al. 1984; see [Section 11.5.2.5](#) below). Its wide use, however, demands that its liabilities as well as its potential be understood.

11.5.2.1 Conditions and Errors in FMR Studies

Nagy (1980, 1989) addressed problems with errors in isotope concentration in the calculation of FMR, and Nagy and Costa (1980) first considered problems of water turnover. In seabirds, a high water content in food is likely to cause a high water turnover rate in the birds. Both of these require validation studies which are difficult to do in the field. However, there have been comparisons of different methods which, until proper validation studies are done, can be useful. For example, Bevan et al. (1994), in their study of Black-browed Albatrosses, used doubly labeled water, oxygen consumption, and heart rate, finding a strong correspondence in all three.

A very different kind of concern comes from looking at the conditions attendant upon the measurement of FMR. The use of doubly labeled water requires sufficient time for differences in the oxygen and hydrogen isotopes to develop but is limited by the inevitable dilution of those isotopes to immeasurable levels over time. In addition, since animal activity is often tied to a circadian rhythm, the exact length of time between samples needs to be a day or some multiple of days. In most seabird studies, the maximum multiple is likely to be two (this multiple can be increased by switching to a more expensive form of analysis which can detect very low levels of isotope; e.g., Pettit et al. 1988). Measurements that miss the 24- or 48-h interval by more than an hour require a back calculation, introducing a new level of uncertainty (K. Nagy, personal communication). In studies of free-ranging animals, these limitations have led investigators to try to maximize their chance of recovering an injected animal by using animals tied to nest sites. This has created an important bias in the DEE literature for seabirds: almost all the studies have been conducted during the breeding season (a notable exception is Gales and Green 1990). Measurements of FMR tell us much about the DEE during reproduction, but little about most other parts of the annual cycle.

Despite the large number of FMR studies on seabirds during the breeding season, not all of them are comparable. Studies done on incubating birds with long periods of unrelieved incubation (e.g., some penguins and procellariiforms, some tropicbirds) are not equivalent to those done on species that exchange incubation duties with their mates every few hours (e.g., Common Terns, *Sterna hirundo*; Ricklefs et al. 1986; [Figure 11.4](#)). Similarly, care must be taken in those species where the period spent at the nest changes during the course of incubation or brooding, or changes between incubation and brooding. Differences within a species may occur due to sex, especially during or just previous to egg-laying when the female costs are almost always elevated (Cary 1996; see [Chapter 12](#)).

Another criticism of the use of doubly labeled water, especially by the proponents of the use of heart rate, is that it often integrates many activities. However, as long as an animal's activities can be monitored, FMR can be partitioned (e.g., Nagy et al. 1984). If the actual manipulation of the animal, for example, by the injection of labeled water, affects its subsequent behavior, the value of the study is compromised. This is the contention of Wilson and Culik (1995) who reported that Gentoo Penguins given 5 mL injections in their pectoralis muscles changed their behavior considerably for the next two days, reducing their activity, especially at sea. However, their injection volume is larger than the 1 mL that would be expected with highly enriched water. In fact, this paper may be interpreted as a caution against using less-enriched isotopic water (which requires larger quantities). Alternatively, special methods might be employed such as using water isotonic with the tissue fluids or putting large amounts of water in noncritical muscles (Wilson and Culik 1995, K. Nagy, personal communication). Birt-Friesen et al. (1989) reported that injected Northern Gannets behaved differently than control birds after a 1-mL injection; but they argued that FMR was unaffected. Similarly, injected Arctic Terns (*Sterna paradisaea*; Uttley et al. 1994) reduced feeding of chicks and Black-legged Kittiwakes (Fyhn et al. 2001) showed a reduction in nest



FIGURE 11.4 Differences in incubation shift length pose problems in comparing FMR studies among species: (a) A Common Tern pair exchanges incubation duties several times a day, while (b) Red-tailed Tropicbirds incubate for 4 to 8 days in a row. (Photos by J. Burger, R. W. and E. A. Schreiber.)

attentiveness compared to controls, though in the latter case, differences disappeared after one day. Comparing the behavior of injected birds to control animals seems a wise precaution.

