ENERGY EXPENDITURE IN ARCTIC SEABIRDS

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To Jorid, Sigrid, Endre and Ingrid

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This thesis is based upon data from laboratory and field studies on Svalbard and in northern Norway. Most of the laboratory work on Svalbard was done at the research station of the Norwegian Polar Institute in Ny-Ålesund (79°N 12°E), while the field studies were done in Kongsfjorden (79°N 12°E), in Hornsund (77°N 15°E) and on Hopen Island (76 °N 25°E). Both the laboratory and field studies in northern Norway were carried out on Hornøya, an island in East Finnmark (70 °N 31°E). Most of the work on which this thesis is based was done while I was a research fellow on the Norwegian Research Programme for Marine Arctic Ecology (PRO MARE) at the Norwegian Polar Institute in Oslo from 1984 to 1990. The final synopsis were written at the Norwegian Institute for Nature Research, Tromsø, while working as a research fellow on the Programme on North Norwegian Coastal Ecology (MARE NOR) from 1990.

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Tromsø, January 1994 Geir Wing Gabrielsen

PREFACE

This dissertation comprises studies on thermoregulation and energy expenditure in Arctic seabirds. It is based on the following papers which are referred to in the text by their Roman numerals:

I. Gabrielsen, G.W., Mehlum, F., Karlsen, H.E., Andresen, Ø. & H. Parker. 1991. Energy cost during incubation and thermoregulation in female Common Eider **Somateria mollissima**. Norsk Polarinstitutt Skrifter 195:51-62.

II. Gabrielsen, G.W., Mehlum, F. & K.A. Nagy 1987. Daily energy expenditure and energy utilization of free ranging Black-legged Kittiwakes. Condor 89:126-132.

III. Gabrielsen, G.W., Mehlum, F. & H.E. Karlsen 1988. Thermoregulation in four species of arctic seabirds. J. Comp. Physiol. B. 157:703-708.

IV. Gabrielsen, G.W., Taylor, J.R.E., Konarzewski, M. & F. Mehlum 1991. Field and laboratory metabolism and thermoregulation in Dovekies (**Alle alle**). Auk 108:71-78.

V. Konarzewski, M., Taylor, J.R.E. & G.W. Gabrielsen 1993. Energy requirements of Dovekie (**Alle alle**) chicks and their contribution to energy expenditure of adults. Auk 110:343-353.

VI. Mehlum, F., Gabrielsen, G.W. & K.A. Nagy 1993. Energy expenditure by Black Guillemots (**Cepphus grylle**) during chick-rearing. Colonial Waterbirds 16:45-52.

VII. Gabrielsen, G.W. 1994. Energy expenditure of breeding Common Guillemots. Can. Wild. Ser. Occ. Papers. (in press)

INTRODUCTION

The population of seabirds breeding in Svalbard, around the Barents Sea and the northern part of the Norwegian Sea are among the largest in the world (Belopol'skii 1957; Zenkevitch 1963; Løvenskiold 1964; Anker-Nilssen and Barrett 1991). In the Arctic, these birds constitute a major component of the marine ecosystem and are an important link between the terrestrial and marine ecosystem through their deposition of nitrogen-rich guano and nutrients from the sea to the land (Norderhaug 1970; Gabrielsen and Mehlum 1989a).

While some seabird species, e.g. Common Eiders (Somateria mollissima), Black Guillemots (Cepphus grylle) and Little Auks (Alle alle) leave the northern Barents Sea area during the winter months, most species, e.g. the Fulmars (Fulmarus glacialis), Kittiwakes (Rissa tridactyla), Glaucous Gulls (Larus hyperboreus), Brünnich's Guillemots (Uria lomvi) and Common Guillemots (Uria aalge) remain in the area all year round (Løvenskiold 1964; Anker-Nilssen et al. 1988). After spending the winter further south, most migrants return in the early spring when the daylength and radiation increase, the sea-ice starts to break up and the mean air temperature is ca. -10 °C. Closely connected to these physical events is an intensive and short period of high primary production and a rapid transfer of this produced energy through the food web from plankton to marine mammals and seabirds (Belopol'skii 1957; Sakshaug et al. 1992). During the short Arctic summer, 2-3 months, most seabirds in the area produce one or two eggs/chicks, often during bad weather and when air temperatures are low.

Different species of seabirds in northern Norway and on Svalbard have different strategies for successful breeding. For example, the Common Eider lays a clutch of 4-6 eggs which is incubated for 24-26 days. The female abstains from feeding and loses 30-45 % of her body mass during incubation (Milne 1963; Korschgen 1977). Once the ducklings are dry, soon after hatching, the female descends to sea with her chicks to feed (Mendenhall 1979). Kittiwakes and Black Guillemots lay 1-3 eggs which are incubated by both parents for 27-31 days. The young are fed by both parents until they are fully grown at 5-6 weeks of age (Barrett and Runde 1980; Cairns 1987). Little Auks, Common and Brünnich's Guillemots lay one egg which is incubated by both sexes for 29-32 days. After hatching, the chick is fed by both parents. Whereas Little Auk chicks remain in the nest for 25-26 days and grow to 2/3 of adult mass before they fly to the sea, the chick of Common and Brünnich's Guillemots leave the ledge when they are 20-22 days old and have only reached 25-30% of the adult body mass (Stempniewicz 1980; Sealy 1973; Furness and Barrett 1985).

Most of the breeding season is a time of high energy demand both for the parent birds and their offspring. Lack (1954), Drent and Daan (1980) and Ricklefs (1983) viewed reproduction as being so energy-demanding that adult birds had to work at near maximum capacity to successfully produce young. Most birds breed when food is plentiful. By breeding during the short summer, Arctic seabirds are able to meet this increase in energy demand. While some direct measurements (using the doubly labeled water (DLW) method) of energy expenditure indicate that many parent birds work below their maximum physiological capacity (see Masman et al. 1989; Weathers and Sullivan 1989), several seabird studies clearly indicate that this group of birds indeed work at or even exceed this "maximum" level (4 times RMR or BMR)(Roby and Ricklefs 1986; Birt-Friesen et al. 1989; Cairns et al. 1990; Peterson et al. 1990; Obst and Nagy 1992). This high energy demand may constrain chick growth and be the main reason for the early fledging strategy in some seabird species.

Basal metabolic rate (BMR) or resting metabolic rate (RMR), the minimum rate of energy expenditure of homeotherms, is the most widely assessed parameter in avian and mammalian energetics. In both birds and mammals the BMR is primarily a function of the body mass (Kleiber 1961). The relation between metabolic heat production and body mass in birds has been discussed by Brody and Proctor (1932), King and Farner (1961), Lasiewski and Dawson (1967) and Aschoff and Pohl (1970). Kersten and Piersma (1987) and Daan et al. (1990) suggested that a high daily energy expenditure (DEE) during breeding should be reflected in a high BMR or RMR. They argued that the metabolic support tissues and organs (especially the heart and kidney mass) have evolved to sustain the power output needed during the period of maximal energy demand i.e. during the chick rearing period. The BMR or RMR should therefore reflect the metabolism of this "machinery" while the bird is resting.

Two earlier studies of seabirds breeding in the north (Scholander et al. 1950a,b,c; Johnson and West 1975) and more recent analysis of metabolic data from seabirds (Ellis 1984; Bennett and Harvey 1987) indicate that BMR or RMR in northern seabirds are over twice as high than could be expected from previous size-based allometric equations.

Thermoregulation

Adult birds and mammals are homeotherms. Birds maintain a high and relatively stable body temperature of about 40 ± 2 °C (Irving 1972), despite large fluctuations in the ambient temperature. For seabirds which live and breed in the Arctic, the temperature gradient between the body core and the surrounding environment can be as much as 50 °C during the the summer. In order to maintain a stable body temperature, these birds must have a good thermal insulation and/or a high rate of heat production in order to compensate for heat loss. Although birds generally lose heat, there are some examples of mammals and birds occasionally gaining heat from solar radiation (Hardy and Stoll 1954; Gabrielsen, unpubl.). However, this heat gain is insignificant and such micro-climatic influences will not be discussed in the present presentation.

The heat balance of any homeotherm with its environment is mathematically expressed by the body heat balance equation (IUPS Commision for Thermal Physiology 1987);

$$S = M \pm W \pm E \pm C \pm K \pm R$$

where S is heat stored in the body, M is the metabolic rate, W is mechanical work, E is evaporative heat transfer, C is convective heat transfer, K is conductive heat transfer, and R is radiant heat exchange. Since Arctic homeotherms are almost always warmer than their surroundings, any heat exchange is largely a result of heat loss through E, C, K and R. Since it is very difficult to measure and distinguish the various avenues of heat transfer within the body and between the body and its environment, the general term "thermal conductance" has been introduced. The thermal conductance is a combined heat transfer coefficient for the whole body. It is a measure of the ease with which heat flows from the body core to the surrounding environment. Thermal conductance (C) is expressed by the equation;

$$C = H/(T_B - T_A)$$

where H is heat production, T_B is deep body temperature and T_A is the ambient temperature (air or water). If the evaporative heat loss (E) is included, the thermal conductance is referred to as "wet" conductance (Aschoff 1981), whereas when E is excluded, it is referred to as "dry" conductance (Whittow 1986). The reciprocal of conductance (1/C) is the total thermal insulation of the animal. In my studies, the Scholander et al. (1950b) model (based on Newton's Law of Cooling) was applied to describe the thermoneutral zone (TNZ), the resting metabolic rate (RMR), the lower critical temperature (LCT) and thermal conductance of seabirds.

Most seabirds exploit marine food resources by either searching for food in the water surface layers or by diving.

Cold stress in the aquatic environment is much higher than in the terrestrial environment since the thermal conductivity and heat capacity of water are respectively 3000 and 25 times higher than that of air (Irving 1972). Seabirds are able to reduce the heat loss by a variety of thermoregulatory effector mechanisms, e.g. by lowering the peripheral temperature (of body extremities or surface) through peripheral vasoconstriction and/or by arterio-venous heat exchanges and the counter-current exchange (Irving and Krog 1955; Steen and Steen 1965; Johansen and Bech 1983; Midtgård 1985). However, thermoregulatory mechanisms when exposed to the aquatic environment have not been part of the present study. For further discussion on this theme see Kooyman et al. (1976), Stahel and Nicol (1982) and Jenssen et al. (1989).

Aim of the study

The aim of the present study was to explain how the different species of seabirds breeding in northern Norway and in Svalbard are adapted to live and breed in the Arctic environment. This was done by examining their resting metabolic rate (RMR), thermal conductance (TC) and field metabolic rate (FMR). The study includes different approaches and methods to determine energy expenditure in free ranging seabirds (both adults and chicks). Data on RMR and FMR in Arctic breeding seabirds will be discussed in relation to similar data from temperate and tropical areas. Energy expenditure data will be discussed in relation to parental investment and different breeding strategies of Arctic seabirds.

Some of the main questions answered in this thesis are: Do Arctic breeding seabirds have a higher RMR and/or better insulation than similar seabirds breeding in temperate and tropical areas? Is a high RMR coupled with a high FMR? If so, does a high FMR in adults constrain chick growth, and is this the main reason for the early fledging strategy in some seabird species?

METABOLIC AND INSULATIVE ADAPTATIONS

The basal metabolic rate (BMR) or resting metabolic rate (RMR) are important components of total energy expenditure, and hence the daily food requirements. Multiples of BMR or RMR have been used to estimate energy expenditure of single individuals (Utter and LeFebvre 1973; King 1974; Ricklefs 1974; Kendeigh et al. 1977; Walsberg 1983) and populations (Furness 1978 and 1990), as well as during activities such as walking, swimming or flying (Raveling and LeFebvre 1967; Prange and Schmidt-Nielsen 1970; Tucker 1972; Fedak et al. 1974). According to King (1974), BMR is a very precise measure since it provides a repeatable measure at the low end of the metabolic "spectrum". This is despite the fact that BMR varies with feeding (Weathers 1979), circadian (Ashoff and Pohl 1970) and seasonal cycles (Kendeigh et al. 1977).

Birds may reduce the conductance or increase the insulation behaviourally or physiologically. They may fluff out their feathers and thereby trap more air between them, they may withdraw their feet or head into the feather or they may allow the peripheral tissue to drop in temperature (Lustick 1984). In birds, feather adjustment is the most important method used to reduce the heat loss. According to measurements on Penguins and Common Eiders, the plumage is responsible for 80-90 % of the total insulation when exposed to air (Le Maho et al. 1976; Stahel and Nicol 1982; Jenssen et al. 1989). Birds resident in northern regions tend to have a heavier plumage than those that migrate every year (Irving 1960), and birds from higher latitudes have better insulation than birds from southern locations (Scholander et al. 1950a,c). Colouration is also important for thermoregulation since birds with darker plumage colours absorb more solar radiation than white birds (Stonehouse 1967; Lustick 1984). Insulation in birds varies both dielly, being low during the active phase (Aschoff 1981), and seasonally, being high during the winter (West 1972; Bech 1980; Mortensen and Blix 1986). All marine birds have subcutaneous fat (Lustick 1984) which may act as both an insulator and an energy source during periods of food shortage.

Resting metabolic rate

Many methods have been used to measure metabolism in birds and mammals. One result is the synonymous use of the terms basal metabolic rate (BMR), standard metabolic rate (SMR) and resting metabolic rate (RMR). Unfortunately it is often difficult to interpret and compare different studies since few report the conditions under which the measurements were made. True BMR is measured when the animal is resting, within the thermoneutral zone (TNZ) in the dark and in a post-absoptive state (Bligh and Johnson 1973). Our metabolic studies (Papers I, III, IV and VII) fulfilled all but one of these conditions. The exception was that they were done under full light conditions in order to simulate the Arctic summer. As a result we define our measurements as being of RMR as opposed to true BMR. Nevertheless, we believe that our measurements are comparable to BMR values in the literature. Being synonymous with BMR and to avoid confusion, I use the term RMR in this thesis.

Despite that the RMR is one of the most commonly measured physiological variables among birds, energy budgets have sometimes been constructed for birds whose RMR is unknown and thus had to be predicted. For such predictions, Lasiewski and Dawson (1967) presented allometric equations for RMR based on the body mass of 58 species of birds, including 5 seabird species. They divided birds into two groups, passerines and non-passerines, with the metabolic rate in non-passerines being lower ($RMR = 327.8\ m^{0.723}$, where RMR is in kJ/day and m is mass in kg) than in passerines ($RMR = 535.9\ m^{0.724}$). Aschoff and Pohl (1970) presented a similar equation where they also accounted for the influence of diurnal rhythm of activity level on RMR. The lowest RMR value was obtained during the resting phase ($RMR = 307.7\ m^{0.734}$) and the highest during the active phase ($RMR = 381.0\ m^{0.729}$). These equations were, however, based primarily on metabolic data from birds from temperate and tropical areas. Very little metabolic data then existed from the Arctic or Antarctic. Weathers (1979) proposed that bird RMR (including 3 seabird species) was a function of breeding latitude with species breeding at high latitudes having higher RMR than those in temperate and tropical areas. Later, Ellis (1984) presented data from 16 Charadriiformes (41 species, mainly Laridae) which supported this view. He found that the ratio of measured to predicted RMR increased from 0.8 in the tropics to 1.8 in Arctic breeding species. His modified equation for RMR = 381.8 $m^{0.721}$ was elevated but parallel to that of non-passerines as predicted by Lasiewski and Dawson (1967). Recently, Bennett and Harvey (1987) quantified deviations in metabolism from a regression fitted to data for 78 bird families (356 species). Their equation for RMR was as follows; RMR = 2.34 $m^{0.67}$ (where RMR is in kJ/day and m is in g). This equation included 10 of the 11 seabird families which also had a higher RMR than expected in relation to their size. Table 1 presents RMR values of 8 species of seabirds measured in Svalbard and on Hornøya. The lowest mean mass-specific RMR values were found in Glaucous Gulls and Eiders (0.88 and 0.86 ml O_2/g·h, respectivly) which are the heaviest birds (Table 1). The highest mean mass-specific RMR value was found in the Little Auks (2.42 ml O_2/g·h) which are the lightest (Table 1) (Paper I, III, IV and VII). These RMR values plus earlier RMR values of northern seabird species (see Table 3) (Scholander et al. 1950b,c; Iversen and Krog 1972a; Johnson and West 1975;

Table 1

Mean body mass (BM±SD), specific resting metabolic rate (RMR±SD), lower critical temperature (LCT) and body temperature (T_B±SD) in eight species of Arctic seabirds. N is number of birds.

Species	N	BM (gram)	RMR (ml O_2/g·h)	(kJ/day)	LCT (°C)	(T_B) (°C)	Source
Kittiwake	16	365± 30	1.64±0.08	289	+4.5	40.2±0.7	*
Glaucous Gull	9	1326±179	0.88±0.07	562	+2.0	39.6±0.5	***
Fulmar	16	651± 83	1.00±0.09	314	+9.0	38.7±0.5	*
Black Guillemot	13	342± 22	1.59±0.12	262	+7.0	39.9±0.3	*
Br. Guillemot	11	819± 73	1.11±0.12	438	+2.0	39.6±0.7	*
Common Guillemot	11	913± 53	1.20±0.03	580	+5.0[a]	39.7±0.5	*****
Little Auk	23	153± 12	2.42±0.13	178	+4.5	40.1±0.4	**
Common Eider	12	1661±251	0.86±0.07	649	+7.0	40.1±0.7	****

[a] LCT from Johnson and West (1975)

From:	
*	Paper III
**	Paper IV
***	Gabrielsen & Mehlum, unpubl.
****	Paper I
*****	Paper VII

Table 2

Resting metabolic rate (RMR) in eight species of Arctic seabirds as measured in this study compared to calculated values from the literature.

Species	BM (g)	RMR This study (kJ/day)	L&D (1967)	A&P (1970)	Ellis (1984)	Ellis Lat. corr.eq. (1984)	B&H (1987)	Gabrielsen et al. (1994)
		A	%A	%A	%A	%A	%A	%A
Kittiwake	365	289	183	158	157	86	236	135
Glaucous Gull	1326	562	140	120	120	66	193	100
Fulmar	651	314	131	113	112	62	174	113
Black Guillem.	342	262	174	150	149	82	223	128
Brünnich's Guillem.	819	438	154	133	132	73	208	112
Common Guillem.	913	580	189	163	162	97	256	136
Little Auk	153	178	211	184	181	103	260	159
Common Eider	1600	649	141	121	120	67	197	100

Data from this study are compared (as % of this study's RMR) to values predicted using to the equations given by Lasiewski and Dawson (L&D) (1967), Aschoff and Pohl (A&P) (active phase) (1970), Ellis (1984) (for seabirds and latitude corrected equation), Bennett and Harvey (B&H) (1987) and Gabrielsen et al. (1994). Sources and number of birds as in Tab. 1.

Table 3

Comparative resting metabolic rate (RMR) of seabirds measured at latitudes above 50°.

Species	BM[a]	N	Latitude	RMR[b]	%RMR[c]	Source
NORTH						
Kittiwake	405	10	57	271	158(136)	Gabrielsen et al. 1994
Kittiwake	420	17	70	304	174(149)	Gabrielsen, unpubl.
Kittiwake	340	2	79	269	179(154)	Brent et al. 1983
Kittiwake	418	6	79	336	193(165)	Krog & Tøien 1984
Kittiwake	365	16	79	289	183(157)	Paper III
Common Guillem.	836	8	57	517	180(154)	Croll & McLaren 1993
Common Guillem.	803	10	57	461	165(141)	Gabrielsen et al. 1994
Common Guillem.	956	5	65	588	185(159)	Johnson & West 1975
Common Guillem.	913	11	70	580	189(162)	Paper VII
Brünnich's Guillem.	803	6	57	595	213(183)	Croll & McLaren 1993
Brünnich's Guillem.	1094	11	57	619	177(152)	Gabrielsen et al. 1994
Brünnich's Guillem.	989	5	65	588	181(155)	Johnsen & West 1975
Brünnich's Guillem.	819	11	79	438	154(132)	Paper III
Brünnich's Guillem.	784	4	79	506	184(158)	Krog & Tøien 1984
Black Guillemot	342	13	79	262	174(149)	Paper III
Fork-tailed S.Petrel	49	16	54	54	146(126)	Iversen & Krog 1972a
Leach's S.Petrel	42	2	54	53	161(136)	Iversen & Krog 1972a
Least Auklet	83	5	56	115	213(183)	Roby & Ricklefs 1986
Little Auk	153	23	79	178	211(181)	Paper IV
Glaucous Gull	1210	2	71	754	201(172)	Scholander et al. 1950b
Glaucous Gull	1326	9	79	562	140(120)	Gabrielsen & Mehlum 1989a
SOUTH						
Common D.Petrel	132	4	54	126	166(142)	Roby & Ricklefs 1986
S.Georgia D.Petrel	119	5	54	122	174(149)	Roby & Ricklefs 1986
Wilson's S.Petrel	36	9	64	37	125(106)	Obst et al. 1987
Wilson's S.Petrel	34	6	64	35	125(106)	Morgan et al. 1992
South Polar Skua	1130	9	64	705	197(169)	Ricklefs & Matthew 1983
South Polar Skua	1250	6	64	708	184(158)	Morgan et al. 1992
Giant-Petrel	3980(M)	2	64	1548	174(150)	Ricklefs & Matthew 1983
Giant-Petrel	3280(F)	6	64	1439	186(160)	Ricklefs & Matthew 1983
Giant-Petrel	3929	6	64	1735	197(169)	Morgan et al. 1992
Kelp-Gull	980	4	64	610	189(162)	Morgan et al. 1992
Blue-eyed Shag	2660	6	64	1317	198(170)	Ricklefs & Matthew 1983

[a] mass in gram
[b] resting metabolic rate in kJ/d
[c] % of predicted RMR based on Lasiewski and Dawson (1967). Values in parantheses are based on Ellis (1984).

Brent et al. 1983; Krog and Tøien 1984; Roby and Ricklefs 1986; Gabrielsen and Mehlum 1989a; Croll and McLaren 1993; Gabrielsen et al. 1994; Paper I, III, IV and VII) confirm findings that seabirds breeding at high latitude have a higher RMR than seabird species of similar body mass measured at low latitudes. In the present study, Arctic breeding seabirds, exposed to ambient temperatures within their thermoneutral zone, maintained an RMR about 13-111% higher than birds in general (compared to Lasiewski and Dawson (1967) and Aschoff and Pohl (1970)) and 12-81% higher than seabirds in general (compared to Ellis 1984) (Table 2). On average, the mean RMR in this study was 65, 43 and 42% higher than Lasiewski and Dawson (1967), Aschoff and Pohl (1970) and Ellis (1984), respectively (Table 2). The RMR values of northern birds are similar to those of Antarctic seabird species (South Polar Skuas (Catharacta maccormicki), Blue-eyed Shags (Phalacrocorax atriceps), Kelp Gulls (Larus dominicanus), Giant Petrels (Macronectes giganteus), Common Diving Petrel (Pelecanoides urinatrix), South Georgia Diving Petrel (P.georgicus) and Wilson's Storm Petrel (Oceanites oceanicus)) which themselves are 25-98 % higher than predicted by Lasiewski and Dawson (1967) (Table 3) (Ricklefs and Matthew 1983; Roby and Ricklefs 1986; Obst et al. 1987; Morgan et al. 1992). High RMR is also found in other northern bird species such as ptarmigans (Lagopus lagopus, L. mutus and L. m. hyperboreus) and ravens (Corvus corax) (West 1972; Schwan and Williams 1978; Mortensen and Blix 1986). The results from the studies above indicate an influence of climate on RMR and is in accordance with earlier observations by Weathers (1979), Hails (1983) and Ellis (1984) that RMR in birds may be a function of breeding latitude.

One exception from the general view of a high RMR in northern seabirds is the result from Fulmars (Procellariiformes) (Table 1 and Table 2) (Paper III). They have a low mass-specific RMR (1.00 ml $O_2/g \cdot h$) which is close to the predicted value for other non-passerines (Ellis 1984; Bennett and Harvey 1987) and nearly identical to that predicted by Adams and Brown (1984) for 10 species of sub-Antarctic Procellariiformes.

The RMR values of all the seabird species studied here were higher than allometric equations predict. This indicates metabolic adaptations to the low air and seawater temperatures to which they are normally exposed (in Svalbard, 2-5°C in air and 0-5°C in water). The adaptive value of a high RMR in seabirds will be a reduced lower critical temperature (LCT). This will reduce energy expenditure (by skeletal muscles) otherwise needed to maintain a constant body temperature at low ambient temperatures. The LCT for Arctic seabirds ranged between 2.0 and 9.0°C (Table 1) (Paper I, III and IV). The species specific LCTs differ mainly due to differences in size and insulation. One should remember that these metabolic studies were carried out during the breeding period when most birds have a naked brood patch. This may have increased the RMR through a reduction in insulation and hence an increase in LCT. However, in Kittiwakes, Glaucous Gulls, Little Auks, Common and Brünnich's Guillemots the LCT (Table 1) is close to the ambient and seawater temperatures in the area. This suggests that these species are not cold stressed during the breeding period. Fulmars and Common Eiders have a LCT of 9.0 and 7.0°C, respectively (Table 1). However, this is compensated for by a low conductance value (good insulation) (Table 4) which results in a relatively low energy expenditure during thermoregulation at ambient temperatures below the LCT.

In temperate and tropical areas, a distinct day/night variance in light intensity is accompanied by a clear variation in RMR and body temperature. Aschoff and Pohl (1970) measured a 20-25% higher metabolism in birds during their active phase (day) than during their resting phase (night). Furthermore the RMR of two species of temperate seabirds measured during the summer decreased 10-15% at night (Gavrilov 1985). In contrast, diurnal phases in RMR and body temperature seem to be absent under continous light conditions of the Arctic summer. Our measurements of RMR, which were made under full light conditions to simulate the Arctic summer, as well as our measurements of body temperatures, using an implanted temperature transmitter (Paper I, III, Gabrielsen, unpubl.), indicate an absence of a nocturnal resting phase. However, since seabirds in the north are active during both the day and the "night", it is inappropriate to talk about the active/ resting phases described by Ashoff and Pohl (1970). The lack of a dark-induced resting phase may therefore be one reason for a high RMR in Arctic seabirds.

However, physiological factors other than those influenced by size, climate and diurnal phase may also contribute to a high RMR in Arctic seabirds. Roby and Ricklefs

(1986) and Gabrielsen et al. (1988)(Paper III) suggested that a bird's physical activity or their mode of life (i.e. diving or surface feeding, soaring/gliding flight as opposed to flapping flight) may influence the RMR. As a result, the skeletal muscles have increased in size and capacity in some of the more active seabird species. This, in turn, depends on a high level of "support" from the organs in the abdominal cavity since the muscles depend on them for fuel, degradation of waste material and repair of tissue. A high activity level is therefore expected to result in a high RMR. The eight species studied here vary greatly in activity levels. Little Auks, Black Guillemots, Common Eiders, Common and Brünnich's Guillemots are divers and Kittiwakes, Fulmars, Glaucous Gulls are surface feeders. While Fulmars and Glaucous Gulls are primarily gliders, Kittiwakes use flapping/gliding flight and Auks use flapping flight only. The latter is the most expensive mode. When using Masman and Klaassen's (1987) equation for calculating flight cost, Fulmars and Glaucous Gulls should have lower flight costs than Kittiwakes which in turn should have a lower flight cost than Auks. Bennett and Harvey's (1987) analysis of seabird RMR at taxonomic level found the highest RMR among the Auks. Since there is a strong positive correlation between RMR and activity (Ellis 1984; Birt-Friesen et al. 1989; Paper III) there is probably a close linkage between BMR and maximum power output. This means that a high RMR should correlate with a high FMR (for further discussion see energy cost of chick rearing, page 49-50).