11.5.2.2 Allometry of FMR

The first allometric treatment of FMR in seabirds was provided by Nagy (1987). Looking at 15 species, he found

$$\text{FMR} = 8.02 \text{ m}^{0.704} \quad (11.10)$$

where FMR is in kJ d^{-1} and m is mass in g. Birt-Friesen et al. (1989) expanded this analysis by looking at 23 species of seabirds. They found

$$\text{FMR} = 12.02 \text{ m}^{0.667} \quad (11.11)$$

with units converted to those in Equation 11.10. They further analyzed these birds by water temperature and activity (see Section 11.5.2.4 below). Nagy et al. (1999) increased the sample size to 36 species of “marine” birds (including four species of shorebirds) and showed a similar relationship:

$$\text{FMR} = 14.25 \text{ m}^{0.659} \quad (11.12)$$

with units as in Equation 11.10. They also presented FMR equations for four seabird orders separately. We compare their equations to ours in Table 11.5. Nagy et al. (1999) report no significant differences based on order, which is in agreement with the findings of Birt-Friesen et al. (1989) and our analysis below. Nagy et al. (1999) also found no scaling effect separating marine and nonmarine birds, but they did find a significant difference in the intercept: marine birds’ FMR averaged 60% higher than that of nonmarine birds.

Our analysis, based on 45 studies on 37 species of seabirds (no shorebirds included), provides the following relationship:

$$\text{FMR} = 16.69 \text{ m}^{0.651} \quad (11.13)$$

with FMR in kJ d^{-1} and mass (m) in g (intercept s.e. = 1.2719; exponent s.e. = 0.0360; $R^2 = 0.910$). The exponent is nearly identical to that of Nagy et al. (1999), but the coefficient is 17% higher. It appears from the last four equations that with the progressive inclusion of more data, the higher the coefficient and therefore the higher the prediction for a seabird of a particular size. This may be because of an increasing proportion of species from very high latitudes. We address this in Section 11.5.2.4 below.

11.5.2.3 FMR/BMR Ratios

For reasons discussed above, most of the FMR data collected in birds has been during the breeding season, which is a time of high energy demand both for parents and offspring. Lack (1954) and Drent and Daan (1980) viewed reproduction as so energy demanding that adult birds had to work at near maximum capacity to produce young successfully; this is no different for seabirds (Ricklefs 1983). However, other authors have found the reproductive effort to be less demanding (e.g., Masman et al. 1989, Weathers and Sullivan 1989). This effort may be represented best as a multiple of BMR, that is, as the FMR/BMR ratio (cf. Drent and Daan 1980, Nagy 1987). Table 11.5 provides FMR/BMR ratios for all seabirds for which both measurements were available. Although the ratio for some species is not particularly high (≤ 3.0), several reach the predicted maximum of 4.0 (Drent and Daan 1980), and others exceed it.

Since Nagy’s (1987) analysis of FMR in a variety of taxa in which comparisons were made with BMR, there has been some tendency to look for parallels in the scaling of FMR and BMR. Koteja (1991) incorrectly attributed that tendency to some authors (see p. 58) but correctly criticized that imputed relationship and, in a reanalysis of BMR and FMR for several groups, concluded that there was no general case for FMR scaling with BMR, although specific cases varied. When we compare our scaling equations for BMR (Table 11.3) and FMR (Table 11.6), it is clear that some of the equations for seabirds, including the overall equation, scale differently. However, that is mainly because of the disparity in the allometric exponents for penguins and especially petrels, because there is some obvious correspondence among charadriiforms and especially pelecaniforms. FMR/BMR ratios shed no light on this question. Our calculations show great variation in all orders. Since both BMR and FMR equations are influenced by latitude, biases in data sets by latitude may affect the results of a comparison. Even a single species can show different FMR/BMR ratios as a function of latitude, as Castro et al. (1992) demonstrated for a shorebird, the Sanderling (*Calidris alba*). Whether the bias in FMR due to reproductive season also affects comparisons cannot yet be assessed.

TABLE 11.5
Body Mass and Field (FMR) and Basal Metabolic Rates (BMR) in Seabirds
by Breeding Region

Order/Species	Body Mass (g)	N	FMR (kJ d ⁻¹)	BMR (kJ d ⁻¹)	FMR/BMR	Latitude/Region (degree)	Source
Sphenisciformes							
Gentoo Penguin	6100	5	3925	1406	2.8	54 S	Davis et al. 1989
<i>Pygoscelis papua</i>							BMR from Brown 1984
Gentoo Penguin	6170	17	5263	1418	3.7	53 S	Gales et al. 1993
<i>P. papua</i>							BMR from Ellis 1984
Chinstrap Penguin	3806	22	4720	1045	4.5	63 S	Moreno and Sanz 1996
<i>P. antarctica</i>							BMR from Brown 1984
Adélie Penguin	3868	18	4002	1039	3.9	64 S	Nagy and Obst 1992
<i>P. adeliae</i>							BMR from Kooyman et al. 1976
Adélie Penguin	3940	24	3787	1233	3.1	64 S	Chappell et al. 1993
<i>P. adeliae</i>							BMR from Chappell and Souza 1988
King Penguin	12900	14	7518	2427	3.1	54 S	Kooyman et al. 1992a
<i>Aptenodytes patagonicus</i>							BMR from Ellis 1984
Macaroni Penguin	3870	6	4380	1188	3.7	54 S	Davis et al. 1989
<i>Eudyptes chrysolophus</i>							BMR from Brown 1984
Jackass Penguin	3170	10	1945	877	2.2	33 S	Nagy et al. 1984
<i>Spheniscus demersus</i>							BMR from Ellis 1984
Blue Penguin	1076	4	986	465	2.1	38 S	Costa et al. 1986
<i>Eudyptula minor</i>							BMR from Stahl and Nicol 1982
Blue Penguin	1050	4	2662	577	4.6	40 S	Gales and Green 1990
<i>E. minor</i>							BMR from B. Green unpublished
Procellariiformes							
Wandering Albatross	10465	17	4485	2260	2.0	46 S	Shaffer 2000
<i>Diomedea exulans</i>							BMR from Brown and Adams 1984
Wandering Albatross	8305	11	3288	1794	1.8	46 S	Adams et al. 1986
<i>D. exulans</i>							BMR from Brown and Adams 1984
Laysan Albatross	3066	8	1803	689	2.6	24 N	Pettit et al. 1988
<i>Phoebastria immutabilis</i>							BMR from Grant and Whittow 1983
Gray-headed Albatross	3890	6	2393	718	3.3	54 S	Costa and Prince 1987
<i>Thalassarche chrysostoma</i>							BMR from Adams and Brown 1984
Southern Giant Petrel	3885	8	4330	1110	3.9	64 S	Obst and Nagy 1992
<i>Macronectes giganteus</i>							BMR from Morgan et al. 1992
Northern Fulmar	728	14	1444	312	4.6	60 N	Furness and Bryant 1996
<i>Fulmarus glacialis</i>							BMR from Bryant and Furness 1995
Antarctic Petrel	618	2	1302	368	3.5	69 S	P. J. Hodum and W. W. Weathers unpublished
<i>Thalassoica antarctica</i>							
Cape Pigeon	440	26	1196	338	3.5	69 S	P. J. Hodum and W. W. Weathers unpublished
<i>Daption capense</i>							
Snow Petrel	245	11	793	174	4.6	69 S	P. J. Hodum and W. W. Weathers unpublished
<i>Pagodroma nivea</i>							

TABLE 11.5
Body Mass and Field (FMR) and Basal Metabolic Rates (BMR) in Seabirds
by Breeding Region