Our RMR measurements of Common Eiders from Svalbard (Paper I) were 23% higher than RMR values reported in central Norway in winter acclimatized Eiders (in resting phase) (Jenssen et al. 1989) suggesting a seasonal difference in RMR. However, our RMR measurements of Kittiwakes (1.61 ml O_2/g·h), also measured in April on Svalbard (79 ^{0}N)(Gabrielsen, unpubl.), and Gavrilov's (1985) study of 16 species of non-passerine species, showed little or no seasonal variation in RMR. It is thus difficult to explain that Scholander et al's (1950b) spring (April) RMR in Glaucous Gulls in Alaska was 47% higher than our summer values (Paper III). In contrast to these RMR measurements, summer acclimatized Willow Ptamigan and Rock Ptarmigan are reported to have a higher metabolic rate (108-122 %) than winter birds (Mortensen and Blix 1986). The advantages of a a low RMR in winter birds would be the resulting low energy expenditure. This would be a reasonable adaptation to the cold and harsh conditions that these birds face during the winter.

Having corrected for latitude, using Ellis' (1984) "latitude-corrected" equation (percentage increment, % BMR = 2.02 lat. + 52.3 relative to the predictions made from the Lasiewski and Dawson (1967) equation), the RMR of seabirds breeding in northern Norway and in Svalbard are up to 40% below the measured values (Table 2)(Paper I, III, IV and VII). Bennett and Harvey (1987), using analysis of variance, found no significant difference in RMRs between families breeding at different latitudes. Despite the large number of families and species used in their analysis, our RMR values were on average 118% higher than theirs. Our RMR data, measured at different latitudes (Paper III; Gabrielsen et al. 1994) also indicate that there is no latitudinal trend in RMR in northern seabirds. A new equation showing the relationship between metabolic rate and body mass was thus presented based on new metabolic measurements of birds both from the Arctic, sub-Arctic and Antarctic areas (Gabrielsen et al. 1994). This equation is based on twice the the number of flying seabirds used by Ellis (1984) and Bennett and Harvey (1987). In the data set, a range of body masses represented at each latitude was included, but there was no correlation between latitude and body mass of birds measured. In 57 species studied (71 measurements, excluding Sphenisciformes), RMR was related to body mass by the equation; $RMR = 424.7\ m^{0.732}$ (RMR in kJ/d and m in kg). The slope of this regression is similar to that of Aschoff and Pohl's (1970) equation for non-passerines in the resting phase (0.734). Since Procellariiformes differ markedly from the general equation (Paper III; Bennett and Harvey 1987) a separate equation was calculated for this group of seabirds (27 measurements); $RMR = 377.9\ m^{0.705}$. The slope of 0.705 is close to the value (0.680) obtained for 10 species of sub-Antarctic procellariiformes by Adams and Brown (1984). When both the Procellariiformes and Sphenisciformes (penguins, which do not fly) are excluded, the equation becomes $RMR = 455.1\ m^{0.746}$ (44 measurements). This time the slope of 0.746 is very close to that calculated by King and Farner (1961) (0.744), Kleiber (1961) (0.75) and Scholander et al. (1950c) (0.75) for homeotherms. However, the equation still over-estimates the RMR in Arctic seabirds by 20% (Table 2). The difference is greater for small seabirds (less than 0.5 kg), while for Arctic seabirds weighing between 0.5 and 2.0 kg this equation gives a good approximation.

In mammals, a failure to standardize measurement criteria when comparing metabolic rates among groups of animals was the main reason why marine mammals were long thought to have elevated metabolism (see Lavigne et al. 1986). This possibility was also raised by Bennett and Harvey (1987) in their analysis of metabolic data from birds.

Direct and indirect calorimetry are the two main methods used to determine RMR in birds. The indirect method is based on determinations of the quantities of oxygen used, quantities of carbon dioxide produced, or the amounts of food utilized. Measurements of metabolic rate based on determinations of oxygen used, carbon dioxide produced, or a combination of the two have most frequently been employed (Gordon 1977).

Two methods have been used to measure oxygen consumption in animals. These are closed- and open-circuit respirometry. When comparing these two methods (Paper VI and VII), the RMR was lower using closed-circuit respirometry (on a body weight basis). Since a strict experimental protocol is presented and the calibration procedure was followed in our open-circuit measurements, but not in eg. Birt-Friesen et al's (1989) and Cairns et al's (1990) closed circuit experiments, it is difficult to explain the difference between the results using the two methods. However, it is possible that the ineffectiveness of the CO_2 absorbent might be a source of error in closed-circuit experiments (Paper VI and VII). Thus, a test of the validity of the measured RMR values by carrying out a controlled comparison of these two methods is needed.

Insulation

For animals living in the cold, Scholander et al. (1950a,c) described two main physiological and behavioral adjustments to maintain a stable body temperature. One was to reduce the heat loss by increasing the insulation, the other was to increase heat production by increasing the metabolism. While the Eiders and Glaucous Gulls, which have a low RMR and low thermal conductance (TC), seem to use the former mechanism, the latter seems to be used by Kittiwakes, Black Guillemots and Little Auks who have a high RMR and high TC value (Table 4) (Paper I, III, IV). As the air temperature decreased below the lower critical temperature (LCT), metabolic heat production increased in all seabird species in order to maintain homeo-thermy. The TC values of 7 seabird species are presented in Table 4 (Paper I, III and IV).

Table 4

Thermal conductance (TC) in seven species of Arctic seabirds during the breeding season compared to literature data.

Species	BM (g)	TC This study (ml O_2/g·h·°C) A	H&K (1967) %A	Asch. (1981) %A	Source
Kittiwake	365	0.0466	115	86	*
Glaucous Gull	1326	0.0248	122	85	***
Fulmar	651	0.0336	113	82	*
Black Guillem.	342	0.0475	113	85	*
Brünnich's Guillem.	819	0.0282	107	77	*
Little Auk	153	0.0630	98	76	**
Common Eider	1600	0.0240	131	90	****

Data from this study are compared (as % of this study's TC) to values predicted using the equations given by Herreid and Kessel (H&K) (1967) and Aschoff (Asch.) (1981). Sources as in Tab. 1.

The lowest TC values were found in Eiders and Glaucous Gulls, (0.0240 and 0.0248 ml $O_2/g\cdot h\cdot{}^0C$, respectively) which are the heaviest birds. The highest TC value was found in Little Auks (0.0630 ml $O_2/g\cdot h\cdot{}^0C$) which are the lighest (Paper I, II and IV). Two of seven seabird species studied, the Black Guillemot and Kittiwake have similar RMR values and body mass (Table 1). When comparing the two, one would expect the Black Guillemot, a diver, to be better insulated than the Kittiwake, a surface feeder. This is not the case, both having similar TC values (Table 4).

In most seabird species the TC were close to the allometric values calculated for birds of similar size (Table 4). Compared to Herreid and Kessel's (1967) equation for dead birds (dry conductance), we obtained values within 98-131% of their predictions and 76-90% of Aschoff's (1981) (active phase) predictions (Table 4). When compensating for respiratory heat loss, which Drent and Stonehouse (1971) estimated to be 12 % of total heat loss, our measurements were even closer to Herreid and Kessel's (1967) predictions than those of Aschoff (1981)(Table 4).

According to Bligh and Johnson (1973), thermal conductance should be expressed as $W/m^2 \cdot {}^0C$ (where W is watt), since heat is lost from the body surface area. It is therefore more appropriate to express the term thermal conductance as a function of body surface area than of body mass. Based on Meeh's (1879) equation $A = k \cdot m^{0.667}$ (where A is the body surface area, m is body mass in kg and k is a constant (for birds = 10) (Benedict (1934)), we calculated that, of the seven species studied, the lowest conductance or the best insulation was found in Common Eiders, while the Little Auks had the highest conductance or poorest insulation (Gabrielsen and Mehlum 1989a).

The TC value also varies with season in seabirds. The present TC values were obtained during the breeding season. For the 7 species in this study, the only winter TC value published is for the Eider. The TC value in winter acclimatized Eiders was 25% lower than that of summer acclimatized Eiders (Jenssen et al. 1989; Paper I). Seasonal variations in TC have also been found in other Arctic and sub-Arctic species (West 1972; Bech 1980; Rintamäki et al. 1983; Barre 1984; Mortensen and Blix 1986). In ptarmigans (Lagopus spp.), the thermal conductance in winter birds were 8-32% lower than in summer acclimatized birds (Mortensen and Blix 1986). A better insulation during the winter was mainly attained through an increase in subcutaneous fat and thicker plumage in winter birds (Mortensen and Blix 1986). A reduced summer insulation in Eiders is probably due to loss of down (used as insulating nest material) and the formation of a naked brood patch from which they may lose heat. Insulation in female Eiders may also be reduced because they lose body mass (mostly fat) during the incubation period (Korschgen 1977; Parker and Holm 1990; Paper III).

When comparing summer TC values of Arctic breeding seabirds (Paper I, III and IV) with more temperate seabird species, we found considerable interspecific variability. TC values of Brünnich's Guillemots measured at Svalbard (79 ^{0}N) were 54% lower than measurements of the same species measured further south (65 ^{o}N)(Johnson and West 1975; Paper III). The TC values of gulls, of similar body size, was lower in temperate areas indicating better insulation than Arctic gulls (Herreid and Kessel 1967; Drent and Stonehouse 1971; Lustick et al. 1978; Gavrilov 1985; Hüppop 1987; Paper III). The TC value in Little Auks was low compared to that of diving petrels (Common Diving Petrel and South Georgia Diving Petrel) of similar body size measured in sub-Antarctic areas (Roby and Ricklefs 1986; Paper IV). Arctic breeding raven (Schwan and Williams 1978) and ptarmigan (West 1972; Mortensen and Blix 1986) had lower TC values than seabirds, indicating that these permanent residents are better cold-adapted than seabirds.

Body temperature

Deep body temperature is dependent on metabolic rate and insulation (or its reciprocal conductance)(Irving 1972). Measurements of body temperature of Arctic bird species clearly show that they do not have higher body temperatures than bird species from the Antarctic, sub-Arctic, temperate and tropical areas (Scholander et al. 1950a,b; Irving and Krog 1954; Drent 1965; Irving 1972; Barrett 1978; Morgan et al. 1992). In the present investigation of 8 seabird species (Table 1)(Paper I, III, IV and VII) the mean body temperature was stable over the whole range of ambient temperatures (between -25 to +20 ^{o}C) at which they were exposed. Fulmars had significantly ($p<0.05$) lower body temperatures than the other species measured.

During summer expeditions to Svalbard in 1838 and 1840, Martins (1845) measured the body temperatures in 10 species of "webfooted" birds to 40.6 °C. We do not know the species included in this study but they probably included Common Eiders, Kittiwakes, Glaucous Gulls and alcids. His value is very close to that presented in later studies of Arctic and sub-Arctic seabirds (Irving 1972; Iversen and Krog 1972b; Paper I, III, IV and VII).

According to Gavrilov's (1985) studies of seabirds in temperate areas (also measured during the summer), changes in body temperature were correlated with changes in metabolic level, which were associated with changes in light intensity. Body temperature measurements of resting Common Gulls (<u>Larus canus</u>) and Black headed Gulls (<u>Larus ridibundus</u>) varied between 38.5-39.0 °C at night and 39.0-40.0 °C during the day (Gavrilov 1985). Measurements of body temperatures by means of an implanted temperature transmitter in Kittiwakes and Brünnich's Guillemots at the island of St. Paul (57 °N), Alaska, showed a clear diel pattern of body temperatures (Gabrielsen et al. 1994). Daytime body temperatures (40.8 and 41.3 °C) was significantly higher than at night (40.1 and 40.5 °C) in Kittiwakes and Brünnich's Guillemots, respectively. This indicates that the body temperature at rest is nearly the same at both St. Paul and at Svalbard during the summer. However, in contrast to Gavrilov's (1985) results, these changes in body temperature was not correlated with an increase or decrease in RMR (Gabrielsen et al. 1994). We have in our metabolic studies which took place in the Arctic (Paper I, III, IV and VII) been unable to find any diel differences in RMR and body temperature when comparing birds measured throughout the 24 hour period. This indicates a lack of any diel resting phase for RMR and body temperature in Arctic seabirds during the summer, which is clearly a response to the contineous daylight in the region.

Seasonal variations in body temperatures are recorded in many Arctic and sub-Arctic bird species (Irving 1972; Gavrilov 1985). The body temperatures in winter acclimatized Common Eider (Jenssen et al. 1989) was significantly ($p<0.05$) lower (1.0-1.5 °C) than the body temperature reported for summer birds (Paper I). Body temperature in Common and Brünnich's Guillemots measured in the present study (paper III)(39.6 and 39.7 °C, respectively) also seem to be higher than measurements (38.9 °C) of the same species at Fairbanks, Alaska (Johnson and West 1975). In the latter study, the authors do not give the exact date of temperature measurements. However, the ambient temperature was 0 °C so it is reasonable to believe that these are autumn/winter/spring adapted birds. Common Eiders, Common and Brünnich's Guillemots stay in northern Norway, in the Barents Sea and south of Svalbard, respectively, during the winter. For these species a low RMR and a low body temperature will be of advantage to economize body resources during the long winter nights.

The Fulmar (paper III) had a significantly ($p<0.05$) lower body temperature (38.7 °C) than the other species studied. This is in accordance with other studies showing that Procellariiformes have lower body temperatures than other non-passerines (McNab 1966; Adams and Brown 1984).

ENERGY COST OF REPRODUCTION

The process of reproduction results in a substantial increase in the energy demand of birds, particularly for the female. The production of an egg or a clutch of eggs creates both energy and nutrient demands that are superimposed upon the normal energy expenditure and activity costs. Prior to egg laying, female birds increase their food intake and body mass by 10-30 % (Parker and Holm 1990; Gabrielsen, unpubl.). This body mass increase is mainly due to the development of reproductive organs and the build up of fat reserves. Depending on the number of eggs laid and if parents share the incubation, most female seabirds lose 10-20 % of their body mass during the egg-laying period. Black Guillemots, Little Auks, Fulmars, Common and Brünnich's Guillemots lay their egg(s) directly on rocky shelves on the bird cliff, under stones or in crevices with little or no nest insulation. Kittiwakes and Glaucous Gulls insulate their nest with plant material, whereas female Common Eiders build well insulated nests lined with a thick layer of down. In contrast to single sex incubators which have to rewarm the eggs after feeding (Haftorn and Reinertsen 1985; Gabrielsen and Unander 1987), most seabirds can maintain a more or less stable egg temperature since one of the parents always incubates the egg(s). Seabirds incubate for prolonged bouts, during which they are inactive or fasting. In Kittiwakes and Brünnich's Guillemot, incubation does not involve a reduction in body mass (Gaston and Perin 1993; Gabrielsen, unpubl.). When relieved at the nest by the mate, the parent bird can easily spend enough time in the feeding area to regain its body mass. In these species, body mass loss (5-10%) occurs soon after hatching (Croll et al. 1991; Gaston and Perin 1993; Gabrielsen, unpubl.). In contrast to most seabirds, female Common Eiders incubate alone and abstain from feeding during almost all the incubation period. This results in a body mass loss of 30-45% between egg laying and hatching (Milne 1963; Korschgen 1977; Parker and Holm 1990; Paper I).

While incubating, the energy cost in seabirds is limited, and determined mainly by the amount of cold stress below the thermoneutral zone. However, once the chick(s) hatch, there is a sharp increase in energy demand of the parent birds (Ricklefs 1983). They must now maintain not only their own requirements, but also those of the chick(s). Apart from feeding the chick, this involves protecting them against predators, and warming them for the first 5-10 days after hatching. The energy invested by the parent seabird during the chick rearing period is thus partly determined by the number of chicks, the growth rate of the chick(s) and, in most species, the distance to the foraging area. However, cold stress, as also experienced during the incubation period, is still an important factor determining energy expenditure during chick rearing.

Estimates of the energy budget of birds have usually been based on time-activity observations combined with laboratory measurements of activity cost (Gessaman, 1973; King, 1974; Kendeigh et al., 1977; Mugaas and King, 1981; Walsberg 1983; Gabrielsen and Mehlum, 1989b). Since seabirds often travel long distances to forage it is difficult to make direct observations of free-ranging individuals. The use of telemetry systems (Kooyman et al., 1982; Hill et al., 1983; Prince and Francis, 1984; Mohus 1987; Gabrielsen and Mehlum 1989b) and the DLW method (Weathers and Nagy, 1980; Williams and Nagy, 1984; Nagy et al., 1984; Bryant et al., 1985; Paper II, IV, V, VI and VII) have helped the collection of energy expenditure data for free ranging birds.

Energy cost of incubation

Hypotheses related to the cost of incubation were first presented by Kendeigh (1963) and King (1973). Kendeigh's model assumed that heat lost from the egg must be balanced by extra heat produced by the parent bird. King argues that the bird's metabolic rate at rest, and the heat produced as a by-product of the embryo's metabolism could substitute at least part of the heat needed to maintain the egg temperature. Several studies have since been made to test these hypotheses. Indirect methods of estimating the cost of avian incubation include measurements of heat loss from eggs (Kendeigh 1963, Walsberg and King 1978), the clutch mass method (West 1960; Ricklefs 1974) and heat budget modelling (Walsberg and King 1978). Direct measurements of incubation cost have included measurements of food intake (Riddle and Brancher 1934; El-Wailly 1966; Brisbin 1964), oxygen consumption or carbon dioxide production (Norton 1973; Mertens 1977, 1980; Biebach 1979; Gessaman and Findell 1979; Vleck 1981; Grant and Whittow 1983; Haftorn and Reinertsen 1985; Tøien et al. 1986; Gabrielsen and Unander 1987), measurements of loss of body mass (Prince et al. 1981; Croxall 1982; Croxall and Ricketts 1983; Grant and Whittow 1983) and the doubly labeled water (DLW) method (Pettit et al. 1988; Gales and Green 1990). While most of these studies have been carried out in the laboratory a few were also based on free-living birds on the nest site. Furthermore, there are a few studies which compare incubating birds with non-incubating birds.

Most studies, usually on single sex incubators weighing less than 0.5 kg, indicated that the energy cost of incubation is equivalent to 1.1-1.3 times RMR (Mertens 1977; Biebach 1979, 1981; Vleck 1981; Haftorn and Reinertsen 1985; Gabrielsen and Unander 1987). However, studies on larger birds that fast during incubation or incubate within their thermoneutral zone, have shown that the metabolic rate is maintained at or below the RMR level of non-incubating individuals (Table 5) (Grant and Whittow 1983; Brown 1984; Grant 1984; Brown and Adams 1984; Pettit et al. 1988; Paper I). In contrast to these studies which used the doubly labeled water method or were based on oxygen consumption, the energy costs of incubation derived from mass loss were estimated at 1.1-2.3 times RMR for petrels and albatrosses (Croxall 1982; Croxall and Ricketts 1983) and 1.1-1.7 times RMR for penguins (Croxall 1982). There are however, very few studies of the energy cost of incubation in Arctic seabirds (see Table 5)(Gaston 1985; Gabrielsen and Mehlum 1989b; Paper I). In incubating Kittiwakes, using an activity recorder combined with measurements of the energy cost of different activities, the energy cost of incubation was calculated to 2.2 times RMR (Gabrielsen and Mehlum 1989b). Using the DLW method, the energy cost of incubation of the same species was estimated to 1.7 times RMR (Table 5) (Gabrielsen and Mehlum, unpubl.). The IMR of incubating Black Guillemots and Brünnich's Guillemots in the high Arctic, also measured using the DLW method, was calculated to 2.1 and 3.0 times their RMR, respectively (Table 5)(Gaston 1985).

Table 5

Measurements of incubation cost (IMR) in seabirds using the doubly labeled water (DLW) method or oxygen consumption method. IMR is compared to resting metabolic rate (RMR) values from the same species.

Species	IMR (kJ/d)	RMR (kJ/d)	IMR/RMR ratio	Method	Source
Macaroni Penguin	1032	1161	0.9	Oxygen Cons.	Brown 1984
Rockhopper Penguin	701	863	0.8	Oxygen Cons.	Brown 1984
Little Penguin	661	426[a]	1.6	DLW	Gales & Green 1990
Wandering Albatross	2415	1755[b]	1.4	Oxygen Cons.	Brown & Adams 1984
Laysan Albatross	618	645	1.0	Oxygen Cons.	Grant & Whittow 1983
Laysan Albatross	689	680[c]	1.0	DLW	Pettit et al. 1988
Bonin Petrel	90	109	0.8	Oxygen Cons.	Grant & Whittow 1983
Leach's Storm Petrel	124	46	2.7	DLW	Montevecchi et al. 1991
Leach's Storm Petrel	103	49	2.1	DLW	Ricklefs et al. 1986
Sooty Tern	140	87[d]	1.6	DLW	Flint & Nagy 1984
Black Guillemot	642[e]	307[f]	2.1	DLW	Gaston 1985
Brünnich Guillemot	1597[e]	535[f]	3.0	DLW	Gaston 1985
Kittiwake	522	316[f]	1.7	DLW	Gabrielsen,unpubl.
Eider	560	601	0.9	Oxygen Cons.	Paper III
Eider	625	601	1.0	DLW	Gabrielsen & Erikstad, unpubl.

[a] RMR from Stahel and Nicol (1982)

[b] Different methods - mask for IMR, box for RMR

[c] RMR from Grant & Whittow (1983)

[d] RMR from MacMillen et al. (1977)

[e] Average IMR

[f] RMR from Gabrielsen et al. (1988)

High IMR values (2.1 and 2.7 times RMR) were also found in incubating Leach's Storm Petrels (Oceanodroma leucorhoa) studied in temperate areas (Table 5) (Ricklefs et al. 1986; Montevecchi et al. 1991). Compared with the RMR values, the IMR values measured in Black Guillemots, Brünnich's Guillemots, Kittiwakes and Leach's Storm Petrels are 1-2 times higher than the IMR value of incubating Common Eiders (measured using the oxygen consumption and the DLW methods) (Table 5) (Paper I; Gabrielsen and Erikstad, unpubl.). The cost of incubation in most seabirds is thus high. Most seabird species in the Arctic have little or no nest insulation. The mean ambient temperature in my study area (mean = +2°C in June at Svalbard) is below their LCT, indicating that they must produce extra heat in order to maintain their own body temperature as well as the optimal egg temperature. This implies an increased energy cost in Arctic breeding seabirds compared to similar species breeding in temperate and tropical areas. However, eggs of the female Eiders are well protected from cold stress in a well insulated nest. The down in the nest reduces the heat loss from both the eggs and the brood patch. The combination of a well insulated nest, a low thermal conductance, a low activity and a high nest attentiveness has enabled the female Common Eiders to reduce the energy cost of incubation to a level close to the RMR level of non-incubating individuals.

When comparing the estimates of energy expenditure based on oxygen uptake or the DLW method with estimates based on mass loss of incubating females (Paper I; Gabrielsen, unpubl.)

large discrepancies appear. In Eiders, the IMR value obtained by mass loss (Korschgen 1977; Parker and Holm 1990; Paper I) as 20-35 % lower than values using oxygen uptake or the DLW method (Paper I; Gabrielsen, unpubl.). Similar IMR comparisons made in other species (penguins, petrels and albatrosses) showed both under- and overestimates using the mass loss method (Grant 1984; Groscales 1988). In the case of the female Common Eiders, the fact that they drink and possibly eat (as recently documented for birds in Holland by Swennen et al. (1993)) towards the end of incubation (Paper I), and that the body water content increased from 51% at egg laying to 63% at hatching (based on body composition analysis)(Parker and Holm 1990) are the main cause of the underestimate, using the mass loss method (Paper I). Similar conclusions were drawn by Groscales (1988) for penguins. According to him, energy expenditure should only be determined in the middle of the starvation period in order to avoid the final period of protein catabolism.

During periods of long-term fasting, mammals and birds go through three different periods; a rapid adaptation period, a long period of economy, and finally a critical period (Kleiber 1961; Le Maho 1983). Common Eider seem to go through the first two periods (Paper I). In geese and penguins, the adaptation period is characterized by a rapid reduction (30-50%) in RMR (Benedict and Lee 1937; Le Maho et al. 1981; Le Maho 1983). However, in the female Common Eider, the IMR level does not drop below the RMR level of non-incubating individuals (Paper I). What is the physiological cause of this apparent discrepancy?

The rates of oxygen consumption and metabolism are influenced by the thyroid hormones (Falconer 1971; Etkin 1978). In some birds (eg. chicken and penguins) the T_3 (triiodothyronine) level normally drops during starvation (May 1978; Cherel et al. 1988). However, in incubating female Common Eiders, there was a stable or even slight increase in the T_3 level indicating that they do not reduce their metabolism (Paper I). Whereas body temperature in starved geese decreased from 40.1 to 39.3 °C (Le Maho et al. 1981), that of the incubating female Common Eiders were stable at 40.1 °C.

IMR data from female Common Eiders (Paper I), and from penguins, albatrosses and petrels (Table 5) support King's (1973) contention that the metabolic rate of a bird at rest can supply all the heat required for incubation. However, IMR data from other seabirds (Table 5) (e.g gulls and auks) support Kendeigh's (1963) hypothesis that extra heat is required to maintain the egg temperature.

Energy cost of chick rearing

According to Ricklefs (1983), parental energy demand is at the maximum during the chick rearing period. There are very few energetic studies of seabirds in which the field metabolic rate (FMR) has been measured during the pre-breeding, incubation and the chick rearing periods in the same species. For example the annual energy demand was determined in Little

Penguins (Eudyptula minor) using the DLW method (Gales and Green 1990). In this species the highest FMR was measured towards the end of the period of chick growth. DLW studies of Leach's Storm Petrels and Wilson's Storm Petrels (Oceanites oceanicus) during the incubation and chick rearing period also revealed a 15% higher energy expenditure during the chick rearing period than during incubation (Ricklefs et al. 1986; Obst et al. 1987; Montevecchi et al. 1991). In Kittiwakes the highest FMR value was obtained during the chick rearing period, being 30% and 15% higher than the pre-breeding and incubation period, respectively (Paper II, Gabrielsen and Mehlum, unpubl.).

During the chick rearing period, the parent bird attending the nest has to brood and protect the chick(s). While at sea, they have to cover their own requirements as well as the energy requirements of their chick(s). The FMR value obtained by the DLW method are thus the sum of the RMR, the cost of thermoregulation, the specific dynamic action (SDA) and the energy cost of different activities (i.e. flying, diving and walking). In contrast to the incubation period, the cost of foraging is a large component of the total FMR during chick rearing.

The FMR values in four species of seabirds obtained during the chick rearing period are presented in Table 6 (Paper II, IV, VI and VII). Kittiwakes had the lowest mean mass-specific FMR (3.24 ml $CO_2/g \cdot h$) and Little Auks the highest (6.68 ml $CO_2/g \cdot h$). This demonstrates that active, small-bodied seabirds require more energy per unit time above resting level

Table 6

Mean body masses (BM±SD), resting metabolic rates (RMR±SD), field metabolic rate (FMR) and FMR/RMR relationships in four species of seabirds during chick rearing. N is number of birds.

Species	N	BM (g)	RMR (kJ/day)	FMR (ml CO_2/g·h)	FMR (kJ/day)	FMR/RMR	Source
Kittiwake	13	383±25	303	3.24±0.92	798	2.6	*
Black Guillem.	11	380±20	291	3.63±0.76	860	3.0	**
Common Guillem.	11	1025±53	593	3.34±0.86	2198	3.8	****
Little Auk	14	164± 9	191	6.68±1.06	696	3.6	***

From:
* Paper II
** Paper VI
*** Paper IV
**** Paper VII

than do active large-bodied seabirds. The mean mass-specific FMR value in Kittiwakes was close to the value obtained in Black Guillemots (Table 6). These two species have nearly the same body mass, have similar RMR and TC values (Table 1 and Table 4) and raise the same number of chicks. The major difference is that Kittiwakes are distance foragers while Black Guillemots are nearshore feeders (Furness and Monaghan 1987; Cairns 1987). The total cost of flying when foraging is probably higher in Kittiwakes (surface foragers using flapping/gliding flight) than in Black Guillemots (a diver using only flapping flight), despite that number of feeds per young per day are similar (Barrett 1978; Cairns 1987) and that the wing loading in Black Guillemots (0.82 g/cm^2, Table 9) is 110 % higher than in Kittiwakes (0.39 g/cm^2, Table 9). While Kittiwakes expend most energy during flight, Black Guillemots probably expend even more when diving.