Order/Species	Body Mass (g)	N	FMR (kJ d ⁻¹)	BMR (kJ d ⁻¹)	FMR/BMR	Latitude/Region (degree)	Source
Antarctic Prion	149	8	391	97	4.0	54 S	Taylor et al. 1997
<i>Pachyptila desolata</i>							BMR from Ellis 1984
Wedge-tailed Shearwater	384	10	614	191	3.2	24 N	Ellis et al. 1983, Ellis 1984
<i>Puffinus pacificus</i>							BMR from Ellis 1984
Georgian Diving Petrel	109	10	464	112	4.1	54 S	Roby and Ricklefs 1986
<i>Pelecanoides georgicus</i>							
Common Diving Petrel	137	13	557	130	4.3	54 S	Roby and Ricklefs 1987
<i>P. urinatrix</i>							
Wilson's Storm Petrel	42	15	157	37	4.2	64 S	Obst et al. 1987
<i>Oceanites oceanicus</i>							
Leach's Storm Petrel	45	8	123	43	2.9	45 N	Ricklefs et al. 1986
<i>Oceanodroma leucorhoa</i>							
Leach's Storm Petrel	47	12	142	45	3.2	47 N	Montevicchi et al. 1992
<i>O. leucorhoa</i>							
Pelecaniformes							
White-tailed Tropicbird	370	10	777	186	4.2	18 N	Pennycuik et al. 1990
<i>Phaethon lepturus</i>							BMR from Ellis 1984
Cape Gannet	2580	10	3380	756	4.5	32 S	Adams et al. 1991
<i>Morus capensis</i>							BMR from Ellis 1989
Northern Gannet	3210	20	4865	1377	3.5	49 N	Birt-Friesen et al. 1989
<i>M. bassanus</i>							BMR from Bryant and Furness 1995
Red-footed Booby	1070	9	1246	401	3.1	16 N	Ballance 1995
<i>Sula sula</i>							BMR from Ellis 1984
Charadriiformes							
Black-legged Kittiwake	392	17	795	310	2.6	76 N	Gabrielsen et al. 1987
<i>Rissa tridactyla</i>							BMR from Gabrielsen et al. 1988
Black-legged Kittiwake	386	15	786	305	2.6	61 N	Golet et al. 2000
<i>R. tridactyla</i>							BMR from Gabrielsen et al. 1988
Common Tern	127	7	343	86	4.0	53 N	Klaassen et al. 1992
<i>Sterna hirundo</i>							BMR from Ellis 1984
Arctic Tern	101	8	335	70	4.8	55 N	Uttley et al. 1994
<i>S. paradisaea</i>							
Sooty Tern	186	14	241	87	2.8	24 N	Flint and Nagy 1984
<i>S. fuscata</i>							BMR from MacMillen et al. 1977
Brown Noddy	195	9	352	95	3.7	24 N	Ellis et al. 1983, Ellis 1984
<i>Anous stolidus</i>							BMR from Ellis et al. 1995
Dovekie	164	13	696	191	3.6	79 N	Gabrielsen et al. 1991b
<i>Alle alle</i>							
Common Murre	1025	11	2198	593	3.7	70 N	Gabrielsen 1996
<i>Uria aalge</i>							
Common Murre	940	4	1790	544	3.3	47 N	Cairns et al. 1990
<i>U. aalge</i>							BMR from Gabrielsen 1996

TABLE 11.5
Body Mass and Field (FMR) and Basal Metabolic Rates (BMR) in Seabirds
by Breeding Region

Order/Species	Body Mass (g)	N	FMR (kJ d ⁻¹)	BMR (kJ d ⁻¹)	FMR/BMR	Latitude/Region (degree)	Source
Thick-billed Murre <i>U. lomvia</i>	1078	12	1783	577	3.1	57 N	E. N. Flint and G. Hunt unpublished BMR from Gabrielsen et al. 1988
Thick-billed Murre <i>U. lomvia</i>	980	5	1860	552	3.4	67 N	Croll 1990 BMR from G. Gabrielsen unpublished
Black Guillemot <i>Cephus grylle</i>	380	10	860	291	3.0	79 N	Mehlum et al. 1993 BMR from Gabrielsen et al. 1988
Cassin's Auklet <i>Ptychoramphus aleuticus</i>	174	9	413	108	3.8	37 N	Hodum et al. 1998 BMR from Ellis 1984
Least Auklet <i>Aethia pusilla</i>	83	24	358	116	3.1	56 N	Roby and Ricklefs 1986
Atlantic Puffin <i>Fratercula arctica</i>	460	9	848	309	2.7	70 N	G. Gabrielsen unpublished BMR from Barrett et al. 1995