The mean mass-specific FMR value (3.34 ml CO_2/g·h, Table 6) obtained in Common Guillemots at Hornøya (Paper VII) was close to the FMR value (3.18 ml CO_2/g·h) obtained in Common Guillemots in the eastern Canadian Arctic (Cairns et al. 1990). The mean mass-specific FMR values in Common Guillemots at these two locations are however 10-30 % higher than the FMR values (2.89 and 2.37 ml CO_2/g·h) obtained in Brünnich's Guillemots measured in the Pribilofs and western Canadian Arctic, respectively (Flint and Hunt, unpubl.; Croll, unpubl.). A lower FMR value is found in Brünnich's Guillemots despite that they breed further north and in colder environments than Common Guillemots. A lower wing loading (1.48 g/cm^2, Table 9), a higher body fat content (20-30 %, Gaston and Perin 1993) and better insulation (TC = 0.0282 ml O_2/g·h, Table 4) in Brünnich's Guillemots compared to Common Guillemots (1.86 g/cm^2 (Table 9), 5-10 % body fat content (Gabrielsen, unpubl.) and TC = 0.0434 ml O_2/g·h (Johnson and West 1975), respectively) may be the main reason for the FMR difference between these two alcids.

In models estimating food consumption of single individuals or populations of seabirds, we often find daily energy budgets based on different allometric equations (Wiens and Scott 1975; Furness 1978 and 1990; Grant 1981; Furness and Cooper 1982; Croxall and Prince 1982; Wiens 1984; Furness and Barrett 1985). Kendeigh et al. (1977) and Walsberg's (1983) equations have been used most often. Kendeigh et al.'s (1977) equation for existence metabolism (EM) in birds (including 8 species of seabirds) integrates RMR, temperature regulation, specific dynamic action (SDA) and different activities of birds held captive in a cage in the laboratory. Their equation enables calculation of EM for individuals of different body mass under a variety of ambient conditions. At an ambient temperature of 0 °C, the following equation is given; $EM = 33.73\ m^{0.50}$ (EM in kJ/d and m in gram). For birds at the nest site, the EM equation may be a useful measure since activity at the nest is probably close to that when caged. This was illustrated in the DLW study of Kittiwakes (Paper II) where the measured FMR of brooding birds was 596 kJ/d (1.9 x RMR). This is only 10% less than the calculated EM (652 kJ/d) using Kendeigh et al.'s (1977) equation. However, while foraging, the FMR in Kittiwakes was 992 kJ/d (3.2 x RMR)(Paper II), which is 52% higher than the calculated EM from Kendeigh et al. (1977). Kendeigh et al.'s (1977) equation does not include thermoreguatory costs other than that caused by the ambient temperature. Nor does it include the cost of other activities such as flying, diving or walking, which, in seabirds, have been estimated to be 5-12, 2-12 and 3-5 x RMR, respectively (see Ellis 1984). When applied to the present FMR data from 4 species the Kendeigh et al. (1977) EM equation underestimates the FMR results by 19-104% (Table 7).

Walsberg (1983) presented a new equation for daily energy expenditure (DEE) in free ranging birds. This equation; $DEE = 13.05\ m^{0.605}$ (DEE in kJ/d and m in gram) was based on energetic studies of 42 bird species, but including only one seabird species, the Emperor penguin (Aptenodytes fosteri). When applied on the present FMR data, this equation underestimated

Table 7

Field metabolic rate (FMR) in four species of arctic seabirds during the chick rearing period compared to literature data.

Species	BM (g)	FMR This Study (kJ/day)	Kendeigh et al. (1977)	Walsberg (1983)	Nagy (1987)	B&H (1987)	Birt-Friesen et al. (1989)
		A	%A	%A	%A	%A	%A
Kittiwake	392	795	119	164	148	138	90
Black Guillem.	380	860	131	181	164	152	100
Common Guillem.	1025	2198	204	254	208	211	124
Little Auk	164	696	161	244	239	205	149

Data from this study are compared (as % of this study's FMR) to values predicted using the equations given by Kendeigh et al. (1977) (0°C), Walsberg (1983), Nagy (1987), Bennett & Harvey (B&H) (1989) for seabirds and Birt-Friesen (1989) for cold water seabirds using flapping flight. Sources as in Tab. 6.

the FMR of northern seabird species by as much as 154% (Table 7). Based on DLW studies on 15 seabird species from many different families, Nagy (1987) presented the following equation for field metabolic rate (FMR); $FMR = 8.02\ m^{0.704}$ (FMR in kJ/d and m in gram). This equation also underestimated the present FMR values by as much as 139% (Table 7). Bennett and Harvey (1987) using metabolic data from 47 species of birds, in which the RMR and active metabolic rate (AMR) were determined in the same species, reached the following equation for AMR; $AMR = 15.14\ m^{0.61}$ (AMR in kJ/d and m in gram). This equation also underestimates the present FMR results by 111% (Table 7). Birt-Friesen et al. (1989), also rewiewing FMR data from seabirds, separated foraging modes (pursuit diving, gliding flight or flapping flight) in seabirds and the oceanographic regime (warm water from cold water) at which they were feeding. They found that birds using flapping flight in cold water were different from other seabird species studied, and presented the allometric equation FMR = 1737.8 $m^{0.727}$ (FMR in kJ/d and m in kg). When this equation was compared to the present FMR results from northern seabirds it gave the best predictions (Table 7)(Paper II, IV, VI and VII).

To maintain a high FMR, the bird must develop a large metabolic apparatus to sustain the high energy turnover throughout the period of chick rearing. While the energy expenditure at basal levels is mainly a result of heat produced by the brain, heart, liver and kidney (Aschoff et al. 1971), the energy expenditure above basal levels is mostly generated by skeletal muscles during active movements and thermoregulation (by shivering and non-shivering thermogenesis)(Kersten and Piersma 1987). Since the muscle depends on the internal organs to function (for fuel, degradation of waste material and repair of tissue), it is believed that the high FMR is the result of the maintenance of a high RMR (Kersten and Piersma 1987; Daan et al. 1990). According to Daan et al. (1990) this is a functional explanation for the near constant ratio (3-4 times RMR) between RMR and FMR. They also suggest a physiological limit or avian ceiling of 4.0 times RMR as proposed by Drent and Daan (1980).

The high FMR in high-latitude seabirds can be explained by the cost of thermoregulation in cold environments and by the foraging mode (flying or diving). In the Little Auk, Common and Brünnich's Guillemot, the FMR/RMR relationship is high (see Tables 6 and Table 8). Ellis (1984) proposed a close

Table 8

Field metabolic rate (FMR) in seabirds using flapping flight in cold water, measured using the doubly labeled water (DLW) method during the chick rearing period.

Species	BM (g)	FMR (kJ/d)	RMR		FMR/RMR ratio	Source
			(ml CO_2/g·h)	(kJ/d)		
Least Auklet	83	358	7.33	116	3.1	Roby & Ricklefs 1986
Georgian Diving Pet.	109	351	5.27	112	3.1	Roby & Ricklefs 1986
Common Diving Pet.	137	417	6.38	130	3.2	Roby & Ricklefs 1986
Little Auk	164	696	6.68	191	3.6	Paper IV
Black Guillem.	380	860	3.63	291	3.0	Paper VI
Kittiwake	392	795	3.16	310	2.6	Paper II
Common Guillem.	1025	2198	3.34	593	3.8	Paper VII
Common Guillem.	940	1790	3.18	344(544[a])	5.2(3.3)	Cairns et al. (1990)
Brünnich Guillem.	1119	2080	2.89	599	3.5	Flint & Hunt, unpubl.
Brünnich Guillem.	1100	1860	2.63	589	3.2	Croll, unpubl.
Northern Gannet	3210	4865	2.44	737(1377[b])	6.6(3.5)	Birt-Friesen et al. 1989
Southern Giant Pet.	3890	4270	2.46	1200[c]	3.6	Obst & Nagy (1992)

[a] RMR from Gabrielsen et al. (1988)

[b] RMR from Bryant and Furness, unpubl.

[c] RMR from Morgan et al. (1992)

Table 9

Wing loading in seven species of seabirds.

Species	N	BM (g)	Wing loading (g/cm^2)
Kittiwake	5	390±20	0.39±0.10
Fulmar	5	650±50	0.52±0.10
Herring Gull	5	940±45	0.51±0.10
Black Guillem.	5	380±25	0.82±0.10
Common Guillem.	5	1010±40	1.86±0.10
Brünnich Guillem.	5	990±30	1.48±0.10
Little Auk	5	165±15	0.98±0.05

From; Gabrielsen, unpubl.

linkage between RMR and the maximum power output, whereas Roby and Ricklefs (1986) and Gabrielsen et al. (1988) (Paper III) suggested that the bird's physical activity may influence the RMR level. According to Birt-Friesen et al. (1989), auks and diving petrels have a higher FMR than other seabirds because they use their wings both for flying and diving. In contrast to penguins in which the wing form is optimized for swimming, the wing form for fulmars and larids is optimized for flying. Since the optimum design for wings differs for flyers and divers one would expect that an intermediate stage would be less effective in both in water and air.

In Table 9, the wing loading in four alcid species, two larids and fulmars are presented. The wing loading of auks, especially Common and Brünnichs Guillemots, are highest while that of the Fulmar, Herring Gull and Kittiwakes are lowest. Since there is a good correlation between the FMR and time at sea in several DLW studies of seabirds feeding in cold water and using flapping flight (Roby and Ricklefs 1986; Birt-Friesen et al. 1989; Obst and Nagy' 1992, Paper VII), the high and variable FMR in alcids is probably associated with high cost of flying and diving, distance flown and depth dived.

In Little Auks, Common and Brünnich's Guillemots there is a strong correlation between FMR and activity levels (Ellis 1984; Birt-Friesen et al. 1989; Paper III and IV). This suggests a strong linkage between RMR and maximum power output in which a high RMR is correlated with a high FMR. Black Guillemots and Kittiwakes have a high mean mass-specific RMR (Table 1). However a high RMR is not correlated with a high

FMR in these two species (Table 6). Because Fulmars have a low wing loading (Table 9) and a low RMR (Paper III), one would expect them also to have a low FMR. As yet, there is no FMR data available from Fulmars during the chick rearing period. However, another species of Procellariiformes, the Wandering Albatross (Diomedea exulans), has a low wing loading, a low RMR value and a low FMR (2.3 x RMR)(Adams et al. 1986). This indicates that a low cost of flight can be associated with a low RMR in Procellariiformes (Gabrielsen and Mehlum 1989a).

Our DLW studies show that the FMR in foraging seabirds during chick rearing varies between 2.6 and 3.8 times the RMR (Table 6; Paper II, IV, VI and VII). This is consistent with Drent and Daan's (1980) "maximum sustained working level" of 3-4 times RMR during the chick rearing period. Most DLW studies of birds, ranging from 83-3890 g in body mass and with similar foraging mode show the same FMR/RMR relationship (Table 8). However, DLW studies of Common Guillemots and Northern Gannets (Sula bassana) in the Canadian Arctic resulted in factors of 5.2 and 6.6 FMR/RMR relationship, respectively (Table 8) (Cairns et al. 1990; Birt-Friesen et al. 1989). In both these studies the RMR was determined using closed respiratory systems. Since the FMR/RMR relationship is very sensitive to the methods used to determine the RMR and since both these studies deviate most when calculated as a) % of predicted values using the equation by Ellis (1984) and b) using body mass (paper VI), it is possible that the high FMR/RMR relationship is an artifact of the technique used for determining RMR. Both used the same respiratory method (the closed-system described by Ricklefs et al. 1984) to determine the RMR level (Birt-Friesen et al. 1989; Cairns et al. 1990; Montevecchi et al. 1991). Since the experimental protocol for measuring RMR is not presented in these studies, it is difficult to explain the RMR difference. Until these analytical problems are solved, one should be careful in using multiples of RMR when calculating FMR in seabirds. Also, since analyses by Bennett and Harvey (1987) indicated that the active metabolic rate (AMR) and RMR relationship is constant in birds during breeding, it is not correct to use a specific relationship to estimate AMR or FMR.

Several factors seem to influence the FMR level in seabirds during the chick rearing period. In Kittiwakes (Paper II) and in Little Auks (Paper IV), the FMR was high during days of heavy wind. In Kittiwakes an increase in wind speed (headwinds) results in an increase in flapping flight which results in elevated energy expenditures. Wind may also influence prey availability through increased wave action (Schneider 1989) and thereby cause problems for Kittiwakes to find food. In Leach's Storm Petrels, Kittiwakes, Common Guillemots, Northern Gannets and Southern Giant Petrels (Birt-Friesen et al. 1989; Montevecchi et al. 1991; Obst and Nagy 1992; Flint, unpubl.; Paper VII) the time spent away from the colony, presumably at sea, was related to FMR.

The diet or feeding habits of Arctic breeding seabirds may also cause an elevation in RMR and FMR levels. McNab (1986) found a dietary correlation with RMR among several species of mammals. While Bennett and Harvey (1987) found no significant association between RMR and differences in diet across several families of birds, McNab (unpubl.) and Nagy and Obst's (1991) analyses of birds indicated that a large part of the FMR variation is associated with the feeding habits. Based on studies of food requirements, using the DLW method (Paper II, IV, VI and VII), Arctic breeding seabirds are calculated to need 40-80% of their own body weight of food per day during the chick rearing period. Such a high food consumption may, in some species, cause a physiological limitation due to digestive bottlenecks (Diamond et al. 1986). High food consumption and time needed for digestion may limit their time budget at sea. A Common Guillemot requires 1-2 hours to process a meal of 80-100 g (Brekke and Gabrielsen, 1994). With a daily consumption need of 440 g, this means that this species uses at least 5-10 hours to process the food. Since Common Guillemots have to digest most of the food at sea in order to reduce the energy costs of flying (Paper VII), they have to spend much of their foraging time to cover their own needs and thus have less time available to feed their chick. Furthermore, Arctic seabirds have an additional problem in that they have to warm the cold food items before digestion. Depending on the size and composition of the meal, the heat increment of feeding (SDA) increases energy expenditure by 15-20% above the RMR level in most seabirds (Gabrielsen, unpubl.). Most of the SDA are used in thermoregulation at temperatures below LCT. For seabirds, especially diving seabirds foraging in cold oceans, which spend many hours to process the food, the SDA is an important component of FMR.

Hails and Bryant (1979) found a correlation between FMR and brood size in Common House Martins (Delichon urbica). By enlarging the brood size from three to four young, the energy expenditure increased by 18%. This is in accordance with our studies of seabirds, which show that the FMR increases by 20-25% in Kittiwakes feeding two chicks compared to one (Paper II, Gabrielsen, unpubl.). The parents of two chicks have to spend more time flying while searching for food, and carry more food back to the nest. Most DLW studies of seabirds have been presented as an average FMR throughout the chick rearing period. In two species of diving petrels (Pelecanoides urinatrix and P.georgicus) and in Little Auks (Roby and Ricklefs 1986; Paper IV) there was no change in adult FMR with respect to chick age. In several studies of Common Guillemots, there was no apparent increase in provisioning rates with increasing chick age (Birkhead 1977; Harris and Wanless 1985). However, Birkhead and Nettleship (1987) found an increase in provisioning in two seasons in Brünnich's Guillemots and in one season in Common Guillemots. The lack of correlation between FMR and chick age in diving petrels and Little Auks is probably due to small sample sizes. In adult Little Penguins, the highest energy cost was found at the end of chick growth (Gales and Green 1990). In Common Guillemots (Paper VII) a weak correlation was found between FMR and chick age, suggesting that adults with older chicks spent slightly more time at sea than adults with smaller chicks.

Chick energetics

After hatching, chicks of different seabirds have varying development patterns which require different pattern of energy allocation from the parent birds. Parents of precocial chicks, such as the Common Eider, use most of their energy to produce eggs, to incubate and to protect their ducklings. Contrary to this strategy, altricial chicks (most seabirds) are dependent on an extensive energy input from their parents in the form of food and warmth through brooding. The allocation of energy by the young to growth, thermoregulation etc. thus affects the time and energy the parents must put into their offspring both on a daily basis as well as over the long term (Dunn 1980). It is thus important to determine the energy costs of the different developmental patterns of seabird chicks to evaluate the constraints they may put on the parent birds.

Ducklings of Common Eiders leave the nest one day after hatching and when they reach the water they can swim, eat and dive (Mendenhall 1979; Blix and Steen 1979). These ducklings are well adapted to cope with the temperature stresses imposed by hatching in the Arctic. While resting in ice water or at ambient temperatures of 0 °C, one day old ducklings are able to maintain a stable high body temperature for several hours. This is possible through a high metabolic rate, close to 4 times the rates at thermoneutrality and good insulation (Steen and Gabrielsen 1986 and 1988). In contrast to Eiders, most seabird chicks have a poorer capacity for thermoregulation. Chicks of Little Auks and Kittiwakes cannot maintain homeothermy until they are 5-6 and 15-16 days old, respectively (Gabrielsen et al. (1992); Paper V). They are also fully dependent of their parents for protection and feeding.

The allocation pattern of metabolisable energy in Kittiwake and Little Auk chicks resembles that found in laboratory-raised tern and gull chicks (Drent and Klaassen 1989, Drent et al. 1992) and in field studies (Dunn 1980; Klaassen et al. 1989). The RMR constitutes 50-55% of total metabolisable energy in both Kittiwake and Little Auk chicks (Gabrielsen et al. (1992); Paper V). However, the cost of thermoregulation in Little Auk chicks is much higher than in Kittiwake chicks. The main reason is a low insulative value of Little Auk chick down and that Little Auk chicks are not brooded for more than 5-7 days (Paper V). Arctic tern (Sterna paradisaea) chicks, which breed in the same area, also have a high cost of thermoregulation (30%)(Klaassen et al. 1989). However, two species of diving petrels, which live at the same ambient temperatures, have lower cost of thermoregulation because they are brooded by one of the parents at night (Ricklefs and Roby 1983; Roby 1991). At a mean ambient temperature of 5 ^{o}C (July), the energy saved by the Kittiwake chick through being brooded is calculated to be close to 20% (Gabrielsen et al. 1992).

The energy expended in activity is small (less than 10%) in Little Auk chicks when compared to other bird species (Dunn 1980; Ricklefs and White 1981; Klaassen et al. 1989; Gabrielsen et al. 1992). Little Auk chicks are inactive in their crevices most of the time and do not start to exercise their wings at the entrance of the crevice until they are two-three weeks old (Paper V). In Kittiwake chicks, a high proportion (20%) of the energy expenditure is allocated to activity. It is initially low, but accelerates at age 10-15 days and onwards (Gabrielsen et al. 1992). The same proportion (20%) was also found in tern chicks in both field and laboratory studies (Drent and Klaassen 1989; Klaassen et al. 1989).

When compared to other seabird chicks of similar body mass, Little Auk chicks have the highest cost of growth (energy-accumulation rate in growing tissues plus the cost of biosynthesis). This is mainly a result of a high body-mass growth rate and a high rate of fat deposition (Paper V). Of the total accumulated energy in Little Auk chicks between days 1 and 21, 58% is in the form of fat (Taylor and Konarzewski 1989). In Kittiwake chicks the energy deposited in tissue constitutes 24% of the total metabolisable energy intake (Gabrielsen et al. 1992). This is similar (23%) to that found in Arctic Tern chicks in Svalbard (Klaassen et al. 1989).

The overall daily energy expenditure of Little Auk chicks is also high when compared to other seabird chicks of similar body mass (Paper V). One might expect that this high energy demand in Little Auk chicks would result in an equivalent high energy expenditure by the parents. However, the amount of energy delivered to the Little Auk chick by one of the parents is only 15 % of that gathered by the parent to meet both its own and its chick's requirements (Table 10). This calculation is based on the period between days 8 and 21, when the chick

Table 10

Proportion of energy gathered by European Starlings, Least Auklets, Diving Petrels, alcids and Kittiwakes delivered to their chicks during period of peak chick food demands.

Species	Adult body mass (g)	Brood size	Adult FMR[a] ml CO_2/(g·h)	Adult energy consumption[b] (kJ/day) A	Food delivered to chick (kJ/adult day) B	Proportion of energy delivered to chick (%; 100 B/[A+B])	Source
European Starling	76	5	6.18	450	460	51	*
Least Auklet	84	1	6.69	465	97	17	**
South Georgia Diving Petrel	109	1	6.53	602	123	17	**
Common Diving Petrel	137	1	6.34	723	101	12	**
Little Auk	164	1	6.68	904	162	15	***
Black Guillemot	381	2	3.63	1121	700	38	****
Common Guillemot	1025	1	3.34	2855	200	7	*****
Kittiwake	383	1	3.15	1007	420	29	******
- " -	383	2	3.57	1141	840	42	

From:
* Ricklefs and Williams (1984), Westerterp (1973)
** Roby and Ricklefs (1986), Roby (1991)
*** Paper IV, Paper V
**** Paper VI, Gabrielsen, unpubl.
***** Paper VII, Gabrielsen, unpubl.
****** Paper II, Gabrielsen et al. (1992)

a Field metabolic rates in birds feeding chicks measured using the doubly labeled water (DLW) method.

b Calculated from FMR, assuming 0.67 energy-assimilation coefficient in European Starling (Ricklefs and Williams 1984) and 0.77 in all others (Brekke & Gabrielsen 1994).

is no longer brooded but is still being fed by both parents.

The energy delivered to the chick per day by one Little Auk parent is similar to that of the Least Auklets and two species of diving petrels (Table 10), but only 1/4-1/3 of that delivered by the European Starlings (Sturnus vulgaris) to their five-chick brood (Roby and Ricklefs 1986), despite the mass-specific FMR and body masses of all species being similar (Table 10). This shows that some seabirds species are less efficient in delivering energy to the nest per unit energy expended. Roby and Ricklefs (1986) suggested that the broods of auklets and diving petrels are restricted to single chicks as a consequence of the high cost of foraging and transport of chick meals.

The results from Little Auk chicks (Paper V) support this view since the mass-specific FMR while feeding the chick was the highest among the species investigated (Table 10). For adult Little Auks, a high cost of flight and the fact that they forage far off-shore explain the high energy expenditure (Paper V). Even further to the extreme are adult Common Guillemots which deliver the equivalent of <10% of their total energy expenditure to their chick (Table 10)(Paper VII; Gabrielsen, unpubl.). A relatively high FMR of adult Common Guillemots during chick rearing is also explained by a high energy cost of flight or diving (Paper VII).

Adult Black Guillemots deliver the equivalent of 2-5 times more energy to their chicks than do adults of Little Auks and Common Guillemots (Table 10). Adult Black Guillemots obtain food for chicks inshore in shallow water (Cairns 1987), and have lower wing loads (Table 9) and thus reduce the flight cost and FMR (Table 6). This enables them to raise two chicks which fledge at 100% of the adult body mass. Adult Kittiwakes which also raise two chicks deliver the same amount of energy to the chicks as Black Guillemots (Table 10). In their case, an off-shore feeding strategy is upweighed by low costs of flight and a low FMR (Table 6). This again enables them to raise 1-3 chicks which attain 100% of the adult body mass at fledging. Adult Least Auklets raise one chick and deliver the the same amount of energy to the chicks as Dovekies (Table 10). However, their inshore feeding strategy have enabled them to raise a chick which attain 108% of the adult body mass at fledging (Roby and Brink 1986).

The parents of Common Guillemots work at a maximum during chick rearing (Table 6 and Table 8). The FMR/RMR ratio in this species is 3.8. It is suggested that Common Guillemots are simply unable to provision chicks beyond <30% of adult body mass at which they leave the nest. This view is in accordance with previous hypotheses put forward by several authors (Sealy 1973; Birkhead 1977; Gaston 1985; Furness and Barrett 1985; Roby and Ricklefs 1986). The parents of Little Auks also work near the maximum during chick rearing (FMR/RMR ratio of 3.6, Table 6 and Table 8). The chicks of Little Auks reach 65-70% of adult body mass before fledging. Common Guillemots and Little Auks both are offshore foragers. However, Little Auks probably have lower flight cost than Common Guillemots, since their wing loading is 50% lower (Table 9). A lower flight cost thus enables Little Auks to provision chicks throughout the fledging period.

SUMMARY

The resting metabolic rate (RMR) and thermal conductance (TC) were measured in 8 species of seabirds ranging in size from Little Auks (165 g) to Eiders (1.6 kg) breeding in northern Norway and in Svalbard (70-80 ^{o}N, 12-31 ^{o}E). The RMRs for seabirds breeding at high latitudes were higher than that of similar species breeding in temperate and tropical areas. In all species measured the RMRs were 12-111 % above those predicted using allometric equations of Lasiewski and Dawson (1967), Aschoff and Pohl (1970) and Ellis (1984). The RMRs presented here suggest a lack of a latitudinal trend indicating that other factors are the main reason for the high and variable RMR in seabirds. Climate, lack of diurnal phase and the birds' activity mode seem to be the main factors causing such a high RMR in seabirds. The lowest thermal conductance (TC) values, or the best insulation, were found in Eiders and Glaucous Gulls, while Little Auks had the highest. In most seabirds, the TC values are close to those predicted by allometric equations. Alcids have lower TC values, or better insulation, than comparable species from temperate and tropical areas. However, Larids have higher TC values than comparable species studied further south.

The cost of incubation is high in most northern breeding seabirds (gulls and alcids). However, the cost of incubation in the female Common Eider was similar to the RMR value of non-incubating individuals.

Estimated and measured incubation costs by female Common Eiders were compared using the mass loss and the oxygen consumption method, respectively. The calculated value was 20-35 % lower than the measured value, and it is suggested that increased drinking or eating near the end of the incubation period is the main reason for the underestimation using the mass loss method.

The field metabolic rate (FMR) during chick rearing in Kittiwakes, Little Auks, Black Guillemots and Common Guillemots varied between 2.6 and 3.8 times their RMR per day. In the Little Auk and Common Guillemot, the high FMR is coupled with a high RMR. The high FMR in these two species is mainly explained by the cost of thermoregulation in cold environments, their off-shore foraging habit and high cost of flying and diving. In Kittiwakes and Black Guillemots, a high RMR is not correlated with a high FMR. A low cost of flight is suggested as being the main cause of a low FMR in these two species.

The allocation pattern of metabolisable energy has been determined in Little Auk chicks. In this species, the RMR constituted 50-55% of the total metabolisable energy budget. In contrast to precocial chicks, such as Eider ducklings, most seabird chicks have a poor capacity for thermoregulation at hatching. However, costs of thermoregulation are reduced through brooding by the parents. In Little Auk chick, the proportion of energy saved by brooding is close to 10% of the total energy expenditure. The energy expended in activity is 10% of the total energy expenditure in Little Auk chicks.

The energy deposited in tissue constitutes 25-30% of the total metabolisable energy intake in Little Auk chicks.

Despite that most seabird chicks have a high energy demand, the energy delivered to the chick by one parent of Little Auks and Common Guillemots is equivalent to less than 15 % of the total energy gathered. In most seabirds the adult FMR does not constrain chick growth. However, in adult Common Guillemots, a high FMR/RMR ratio may constrain chick growth and be the main reason for the early fledging strategy of this species. Adult Little Auks also have a high FMR/RMR ratio. A lower wing loading than Common Guillemots enables them to feed chicks until they reach a fledging mass which is 65-70% of the adult body mass. In adult Kittiwakes and Black Guillemots, FMR/RMR ratios of 2.6 and 3.0, respectively, have enabled them to raise multiple chick broods which fledge at 100% of the adult body mass.

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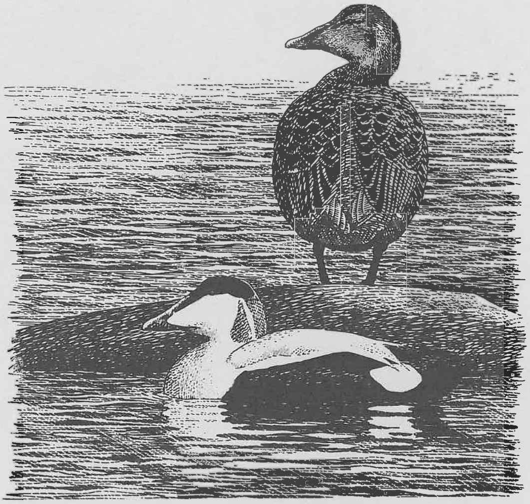
Paper I



Energy cost during incubation and thermoregulation in the female Common Eider *Somateria mollissima*

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Gabrielsen, G.W., Mehlum, F., Karlsen, H.E. Andresen, Ø. & Parker, H. 1991: Energy cost during incubation and thermoregulation in the female Common Eider *Somateria mollissima*. *Norsk Polarinstitutt Skrifter 195*, 51–62.

Metabolic rate during incubation (IMR) was measured in two wild incubating Eiders at Ny-Ålesund, Svalbard (79°N). IMR, measured toward the end of incubation (day 15–20), averaged 0.80 ml O_2/g·h. The respiratory quotient (RQ) was 0.70, indicating that fat was the major metabolic fuel during this long period of fast. Both birds showed a decrease in mean daily energy expenditure with decreasing body mass but no significant decrease in specific resting metabolic rate.

Thermoregulation was studied in 12 non-incubating Eiders in the laboratory. Resting metabolic rate (RMR) averaged 0.86 ml O_2/g·h, thermal conductance (TC) 0.0240 ml O_2/g·h·°C and deep body temperature 40.1°C. The RMR value of non-incubating Eiders tended to be 7.5% higher than the IMR value of incubating birds ($0.05 > p > 0.10$, t-test). Both IMR and RMR values were above predicted values based on equations by Lasiewski & Dawson (1967) and Aschoff & Pohl (1970). TC was lower than values predicted from equations of Herreid & Kessel (1967) and higher than those predicted by Aschoff (1981).

Calculation of daily energy expenditure (DEE) during incubation (day 20) based on weight loss was 24% and 29% less, respectively, than DEE measurements derived from indirect calorimetry of incubating and non-incubating eiders. Measurements of water influx rate close to hatching suggested that Eiders increased their water consumption then.

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Introduction

The energy cost of incubation in birds has been estimated from measurements of loss of body mass (Prince et al. 1981; Croxall 1982; Croxall & Ricketts 1983; Grant & Whittow 1983), oxygen consumption (Norton 1973; Ricklefs 1974; Biebach 1979; Gessaman & Findell 1979; Vleck 1981; Haftorn & Reinertsen 1985; Gabrielsen & Unander 1987) and the doubly labelled water (DLW) technique (Pettit et al. 1988). Most metabolic studies have been performed in the laboratory and few on free-living birds (Brown 1984; Grant & Whittow 1983; Brown & Adams 1984), and most have shown the energy cost of incubation to be greater than the basal metabolic rate. Grant & Whittow (1983) and Brown (1984) however, reported the oxygen consumption of incubating Laysan Albatross (*Diomedea immuntabilis*) and Marcaroni Penguins (*Eudyptes chrysolophus*) to be significantly lower than that of non-incubating resting birds.

Female Common Eiders (hereafter called Eiders) abstain from feeding during 25 days of incubation resulting in a weight loss of 30–45% (Maline 1963, 1976; Cantin et al. 1974; Korschgen 1977). Little is known about the physiological adaptations to fasting in birds. Geese and penguins show a 30–50% decrease in resting metabolic rate (RMR) after 30 days of fasting (Benedict & Lee 1937; Le Maho et al. 1981). The thyroid hormones are involved in controlling oxygen consumption and metabolic rate (Falconer 1971; Etkin 1978). In birds it has been demonstrated that the level of thyroxin (T_4) increases while triiodothyronine (T_3) decreases after food deprivation (May 1978).

In this study we measured oxygen consumption and plasma concentrations of thyroid hormones of both incubating and non-incubating Eiders.

Estimates of energy expenditure based on oxygen uptake were compared to values calculated from weight loss of incubating females. Close to hatching we used tritium to study the water influx rate to determine if birds were drinking water toward the end of the incubation fast, as this could influence calculations of energy expenditure based on weight loss.

Material and methods

Metabolic Rate Measurements

Field work.—The field work was carried out at Ny-Ålesund on the north-western coast of Spitsbergen, Svalbard (Fig. 1). During the summer of 1983 we studied the incubation metabolic rate in two female Eiders nesting close to the settlement of Ny-Ålesund. On the fifteenth day of incubation each nest with clutch (4 and 5 eggs) and down was removed from the nest bowl and placed inside a plexiglass box (40 × 30 × 30 cm) at the original nest site. This procedure required about 30 minutes, and the females returned to the nest within 10–20 minutes to resume incubation. The chamber consisted of two hinged parts, the upper part of which was lowered down from a distance with a rope before performing the measurements (Fig. 2). The incubation metabolic rate (IMR) was measured in an open system in which the plexiglass box functioned as the metabolic chamber. The chamber was connected to a carbon dioxide (Binos-1, Leybold-Heraeus) and an oxygen (S-3A, R-1 and N-22M, Applied Electrochemistry Inc.) analyzer by means of a plastic tube. Air was dried and pumped through the system with a flow of 3.5–4.0 l/min. Airflow was measured in each experiment with a Tri-Flat flowmeter (10 A 3200, Fischer & Porter). Temperature in the box and in the bottom of the nest was measured with copper-constantan thermocouples connected to a digital thermometer (2190A, Fluke). Both birds were weighed at the end of the experimental period using a Pesola spring balance (±5 g). In order to reduce overheating in the plexiglass box, we performed metabolic measurements only on cloudy days. Measurements were performed 1–2 times daily in 2–3 hour periods. All measurements were performed between day 15 and 20 of incubation.

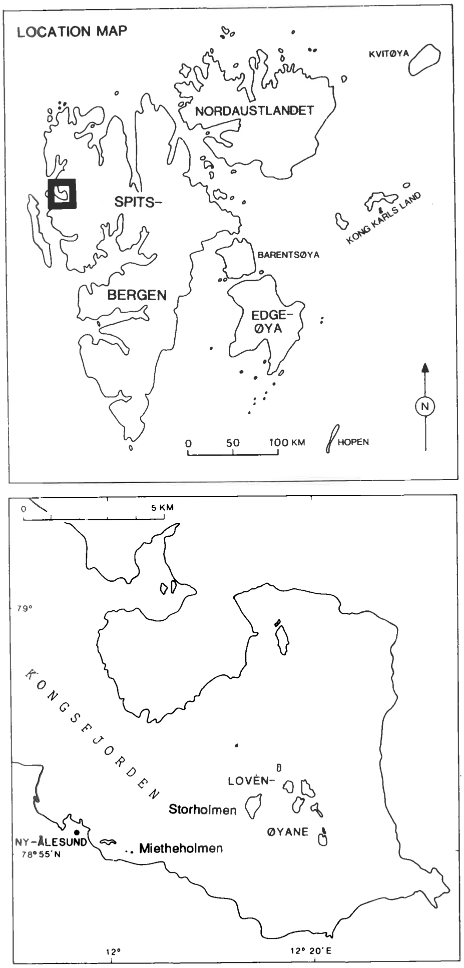

Fig. 1. Over, the Svalbard archipelago (with the exception of Bjørnøya to the south) showing the inner Kongsfjorden area and the location of Ny-Ålesund (enlarged, under) where the field work was carried out.

Laboratory study.—The laboratory study of 12 non-incubating adult females was carried out at the research station of the Norwegian Polar Research Institute in Ny-Ålesund during the summers of 1984–85. Birds were either captured on the nest using a bamboo pole with a nylon snare or caught with a net-gun (Coda Enterprises) while swimming. They were kept in individual outdoor cages without food for 1–2 days and given water ad lib. Metabolic measurements were performed within a minimum of 12 hours after capture according to the methods described by Gabrielsen et al. (1988). A metabolic chamber

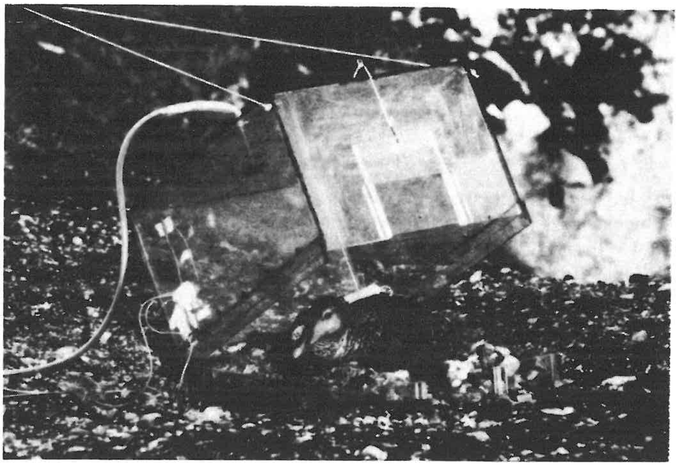

Fig. 2. A wild Eider duck incubating in a respiration chamber.

was briefly placed inside a climatic chamber where temperature could be controlled within ±1°C from −25 to +30°C. Instrumentation was the same as that used in the study of incubating Eiders with the exception of air flow which was measured with a flowmeter (F 113, Hi-Tec) connected to a readout (Model E-0020). Temperature in the climatic and metabolic chambers was measured by thermocouples connected to a Fluke thermometer. Body temperature was measured continually by means of an epoxy-coated thermocouple inserted approximately 7 cm into the colon. Birds were exposed to a given chamber temperature for a minimum of 1.5–2.0 hour periods. The measurements were performed under full light conditions since these birds experience 24 h of daylight during the breeding season. Oxygen consumption (ml O_2/g·h) and CO_2-preduction (ml CO_2/g·h) were measured during stable resting periods. Respiratory quotient (RQ) and energy expenditure (kJ/day) were also calculated. In calculating energy expenditure from oxygen consumption the conversion coefficient of 4.7 kcal per litre oxygen (RQ = 0.71) was used (Schmidt-Nielsen 1983; 1 kcal = 4.185 kJ). The final values for oxygen consumption and CO_2 production are accurate within ±5%. All results are given at STPD and mean values are shown with ± standard deviation.

Body weight measurements

Females nesting on the islands of Storholmen and Mietheholmen in the Kongsfjorden area were captured and weighed throughout incubation. The number of days each bird had incubated was estimated by measuring the density of the eggs in the nest. Egg weights in air were measured on a battery operated Ohaus digital scale (accuracy ±0.1 g) and in water on a 50 g Pesola spring balance (accuracy ± 0.1 g). From mean egg density the number of days the female has been incubating could be estimated by using the equation $y = 1634.788 - 4878.271\,x + 5034.848\,x^2 - 1777.747\,x^3$ (y = days of incubation, **x** = mean density of eggs). By using this equation it was possible to determine the number of days of incubation to within ± 2.5 days ($p < 0.01$) (Karlsen et al. in prep.).

Body weights of Eiders prior to egg-laying and 7–14 days after incubation were obtained from birds captured with a net-gun in Kongsfjorden.

Thyroid hormones

Birds collected for body weight measurements were also used for studies of plasma concentrations of thyroid hormones. A blood sample (2–3 ml) was taken from the wing vein using a heparinized syringe. The blood samples were kept on ice during transport to the laboratory for centrifugation. Plasma was thereafter stored at − 20°C until assayed at the Norwegian College of Veterinary Medicine in Oslo, Norway. The total thyroxine (T_4) level in the plasma was determined by radioimmunoassay described by Larsen et al. (1973) and modified by Andresen et al. (1980). The antiserum used has been described by Kruse (1976). The total triiodothyronine (T_3) level in the plasma was measured by a commercially available solid phase radioimmunoassay (Coat-a-Count, Diagnostic products Corp., Los Angeles, USA).

Water influx rate

Ten incubating Eiders close to hatching (mean = 23 days) were injected in the pectoral muscle with 0.75 ml tritium (1.34 mCi in each bird) and weighed before release. One to two hours after the injection, when the isotope had mixed thoroughly in the body water fluid (Degen et al. 1981; Williams & Nagy 1984), we recaptured the birds to obtain the initial blood sample. Blood samples were taken from the wing vein and the birds were released. Over the next 2–3 days we recaptured, weighed and sampled 6 of these birds once or twice. Blood samples were stored in heparinized microhematocrit capillary tubes and vacuum-distilled to obtain pure water. Isotope levels in water were measured by liquid scintillation spectrometry (Wood et al. 1975). Water flux rates were calculated by using equation 4 in Nagy and Costa (1980). Water volumes at recapture were calculated as initial fractional water content multiplied with body mass at recapture.

Thermal Conductance

Thermal conductance (TC) in non-incubating birds was calculated from the mass specific metabolic rate at ambient temperatures below the lower critical temperature. The TC was calculated by dividing oxygen consumption by the difference between body and ambient temperature at ambient temperatures below 0°C. TC (ml $O_2/g \cdot h \cdot °C$) is expressed as "wet" conductance since evaporative heat loss was not excluded.

The lower critical temperature was determined from the intersection of the lines representing metabolic rate at low ambient temperatures and the line representing resting mean metabolic rate in the thermoneutral zone.

Results

Ambient, chamber, and nest temperatures

In Ny-Ålesund the means for daily ambient, maximum and minimum temperatures for June 1983 were 2.1, 4.0 and 0.6°C respectively. In July, respective temperatures were 5.2, 7.2 and 3.6°C (The Norwegian Meteorological Institute). While performing the field metabolic studies of female Eiders the mean temperature in the metabolic chamber and nest were 12.2°C (SD = 4.7°C) and 31.9°C (SD = 2.5°C) respectively.

Body weight loss during laying

Immediately prior to egg-laying the mean body weight of females was 2,442 g (SD = 149, n = 6). Some of these birds, however, may have already laid 1–2 eggs despite having been caught on the water. Female Eiders often cover their first egg and return to the water for some time before egg-laying is resumed. After laying the second egg, however, they leave the nest only occasionally for short periods (Hagelund & Norderhaug 1975). At the start of incubation female body weight averaged 2,106 g (SD = 156, n = 11) (Fig. 3) or 336 g less than pre-laying weight. The mean density of the eggs of these birds was 1.075 which is close to the density of freshly laid Eider eggs (Rahn et al. 1983). The average number of eggs produced by female Eiders nesting on Storholmen in 1984 was 4.4 g (Mehlum 1991a, this volume). With a mean initial egg weight of 98 g, this gives a mean clutch weight of 392 g. Thus this initial weight loss can mainly be ascribed to egg production.

Body weight loss during incubation

The mean body weight of female Eiders at hatching was 1,357 g (SD = 71, n = 16). The total weight loss during 25 days of incubation was 749 g or 35.6%. Weight loss from pre-incubation to hatching was 1,085 g or 44.4%.

Assuming an incubation period of 25 days, the average weight loss was 30 g per day. Weight loss, however, was clearly a non-linear function of time (Fig. 3). (Polynominal regression $y = 2114.5 - 52.188\,x + 1.064\,x^2 - 0.006\,x^3$, $r^2 = 0.80$, y = body weight, x = days of incubation).

The mean body weight of the birds, accompanied by their ducklings and caught 7–14 days after the main hatching period, was 1,713 g (SD = 136, n = 4). Since these birds were not accompanied by other females, we assume that these Eiders had laid and incubated.

Thyroid hormones

The variation in plasma T_3 and T_4 concentrations are shown in Fig. 4. Mean T_3 concentration was

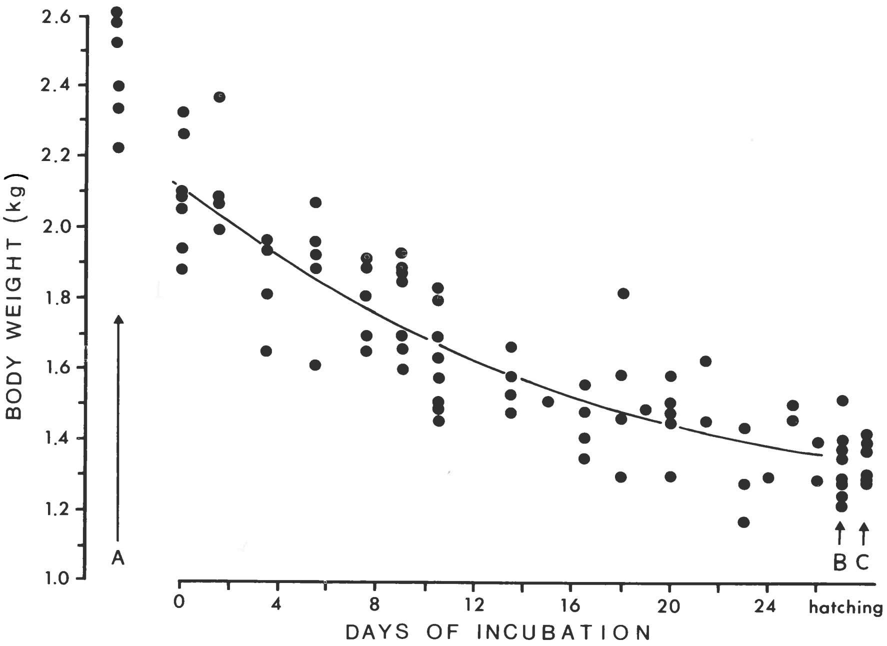

Fig. 3. Body weight of female Eiders before egg-laying (A), during incubation, at hatching (B), with newly hatched chicks but still in nest (C) and with ducklings 10–14 days after the main hatching period (D). Number of days of incubation was determined by the mean density of eggs in the nest using the following equation: $y = 1634.788 - 4878.271x + 5034.848x^2 - 1777.747x^3$ (y = days of incubation, x = density of eggs).

The weight loss curve is based on the following equation: $y = 2114.5 - 52.188x + 1.064x^2 - 0.0063x^3$ (y = body weight, x = days of incubation).

1.65 ng/ml (SD = 0.65, n = 80) and varied between 0.53 and 4.50 ng/ml. The egg-laying T_3 level was 1.48 ng/ml (SD = 0.81, n = 6) and 10–14 days after hatching level was 1.65 ng/ml (SD = 0.65, n = 4). Plasma T_3 levels increased throughout the incubation period ($y = 0.044x + 1.062$, $p < 0.001$, $r^2 = 0.23$, y = plasma T_3 concentration, x = days of incubation). There was no significant variation in plasma T_4 levels throughout the study period ($y = 0.028x + 13.841$, $r^2 = 0.00$, y = plasma T_4 concentration, x = days of incubation). The mean T_4 concentration was 14.26 ng/ml (SD = 4.68, n = 87) and varied between 5.8 and 35.5 ng/ml. The egg-laying T_4 level was 11.28 ng/ml (SD = 5.33, n = 6), and 10–14 days after hatching the level was 17.93 ng/ml (SD = 6.82, n = 4).

Incubating Metabolic Rate

The mean body weight of the two incubating female Eiders, measured at day 20, was 1540 g and 1580 g. The females did not struggle when the upper part of the metabolic chamber was lowered. Stable measurements were obtained within 1 hour. The mean incubating metabolic rate (IMR) was 0.80 ml O_2/g·h (SD = 0.02, n = 13) and the corresponding mean RQ was 0.70 (SD = 0.01). The mean daily energy expenditure of the incubating Eiders decreased as body weight decreased, though there was no significant decrease in the specific metabolic rate throughout the experimental period. The mean energy expenditure was calculated to 604.4 kJ/d (SD = 15.1, n = 2).

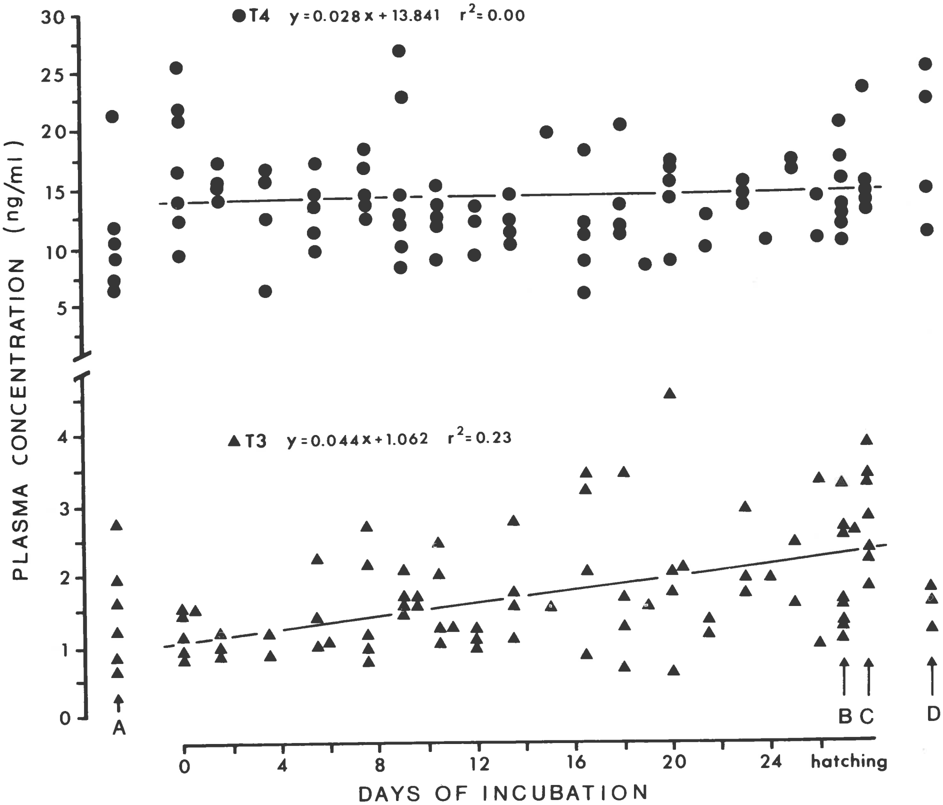

Fig. 4. Plasma concentrations of thyroxine and triiodothyronine in birds at egg-laying, during incubation and 10–14 days after hatching. A, B, C and D as in Fig. 3.

Resting Metabolic Rate/Thermal Conductance

The mean body weight of the 12 non-incubating Eiders was 1,661 g (SD = 251, number measurements = 18). This weight was used when calculating the mean metabolic rate. Birds caught on the nest did not differ ($p < 0.05$) in RMR from those caught while swimming. The mean RMR value at thermoneutrality was 0.86 ml O_2/g·h (SD = 0.07) (Fig. 5). The corresponding mean RQ was 0.71 (SD = 0.02). The RMR value of non-incubating females tended to be 7.5% higher than the IMR values of incubating birds ($0.05 < p < 0.10$, t-test).

The mean daily energy expenditure (DEE) of the resting non-incubating Eiders (1,600 g) at thermoneutrality was calculated to be 649.4 kJ/d (SD = 52.9, n = 12).

The average body temperature was 40.1°C (SD = 0.7, number of measurements = 18). Oxygen consumption increased linearly below the lower critical temperature of 7°C. The regression line ($y = 1.052–0.025\,x$, x = amb. temp., y = ml O_2/g·h) intersected the abscissa close to Eider body temperature. Thermal conductance (TC) was 0.0240 ml O_2/g·h·°C.

Energy budget calculation based on weight loss

Calculation of DEE during incubation based on weight loss (Fig. 3) was done for birds between 19 and 20 days of incubation. The daily weight

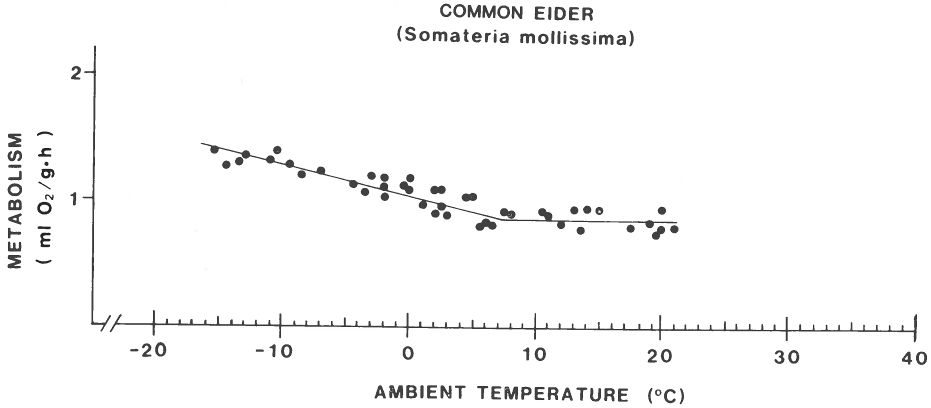

Fig. 5. Oxygen consumption and energy expenditure of non-incubating female Eiders at different ambient temperatures. The regression line below the lower critical temperature intersected the abscissa at an ambient temperature close to the measured body temperature.

loss on day 20 was 17.7 g. Since there was no value available for body composition between day 19 and 20, we have used an average value for loss of fat and protein throughout incubation. Body composition analysis of Eiders from Maine, USA (Korschgen 1977) and Svalbard (Parker & Holm 1990) indicate that based on a weight loss of 17.7 g/day, 11.0 g is lost as fat, 1.8 g as protein and 4.8 g as water. The energy equivalents of fat and protein were 38.53 kJ/g and 19.67 kJ/g, respectively (Parker & Holm 1990). Based on body weight loss, DEE during incubation at day 20 was calculated to 460 kJ/day. This is 24% and 29% lower than the DEE values obtained by indirect respirometry on incubating and non-incubating birds, respectively.

Water influx rate

The mean body weight of 6 incubating female Eiders (measured close to hatching) was 1,438 g (SD = 121, n = 8) (Table 1).

During the study period (2–3 days) the body mass change was 1.26%/day, i.e. a loss of 18.1 g per day. The water influx rate was 90.06 ml/day (SD = 56.36, n = 8). Based on a weight loss of 18.1 g per day the metabolic water production was calculated to 12.3 g per day using values of 0.11 g water formed per kcal burned (Schmidt-Nielsen 1983). One bird (No. 446), during the first experimental trial, had a water influx rate of only 18.11 ml/day, while all the others varied between 37.65 and 194.45 ml/day (Table 1). These values indicate that female Eiders consumed water close to or at hatching.

Discussion

In previous studies on small bird species (<0.5 kg) the energy cost during incubation has been estimated to be 15–30% higher than the resting metabolic rate (RMR) of non-incubating birds (Biebach 1979, 1981; Vleck 1981; Haftorn & Reinertsen 1985; Gabrielsen & Unander 1987). Small birds often have limited resistance to starvation and leave the nest periodically to forage. Recently, studies of larger birds that tolerate periods of fasting and show high nest attendance have revealed incubation costs similar to or lower than RMR or non-incubating individuals (Grant & Whittow 1983; Grant 1984; Brown & Adams

Table 1. Water influx rate in incubating Eiders at Ny-Ålesund, Svalbard, 1987.

Bird No.	Body weight (gram)	Body weight change (%/day)	Water influx rate (ml/day)
444	1,470	−1.42	121.14
445	1,295	−2.45	81.04
446	1,420	−0.75	18.11
446	1,405	−2.14	77.34
447	1,285	−0.82	194.45
448	1,420	−0.76	54.63
450	1,600	−0.33	37.65
450	1,610	−1.42	147.89
Mean	1,438	−1.26	90.06
SD	121	0.74	56.36

1984; Brown 1984; Groscolas 1988; Pettit et al. 1988). Metabolic measurements of incubating Eiders within the thermoneutral zone in our study indicated the energy cost during incubation to be similar to or slightly lower than RMR of non-incubating birds.