TABLE 11.6
Comparison of Allometric Equations for FMR by Order

Taxon	This Study	R ²	s.e. Intercept	s.e. Exponent	Nagy et al. 1999
All Seabirds	16.69 m ^{0.651} (N = 37)	0.910	1.210	0.028	14.25 mass ^{0.659} (N = 36) ^a
Charadriiformes	11.49 m ^{0.718} (N = 12)	0.814	1.716	0.095	8.13 mass ^{0.77} (N = 13) ^{a,b}
Pelecaniformes	3.90 m ^{0.871} (N = 4)	0.953	4.209	0.196	4.54 mass ^{0.844} (N = 4)
Procellariiformes	22.06 m ^{0.594} (N = 14)	0.921	1.350	0.047	18.4 mass ^{0.599} (N = 11) ^c
Sphenisciformes	21.33 m ^{0.626} (N=7)	0.681	3.908	0.162	4.53 mass ^{0.795} (N = 7)

Note: The general form of the equation is $FMR = a \text{ mass}^b$, with FMR in units of kJ d⁻¹ and mass (m) in g. N refers to number of species; in this study, the number of sources is typically larger and may be found in Table 11.5.

^a This equation includes four species of shorebirds; shorebirds are not included in our equations.

^b This equation has been corrected to: $8.49 \text{ mass}^{0.77}$ for N = 15 (K. Nagy, pers. comm.).

^c This equation has been corrected to: $17.9 \text{ mass}^{0.600}$ for N = 10 (K. Nagy, pers. comm.).

11.5.2.4 Correlates and Influences on FMR

Ellis (1984) showed a relationship between BMR and various activities. In general, he found that more active life styles were associated with higher values of BMR. Birt-Friesen et al. (1989) did a similar analysis for FMR values in seabirds. They found FMR to be higher in birds living in colder waters and having flapping flight. We also tested FMR as a function of latitude or region, ocean regime, season, activity mode, as well as body mass. Of all those parameters, only mode and latitude increased the ability of body mass to predict FMR. Of those two, latitude was most important, so the relationships can be expressed by the equation

$$\text{FMR} = 9.014 \text{ m}^{0.655} \cdot [\exp_{10}(\text{latitude})]^{0.0048} \quad (11.14)$$

with FMR in kJ d^{-1} and mass (m) in g (intercept s.e. = 1.233; body mass exponent s.e. = 0.023; latitude exponent s.e. = 0.001; $R^2 = 0.951$). This seems to validate the possibility that the equation describing FMR as a simple allometric equation (11.13) is affected by a sample with a geographic bias.

Another correlate of FMR is activity mode (e.g., flapping vs. gliding flight; plunge diving; etc.). When that parameter is included in our analysis, however, we failed to find a statistically significant relationship. Thus, we are unable to confirm statistically the assertion of Birt-Friesen et al. (1989) that mode of activity is related to FMR. Additional data may change that in the future and taxon-specific data might also show relationships not found in our analysis.

Other factors may play a role in the value of FMR. Growth of chick(s) and number of chicks have a great influence on FMR in Black-legged Kittiwakes: adults raising larger chicks and several chicks have a higher FMR than those raising smaller chicks and broods of one (Gabrielsen et al. 1987, Gabrielsen 1996, Fyhn et al. 2001). In most seabird studies, time away from the colony (and distance) is the most important factor associated with higher FMR (Gabrielsen et al. 1987, 1991b, Birt-Friesen et al. 1989, Gabrielsen 1996, Shaffer 2000). Wind also has an influence on FMR in seabirds. Gabrielsen et al. (1987, 1991b) reported that FMR increased with wind speed in Black-legged Kittiwakes and Dovekies, respectively. Furness and Bryant (1996) found an inverse relationship for Northern Fulmars. The difference is due to differences in the modes of flight: Kittiwakes and auks are flap flyers, while most petrels use substantial gliding. Wind is beneficial to the flight of the latter, but not necessarily the former. This influence on flight costs (also discussed in Section 11.4.3) affects FMR.