Our indirect measurement of daily energy expenditure (DEE) in incubating birds (604 kJ/day) was higher than Korschgen's (1977) of 401 kJ/day, Parker & Holm's (1990) of 490 kJ/day, and ours of 460 kJ/day. This difference may be due in part to the random fluctuations associated with small samples. Also, the contribution of the embryos to the total energy cost of incubation increases as incubation proceeds. In a study of the Blue Tit (*Parus caeruleus*) Haftorn & Reinertsen (1985) calculated that during the last days of incubation the clutch (13 eggs) accounted for 15% of the total oxygen consumption. In a similar study of incubating American Kestrels (*Falco sparvarius*) Gessaman & Findell (1979) estimated that during the last 5 days of incubation the clutch of five eggs contributed 19–25% of the total energy required for incubation. In three species of shorebirds Norton (1973) estimated that embryos close to hatching contributed 35–40% of the total energy cost of incubation. Steen & Gabrielsen (1988) calculated that a clutch of four pipped eggs contribute 125 kJ/d or 20% of the total DEE of incubating Eiders. In the present study, oxygen consumption and carbon dioxide production of the eggs was not subtracted from the incubation metabolic rate (IMR) measurements. However, based on a study of oxygen uptake in common fowl eggs Høiby et al. 1983), the oxygen uptake in Eider eggs incubated 15–20 days was calculated to vary between 12–15% of the total DEE. Therefore, the IMR in incubating individuals may be about 20–25% lower than the RMR of non-incubating birds.

Nest insulation may also reduce the net energy expenditure of an incubating bird relative to that of a non-incubating individual. Walsberg & King (1978) found the energy expenditure in the Red-winged Blackbird (*Agelaius phoenicus*), Willow Flycatcher (*Empidonax traillii*) and White-crowned Sparrow (*Zonotrichia leucophrys*) to be 15–18% less when incubating in a bowl-shaped nest than when perched in the open. Gessaman & Findell (1979) concluded that incubation in American Kestrels could be accomplished at the level of adult resting metabolism due partly to embryonic heat production and nest insulation. Our study, as well as previous studies on incubating penguins (Brown 1984; Groscolas 1988), albatrosses (Grant & Whittow 1983; Brown & Adams 1984; Pettit et al. 1988) and petrels (Grant & Whittow 1983), supports King's (1973) contention that the metabolic rate of a bird at rest can supply all the heat required for incubation, at least in some species.

Energy expenditure during incubation depends in part on nest attentiveness (Vleck 1981). Many smaller species of birds in particular have limited resistance to starvation and are obliged to forage regularly during incubation. The energy cost of rewarming the eggs increases with increased time away from the nest and lower ambient temperature (Gabrielsen & Steen 1979; Biebach 1986; Tøien et al. 1986). This extra energy cost is avoided when the incubation is shared by both parents. In contrast, many larger birds incubate for weeks without eating. Mehlum (1991b, this volume) found that female Eiders left the nest for an average of 4–5 min every second day, and they always covered the eggs with down before leaving. Consequently, egg temperature decreased less than 1°C during their absence time. Thus Eiders normally experience a low egg rewarming cost during incubation.

The mean ambient temperature measurement in Ny-Ålesund in June was 2.1°C which indicates that Eiders incubate at temperatures below the thermoneutral zone of non-incubating birds much of the time. Several of the non-incubating Eiders used in the metabolism measurements still had remnants of a brood patch. This probably resulted in an overestimation of the lower critical temperature as the down-lined nest would prevent considerable heat loss from the brood patch. The lower critical temperature of Eiders in winter is −6°C (Jenssen et al. 1989) or considerably lower than the 7°C measured in the present study. Microclimatic influences such as solar radiation have a positive effect on heat balance. Behavioural changes may also reduce heat loss, e.g. the lowest IMR values were obtained at low ambient temperatures when the bird put its bill under the wing feathers.

According to studies by Le Maho (1983) fasting penguins and geese go through three different periods during long-term fasting: a rapid adaptation period, a long period of economy, and finally a critical period. In geese the adaptation period is characterized by a rapid reduction in specific metabolic rate, the economy period by a slow decrease in body weight and RMR but with no decrease in specific RMR, and the critical period by drop in body mass which was not accompanied with a change in RMR (Le Maho et al. 1981; Le Maho 1983). Our measurements of body weight and IMR indicate that the period of adaptation and economy are also present in incubating Eiders. Unfortunately we do not have metabolic measurements from the beginning of incubation, but Le Maho et al. (1981) in their studies of geese suggest that the main reduction in metabolic rate appears at this time. While we found a slight (7.5%) difference between specific IMR and RMR in Eiders, and a 20–25% difference when subtracting for the eggs, there was a 17% difference between starved and normal geese (Le Maho 1983).

Measurements of thyroxin (T_4) and triiodothyronine (T_3) in Eiders indicated that while the level of T_4 was stable throughout the incubation period, there was a small but significant increase in T_3. This increase in the T_3 level contrasts with results from corresponding studies on chickens and penguins (May 1978; Cherel et al. 1988) which showed that the T_3 level was depressed after food deprivation. The thyroid hormones are involved in controlling heat production, and we suggest that the levels of these hormones are kept high in incubating Eiders because of heat requirements associated with the incubating eggs. Measurements of body temperature support this theory, for while body temperature in starved geese decreased from 40.1°C to 39.3°C (Le Maho et al. 1981), female Eiders showed a body temperature of 40.1°C up until day 20 of incubation.

Eiders show body weight reductions in the vicinity of 45% during breeding (Milne 1963, 1976; Cantin et al. 1974; Korschgen 1977). The present study showed a 44.4% decrease in body weight from the start of egg-laying until hatching and a 35.6% decrease during incubation. Our metabolic measurements gave a respiratory quotient value of 0.70, indicating that fat was the major fuel during incubation fasting in Eiders. Parker & Holm (1990) calculated from body composition analysis that lipid accounted for 91.8% of the total energy expenditure during incubation in Eiders. Le Maho et al. (1981) found a 39% reduction in body weight after 40 days of fasting in geese, and that lipid accounted for 95% of the energy expended.

Lasiewski & Dawson (1967) provided an allometric equation for basal metabolic rate (BMR) in non-passerines based on body mass. Aschoff & Pohl (1970) made a similar equation which in addition accounted for the influence of diurnal rhythm on BMR. Our IMR and RMR measurements (of birds in resting or β-phase and within the thermoneural zone) were 130–149% of those predicted from these equations. RMR values obtained in this study, RMR measurements of arctic seabirds (Gabrielsen et al. 1988) as well as Prinzinger & Hanssler's (1980) metabolic study of 24 different non-passerine birds in which 11 species were Anseriformes, reveal RMR values above the values predicted from these equations.

According to Aschoff & Pohl (1970) there is a 20–25% difference in metabolism in non-passerine birds during their active (α) versus their resting place (β) phase. Our RMR measurements of Svalbard Eiders were 23% higher than RMR values reported from central Norway in winter acclimatized birds (in resting phase) (Jenssen et al. 1989). The body temperature in summer acclimatized Eiders is 0.5–1.0°C higher than in winter birds (Jenssen et al. 1989). Summer acclimatized Willow Ptarmigan *(Lagopus lagopus)* and Rock Ptarmigan *(Lagopus mutus)* are also reported to have a higher metabolic rate than winter birds (Mortensen & Blix 1986).

Disappearance of a diurnal resting phase in arctic birds during the summer has been described in ptarmigan and seabirds (West 1968; Stokkan et al. 1986; Gabrielsen et al. 1988). In temperate areas there is a distinct day/night variance in light intensity. This is accompanied by a clear variation in RMR and body temperature (T_B). In contrast, diurnal phases in RMR and T_B seem to fade away under continual light conditions of the arctic summer. It therefore seems inappropriate to talk about active/resting phases (Aschoff & Pohl 1970) during arctic summers. When comparing measured with predicted metabolic rates it is important that experimental conditions are standardized.

Metabolism of non-incubating Eiders increased as ambient temperature decreased in the usual homeothermic linear fashion. Thermal conductance was very close to the allometric values calculated for birds of similar body size. When using Herreid & Kessel's (1967) equation for dead birds (dry conductance), we obtained values 131% greater than those predicted, while Aschoff's (1981) equation (α-phase) gave 90% of the predicted value. When compensating for respiratory heat loss, which according to Drent & Stonehouse (1971) is estimated to be 12%, a better agreement with Aschoff's (1981) than Herreid & Kessel's (1967) equation was obtained. Compared to other summer acclimatized arctic birds such as the Raven *(Corvus corax)* (Schwan & Williams 1978) and Ptarmigan (West 1968; Mortensen & Blix 1986), the TC value in Eiders was similar. The TC in winter acclimatized Eiders (Jenssen et al. 1989) was 25% lower than our measurements. A reduced summer insulation is also described in the Brent Goose *(Branta bernicla)* (Irving et al. 1955), Wild Turkeys *(Meleagris galloparo)* (Gray & Prince 1988) and in Ptarmigan (Mortensen & Blix 1986). It is most likely through the naked brood patch that incubating birds lose most heat, which is probably the main reason for the higher TC and LCT measured in summer acclimatized Eiders.

Studies of water content in starved geese have shown that while the extracellular fluid volume was maintained throughout fast, there was an increase after 21 days of fasting. (Le Maho et al. 1981). Studies from body composition of Eiders performed by Parker & Holm (1990) showed that water content increased from 51 to 63% from egg-laying until hatching. It may be argued that this increase was due to depletion of body fat, relative to protein, but our studies of water turnover rates at the end of incubation suggested that Eiders also increase water consumption at this time. A water influx rate of 90 ml/day and a metabolic water production of 20 ml/day would give a water intake of 70 ml/day. Edema associated with starvation is well-known in mammals (Keys et al. 1950). Birds may drink to maintain a steady body mass when approaching a critical weight level (Stage III, as pointed out by Le Maho et al. 1981). This stage is characterized by increased protein utilization as fat reserves disappear and by as rapid drop in body weight. It has also been suggested that drinking at the end of incubation may lead to an underestimation of DEE when calculations are based only on weight loss (Groscolas 1988). According to Groscolas (1988), DEE in penguins should only be determined in the middle part of the starvation period in order to avoid the final period of protein catabolism. Caution should therefore be exercised when using weight loss to calculate DEE in starved birds.

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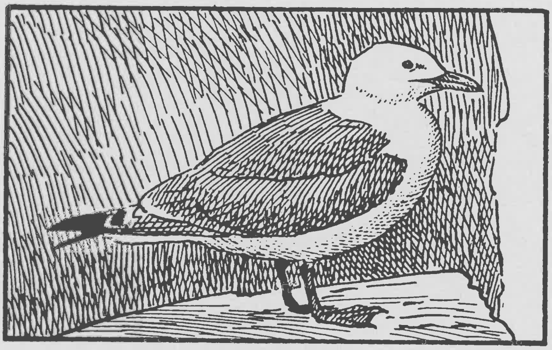
Paper II



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DAILY ENERGY EXPENDITURE AND ENERGY UTILIZATION OF FREE-RANGING BLACK-LEGGED KITTIWAKES[1]

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Abstract. Rates of CO_2 production by breeding Black-legged Kittiwakes (*Rissa tridactyla*) (mean mass, 386 g) were measured by using doubly-labeled water. Kittiwakes alternated days on and off the nest, while they brooded their nestlings. Field metabolic rates (FMR) in nonforaging birds averaged 2.43 ml CO_2/g·hr, or 596 kJ/day. This is 1.9 times the basal metabolic rate (BMR), measured in the laboratory to be 1.31 ml CO_2/g·hr, or 314 kJ/day. FMRs in foraging birds averaged 4.04 ml CO_2/g·hr, or 992 kJ/day which is 3.2 times BMR.

The rate of food consumption by an adult kittiwake, calculated on the basis of the chemical composition and digestibility of capelin (*Mallotus villosus,* the most important dietary item at Hopen Island) was 315 g of fresh matter per bird every other day. A colony of 3,000 breeding pairs of kittiwakes at Hopen Island, using the fishing grounds around the island, would consume about 1,245 kg of fresh fish per day, and add about 76 kg (dry matter) of guano to the marine ecosystem during the chick-rearing period.

Key words: Arctic; seabird energetics; doubly-labeled water; field metabolic rate; food consumption.

INTRODUCTION

The Barents Sea and the waters surrounding Svalbard are highly productive and support large populations of marine mammals and one of the world's greatest concentrations of seabirds (Zenkevitch 1963). These birds constitute a major component of the marine ecosystem and they form an important linkage between the terrestrial and marine ecosystems in the Svalbard area. Black-legged Kittiwakes (*Rissa tridactyla*) comprise a large fraction of the seabird biomass. Thus, studies of kittiwake feeding habits, food requirements, and assimilation efficiency are of great importance in order to determine the energy flow through the ecosystem.

Until recently, the role of seabirds in the arctic marine food chain has been estimated from models of seabird energetics (Wiens and Scott 1975, Furness 1978, Croxall and Prince 1982, Furness and Cooper 1982, Furness and Barrett 1985), which are based on time-energy budget (TEB) studies of individual species. The TEB method involves field measurements of the amounts of time that birds spend in various activities, along with laboratory-based estimates of the energetic cost of these activities (Gessaman 1973, King 1974, Kendeigh et al. 1977). The TEB method is difficult to apply to many seabirds, because they travel long distances to forage and may be unobservable for days at a time. Moreover, recent studies have shown that TEB estimates may contain large errors, depending on the specific TEB method that is employed (Williams and Nagy 1984a, Weathers et al. 1984, but see Nagy et al. 1984).

It is now possible to measure field metabolic rates (FMR) of birds directly, by using the doubly-labeled water method. This technique, used in conjunction with time budget measurements and determinations of diet composition, has yielded much information about food and energy requirements of wild birds (Weathers and Nagy 1980, Williams and Nagy 1984a, Nagy et al. 1984, Bryant et al. 1985). Validation studies on birds have shown that DLW measurements are within ±10% of direct gravimetric measurements of CO_2 production, indicating reasonable accuracy for such studies (Williams and Nagy 1984b).

The main goal of the present study was to determine the field metabolic rates and food requirements of breeding Black-legged Kittiwakes.

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MATERIALS AND METHODS

BIRDS

Black-legged Kittiwakes breeding on Hopen Island (76°30′N and 25°03′E), in the Svalbard archipelago, were studied from 31 July until 8 August 1984. Between 2,000 and 3,000 pairs of kittiwakes breed annually in the colony we studied on the eastern coast of Hopen. Kittiwakes on Hopen lay one or two eggs and they usually fledge one chick (R. T. Barrett, unpubl.). Kittiwake chicks were about 5 to 10 days old when we performed our study, and both parents were making foraging trips.

WEATHER

The weather conditions were measured at Hopen Radio, 500 m away from the colony, every third hour. The weather during the study period was characterized by low temperatures, fog, and strong winds. The mean air temperature was 4.4°C (range, 1.2–12°C), daily average rainfall was 0.4 mm (range, 0.1–1.2 mm) and mean wind speed was 9 m/sec (range, 2–24 m/sec). The ocean surface temperature was about 3.0°C. There was continuous, 24 hr light at Hopen during the study period.

DLW

Metabolic rates (CO_2 production) and water flux rates were measured using the doubly-labeled water method (Lifson and McClintock 1966, Nagy 1980, Nagy and Costa 1980) in one or both members of breeding pairs. A total of 24 adult kittiwakes were caught on the nest. Each was placed in a nylon bag and carried to the field laboratory 500 m from the colony. Birds were injected in the pectoral muscle with 1.2 ml of water containing 97.11% oxygen-18 and 0.4 mc of tritium, and were held in a wooden box for 1.0 to 1.5 hr while the isotopes mixed thoroughly in body water fluid (Degen et al. 1981, Williams and Nagy 1984b). Birds were weighed to ±5 g on a Pesola spring balance, head and bill lengths were measured to ±1 mm to determine sex (males > 92 and females < 92 mm) (Mehlum, unpubl.), and each was marked with individual patterns on the head using picric acid and indian ink. A blood sample (ca. 1 ml) was taken from a wing vein before release. Most of the birds returned to their nest within 10 to 30 min after release, and all were relieved at the nest by their mates during the next 24 hr. Over the next eight days, marked birds were recaptured, weighed, and sampled, some more than once. Visual observations of the colony were made four times each day to check if birds were present. We obtained separate measurement intervals covering brooding of young only ("on nest"), as well as periods away from the nest ("off nest") that included foraging.

Blood samples were centrifuged in heparinized microhematocrit capillary tubes, and were vacuum-distilled to obtain pure water. Isotope levels in the water were measured by liquid scintillation spectrometry (for tritium) and proton activation analysis (for oxygen-18, Wood et al. 1975). Rates of CO_2 production were calculated by using equation 2 in Nagy (1980), and water flux rates were calculated by using equation 4 in Nagy and Costa (1980). Body water volumes were estimated at initial capture from dilution of injected oxygen-18 (Nagy 1980). Water volumes at recaptures were calculated as initial fractional water content multiplied with body mass at recapture.

FOOD CONSUMPTION

Field metabolic rates were converted from units of CO_2 production to units of energy (J) by using the factor 26.5 J/ml CO_2. This factor was calculated from the chemical composition of capelin (74.4% water, 10.1% fat, 13.4% protein, and 1.9% ash; Utne 1976), using energy equivalents for fat and protein from Schmidt-Nielsen (1975). This calculation involves the assumption that the proportions of dietary fat and protein assimilated were the same as their proportions in the diet, and that kittiwakes ate only capelin during our study. In fact, kittiwakes fed primarily on capelin, but they consumed some arctic cod and various species of crustaceans as well (Mehlum and Giertz 1984; Lydersen et al. 1985; Giertz et al. 1985; R. T. Barrett, pers. comm.). However, the conversion factors for these diet items should be within 10% of that for capelin, due to similarities in the conversion factors for protein and fat (Schmidt-Nielsen 1975).

The amount of food an adult kittiwake would have to consume to satisfy its daily energy requirement (as measured with doubly-labeled water) was calculated from the energy content and energy assimilation efficiency for capelin. These fish contain 25.7 kJ/g dry matter, and 76% of this energy is available for metabolism by kittiwakes (Gabrielsen, Mehlum, and Brekke, unpubl. data). Thus, with a water content of 74.4%,

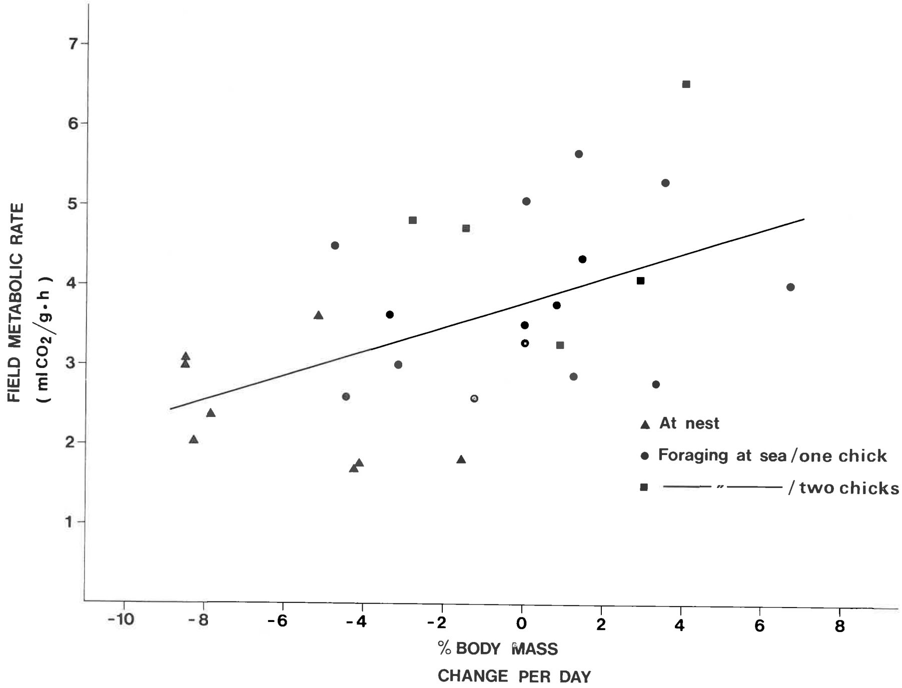

FIGURE 1. Relationship between field metabolic rate, measured with doubly-labeled water, and rate of increase or decrease in body mass for breeding adult kittiwakes at Hopen. The line is the least squares regression, where $y = 3.82 + 0.16x$, $r^2 = 0.26$, $F_{1,26} = 9.06$, $P < 0.01$.

capelin contain 5.0 kJ metabolizable energy per g of fresh matter.

STATISTICS

Two-tailed t-tests were used to determine the significance of differences between means. Results are reported as mean ± standard deviation. The regression line in Figure 1 was calculated by using the least-squares method of linear regression.

RESULTS

BODY MASS

Female kittiwakes had significantly lower body masses (367 ± 11 g) than did males (399 ± 29 g, $P < 0.01$). However, there were no significant differences in mass-specific rates of CO_2 production or water flux, or rates of body mass change between sexes, so mean body mass (386 g) and mean values for the rate processes were used in subsequent calculations. Kittiwakes maintained body masses on average while foraging, but they lost body mass while brooding on their nests (Table 1).

FIELD METABOLIC RATE

Basal metabolic rate (BMR) measured in the laboratory was 1.31 ml CO_2/g·hr or 314 kJ/day (Gabrielsen et al., unpubl.). Field metabolic rate (CO_2 production) of foraging birds averaged 4.04 ± 1.11 ml CO_2/g·hr which is equivalent to 992 ± 273 kJ/day, or 3.16 times BMR (Table 1). Nonforaging birds had significantly lower ($P < 0.01$) metabolic rates, averaging 2.43 ± 0.73 ml CO_2/g·hr, or 596 ± 179 kJ/day (1.90 times BMR).

There was a tendency (not statistically significant) toward higher field metabolic rates during foraging in parents that had two chicks (4.71 ± 1.41 ml CO_2/g·hr, $n = 3$) than in parents having one chick (3.87 ± 1.01 ml CO_2/g·hr, $n = 16$; see Fig. 1). There was a significant correlation between field metabolic rate and % body mass

TABLE 1. Field metabolic rate, water influx and body mass of adult kittiwakes on Hopen Island, 31 July to 8 August 1984.

		Body mass		Field metabolic rate		Water influx rate	Measurement period (days)
Animal	Sex	Mean, g	Change, %/day	ml CO_2/g·hr	kJ/day	ml/day	
While off nest							
2	M	452.5	−3.38	3.64	1,048	115	0.98
2†	M	447.5	+1.29	5.69	1,619	277	0.99
3	M	387.5	+0.89	3.78	932	158	1.48
4*	F	352.5	+2.90	4.12	924	171	1.47
4*†	F	367.5	+4.00	6.60	1,543	366	1.02
5	F	372.5	+1.25	2.87	680	143	1.07
5†	F	375.0	0	5.19	1,238	241	1.45
8†	M	395.0	+3.49	5.31	1,334	246	1.45
8	M	412.5	+3.31	2.78	729	217	1.10
9	M	402.5	−3.08	3.01	771	217	2.02
10*†	F	367.5	−2.85	4.83	1,129	196	1.43
10*	F	362.5	+0.88	3.30	761	231	1.57
11†	M	432.5	+1.41	4.37	1,202	190	0.82
11	M	435.0	0	3.30	703	198	1.05
13	M	400.0	−4.46	2.62	667	209	1.12
15	M	387.5	−1.16	2.60	641	137	1.11
15	M	377.5	−4.79	4.51	1,083	244	0.83
19	M	400.0	+6.64	4.04	1,028	207	1.13
21*	F	365.0	−1.49	4.73	1,098	172	1.86
23	F	340.0	0	3.54	765	179	1.66
Mean		391.6	+0.24	4.04	995	206	
SD		31.5	3.01	1.11	290	56	
While on nest							
6	F	367.5	−8.30	2.06	481	51	0.82
6	F	362.5	−4.23	1.70	392	27	1.02
7	F	342.5	−1.57	1.83	399	34	0.93
12	F	387.5	−7.87	2.36	582	38	0.82
19	M	400.0	−8.52	3.00	763	46	0.88
20	M	395.0	−8.53	3.11	781	36	0.89
20	M	372.5	−4.15	1.74	412	47	0.97
23	F	365.0	−5.20	3.61	838	33	0.83
Mean		374.1	−6.05	2.43	581	39	
SD		19.1	2.63	0.73	188	8	

* Nest contained two chicks.
† Off nest during windy day.

change per day in kittiwakes (Fig. 1; least-squares regression analysis; $F_{1,26} = 9.06$, $P < 0.01$). Weather conditions also affected field metabolic rate. There was a significant increase ($P < 0.001$) in energy expenditure of foraging birds during a 24-hr period of strong southwesterly winds from 3.44 ± 0.59 ml CO_2/g·hr ($n = 5$, wind speed = 7.8 m/sec) before, or 3.67 ± 0.92 ml CO_2/g·hr ($n = 6$, wind speed = 8.3 m/sec) after strong winds to 5.33 ± 0.77 ml CO_2/g·hr ($n = 6$, wind speed = 12.8 m/sec) during strong winds.

Rates of water influx were highest ($P < 0.01$) when kittiwakes were off their nest (Table 1). Body water contents averaged 61.4 ± 2.2% of body mass ($n = 17$).

Visual observation of six marked birds by telescope, checked each 30 min, showed that kittiwakes at Hopen Island spent an average of 23 hr away from the nest (range, 17.0–29.5 hr). Both parents participated in brooding and feeding of the chicks. The brooding birds remained on the nest until relieved by their mates. Three of 17 studied kittiwakes raised two chicks.

FOOD CONSUMPTION

The amount of food a typical adult kittiwake would have to consume to satisfy its own energy requirements was calculated from field metabolic rate measurements as follows. Energy expenditure during one day on the nest was 597 kJ/bird, and one day foraging cost 992 kJ/bird to give a total two-day expenditure of 1589 kJ/bird. At a metabolizable energy yield of 5.0 kJ/g fresh mass of food (see above), the kittiwake must consume 315 g fresh food or about 82% of its body mass. All of this food would be consumed on the day the bird foraged.

We can check this estimate of feeding rate by calculating its associated water influx rate, and comparing this with actual influxes measured with tritiated water. A mass of 315 g of capelin, at 74.4% water, contains 234 ml of H_2O. Metabolically-produced water, from oxidation of assimilated protein and lipid, would provide an additional 0.122 ml H_2O/g fresh food (conversion factors from Schmidt-Nielsen 1975), for a total water yield of 272 ml H_2O/315 g capelin consumed. This is about 11% higher than the measured two-day water influx of 245 ml H_2O/bird (Table 1). The difference may be due to our assumption that 100% of the diet was capelin, which has a relatively high water content. Ingestion of other foods with lower water contents would improve the agreement. Moreover, measured water influxes in Table 1 may underestimate those in kittiwakes maintaining steady-state, because our experimental birds, on average, were slowly losing body mass (Table 1). Thus, they were probably not eating quite enough food to meet their energy expenditures, with the difference coming from energy stored in their bodies. This comparison suggests that the feeding rate estimated from energy expenditure is reasonable, and that kittiwakes consumed little or no sea water while foraging.

DISCUSSION

The FMR of free-ranging kittiwakes was ca. 1.9 times BMR when brooding and ca. 3.1 times BMR when they were off their nests. These values are in accordance with studies of other species in which isotopically-labeled water has been used on breeding birds (Utter 1971, Utter and LeFebvre 1973, Hails and Bryant 1979, Bryant and Westerterp 1980, Weathers and Nagy 1980, Nagy et al. 1984, Ricklefs and Williams 1984). Hails and Bryant (1979) found higher FMR in male Common House-Martins (*Delichon urbica*) feeding their broods. Male European Starlings (*Sturnus vulgaris*) expended less energy during the middle of the nesting period than females (Ricklefs and Williams 1984). In our study there was no significant difference between males and females in FMR. Our study was performed during a short period when the adults were brooding and feeding their chicks. A longer experimental period, more measurements, and stable weather conditions are required to explore for possible sexual differences in FMR. Feeding modes are probably very different in seabirds as compared with house-martins or starlings. Seabirds forage at a much longer distance from the nest than do martins or starlings.

At Hopen both parents shared in feeding of their chicks. Three of 17 parents studied were feeding two chicks. FMRs averaged ca. 3.0 times BMR in parents feeding one chick, and ca. 3.6 times BMR in parents feeding two chicks, but this difference is not statistically significant due to high variability in FMR data (Fig. 1). Although Ricklefs and Williams (1984) found that FMR was independent of brood size in starlings, Hails and Bryant (1979) found a significant correlation between FMR and brood mass in male house-martins. An increase in brood size from three to four young entails an average increase in energy expenditure by female house-martins of 18%. This is in accordance with our study which indicated an FMR increase of 20% in kittiwakes feeding two chicks. The parents of two chicks probably have to spend more time flying while searching for food, and they may also spend more energy to carry a greater mass of food from the foraging area. Purple Martins (*Progne subis*) and house-martins showed an increase in energy expenditure with increased rate of food delivery to the brood (Utter and LeFebvre 1973, Hails and Bryant 1979, Bryant and Westerterp 1983).

Bryant and Westerterp (1983) found a significant correlation between FMR and weather factors (ambient temperature and windspeed). Fair weather (warm and calm days) resulted in higher energy expenditure. This was associated with better food supply (flying insects), more time spent in flight and a greater amount of food brought to the nestlings. Foraging kittiwakes showed a significant increase in FMR during one day of heavy wind. This is probably not due to an increased cost of capturing prey, but rather to an increased energy cost for flapping flight. The energy cost of flight in free-living birds should not be calculated as a given multiple of BMR, as is done in many models (summarized by Flint and Nagy 1984). Behavior and aerodynamic properties are certainly important factors, but weather also has a large influence on the energy expenditure during flight. High wind increases flapping time at the expense of gliding or soaring in kittiwakes.

Behavioral observations of six marked pairs of kittiwakes on Hopen island showed that they spent an average of 23 hr away from their nests during the chick rearing period. We assume that kittiwakes spent much of their time foraging while not on their nests, but they may also have been resting at the breeding island. During the experimental period, flocks of several hundred kittiwakes were often seen resting close to the breeding colony. Most often these birds were sitting with their heads under their wings, but they were also seen preening. Thus, our measurements of FMR and water flux during off-nest periods may include periods of rest as well as foraging bouts.

Kendeigh et al. (1977) provide equations for estimating daily energy expenditure of birds, and these have often been used in models for estimating energetics of seabird populations (Wiens and Scott 1975, Furness 1978, Furness and Cooper 1982, Furness and Barrett 1985). These equations compensate for the effect of temperature on energy metabolism, but Kendeigh et al. (1977) suggest that they may underestimate metabolism for birds breeding at high latitude. Nagy et al. (1984) made DLW measurements of FMR in Jackass Penguins (*Spheniscus demersus*), and found close agreement with the predictions from Furness and Cooper's (1982) bioenergetic model, which is based on Kendeigh's equations. Kendeigh's equation (0°C) predicts a daily energy expenditure for a 386-g kittiwake of 443 kJ/day. Actual FMRs were 36% higher in kittiwakes on the nest, and 123% higher for birds off the nest.

Walsberg's (1983) equation for daily energy expenditure, based on studies of 42 avian species, gives an estimate of 479 kJ/day for a 386-g kittiwake. Actual FMRs were 21% higher (on nest) and 108% higher (off nest, Table 1). These comparisons indicate that caution should be taken when modelling energetics of northern seabirds using equations by Kendeigh et al. (1977) and Walsberg (1983) to estimate daily energy expenditure.

A breeding kittiwake eats an average of 315 g of fresh capelin every other day (assuming a diet of capelin only). This represents only the food an adult needs for its own energy requirements, and does not include food given to its young. Based on metabolism and growth rate measurements on growing kittiwake chicks (Gabrielsen and Mehlum, unpubl.), and assuming that they have the same assimilation efficiency as adults, we estimated that a 10-day-old chick would consume about 100 g of fresh food each day. Thus, the food requirements of the two adults and one chick (age 10 days) at a typical nest would be 415 g fresh fish per day. A colony of 3,000 breeding pairs (including one chick in each nest) of kittiwakes would therefore consume about 1245 kg of capelin per day. At a dry matter digestibility of about 75% (Gabrielsen and Mehlum, unpubl.), we estimate that about 76 kg (dry matter) of nitrogen-rich guano is added to the Hopen island ecosystem each day by this colony alone. Much of this guano is deposited on the terrestrial portion of the system.

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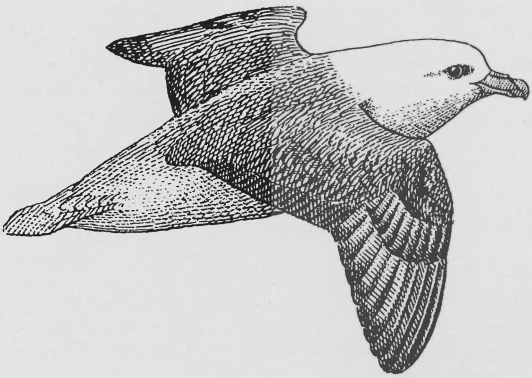
Paper III



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Thermoregulation in four species of arctic seabirds

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Summary. Thermoregulation was studied in four species of seabirds in Ny-Ålesund, Svalbard. The major findings of the study are:

1. Resting metabolic rates (RMR) were 1.64, 1.00, 1.59 and 1.11 ml O_2/g·h, thermal conductance (TC) 0.0466, 0.0336, 0.0475 and 0.0282 ml O_2/g·h·°C and body temperature (T_b) 40.2, 38.7, 39.9 and 39.6 °C, in Kittiwakes, Fulmars, Black and Brünnich's Guillemots, respectively.

2. RMR values from all four species were above predicted values based on equations from Lasiewski and Dawson (1967), Aschoff and Pohl (1970) and Ellis (1984). In Kittiwakes the measured RMR values were 183%, 158% and 156% of predicted values while in Fulmars only 131%, 113% and 112%.

3. Thermal conductance was lower, i.e. insulation better, in Fulmars and Brünnich's Guillemots compared to Kittiwakes and Black Guillemots. TC values obtained in this study were different from values predicted from equations of Herreid and Kessel (1967) and Aschoff (1981). While Herreid and Kessel's values were somewhat elevated, Aschoff's equation gave values below our measurements.

4. Low ambient temperatures and the birds' activity level are suggested as the major reason for high RMR in Kittiwakes, Black and Brünnich's Guillemots.

5. The RMR values measured in Fulmars did not differ from those of Procellariiformes studied in sub-Antarctica. It is suggested that the lower metabolic rate and body temperature enable Fulmars to survive extended periods of fasting.

Introduction

The Kittiwakes, Fulmars and Brünnich's Guillemots constitute the most numerous seabird species in the Barents Sea. In order to determine the energy flow through the arctic marine ecosystem it is important to determine seabirds' resting metabolic rate (RMR) as well as their thermoregulation when exposed to different ambient temperatures (T_a). Energy budget calculations of free ranging birds have often been related to RMR. Multiples of RMR have been used to estimate energy expenditure of single individuals (Utter and LeFebvre 1973) and populations (Furness 1978) as well as during activities such as walking, swimming or flying (Raveling and LeFebvre 1967; Prange and Schmidt-Nielsen 1970; Tucker 1972; Fedak et al. 1974). Energy expenditure of a bird at rest is strongly influenced by T_a. The extent of this influence in different species is shown by the thermal conductance (TC). In addition to direct measurements in the field and laboratory, RMR and TC in birds have been estimated from various allometric equations (Aschoff and Pohl 1970; Lasiewski and Dawson 1967; Herreid and Kessel 1967; Aschoff 1981). Such estimates are frequently used in models of seabird energetics in which RMR and TC are unknown.

In only two studies of seabirds, living and breeding in the arctic, have such values been directly measured (Scholander et al. 1950; Johnson and West 1975). Both studies gave RMR and TC values well above the predicted ones.

The aims of this study were (1) to determine RMR, T_b and TC in four species of arctic seabirds,

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Abbreviations: *RMR* resting metabolic rate; *TC* thermal conductance; T_a ambient temperature; T_b cloacal temperature; T_c lower critical temperature; *RQ* respiratory quotient; V_{O_2} oxygen consumption

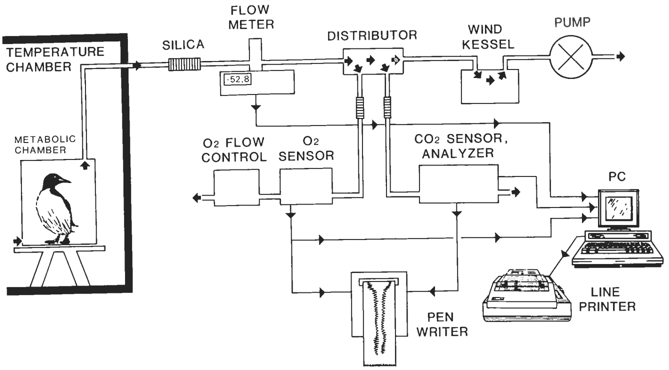

Fig. 1. Experimental set-up for recording oxygen consumption and carbon dioxide production in seabirds

(2) to compare these measurements with others and with theoretical estimates and (3) to give new insights into the thermoregulation of arctic breeding seabirds.

Materials and methods

Experimental birds. The study was carried out at the Research Station of the Norwegian Polar Research Institute in Ny-Ålesund (79 °N), Svalbard. A total of 16 adult Black-legged Kittiwakes (*Rissa tridactyla*), 16 Fulmars (*Fulmarus glacialis*), 13 Black Guillemots (*Cepphus grylle*) and 11 Brünnich's Guillemots (*Uria lomvia*) of both sexes was studied during June/July in 1984, 1985 and 1987. Birds were either trapped on the nest, using a bamboo pole with a nylon snare or they were caught in flight with a net-gun (Coda Enterprises). The birds were kept in individual outdoor cages for 1–2 days. They were not fed but were given water ad libitum. The first metabolic measurement was done 10–12 h after capture.

Metabolic rate measurements. A metabolic chamber was placed inside a climatic chamber where the T_a could be controlled within +1 °C from −25 to +30 °C (Fig. 1). The metabolic chamber was of plexiglass which allowed continuous TV surveillance. $\dot{V}_{O_2}$ and CO_2 production were measured in an open system using an oxygen analyzer (Applied Electrochemistry Inc.) and a carbon dioxide analyzer (Binos-1, Leybold-Heraeus). Air was dried with silica. Air flow (2.5–4.0 l/min) was measured with a flowmeter (Hi-Tec, F113) connected to a readout (Model E-0020). The air flow was adjusted to keep CO_2 levels in the chamber between 0.3% and 1.0%. The instruments were calibrated with ambient air before each test.

T_a in the climatic and metabolic chambers were measured with copper-constantan thermocouples connected to a digital thermometer (Fluke, 2168 A). T_a in the metabolic chamber was measured 3–5 cm above the birds' body surface. T_b of the birds was measured continuously with an epoxy-coated thermocouple inserted about 3 cm into the colon of the birds. Each bird was measured at 2–5 different T_a. Body weights were measured at the start and at the end of each experiment, using a Metler PE 16 balance (accuracy ±0.1 g). During each test, the bird was exposed to a given temperature for at least 1.5–2.0 h. All measurements were done under full light conditions in the climatic chamber, since these birds experience 24 h of daylight during the breeding season. At each T_a, $\dot{V}_{O_2}$, CO_2-production, flow rate and T_b were read by a computer (Apricot PC) every 30 s when a stable resting period was obtained. $\dot{V}_{O_2}$ (ml O_2/g·h), CO_2-production (ml CO_2/g·h), RQ and energy expenditure (kJ/bird·day and Watt/bird) were calculated. Oxygen and carbon dioxide content in the outflow gas were determined to the nearest 0.01%. The final values for $\dot{V}_{O_2}$ and $\dot{V}_{CO_2}$ are accurate to within ±5%. All results are given at STPD.

Thermal conductance. Thermal conductance (TC) was calculated from the mass specific metabolic rate and at T_a below T_c. The regression line was calculated by dividing the $\dot{V}_{O_2}$ by $T_b - T_a$ at a T_a below 0 °C. TC should be expressed as W/m·°C (Bligh and Johnson 1973). However, in order to compare our results with those of Herreid and Kessel (1967) and Aschoff (1981), TC was expressed as ml O_2/g·h·°C. TC is expressed as 'wet' conductance since evaporative heat loss from respiration was not excluded. In calculating energy expenditure from $\dot{V}_{O_2}$, the conversion coefficient of 4.8 kcal per liter oxygen ($RQ = 0.75$) was used (Schmidt-Nielsen 1975; 1 kcal = 4.185 kJ).

The lower critical temperature (T_c) was determined from the intersections between the lines representing metabolic rate at low T_a and the lines representing RMR in the thermoneutral zone.

Results

Resting metabolic rate

The mean body weight value from each species was used (see Table 1) when calculating the metabolic rate.

Fulmars, Black and Brünnich's Guillemots settled down in the metabolic chamber within a few minutes and stable measurements were obtained within 1 h. The Kittiwakes, however, initially showed restless behavior, and stable measurements were not obtained before 1 to 2 h.

The mean RMR values are given in Table 1. The corresponding mean RQ were 0.73±0.01,

Table 1. Body weight (mean ± SD), resting metabolic rate (RMR, ml O_2/g·h, mean ± SD), thermal conductance (TC, ml O_2/g·h·°C) and lower critical temperature (T_c, °C) in four species of seabirds in Svalbard. N is number of birds

Species	N	Body mass (g)	RMR (ml O_2/g·h)	TC (ml O_2/g·h·°C)	T_c (°C)
Rissa tridactyla	16	365.0 ± 29.8	1.64 ± 0.08	0.0466	+4.5
Fulmarus glacialis	16	651.0 ± 83.4	1.00 ± 0.09	0.0336	+9.0
Cepphus grylle	13	342.2 ± 22.3	1.59 ± 0.12	0.0475	+7.0
Uria lomvia	11	819.3 ± 72.7	1.11 ± 0.12	0.0282	+2.0

0.73 ± 0.01, 0.72 ± 0.01 and 0.72 ± 0.01. Fulmars had a significantly lower specific RMR than Kittiwakes, Black and Brünnich's Guillemots. Kittiwakes showed the highest specific RMR, about 64% higher than those of the Fulmars.

All metabolic measurements were performed during full light conditions in order to simulate the arctic summer. We found no significant difference between RMR values measured during the day (9^{00}–15^{00}) and those measured during the night (21^{00}–03^{00}). This indicates, under the given experimental conditions, that there was a lack of diurnal rhythmicity in the RMR of all four species studied.

The mean daily energy expenditures of birds studied, at thermoneutrality, are given in Table 2. All these values are higher than those predicted by Lasiewski and Dawson (1967), Aschoff and Pohl (1970) and Ellis (1984). In energy expenditure they were most pronounced in Kittiwakes (183%, 158% and 156% of predicted values, respectively) while they were lowest in Fulmars (131%, 113% and 112% of predicted values, respectively). In general all RMR values obtained in this study were above the predicted equations.

Metabolism at low ambient temperatures

The RMR at different T_a are presented in Fig. 2. T_b was stable over the whole range of T_a, 40.2 ± 0.7, 38.7 ± 0.5, 39.9 ± 0.3 and 39.6 ± 0.7 °C in Kittiwakes, Fulmars, Black and Brünnich's Guillemots, respectively. Kittiwakes, which had the highest RMR, also had the highest T_b, while Fulmars, which had the lowest RMR had the lowest T_b. The T_b difference in the last two species was significant ($P < 0.001$, t-test).

Below T_c $\dot{V}_{O_2}$ increased linearly in all species. The regression line intersected the abscissa close to T_b in all species. The regression equations in Kittiwakes, Fulmars, Black and Brünnich's Guillemots were $y = 1.87 - 0.05x$, $y = 1.34 - 0.04x$, $y = 1.93 - 0.04x$ and $y = 1.14 - 0.03x$, respectively. TC and T_c values are given in Table 1. The insulation in the Fulmar is 39% better than in the Kittiwake, while it is 68% better in the Brünnich's Guillemot compared to the Black Guillemot. TC values obtained in this study were different from values obtained by equations made by Herreid and Kessel (1967) and Aschoff (1981) (Table 2).

Discussion

True basal metabolic rate (BMR) is measured when the organism is resting, during the dark-phase and in the post-absorptive state within the thermoneutral zone (Bligh and Johnson 1973). In our study the birds were physically inactive during measurement and they fasted 10–12 h prior to each experiment. Yet, in all likelihood, the birds were excited and we therefore do not claim to have measured true BMR but rather resting metabolic rate (RMR). Nevertheless we think that our measurements are comparable to values termed BMR in the literature.

Aschoff and Pohl (1970) have shown a 20–25% difference in metabolism in birds during their ac-

Table 2. Resting metabolic rate and thermal conductance in four species of seabirds

Species	Mean body mass (g)	Mean resting metabolic rate				Thermal conductance		
		This study (kJ/bird·day)	L&D (1967)	A&P (1970)	Ellis (1984)	This study (ml O_2/g·h·°C)	H&K (1967)	A (1981)
Rissa tridactyla	365	289	183	158	156	0.0466	115	86
Fulmarus glacialis	651	314	131	113	112	0.0336	113	82
Cepphus grylle	342	262	174	151	149	0.0475	113	85
Uria lomvia	819	438	154	133	132	0.0282	107	77

Data from this study are compared (as %) to values predicted according to the equations given by Lasiewski and Dawson (1967), Aschoff and Pohl (α-phase) (1970), Ellis (1984), Herreid and Kessel (1967) and Aschoff (1981)

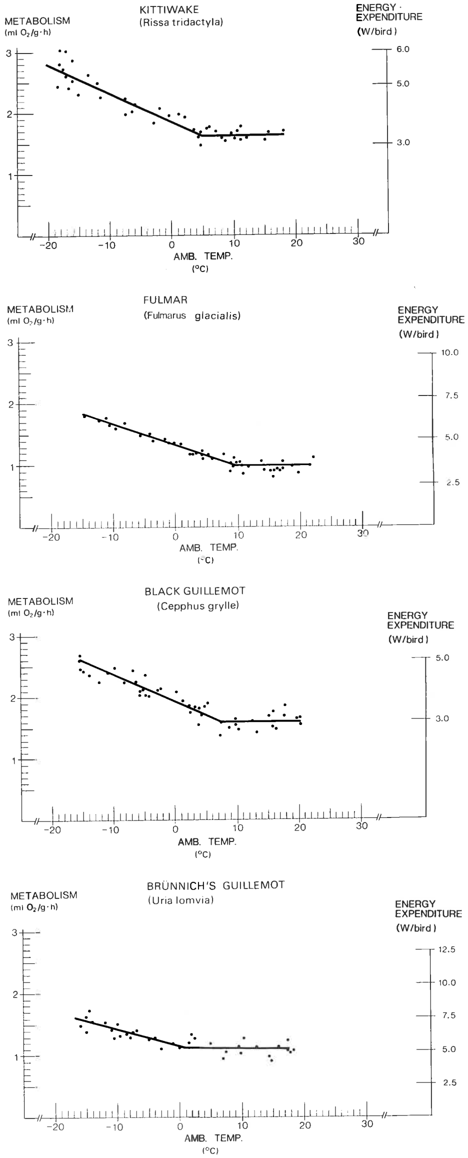

Fig. 2. Oxygen consumption of Kittiwake, Fulmar, Black Guillemot and Brünnich's Guillemot at different T_a. The regression lines below T_c intersected the abscissa at the ambient temperatures close to the measured T_b. The horizontal lines were drawn through the mean values obtained at thermoneutrality

tive (α) versus their resting (ϱ) phase. Our experiments were performed during full light conditions, due to the midnight sun during the arctic summer. When measurements during day and at night were compared, we were unable to find a diurnal cycle in T_b and RMR. These results, together with measurements of T_b by telemetry (Gabrielsen, unpublished), indicate that there is little or no diurnal rhythmicity in seabirds studied in Svalbard. Disappearance of a nocturnal resting phase during summer has also been described for other arctic birds (West 1968; Stokkan et al. 1986).

Lasiewski and Dawson (1967) provided an allometric equation for BMR in non-passerines based on body mass. Aschoff and Pohl (1970) made a similar equation, which accounted for the influence of the diurnal rhythm on BMR. Ellis (1984) based his equation on metabolic measurements of seabirds only. His equation was elevated but parallel to that of all non-passerines as predicted by Lasiewski and Dawson (1967). Prinzinger and Hänssler's (1980) metabolic measurements of 24 species of non-passerines, our measurements, and those by Scholander et al. (1950) and Johnson and West (1975), reveal RMR well above the values predicted from these equations. Adult Kittiwakes (365 g) for example, showed RMR values which were 183, 158 and 156% of these predicted values, respectively. These results indicate an influence of climate on RMR. This is in accordance with earlier observations by Weathers (1979), Hails (1983) and Ellis (1984) that BMR in seabirds is a function of breeding latitude. Other bird species, living and breeding in the north, also show a higher RMR than predicted (West 1972; Schwan and Williams 1978; Mortensen and Blix 1985). However, this study on Kittiwakes, Black and Brünnich's Guillemots indicates that other factors than size, diurnal phase and climate may additionally account for their high RMR. Ellis (1984) found that seabirds that feed below the water surface have higher metabolic rates than birds feeding on the surface. On the contrary, the study by Scholander et al. (1950) of Glaucous Gulls (*Larus hyperboreus*) and our study of Kittiwakes, show that both these surface feeders have a higher RMR value than the Alcidae, which are typical divers. A possible explanation for the difference in RMR between Laridae and Alcidae is better cold adaptation in the Alcidae since they are more exposed to low sea water temperatures. The difference may also be related to physical activity. Their modes of life are different. Kittiwakes and Glaucous Gulls, which are surface feeders, use more energy to search for food compared to Black and Brünnich's Guillemots, which are divers. In birds the energy cost of diving is less than that of flying. While the cost of diving is 1.2–2 times RMR, the cost of flying varies from 6–12 times RMR (Butler and Woakes 1982). Active birds, compared to less active birds, are known to have higher $\dot{V}_{O_2}$ max, increased ventilation volume, higher mitochondrial volume (more aerobic enzymes) and a higher cardiac output (Butler 1982). These behavioral and physiological differences may explain some of the RMR differences between Laridae and Alcidae.

The Fulmar studied had a significantly lower T_b than the other species studied. This is in accordance with other studies showing that Procellariiformes have T_b's significantly lower than other non-passerines (McNab 1966; Warham 1971; Adams and Brown 1984). According to McNab (1966) the low T_b of Procellariiformes suggests a low BMR and/or a high rate of heat loss. We found that the Fulmar, despite its body weight being 170 g below Brünnich's Guillemot, possesses nearly the same insulation (Table 1). In accordance with the low T_b and TC we also measured a low RMR.

RMR of the Fulmar is close to those predicted from other non-passerines. They are nearly identical to those predicted by Adams and Brown (1984) for 10 species of sub-Antarctic Procellariiformes. The Fulmar is found in the Svalbard region throughout the year. A low BMR, T_b, good insulation together with its ability to store oils in the proventricular part of the intestine (Rosenheim and Webster 1927; Imber 1976) are the most important factors to survive the long winter nights in the Arctic with extended periods of fasting. At the island of Jan Mayen (71 °N), trappers have recorded Fulmars coming midwinter to settle at the bird cliffs. When arriving the birds were plump and had large breastmuscles, but after a fortnight on the cliffs they became very thin (Løvenskiold 1964).

When calculating energy cost of flight, according to the equation by Masman and Klaassen (1987), Fulmars have a lower flight cost compared to Kittiwakes. It therefore appears that Fulmars, even though they fly a lot, still retain a low RMR as a result of their low flight cost. Thus their activity pattern or manner of flying affects their RMR in a predictable way.

Scholander et al. (1950) described two main adjustments for animals living in the cold. One was to lower the heat loss by increasing the insulation, the other was to increase the heat production during cold stress by raising the metabolism. While the Fulmars and Brünnich's Guillemots seem to use the former mechanism, the latter principle seems to be used by the Kittiwakes and Black Guillemots. As T_a decreased, metabolism increased in the usual homeothermic linear fashion in all species studied. TC's in the four species were very close to allometric values calculated for alert birds of similar body size. By using Herreid and Kessel's (1967) equation for dead birds (dry conductance), we got values 107 to 115% of predicted, while using Aschoff's (1981) equation (α-phase) we got 77–86% of the predicted value. When compensating for respiratory heat loss, which according to Drent and Stonehouse (1971) is 12%, we got better agreement with Herreid and Kessel (1967) than with Aschoff (1981). Compared to other arctic bird species, the raven (*Corvus corax*) and the ptarmigans (*Lagopus* spp.), adapted to the cold (Schwan and Williams 1978; West 1972; Mortensen and Blix 1985), TC's were higher in all seabirds studied. When comparing seabirds of similar body size measured in the temperate areas (see Aschoff 1981), TC in arctic living seabirds is lower. The Fulmar has 19% higher TC values than Brünnich's Guillemot. As a result of a reduced metabolism in Fulmars the T_c is higher compared to other species. This is compensated by good insulation which is important, especially when 'fasting'.

Energy budgets from seabirds are often presented in terms of 'predicted metabolic rate', especially in models of seabird energetics (Wiens and Scott 1975; Furness 1978; Croxall and Prince 1982; Furness and Barrett 1985). Kendeigh's et al. (1977) equations are frequently used in model studies explaining the interactions of seabirds and fish populations. These equations include BMR, temperature regulation, specific dynamic action and energy expenditure of locomotion while the bird is 'caged' and is not compensated for climate. When applied to daily energy budgets for Kittiwakes (independently studied by Gabrielsen et al. (1987) using the doubly labeled water technique) this direct method gave results which were 36% higher than predicted on nest and 123% higher off nest.

The results reported here and in other studies (Ellis 1984) suggest that the physiological factors are not only related to geographic locality (Schwan and Williams 1978), but also to the birds' activity level. In addition the study shows that great caution should be taken when seabird energetics are modelled using only allometric equations.

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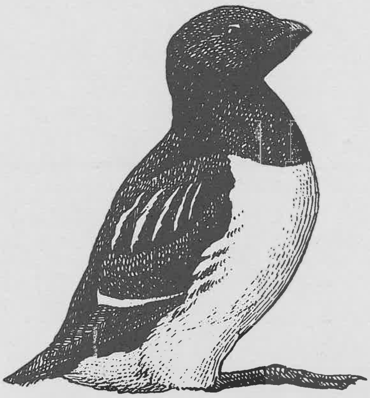
Paper IV



FIELD AND LABORATORY METABOLISM AND THERMOREGULATION IN DOVEKIES (*ALLE ALLE*)

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ABSTRACT.—The Dovekie (*Alle alle*) is an abundant seabird in the high Arctic. We studied Dovekie energetics by measurements of resting metabolic rate (RMR) in the laboratory and rates of CO_2 production (with doubly labeled water, DLW) of free-living adults during the chick-rearing period. Within the thermoneutral zone, resting metabolism was 2.42 ± 0.13 ml $O_2 \cdot g^{-1} \cdot h^{-1}$ (177.9 ± 9.6 kJ/day). These values were 84–112% greater than predicted for non-passerines. Thermal conductance (C) was 0.0630 ± 0.0029 ml $O_2 \cdot g^{-1} \cdot h^{-1} \cdot {}^{\circ}C^{-1}$, which was close to or lower than allometric values of birds of similar body size. Field metabolic rate (FMR) was 6.68 ± 1.06 ml $CO_2 \cdot g^{-1} \cdot h^{-1}$ (696.1 ± 103.7 kJ/day). This is the highest FMR value, corrected for body mass, yet published for seabirds studied by the doubly labeled water method during the chick-rearing period. The high wing loading of Dovekies implies that flight cost may be high, resulting in a high FMR. Despite a high FMR, Dovekies had an FMR/RMR ratio of 3.9, similar to values reported for other species in other regions during chick-rearing. We estimated that the amount of plankton (mainly *Calanus finmarchicus*) consumed each day by Dovekies equaled 80% of their body mass. A colony of 70,000 pairs of Dovekies (assuming one 14-day-old chick in each nest) would consume 21.9 tons of fresh zooplankton per day, and would add approximately 2.1 tons (dry mass) per day of guano to the marine and terrestrial ecosystems over this period. *Received 4 January 1990, accepted 13 July 1990.*

THE DOVEKIE (*Alle alle*) is the smallest (163 g) and the most abundant seabird species of the Svalbard archipelago. The largest breeding colonies, which comprise several hundred thousand pairs, are on the western coast of Spitsbergen (Løvenskiold 1964). Dovekies feed offshore during the breeding season, and have been observed as far as 150 km from the colonies (Byrkjedal et al. 1974, Brown 1976). Some Dovekies also feed inshore (Hartley and Fisher 1936, Evans 1981). Near Hornsund, Svalbard (77°N), the birds feed mainly offshore (Konarzewski and Taylor pers. obs.). The diet consists primarily of planktonic copepods (Norderhaug 1980; Evans 1981; Lydersen et al. 1985; Weslawski, Taylor, and Konarzewski unpubl. data). The large populations of Dovekies are the major avian predators on marine copepods in the Svalbard area. Dovekies spend most of their time at sea, and may play an important role in recycling nutrients in arctic marine ecosystems. They also have a significant impact on terrestrial ecosystems by transporting organic matter and nutrients from sea to land (Norderhaug 1970, Taylor and Konarzewski unpubl. data).