11.5.2.5 Partitioning FMR

FMR, in conjunction with time-activity budgets, leads to a partitioning of DEE into specific activities. Birt-Friesen et al. (1989) reported the cost of flying and pursuit diving in six seabirds to average $5.25 \times \text{BMR}$, but that included their own multiple for Northern Gannets ($11.3 \times \text{BMR}$). If the BMR value from Bryant and Furness (1995) is used instead, their multiple becomes $6.4 \times \text{BMR}$. Flight costs estimated this way in two other seabirds (where flight has a wind-assisted component) are Red-footed Boobies ($4.5 \times \text{BMR}$; Ballance 1995) and Northern Fulmars ($4.5 \times \text{BMR}$; Furness and Bryant 1996). Arnould et al. (1996) reported that flight was not a limiting activity for Wandering Albatrosses during foraging trips. Shaffer (2000) confirmed that, finding a very low FMR in Wandering Albatrosses due to a low cost of flight. The only factor which had an influence on FMR was number of landings. For most albatrosses the highest cost is probably associated with getting airborne, particularly in the absence of wind. Shaffer (2000) compared FMR in several albatross species. All of them had a cost of flight between 2 and $3 \times \text{BMR}$. Costs of swimming and diving, occasionally calculated as FMR partitions, are discussed in Section 11.4.3.1.

If greater activity can be correlated with higher values of DEE, can sleep be an energy-reducing mechanism? Stahel et al. (1984) addressed that question for Blue Penguins; they found it to represent a trivial savings (2.4% of DEE) in that species. A logical partition for an FMR study might seem to be the cost of molt. However, using FMR to estimate the cost of molt may be problematic, since molting birds sometimes compensate by reducing activity (Groscolas 1990, Murphy 1996).

One of the more common partitions presented for free-ranging seabirds has been the cost of being at sea. In some sense, this is the real cost of foraging: it includes costs associated with flying, swimming and diving, and thermoregulation; but it may also include the costs of social interactions and other undescribed activities. Because it is an integrated value, it is likely to be less than locomotion, but more than nest attendance. Birt-Friesen et al. (1989) found the cost of being at sea in 11 species of seabirds to be $3.78 \times \text{BMR}$. Furness and Bryant (1996) found that FMR at sea varied greatly among individuals, ranging from 1.40 to $7.85 \times \text{BMR}$; this probably reflected the

effects of variable winds, as discussed above. Montevecchi et al. (1992) found at-sea FMR to increase with time spent at sea. At sea FMRs, expressed in ratio with BMR, are often high compared to the overall FMR/BMR ratios reported in [Table 11.5](#), especially among penguins (Nagy et al. 1984, Davis et al. 1989, Kooyman et al. 1992b, Nagy and Obst 1992, Moreno and Sanz 1996), but also among gannets (Adams et al. 1991), ranging from about 4.5 to over $8.0 \times$ BMR. The data set is biased toward high-latitude species, however, and comparable work on low-latitude seabirds would be useful in developing generalizations.

Studies of locomotion, especially diving, have often been done on seabirds where extrapolations to foraging costs and even total food requirements were easily made (e.g., Culik and Wilson 1991a, Grémillet and Wilson 1999, Luna-Jorquera 2000). These extrapolations lend themselves easily to considerations of population, and ultimately community, energetics.

11.6 COMMUNITY ENERGETICS

The ability to estimate the DEE of seabirds has always held out the possibility of converting energy costs to food requirements. It has also promised the ability to extrapolate from individuals to populations and ultimately to communities. The literature on seabird population and community energetics is too broad to treat comprehensively here. Instead, using examples, we will indicate areas where there have been problems and areas which have proven especially fruitful. It should be noted that many DEE studies have extrapolated their energy costs to the numbers of fish, squid, krill, etc. required by an individual seabird or a population (e.g., Nagy et al. 1984, Fitzpatrick et al. 1988, Cairns et al. 1990, Adams et al. 1991, Gabrielsen et al. 1991b, Montevecchi et al. 1992, Nagy and Obst 1992, Mehlum et al. 1993, Moreno and Sanz 1996). Far fewer studies of seabird community energetics exist.

Extrapolations from individuals to populations and communities has always required very specific information: (1) the food eaten, (2) caloric value of the food, (3) an estimate of the efficiency of assimilation, (4) the size of the population(s), (5) the period of time of an event (e.g., the breeding season), and (6) the number of chicks, if any. But pivotal to such an extrapolation is an estimate of the energy demands of individuals. Many of the early studies (e.g., Wiens and Scott 1975, Furness 1978, Croxall and Prince 1982, Furness and Cooper 1982, Pettit et al. 1984) used allometric predictions of existence metabolism to estimate energy requirements at the individual level. The problems inherent in such an approach were discussed in Section 11.5.1.3 and would be extended to those populations and communities.

Although we are particularly critical of the use of EM in energetics studies, the use of any allometric model carries with it some uncertainty. One equation so used in the past was for BMR (discussed above in Section 11.5.1.1), although Schneider et al. (1986) used alternative equations to model community energetics involving seabirds of the Bering Sea. If the energy costs of different activities such as flight, gliding, swimming, and walking are known absolutely or as multiples of BMR, and the time spent in each activity is known, it is possible to calculate energy budgets for free-living seabirds (Croxall and Briggs 1991). However, the use of this method to determine the food harvest of a seabird community requires not only accurate measurements of the cost of different activities, but detailed time budgets for different periods in many seabird species. Good data on costs are especially lacking, except for a few species and groups. The same can be said about time budgets. While the activities of birds in the colony are easy to document, good studies of time-activity budgets of seabirds once they leave the colony (during or outside the breeding period) are few.

The advent and accessibility of doubly labeled water studies, providing FMR values for the birds actually studied, have ended much of the uncertainty associated with individual energy budgets in the construction of larger-scale studies. Furthermore, if diet, chemical composition, and assimilation efficiency (Brekke and Gabrielsen 1994) are known, it is also possible to calculate the food consumption using this method. This has become the basis of more recent studies on population and community energetics. However, other problems remain.

Most data on seabird FMR have been collected during the breeding season, with the majority of bioenergetic models being based on data obtained during incubation and chick rearing. With the exception of the study by Gales and Green (1990), virtually no FMR data have been collected outside the breeding season. That is, bioenergetics models which cover the whole year were based on extrapolations of breeding season data. Gales and Green (1990) found that although chick-rearing in Blue Penguins takes up only 16% of their annual cycle, it accounts for 31% of the annual energy budget. Only recently have models integrated data from breeding colonies with extensive data from birds at sea (e.g., Diamond et al. 1993, from the Canadian Arctic and a report, Anonymous 1994, from the North Sea). Although we have good energetics data from adult breeding birds, we have very little information concerning the energetics of chicks, juveniles, and nonbreeding birds. Most seabirds do not start to breed before they are 4 to 8 years old. In some extreme cases, as in many Procellariiformes and Pelecaniformes, breeding may not begin before 8 to 10 years. Surely, the activity budgets of breeding and nonbreeding birds must differ. Finally, most studies are from high latitudes, especially in the northern hemisphere (Wiens 1984, Furness and Barrett 1985, Croxall 1987, Duffy et al. 1987, Barrett et al. 1990, Furness 1990, Bailey et al. 1991, Diamond et al. 1993, Mehlum and Gabrielsen 1995), and may introduce geographic bias.

Based on the published literature from different parts of the world, the potential impact by seabird communities on fish stocks has been estimated to vary between 5 and 30% of the local annual fish production (Wiens and Scott 1975, Furness and Cooper 1982). Two Norwegian studies suggest that, under very special circumstances, seabird predation has the potential to negatively influence recruitment into some commercial fisheries (Barrett et al. 1990, Anker-Nilsen 1992). However, these estimates were crude and need to be validated. To quantify the impact of seabird populations or communities on fish stocks, it is necessary to estimate the proportion of fish consumed by a seabird population or community in a defined area. That brings us back to the relationship between energetics and demographic variables (e.g., population size and age structure). However, some of these variables will change daily and seasonally, so that an annual figure can be computed only by using values throughout the year. Once again, extrapolations from known periods to unknown periods are likely to add new sources of error of unknown magnitude.

The overexploitation of fisheries by humans may leave seabirds without adequate resources. That being the case, it is important to move from models to actual measurements in order to minimize extrapolations.