High-latitude seabirds during the chick-rearing period have high values of resting metabolic rate (RMR) within the thermoneutral zone, and a high field metabolic rate (FMR) when compared with tropical and temperate species (Johnson and West 1975; Ricklefs et al. 1986; Roby and Ricklefs 1986; Obst et al. 1987; Gabrielsen et al. 1987, 1988). The FMR/RMR ratio in high-latitude seabirds varies between 3 and 4, which is consistent with Drent and Daan's (1980) proposal of a "maximum sustained working level" of 4 times basal metabolic rate (BMR) during chick-rearing. The Dovekie activity pattern during chick-rearing reflects a high energy expenditure. Each parent makes approximately 3–5 trips between nesting and feeding areas daily (Norderhaug 1980, Evans 1981, Stempniewicz and Jezierski 1987, Konarzewski and Taylor pers. obs.). Dovekies have only one chick, which is brooded for 5–7 days (Norderhaug 1980, Taylor and Konarzewski pers. obs.).

Dovekies and other alcids practice both aerial and underwater locomotion. They use their wings for propulsion, and the media differ sub-

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stantially in density and in buoyancy. Flying auks probably represent a compromise between birds adapted for locomotion in air and in water (Storer 1960). Compared with other seabirds of the same mass, auks have reduced wing span and wing area (Masman and Klaassen 1987, Pennycuick 1987). Thus, we expect a high energetic cost of aerial locomotion and pursuit diving in the Dovekie. The cost of flight and swimming, measured on free-living birds by the doubly labeled water (DLW) method, ranged between 4.8 and 11.6 times BMR (LeFebvre 1964, Utter and LeFebvre 1973, Flint and Nagy 1984, Nagy et al. 1984). Because of the expected high cost of existence in Dovekies, we felt it important to determine whether FMR and RMR are consistent with these values, and whether the FMR/RMR ratio supports the "maximum sustained working level" hypothesis (Drent and Daan 1980). We used the DLW method to measure FMR of the Dovekie during the chick-rearing period. To determine the FMR/RMR ratio of free-living Dovekies, we also measured rates of metabolism in the laboratory. We estimated food consumption based on water flux rates and the chemical composition of the diet. Finally we estimated food requirements of a population of Dovekies to assess their influence on the arctic marine ecosystem.

METHODS

We studied Dovekies breeding in Krossfjorden (79°N, 11°W) and in Hornsund (77°N, 15°W), Svalbard, from July to mid-August 1986. Laboratory studies were performed at the research station of the Norwegian Polar Research Institute in Ny-Ålesund (32 km south of Krossfjorden). Adult Dovekies ($n = 23$) were studied in the laboratory during their incubation period. Birds were either trapped in the nest or caught with a mist net. Birds used in the laboratory study were kept in an outdoor cage for 1–1.5 days and fed frozen *Parathemisto* sp.

The field studies were conducted at the Dovekie colony (Ariekammen) on the northern shores of the Hornsund Fjord (Norderhaug 1980; Stempniewicz 1980, 1981). Approximately 70,000 pairs of Dovekies breed annually in the Ariekammen colony (Taylor and Konarzewski in prep.), and 400,000 pairs are estimated to breed on the northern mountains of the Hornsund Fjord (Bakken pers. comm.). During the last days of incubation, we fitted 25 nests with traps. These nests were inspected daily before the DLW experiments to determine the date of hatching. Chicks were 7–20 days old when we performed the DLW measurements on adults. At that age chicks are already homeothermic (Konarzewski and Taylor pers. obs.).

Resting metabolic rate measurements.—RMR was measured both during the day and at night. Metabolic measurements at Ny-Ålesund, were as described by Gabrielsen et al. (1988). Briefly, a metabolic chamber (4.5 l) was placed inside a climatic chamber where the ambient temperature could be controlled within ± 1°C from −25 to +30°C. We measured air flow (1.5–2.0 l/min) with a mass flow meter (Model F 113, Hi-Tec) connected to a readout (Model E-0020, Hi-Tec). Oxygen consumption and CO_2 production were measured with an Applied Electrochemistry oxygen analyzer and a Leybold-Heraeus (BINOS-1) CO_2 analyzer. Temperatures in the climatic and metabolic chamber were measured by thermocouples connected to a Fluke thermometer. Body temperature was measured during metabolism trials by a small thermocouple inserted ca. 2–3 cm into the cloaca. The first metabolic measurement was made within 10–12 h of capture. Eight to ten hours before metabolic trials, birds were denied food. All birds were exposed to a given chamber temperature 1–3 times for at least 1.5–2.0 h. We measured metabolism under full light conditions in the climatic chamber and while the bird was resting, as determined by inactivity of the bird (observed by video). We calculated O_2 consumption ($ml\ O_2 \cdot g^{-1} \cdot h^{-1}$), CO_2 production ($ml\ CO_2 \cdot g^{-1} \cdot h^{-1}$), respiratory quotient (RQ), and energy expenditure (kJ/day) at STPD.

We calculated thermal conductance (C) from the mass-specific metabolic rate ($\dot{V}O_2$) at an ambient temperature (T_a) below lower critical temperature, according to the formula: $C = \dot{V}O_2/(T_b - T_a)$, where T_b is the body temperature of the bird. Thermal conductance is expressed as "wet" conductance because evaporative heat loss from respiration was included.

All birds used in laboratory experiments were released in the colony.

Doubly labeled water studies in the field.—Metabolic rates (CO_2 production) and water flux rates were measured by the DLW method (Lifson and McClintock 1966, Nagy 1980, Nagy and Costa 1980) in one or both members of a breeding pair. The mean error of this method ranged between −4.9 and +6.5% (Williams and Prints 1986).

We trapped 28 adults at the nest. We injected 0.5 ml $H_2{}^{18}O$, containing 97.11 atom % oxygen-18 and 0.4 mCi tritium, into the pectoral muscle. The birds were held in a wooden box for 1.0 h while the isotopes equilibrated with body water (Degen et al. 1981, Williams and Nagy 1984). Birds were weighed to the nearest 1 g on an Ohaus (C 501) digital balance. Each bird was marked on the breast with individual patterns in india ink. Blood samples ($3 \times 70\ \mu l$) were taken from a wing vein. We retrapped 15 birds within one or two days, some of them more than once; and a second blood sample was taken. The colony was monitored continuously to establish the presence of experimental birds. Two background samples were taken from control birds at the start and at the end of the experimental period. The background for oxygen-18 was 0.2030 atom % and 30.0 cpm for tritium. Measurements of FMR by DLW become unreliable as final oxygen-18 value approaches background. We excluded all blood samples with final oxygen-18 enrichments within 8% of background.

Blood samples were stored in flame-sealed, heparinized microhematocrit capillary tubes, and were vacuum-distilled to obtain pure water. Isotope levels in the water were measured by liquid scintillation spectrometry (for tritium) and proton activation analysis (for oxygen-18) (Wood et al. 1975) by Ken Nagy, University of California, Los Angeles, California, USA. Rates of CO_2 production were calculated with eq. 2 in Nagy (1980). Water flux rates were calculated from eq. 4 in Nagy and Costa (1980). Body water volume was estimated from the regression equation:

$$\text{body water (ml)} = 7.70 + 0.589\ (\text{wet body mass, g})$$

($r^2 = 0.89$, $P < 0.0001$, $n = 27$). We dried carcasses of adult birds caught in the colony during feeding of the chicks to constant weight (Taylor and Konarzewski in prep.). We used this equation to estimate the mass of water in the body of each bird at each sampling time.

Food consumption.—We collected food samples from the gular pouches of adult Dovekies that fed chicks in the colony. We assumed that the diet given to the chick was the same for adults. The copepod (*Calanus finmarchicus*) made up 8.5% of fresh mass of food (105 food samples); other crustaceans contributed the rest (Weslawski, Konarzewski, and Taylor unpubl. data). Field metabolic rates (FMR) were converted from units of CO_2 production to units of energy by the factor 26.5 J/ml CO_2. This factor was calculated from the chemical composition of Dovekies' food samples (76% water in fresh mass; 36.8% of lipid, 47.9% of proteins, and 15.3% of minerals in dry mass [Taylor and Konarzewski unpubl. data]). Energy equivalents for fat and protein were from Schmidt-Nielsen (1975). For our calculation, we assumed that the proportions of assimilated dietary fat and protein were the same as their proportions in the diet. We calculated the amount of food an adult Dovekie would have to consume to satisfy its daily energy requirement (as measured with DLW) from the energy content of food samples and energy assimilation efficiency. Because there are no assimilation efficiency studies of adult Dovekies, we used the value of 0.80 obtained in fledglings (Taylor and Konarzewski unpubl. data). The food of Dovekies contains 28.1 kJ/g dry matter (Taylor and Konarzewski unpubl. data). Thus, with a water content of 76%, the food contains 6.75 kJ/g of wet mass, or 5.3 kJ metabolizable energy per gram of fresh matter.

Weather.—Weather conditions during the field experiments were obtained from the Polish Polar Research Station, 1 km from the Dovekie colony. Air temperatures, horizontal visibility, and wind speed were measured every third hour. Precipitation was recorded four times daily. For each bird used in the field experiment, precipitation and the mean values of all of the above weather factors were calculated for the period of measurement of field metabolic rate (i.e. between the first and second blood sampling).

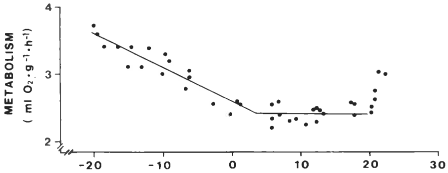

Fig. 1. Oxygen consumption rates of Dovekies at different ambient temperatures.

Mean values are ±SD unless noted otherwise.

RESULTS

Resting metabolic rate.—The lower critical temperature, defined as the intersection between the RMR line and the line that describes the dependence of metabolic rates on T_a, was 4.5°C (Fig. 1). The regression for Dovekies was $y = 2.61 - 0.05x$ ($y = \text{ml } O_2 \cdot g^{-1} \cdot h^{-1}$, x = ambient temperature; T_a range from -20 to $+1.5$°C; $n = 21$). Conductance (C) was 0.0630 ml $O_2 \cdot g^{-1} \cdot h^{-1} \cdot {}^\circ C^{-1}$ (SD = 0.0029, $n = 25$). The division of the points (Fig. 1) into two segments gives the lowest residual sum of squares for all points when the intersection of these lines falls on ambient temperature ca. +5°C (as in Fig. 1).

The mean (±SD) resting metabolic rate (RMR) of Dovekies at thermoneutrality was 2.42 ± 0.13 ml $O_2 \cdot g^{-1} \cdot h^{-1}$ ($n = 16$) or 177.9 ± 9.6 kJ/day (Fig. 1). The mean respiratory quotient (RQ), within the thermoneutral zone, was 0.75 ± 0.02, ($n = 16$), and body temperature was 40.1 ± 0.4°C ($n = 10$). Just after the capture in the colony, the mean body mass of birds used for RMR measurements was 162.3 ± 12.2 g. Body mass dropped significantly because of starvation before metabolic trials ($P < 0.0001$, t-test), and during the metabolic measurements mass averaged 152.5 ± 12.2 g. The latter mean was used for calculation of the mass-specific RMR.

Field metabolic rate.—Field metabolic rate (FMR) of free-ranging birds averaged 6.68 ml $CO_2 \cdot g^{-1} \cdot h^{-1}$, or 696.1 kJ/day (Table 1). The mean body mass of birds in FMR measurements was 164.3 ± 9.5 g ($n = 13$), and was not different from initial body mass of birds used in laboratory measurements ($P > 0.65$, t-test). The FMR/RMR ratio (based on whole-body rates of metabolism) was 3.9.

The weather during the study period was characterized by high precipitation, fog, and strong winds. Mean air temperature was 4.4°C (range, 2.6–7.0°C), mean daily precipitation was 4.1 mm (range, 0–41 mm), and wind speed was 3.4 m/s (range, 0–18 m/s). According to satellite maps, the mean ocean surface temperature was 2.6 (50 km) and 4.7°C (100 km) between Hornsund and the open sea.

We analyzed possible dependence of FMR (kJ/day) on weather conditions (average horizontal visibility [km], average air temperature [°C], average and maximum wind velocity [m/s], precipitation [mm]), and body mass. We used the body mass as an independent variable to avoid statistical problems with analyzing ratios such as mass-specific metabolic rates (Blem 1984). The wind speed appeared to be the only significant weather factor:

$$\text{FMR (kJ/day)} = 3.81 \cdot \bar{W} + 17.07 \cdot V$$

where $\bar{W}$ = mean body mass (in g; partial regression coefficient significant at $P < 0.0001$), V = wind speed (m/s, $P < 0.05$). For FMR, SE = 94.7, $n = 13$. Similar analysis of dependence of FMR on body mass change (between the first and second blood sampling) and the age of chicks was not significant ($P > 0.05$).

Water influx rate in Dovekies was 136.6 ± 31.7 ml/day ($n = 18$) (Table 1).

Food consumption.—Daily energy expenditure in free-ranging birds averaged 696 kJ/day. At a metabolizable energy yield of 5.3 kJ/g fresh mass of food, the Dovekie must consume 131.3 g fresh food or approximately 80% of its body mass per day. We checked this estimate of feeding rate by calculating water influx rate, and compared this value with the actual influxes measured with tritiated water. A mass of 131.3 g of food, with a water content of 76%, contains 99.8 ml of water. Metabolic water production from oxidation of assimilated proteins and lipids would provide an additional 0.122 ml water per gram of fresh food (conversion factors from Schmidt-Nielsen 1975), or 15.7 ml water. This yields a total of 115.5 ml water when consuming 131.3 g of food, which is about 15% lower than the measured water influx of 136.6 ml water per bird (Table 1).

DISCUSSION

Basal metabolic rate (BMR) refers to measurements of resting organisms in a postabsorptive state within their thermoneutral zones (Blight and Johnson 1973). Our measurements were similar to BMR measurements, but they were done under full light conditions. This simulated arctic summer conditions. We measured resting metabolic rate (RMR) rather than basal metabolic rate. Nevertheless we believe our measurements are comparable to BMR.

We used published regression equations (alpha-phase) for nonpasserine birds to predict resting metabolic rate (RMR) in Dovekies within the thermoneutral zone (Lasiewski and Dawson 1967, Aschoff and Pohl 1970). For a Dovekie (153 g) the measured RMR value was 212% and 184% of the predicted values. Similar predicted values were obtained by Roby and Ricklefs (1986) in their study of Least Auklets (*Aethia pusilla*) and diving petrels (*Pelecanoides* spp.), whose ecology is similar to that of Dovekies. The RMR value obtained for Dovekies agrees with earlier observations (Weathers 1979, Hails 1983, Ellis 1984), which showed that BMR is a function of breeding latitude. Species that breed at high latitudes have a higher BMR than those in temperate and tropical areas. However, factors other than relative size, diurnal phase, and climate may contribute to the high RMR in the Dovekie. Roby and Ricklefs (1986) and Gabrielsen et al. (1988) suggested that the birds' physical activity or their mode of life may influence the RMR. Ellis (1984) proposed a close linkage between BMR and maximum power output. This means that a high field metabolic rate (FMR) may correlate with a high RMR.

We calculated thermal conductance (C) as 98% of that predicted by Herreid and Kessel's (1967) equation for dead birds (dry conductance) and 76% of Aschoff's (1981) value (alpha-phase) predicted for a 152.5 g bird. After compensating for respiratory heat loss (Herried and Kessel's equation), we found that the C value in Dovekies was higher than predicted from mass. When compared with temperate seabirds of similar body size, conductance of Dovekies was low. This implies greater insulation than in the Georgian Diving Petrel (*Pelecanoides georgicus*; Roby and Ricklefs 1986). The average ambient temperature in the Svalbard approached the birds' lower critical temperature (T_{LC} = 4.5°C), which implies that these birds may not be cold-

TABLE 1. Rates of body mass change, water influx, and field metabolism of breeding Dovekies in Hornsund.

	Body mass			Metabolic rate			
Bird No.[a]	Mean (g)	Change (g/day)	Water influx rate (ml/day)	(ml $CO_2 \cdot g^{-1} \cdot h^{-1}$)	kJ/day	Measurement period (days)	Age of chicks (days)
86A	154.3	−2.4	99.1	6.90	677.3	1.06	7
94A	168.0	−5.8	131.7	7.58	809.6	1.74	11
94A	159.0	7.8	138.4	8.48	857.4	0.90	16
94A	162.5	0.0	115.3	4.91	507.3	0.88	17
94B	167.5	−4.9	131.6	6.43	685.5	1.01	15
94B	162.5	−6.7	133.9	6.10	630.6	1.64	20
13A	166.0	−4.4	108.6	—	—	2.27	12
13B	167.0	−0.5	122.2	6.42	681.5	2.07	16
45A	160.5	7.7	182.1	8.65	882.6	1.17	11
18A	188.5	0.8	100.4	5.63	674.5	1.30	12
85A	158.0	7.3	212.8	—	—	1.91	11
33A	150.5	−4.0	91.2	6.54	625.6	1.25	8
48A	157.3	4.0	169.4	6.74	673.8	1.88	12
48B	174.3	−1.5	145.7	—	—	2.94	16
84A	173.5	−2.9	128.1	6.64	732.9	1.05	7
67A	164.5	0.0	128.1	5.83	610.0	1.63	15
81A	153.5	−1.1	143.2	—	—	2.64	15
RSA	160.0	3.0	176.5	—	—	2.01	20
Mean	163.7	−0.2	136.6	6.68	696.1		
SD	9.0	4.6	31.7	1.06	103.7		
n	18	18	18	13	13		

[a] A and B indicate two birds of the same pair.

stressed while on land. However, when foraging at sea, water may compress feathers. This increases thermal conductance, and results in increased metabolism at the 2–4°C water temperature.

The FMR in auks and petrels, is elevated in comparison with other seabirds (Birt-Friesen et al. 1989). However, auks and diving petrels also use their wings for underwater locomotion. Because the optimum design of wings is different for flying in air and swimming underwater, an intermediate stage would involve a loss of efficiency in each medium. The wing area of auks is approximately 40% that of Procellariiformes and 30% below marine larids. Wing length is only 60% of Procellariiformes and 50% of marine larids (Jouventin and Mougin 1981). The same tendency—but carried to extremes—is present in penguins, where the wing is presumably optimized for swimming (Jouventin and Mougin 1981).

The FMR of Dovekies, corrected for body size, is the highest among all seven cold-water seabird species that use wings for propulsion in water (Table 2). The wing area of auks falls in the lower extreme of the range of all flying birds (Greenwalt 1962). Very low wing area in Dovekies produces high wing loading (the ratio of body mass to wing area). The wing loading in Dovekies (0.98 g/cm^2; Stempniewicz 1982), is 243% of that predicted for a "typical" bird (Viscor and Fuster 1987). This, together with the presumably high energetic cost of flying long distances to feeding areas (Brown 1976), may account for high FMR in Dovekies.

Dovekies as well as Kittiwakes (*Rissa tridactyla*; Gabrielsen et al. 1987) showed increased FMR with increased wind speed. There is a negative effect of wind speed on the increase in body mass and lipid reserves of Dovekie chicks (Konarzewski and Taylor 1989). It is unlikely that chick growth is directly affected by wind because chicks are relatively well protected in nest crevices (Konarzewski and Taylor 1989). Presumably under windy conditions the FMR of adults is altered sufficiently to change the chicks' food intake.

In seabirds the breeding period represents a period in which the energy demands upon the parent are thought to be at a maximum (Ricklefs 1983). We found no relationship between adult FMR and the age of their chicks 7–20 days of age. Food consumption by chicks is relatively stable during this period (calculated from water influx; Taylor et al. unpubl.). The food consumption of Dovekie chicks increased only 35%

TABLE 2. Field metabolic rates (FMR) of cold-water seabirds that use wings for propulsion in water, measured by doubly labeled water during chick-rearing period.

Species	Body mass (g)	FMR (kJ/day)	Observed FMR vs. predicted[a] (%)	Source
Least Auklet (*Aethia pusilla*)	84	358	125	Roby & Ricklefs 1986
South Georgia Diving Petrel (*Pelecanoides georgicus*)	109	464	134	Roby & Ricklefs 1986
Common Diving Petrel (*P. urinatrix*)	137	557	137	Roby & Ricklefs 1986
Dovekie (*Alle alle*)	164	696	149	Present study
Black Guillemot (*Cepphus grylle*)	381	863	100	Mehlum, Gabrielsen & Nagy unpubl.
Common Murre (*Uria aalge*)	940	1,871	113	Cairns unpubl.
Thick-billed Murre (*U. lomvia*)	1,119	2,080	110	Flint et al. prelim. unpubl. data

[a] Predicted from the equation of Birt-Friesen et al. (1989) relating FMRs of cold-water seabirds that use flapping flight to their body weight.

between days 8 and 14, and it remained stable until day 21 (Konarzewski et al. in prep.). The lack of dependence of adult FMR on chicks' age agrees with data obtained for two species of diving petrels (Roby and Ricklefs 1986).

In many breeding birds, free-living parents use energy at 3.1–4.3 times their RMR (Hails and Bryant 1979, Bryant and Westerterp 1983, Utter 1971, Utter and LeFebvre 1973, Williams and Nagy 1984, Nagy et al. 1984, Gabrielsen and Mehlum 1989; but see Williams 1988). Drent and Daan (1980) proposed a maximum sustained working level of 4 × RMR during chick rearing. Dovekies show the same ratio, despite the fact that these birds differ in other ways from most species studied in other geographical regions. We strongly support Drent and Daan's (1980) hypothesis of the maximum sustained working level.

We estimated food consumption from energy requirements of free-ranging Dovekies. We calculated that adult Dovekies eat approx. 131 g of plankton daily during chick rearing. This includes only the adult needs and excludes food given to the young. Based on the water influx rate in growing Dovekie chicks, water content of their food, and its energetic value (Konarzewski et al. unpubl.), we calculated that a 14-day-old chick consumes 51 g fresh plankton each day. Food requirements of two adults and one chick would total 313 g fresh plankton per day. There are approx. 70,000 pairs of Dovekies in the Ariekammen colony (Taylor and Konarzewski unpubl.), and we estimate that the colony will consume 21.9 tons of *C. finmarchicus* each day. We estimate that approx. 2.1 tons (dry matter) of nitrogen-rich guano are added to the Hornsund marine and terrestrial ecosystems each day.

The amount of food consumed by adult Dovekies may be even larger. We found that water influx calculated from water content of the plankton and oxidation of its fat and protein was 15% lower than water influx measured with DLW. However, the higher measured values may be due to the mode of foraging of Dovekies (presumably they consume some sea water while feeding on copepods). The food is carried by the parents in an extensible gular pouch. This may allow water exchange because the food is in contact with the mucous membrane.

The Dovekie is the only Atlantic seabird that feeds mainly on copepods. The species has a high energy demand balanced by high food consumption, and may therefore have an impact on both the marine and the terrestrial ecosystems, where it deposits a large amount of nutrients.

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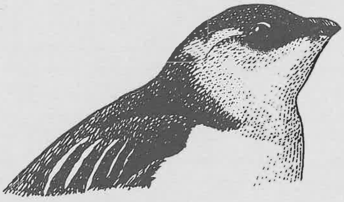
Paper V



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CHICK ENERGY REQUIREMENTS AND ADULT ENERGY EXPENDITURES OF DOVEKIES (*ALLE ALLE*)

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ABSTRACT.—We constructed an energy budget for Dovekie (*Alle alle*) chicks in West Spitsbergen by measuring energy metabolism, rate of accumulation of energy in growing tissues, and body water turnover rate, the last serving as the basis for energy-consumption calculations. The energy budget of a "typical chick" was calculated for chicks measured in 1986 and 1987. Mass-specific resting metabolic rate in Dovekie chicks peaked at days 7 to 10 and then declined considerably. Thermal conductance decreased by 60% between hatching and fledging. Energy deposition in growing tissues, resting metabolic rate, and energy consumption reached maximum values midway through the fledging period. Chicks examined in 1984 had 11% lower growth rate than 1986 and 1987 chicks, and their energy deposited in tissues between hatching and the age of peak body mass before fledging was 17% lower. Energy requirements of Dovekie chicks were much higher than those of other seabird chicks of similar body mass. We attribute this to the arctic nesting of Dovekies. We compared energy demands of Dovekie chicks with those of adults reported in another study. Despite high chick energy demands, energy delivered to the chick by one parent was only 15% of the total energy gathered by the parent (to meet both its own and the chick's needs). We suggest that this reflects a high cost of foraging in adult Dovekies. Additionally, high energy demands of chicks may contribute to the high energy expenditures of adults. This may be a major contribution to the restriction of a Dovekie brood to one chick and to the low chick body mass at fledging. *Received 6 January 1992, accepted 27 May 1992.*

THE ABILITY of parents to provide food for offspring is generally considered a major factor shaping reproductive strategies of birds with nidicolous young. Parents should raise the greatest possible number of young permitted by food availability (Lack 1968) and optimized with respect to the trade-off between investment in a given brood and probability for future reproductive success (Williams 1966, Charnov and Krebs 1974). Brood-size reduction is the primary means of matching reproductive effort to declines in parental foraging capacity. Depression of chick growth rate is a means of fine tuning the adjustment. The latter is especially important in birds that lay small clutches, where the integer steps of adjusting clutch size become too crude (Ricklefs 1968). The adaptive value of growth rate adjustment is based on the assumption that change in growth rate results in substantial change in chick energy requirements, but this assumption has not been consistently supported (for a recent discussion see Klaassen et al. 1992).

Seabirds have much lower reproductive rates than most terrestrial birds (Lack 1968). In many seabird species, adults lay one-egg clutches, forage at long distances from their breeding colonies, and feed their chicks infrequently. Presumably, the severely limited ability of adult birds to deliver food requires that reproductive effort be adjusted to a minimum anticipated level, resulting in slow chick growth in most seabird species (Ricklefs 1983).

Among seabirds, alcids (family Alcidae) offer a good opportunity for comparative studies of growth patterns and factors leading to clutch reduction. Alcids exhibit three patterns of posthatching development: precocial, semiprecocial, and intermediate. Chicks of intermediate

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species go to sea when flightless and weighing only about one-quarter of adult mass. Semiprecocial alcids stay in the nest much longer, exhibiting a wide variety of growth patterns (Sealy 1973).