11.7 SPECULATIONS AND FUTURE RESEARCH DIRECTIONS

We return to Calder and King's (1974) challenge to their readers: is it better to add more species to such a mass of BMR data now or to ask new questions? Having spent many years in search of more data, we see now the possibility of asking intriguing and new questions. In particular, in what ways is BMR a product of natural selection? Is it a function of ecological considerations such as reproductive output, as McNab (1980a) and Hennemann (1983b) proposed, but perhaps in a more complex way? Is it a response to climate as originally suggested by Scholander et al. (1950b)? Is it phylogenetic baggage set in each order by the exigencies of an ancient and more selective regime and modified now only in minor ways? Are BMR and FMR linked as originally suggested by Nagy (1987) or is that truly a spurious relationship (Koteja 1991)? Is BMR linked to summit metabolism (a concept not really addressed in this review) or to any kind of upper end metabolic measurement?

Seabirds often live in extreme environments, where air and sea can put conflicting demands on their thermoregulatory abilities. We have indicated areas where some very interesting work has begun; future work should amplify this. We suggest that such work needs to be done in warm waters as well as cold and should look at temperature regulation during a variety of activities such as diving and flight as well as land-based activities.

The challenge of Calder and King (1974) is very much with us as we assess our knowledge of energetics based on FMR values. We have more data than we did 20 years ago on FMR in

seabirds, but those data now appear to be both narrow and diverse. Our FMR data are still almost entirely based on breeding birds; we lack a real database for the evaluation of DEE in seabirds measured outside the breeding period. At the same time, in the FMR data we do have, studies cover varying aspects of birds' lives (incubation, brooding, life at sea, life on land) and are not all comparable. Future studies should add to the database so that analyses of each of these facets of seabird life can be reviewed and compared. Studies which investigate the factors that affect FMR (growth, age, distance to foraging areas, cost of flight/diving) will be important to address in future research on energetics in seabirds. Additionally, future energetic studies should involve whole-year energy expenditure using on-board data storage of heart rate, body temperature, diving depths, and time in water whenever possible. This will surely require addressing the use and efficacy of external and internal devices. One of the challenges of the future will be to further partition DEE into particular activities. This work has already begun and is summarized above, but it is unclear if that will be the province of further FMR work or the domain of new methods such as heart rate.

The dilemma of Calder and King is not particularly Gordonian. It will be resolved by both data collection and the formulation of new questions, just as it has been for the last quarter of a century. We expect that the latter will lead the former, however, and that should provide some fascinating work for all of us.

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APPENDIX 11.1 TERMS USED IN THIS CHAPTER

- ADL Aerobic dive limit — the maximal dive duration without measurable postdive lactate levels.
- BMR Basal metabolic rate — the minimal metabolic rate measured under specified conditions, including being at rest, post-absorptive, and in the thermoneutral zone (TNZ).
- C Thermal conductance — the coefficient of heat transfer that describes the increase in metabolism that accompanies decreases in temperature in an endotherm; wherever possible values of C reported here are minimal.
- C_f Cost of feather production.
- COT Cost of transport — the metabolic expenditure needed to move a unit of mass a unit distance.
- DEE Daily energy expenditure — the daily energy budget.
- EM Existence metabolism — the energy it takes to stay alive, thermoregulating at a particular temperature, with minimal activity; as developed for birds, it does not include any of the BMR restrictions.
- FMR Field metabolic rate — the DEE typically measured in free-ranging animals using isotopically (usually doubly) labeled water.
- f_H Heart rate.
- HIF Heat increment of feeding (see [SDA](#)).
- LCT Lower critical temperature — the lower limit of the zone of thermoneutrality (TNZ).
- ME Metabolizable energy — ingested energy which is assimilated and used in the DEE.

- T_b Deep body temperature.
- RMR Resting metabolic rate — the rate of metabolism of an animal at rest; the postabsorptive condition is not always specified and it may not be in its TNZ or in air, hence it may be the same or different from BMR.
- RQ Respiratory quotient — the ratio of the volume of CO_2 produced to the volume of O_2 consumed in an animal.
- SDA Specific dynamic action — the cost of digestion; typically measured as an increase in the heat budget of an animal.
- SMR Standard metabolic rate (see [BMR](#)).
- T_b Body temperature.
- T_e Operative temperature — an environmental temperature that integrates air temperature, insolation, wind speed, etc.
- TNZ Thermoneutral zone — the environmental temperature range to which metabolic rate is insensitive; a condition of BMR.



Atlantic Puffin Entering Burrow with Sand Eels for Its Chick