In an attempt to shed light on why Dovekies (*Alle alle*) lay single-egg clutches and on the selective forces shaping their growth pattern, we studied energy requirements of Dovekie chicks. The Dovekie is a small (160-g) planktivorous alcid that breeds only in the Arctic and raises a single semiprecocial chick (Birkhead and Harris 1985). The growth rate of Dovekie chicks is not as low as in many seabird species, but at fledging they attain only 65 to 70% of adult body mass (Stempniewicz 1980, Konarzewski and Taylor 1989). The average nestling period is 27 days and they attain peak nestling body mass in three-fourths of that time. Then there is a slight recession in body mass prior to fledging, but chicks continue to grow feathers and accumulate macroelements in their bodies (Stempniewicz 1980, Taylor and Konarzewski 1992).

We studied energy accumulation and metabolism, and constructed energy budgets for Dovekie chicks. We also compared energy requirements of chicks with those of their parents (reported in Gabrielsen et al. 1991). We calculated the energy delivered to the chick as a ratio of total energy gathered by the parent, and compared it with the same ratio in other alcid species, as well as with diving-petrels (alcids' ecological counterparts in the Southern Hemisphere). Metabolic rates of adult Dovekies feeding chicks are extremely high (Gabrielsen et al. 1991), and we attempted to determine to what extent the energy requirements of chicks contribute to high energy-expenditure rates of adults.

MATERIALS AND METHODS

All chicks used in this study were from the Dovekie colony on the southern slopes of the Arie Mount (Ariekammen), Hornsund Fjord, West Spitsbergen (77°00'N, 15°22'E). Marked nests were inspected daily at the time of hatching and the ages of chicks, thus, were known to within one day.

Chicks used for the determination of energy content in tissues and, hence, energy accumulation with growth were collected in 1984, 1986 and 1987. The same chicks also were used for analyses of gross body composition (water, petroleum ether-extractable lipids, lean dry mass) reported in Taylor and Konarzewski (1989). All details of collection methods and carcass analysis are given in that paper.

The dry homogenates from 64 chicks collected in 1984 and from 19 of 37 chicks collected in 1986 were combusted in a Berthelot-type adiabatic bomb calorimeter. Two or three 1-g aliquots from each chick were used. Birds represented all developmental stages up to the fledging age of 27 days. The regression line of energy density on fat content (%) in the dry chick carcasses was calculated and used for prediction of energy densities of all 1986 and 1987 chicks (these chicks were used to calculate energy budget of a "typical chick"; see Results). Energy density of fresh tissue was obtained by correcting the energy density of dry material for natural water content. To avoid inconsistency due to different methods of determination of energy content of 1984 and 1986–1987 chicks, the statistical interyear comparison of chick energy contents was performed on the values derived from the body composition, assuming 1 g fat is equivalent to 38 kJ, and 1 g of dry nonlipid matter is equal to 20 kJ. Such energy contents were on average 1% lower than those from direct determination.

The measurements of metabolic rate of the chicks were made in 1987 in the Polish Polar Station at Hornsund, 1 km south of the bird colony. Oxygen consumption and carbon-dioxide production of chicks were measured with a flow respirometer "Spirolyt" (Junkalor) with a paramagnetic analyzer for O_2 and diaferrometric for CO_2. Chicks were tested in 0.3- to 1.4-L chambers, depending on chick age and size. The rate of air flow through the chamber was set between 10 and 30 L/h, which produced an increase in CO_2 content in the expired air not exceeding 1.2% that of ambient air. The air leaving the chamber passed through silica gel to remove water before entering the analyzers. The chicks were placed in the chambers within 30 min of removal from the nest. Measurements on one- and three-day-old, largely poikilothermic chicks were taken at air temperatures in the chamber of 25° to 30°C, and 25°, respectively. Air temperature measured in the chamber was stabilized within ±0.5° by submersion of the chamber in a water bath. The chambers with older (homeothermic) chicks were placed outdoors; hence these measurements were performed in 5° to 10°, which approximates well the range of air temperatures in Dovekie nest crevices during chick rearing (Konarzewski and Taylor 1989). Trials lasted 1.5 to 2.5 h with gas exchange recorded over the last 20 to 30 min. Trials were prolonged when birds were excessively active, and some measurements were excluded from calculations due to chicks' restlessness. Body temperature of the chicks was measured immediately after each trial with a thermistor probe (±0.1°C) inserted 3 to 4 cm into the cloaca. After the experiments, all birds were returned to their nests, where they were invariably accepted by their parents. Body temperatures of other chicks, one to five days old, were also measured in the colony immediately after removal from the nest. All measurements were taken between 0900 and 2000 local time.

All gaseous values were converted to standard conditions (STP). When converting gasometric data into energy values, the caloric equivalent of oxygen volume was determined independently for each measurement according to the observed respiratory quotient. Thermal conductance of chicks (ml O_2/[g h °C]) was calculated as:

$$VO_2/[(T_b - T_a)M], \tag{1}$$

where VO_2 is oxygen consumption (ml O_2/h), T_b is body temperature (°C), T_a is ambient temperature (°C), and M is body mass (g).

The energy consumed by chicks was calculated from water-influx rates measured in the chicks in the colony in 1986 using the tritiated-water method (Lifson and McClintock 1966, Nagy and Costa 1980), and known water and energy content of food. In the field, chicks were injected with 0.4 ml tritiated water (containing 0.32 mCi tritium) into the pectoral muscle using a laboratory-calibrated syringe. We allowed 1 h for the tritiated water and body water to equilibrate, after which each chick was returned to its nest, it was weighed to the nearest 0.1 g, and a blood sample (20–30 μl) was taken from the vein in the foot. Second and third blood samples were taken from each chick after 12 and 24 h; thus, each chick gave two 12-h measurements of water flux rates. Near-fledging chicks (25 to 26 days) were bled only once (after 24 h). Two background blood samples were taken from uninjected chicks. The blood samples were stored in flame-sealed, heparinized microhematocrit tubes, and were vacuum-distilled to obtain pure water. The water was assayed for tritium activity by liquid-scintillation spectrometry. Water efflux and influx were calculated using equations 4 and 6, respectively, of Nagy and Costa (1980). The volume of water (TBW, ml) in the body of each bird at each sampling time was estimated from regression equations calculated from raw data of Taylor and Konarzewski (1989), relating TBW to live wet mass (M, g) in chicks collected in 1986 and 1987. These data were obtained by drying chicks to constant mass. For young chicks (4 to 13 days of age),

$$\mathrm{TBW} = 3.12 + 0.6485\ M \tag{2}$$

(SE = 0.97, $r^2 = 0.997$, $P < 0.001$, $n = 47$), and for older chicks (19 to 27 days),

$$\mathrm{TBW} = 15.79 + 0.491\ M \tag{3}$$

(SE = 1.91, $r^2 = 0.842$, $P < 0.001$; $n = 35$).

Dovekie chicks do not drink; hence, water influx (W_i, ml/day) is from water in food (W_f, ml/day) and metabolic-water production (W_m, ml/day):

$$W_i = W_f + W_m. \tag{4}$$

The amount of water in the food equals the fresh mass of the food (M_f, g) times the fraction of water in the food (F_w, dimensionless):

$$W_f = M_f F_w. \tag{5}$$

The estimated metabolic-water production (water from food catabolism) was corrected for lipid and lean-dry-mass (mainly protein) change in growing tissues, assuming that the food fraction that is not catabolized but allocated toward body-mass growth yields no metabolic water. When body mass decreases, as in chicks near fledging (days 25–26), the correction adds the water from body-tissue catabolism.

$$W_m = M_f E_d E_a C - (\Delta M_l \cdot H_l + \Delta M_p \cdot H_p), \tag{6}$$

where E_d is energy density of fresh food (kJ/g), E_a is food assimilation efficiency (dimensionless), C is a conversion factor (ml H_2O/kJ metabolized), ΔM_l and ΔM_p are tissue-lipid and protein mass changes (g/day), respectively, H_l and H_p are the metabolic-water yields (ml/g) of these tissues. The values used are: $F_w = 0.76$, $E_d = 6.75$ kJ/g, and $E_a = 0.80$ for Dovekie chicks' food (Taylor and Konarzewski 1992); $C = 0.026$ ml H_2O/kJ (Schmidt-Nielsen 1990:333). Lipid and protein (lean dry mass) changes in growing chicks in 1986 and 1987 are from Taylor and Konarzewski (1989). H_l and H_p were assumed to be 1.07 and 0.50 ml H_2O/g, respectively (Schmidt-Nielsen 1990:333). The values from equations (5) and (6) were substituted in (4), and the latter was solved for food intake (M_f), which was converted to energy units.

To calculate water flux with the tritiated-water method, several assumptions are required (Nagy and Costa 1980). The most critical of these for growing animals is that tritium labels body water only. The incorporation of tritium into newly synthesized tissue would cause an overestimate of water-flux rates, because the specific activity of tritium in body water would decline owing to isotope binding as well as water influx, assuming that the binding occurs after the initial bleeding. If 10% of the decline in tritium-specific activity in our chicks during the 24 h after initial sampling was due to the incorporation of tritium, our values of water influx and food consumption might be overestimated by up to 16%. However, there are four reasons to expect that the values are not overestimated. First, the preliminary validation experiment by Gabrielsen et al. (1992) showed a very good agreement between food consumption calculated from water influx measured by the tritiated-water method and simultaneous direct determination of the amount of food consumed by Kittiwake (*Rissa tridactyla*) chicks. Second, two independent estimates of food consumption for the same Gentoo Penguin (*Pygoscelis papua*) chicks, derived from water- and sodium-influx rates (using tritiated water and ^{22}Na), were within 2% of each other (Robertson et al. 1988). Third, incorporation of tritium was estimated as only 0.1% of the total administered dose in nestling Glaucous-winged Gulls (*Larus glaucescens*; Hughes et al. 1987), and less than 2% in Chukar chicks (*Alectoris chukar*; J. B. Williams in Williams and Nagy 1985). Fourth, the

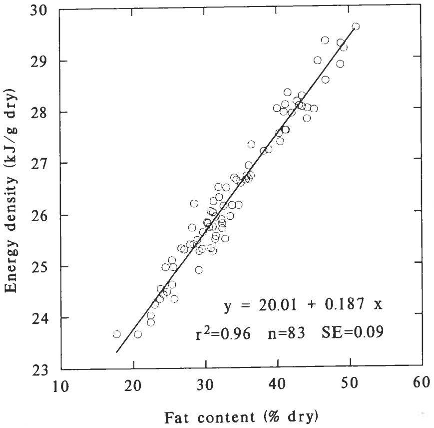

Fig. 1. Relationship between energy density and fat content in dry body mass in Dovekie chick. SE is standard error of estimate.

most convincing argument that our values of food consumption are not overestimated comes from the inspection of the Dovekie chick energy budget itself. The assimilated energy, calculated from food consumption via the tritiated-water method, is exactly equal to (and cannot be lower than) the sum of independently measured resting metabolic rate and the rate of energy accumulation in growing tissues at the age of maximum body-mass growth rate (i.e. when probability of tritium incorporation into newly synthesized tissue is highest).

The relationship between the chicks' body mass and age until the age of peak body mass was described by the Richards curve (Nedler 1962) fitted to the data using a weighted least-square method and the Marquardt algorithm (Bevington 1969). Richards growth curves were compared with an F-test (White and Brisbin 1980).

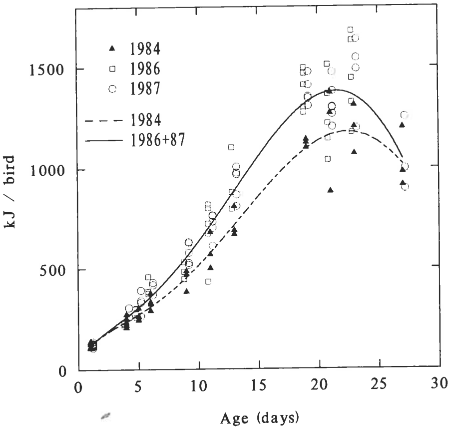

Fig. 2. Changes in energy content of Dovekie chicks with age. Relationships described with polynomials.

RESULTS

Energy content of tissues.—We found a highly significant dependence of energy density upon fat percentage in dry body mass of Dovekie chicks ($r^2 = 0.96$, Fig. 1). This enabled us to accurately estimate the energy density and, thus, total energy content of all 1986 and 1987 chicks.

Energy content of chicks differed among the three study years (Fig. 2). Energy content of 1984 chicks was significantly lower in the linear portion of its dependence on chicks' age (days 9 to 19) as revealed by ANCOVA followed by the Tukey test ($P < 0.05$). Energy contents of 1986 and 1987 chicks did not differ at these ages ($P > 0.05$). At the same time there were no differences among the slopes of three lines ($P > 0.10$). The maximum energy content, achieved on days 19 to 23 (the age of maximum body mass throughout nestling period) was also significantly lower in 1984 chicks than in 1986–1987, with no difference between 1986 and 1987 (ANOVA, Tukey test at $P = 0.05$). Lower energy content of 1984 chicks was due to lower fat content, as there was no difference in lean dry mass of chicks among years (Taylor and Konarzewski 1989). Energy contents of 1986 and 1987 chicks were lumped and used for further basic calculations of energy budget. Energy content of chicks decreased before fledging (Fig. 2) together with a decline in body mass and mass of fat (Taylor and Konarzewski 1989).

Metabolic rates.—Dovekie chicks are poikilothermic until day 5 (Konarzewski and Taylor unpubl. data). Body temperature in one- to five-day-old chicks measured immediately after their removal from the nest, usually from under a brooding parent, was 38.4 ± SD of 0.7°C ($n = 49$). The regression of body temperature on age was not significant ($P > 0.05$). There were no significant differences in body temperatures between chicks examined in the colony and used in metabolic trials on their first and third days of life (Table 1; t-test, $P > 0.05$). This means that air temperature in the metabolic chambers was similar to operative temperature experienced by young chicks during brooding. The conditions within the metabolic chamber also

TABLE 1. Body temperature, oxygen consumption, respiratory quotient (RQ), and thermal conductance in Dovekie chicks of various ages; means ± SD. All parameters measured at ambient temperatures of 25° to 30°C in one-day-old chicks, at 25° in three-day-old chicks, and within range of 6° to 11° in older chicks.

Age (days)	n	Body mass (g)	Body temperature[a] (°C)	Oxygen consumption (mg/[g h])	RQ	Thermal conductance (ml O_2/[g h °C])
1	18	22.4 ± 2.4	38.0 ± 0.7	2.46 ± 0.35	0.63 ± 0.03	0.242 ± 0.043 (115)[b]
3	15	31.6 ± 3.8	38.9 ± 0.4	3.11 ± 0.35	0.69 ± 0.03	0.225 ± 0.024 (127)
7–10	14	69.8 ± 9.3	39.2 ± 0.5	4.38 ± 0.25	0.71 ± 0.02	0.145 ± 0.010 (120)
13–15	19	103.2 ± 14.7	39.7 ± 0.3	3.86 ± 0.25	0.74 ± 0.04	0.124 ± 0.010 (123)
20–22	17	124.6 ± 13.1	39.7 ± 0.3	3.06 ± 0.27	0.75 ± 0.02	0.100 ± 0.008 (109)
25–27	12	115.3 ± 9.8	39.8 ± 0.3	3.13 ± 0.29	0.69 ± 0.05	0.100 ± 0.011 (105)

[a] Measured after metabolic trial.

[b] Thermal conductance, as percent of value predicted from Aschoff's equation (1981) for adult nonpasserine birds of same body mass during activity time, given in parentheses.

approximated the natural thermal environment of older, homeothermic chicks. Dovekies nest in crevices in talus. The chick, even when not brooded, is well protected against wind and solar radiation.

Mass-specific resting metabolic rate peaked 7 to 10 days posthatch; then it declined considerably to days 20 to 22, and changed little up to fledging (Table 1). The respiratory quotient (RQ) averaged 0.74 in 7- to 22-day-old chicks and decreased in near-fledging chicks. Thermal conductance decreased continuously with age and dropped 60% between hatching and fledging (Table 1).

Metabolic rates and energy contents used for construction of energy budget were not measured in the same chicks, but body masses of chicks of these two groups did not differ. There was no difference between two Richards curves relating body mass to the age of chicks (up to the peak of body mass, day 21) fitted to the two data sets ($P > 0.20$). The parameters of the Richards growth curve fitted to the lumped data, as well as body masses of chicks in consecutive days, calculated from the curve, are given in the Appendix. Mean maximum growth rates, calculated as the instantaneous growth rate at the point of inflection (i.e. day 8) of the Richards curve (Nedler 1962, Hussell 1972) was 7.5 g/day, similar to that measured in other years in the same colony by other authors: 7.7 and 7.1 g/day in 1963–1964 and 1974–1975, respectively (Norderhaug 1980, Stempniewicz 1980).

Chicks' energy budget.—Resting metabolic rates reached maximum values on days 16 and 17 (Fig. 3). The rate of energy deposition in growing tissues calculated from the curve in Figure 2 (1986–1987) increased gradually after hatching, peaked only a few days earlier than resting metabolic rate, dropped in the next few days and became negative prior to fledging (Fig. 4). Thus, the sum of these two parameters, being the rate of resting energy assimilation (not including costs of activity of chicks) (A_r) reached its peak on day 14 (Fig. 4). This is exactly midway through the nestling period, as chicks fledged on average on the 27th day after hatching (Stempniewicz 1980, Konarzewski and Taylor unpubl. data). The energy deposited in tissues between days 1 and 21 (i.e. when deposition rate was positive) amounted to 1,254 kJ and constituted 29% of the A_r. The total A_r was 4,258 kJ by day 21.

We assumed that the cost of biosynthesis is one-third the rate of energy accumulation

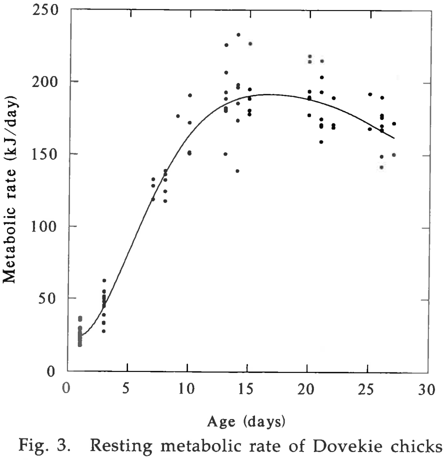

Fig. 3. Resting metabolic rate of Dovekie chicks as function of age. Curve is a polynomial. See Methods for ambient temperatures.

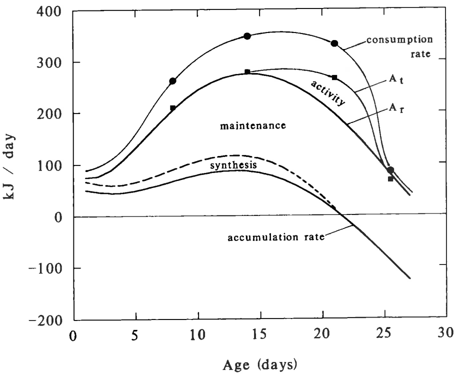

Fig. 4. Energy budget of a typical Dovekie chick. Circles represent energy consumed by chick as calculated from water-influx rates. Squares represent total energy-assimilation rate (A_t), calculated as the consumption rate multiplied by the assimilation coefficient. A_r is resting assimilation rate (not including activity costs), equal to resting metabolic rate plus accumulation rate. A_t is equal to A_r between days 1 and 15. Resting metabolic rate is partitioned into maintenance costs and costs of synthesis of body tissue.

(Ricklefs 1974). Maintenance energy is the resting metabolic rate minus the cost of biosynthesis. Maintenance energy constituted 60% of A_r over the chick's first 21 days of life.

Figure 4 also presents the energy consumed by chicks calculated from water-influx rates. In all age classes except fledglings, the water-influx rate was significantly correlated with body-mass change (Table 2). To unify energy consumed by chicks calculated from water influx with the data on resting metabolic rates and energy content of tissues, we used body-mass change in chicks derived from the Richards growth curve mentioned above. These body-mass changes in chicks and regressions in Table 2 gave adjusted water-influx rates in chicks as a basis for calculation of food consumption (Table 2). The maximum rate of energy consumption occurred at the same age as did the maximum A_r, at the midpoint of the fledging period (Fig. 4, Table 2). The abrupt drop in consumption after day 21, accompanied by a recession in body mass and energy content of tissues (Fig. 2) is caused by cessation of chick feeding by the female parent; the chick is fed only by the male at that time (Taylor and Konarzewski in prep.).

We also estimated the total assimilated energy (A_t; Fig. 4) by multiplying energy consumed by 0.80, the energy assimilation efficiency in Dovekie chicks (Taylor and Konarzewski 1992). The energy deposited in tissues up to day 21 constituted 26% of the A_t at that time. The difference between A_t and A_r is approximately the energy expended in activity. The estimated costs of activity were negligible over the first half of the nest period and attained 32% of A_t (48% of resting metabolic rate) in 21-day-old chicks (Fig. 4).

The mean maximum body-mass growth rate was 6.7 g/day in 1984, 11% less than in 1986–1987, and the two growth curves differed significantly ($P < 0.01$). The total energy deposited in tissues by the chick between 1 and 21 days of age in 1984 (calculated from lower curve in Fig. 2) was 17% lower than in 1986–1987.

DISCUSSION

Energy budget of chick.—A comparison of the rates of energy assimilation minus the costs of activity (A_r) in seabird chicks of similar body

TABLE 2. Water influx rates and estimated food consumption of Dovekie chicks.

Age	Mean body mass (g)	Water influx (WI, ml/day) vs. body-mass change (BMC, g/day)					Adjusted water influx[d]	Food consumption	
(days)[a]	$\bar{x} \pm$ SD (n)[b]	Equation	P[c]	r^2	SE	n	(ml/day)	g/day	kJ/day
7–9	67.9 ± 6.8 (10)	WI = 24.0 + 1.235 BMC	0.01	0.37	10.0	17	33.2	38.8	262
13–15	94.7 ± 8.6 (9)	WI = 37.9 + 1.290 BMC	0.0001	0.68	13.0	18	44.7	51.5	348
20–22	126.1 ± 9.3 (9)	WI = 45.2 + 0.848 BMC	0.005	0.44	12.8	18	44.3	49.2	332
25–26	118.5 ± 8.7 (10)	WI = 13.7[e]			1.2	10	13.7	12.7	86

[a] 20–22 days is age of peak body mass in nest; Dovekie chicks fledge on average on day 27 after hatching.

[b] n is number of chicks.

[c] Significance level of regression slope (t-test).

[d] See text.

[e] Mean value; regression not significant ($P > 0.4$).

mass reveals that A_r of Dovekie chicks is one of the highest (Fig. 5A). This can be partially attributed to their very high cost of growth (energy-accumulation rate in growing tissues plus cost of biosynthesis), the highest among all species shown in Figure 5, which results from the combination of a rather high body-mass growth rate and high rate of fat deposition. Of the total accumulated energy in Dovekie chicks between days 1 and 21, 58% is in the form of fat (Taylor and Konarzewski 1989).

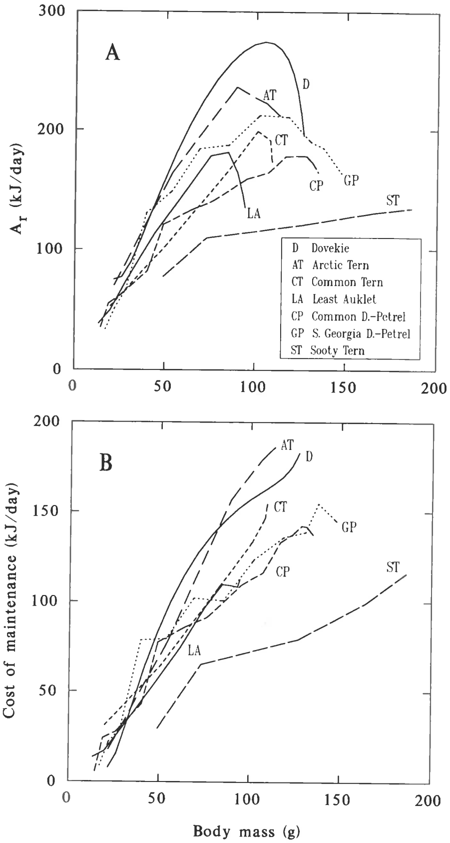

Fig. 5. Energy expenditures of Dovekie chicks and other seabird chicks of similar body mass: Arctic Tern (*Sterna paradisaea*; Klaassen et al. 1989); Common Tern (*S. hirundo*) and Sooty Tern (*S. fuscata*; Ricklefs and White 1981); Least Auklet (*Aethia pusilla*), South Georgia Diving-Petrel (*Pelecanoides georgicus*), and Common Diving-Petrel (*P. urinatrix*; Roby 1991). (A) Rates of resting energy assimilation (A_r; see Fig. 4 and text for definition); (B) Costs of maintenance (resting metabolic rate minus cost of biosynthesis).

The high cost of maintenance similarly contributes to high A_r and to interspecific differences (Fig. 5B). Maintenance costs comprise "basal" costs (within thermoneutral zone), the costs of thermoregulation, and the calorigenic effect of food. High costs of thermoregulation in Dovekie chicks may be one of the causes of their high maintenance costs, as air temperatures in Dovekie nest crevices during chick development range between 3.6° and 11.1°C (mean = 6.5°; Konarzewski and Taylor 1989). The high costs of maintenance in Dovekie chicks are not caused by the poor insulative value of their down; thermal conductance of homeothermic chicks was not higher than 123% of the minimal conductance of adult nonpasserine birds of the same body mass (Table 2), and the conductance we obtained in our chicks was not always minimal. Different costs of thermoregulation alone cannot explain the differences in cost of maintenance in chicks shown in Figure 5B. Chicks of the two species of diving-petrel have much lower costs of maintenance, despite living in similar ambient temperatures (Roby 1991). Moreover, costs of thermoregulation might be of limited significance even in small polar birds, as they accounted for only 30% of maintenance costs in Arctic Tern chicks (Klaassen et al. 1989). On the other hand, estimated maintenance costs are lower in Least Auklet chicks than in the closely related Dovekie due to the correction for parental brooding made for Least Auklet chicks even close to fledging when calculating their energy budget (Roby 1991). Brooding was considered in Dovekie chicks only when younger than seven days (Norderhaug 1980). Even fledgling Least Auklet nestlings are attended by parents at night, while Dovekie chicks are fed 24 h a day in continuous light of Arctic summer (Stempniewicz and Jezierski 1987). It is also possible that presumably high metabolic rates in thermoneutrality bring about high cost of maintenance in Dovekie chicks. Basal metabolic rates of adult birds from high latitudes generally exceed those of species from lower latitudes (Weathers 1979). The basal metabolic rates of adult Dovekies are equal to 212% of the rate expected for bird species of the same body mass (Gabrielsen et al. 1991), while the same figures in adult Least Auklets, South Georgia Diving-Petrels, and Common Diving-Petrels are 191, 156, and 150%, respectively (Roby and Ricklefs 1986). Klaassen and Drent (1991) also showed a positive correlation between resting metabolic rates in hatchlings and latitude.

Energy expended on activity is rather small in Dovekie chicks when compared with that expended by other bird species (Dunn 1980), as the chicks usually remain inactive in their nest crevices (pers. observ.). The highest estimated costs of activity, which occur on about day 21, result from chicks exercising their wings at the entrance of the crevice, an activity that starts at the age of 15 days (Stempniewicz 1981, and our own observations). Despite low activity costs, the consumed and assimilated energy is relatively high; the peak assimilated energy (maximum A_t) is 31% higher than that predicted for a chick of the same mass and age at fledging (from equation 14 by Weathers 1992).

The difference between Dovekie-chick energy requirements (measured in absolute values) and those of other seabird chicks is greatest at older ages (Fig. 5A). This large difference may contribute to the fact that, in contrast to all other species shown in Figure 5, Dovekie chicks attain only 65 to 70% of adult mass at fledging. High maintenance costs that increase with age (Fig. 5B) and appearance of activity costs at older age in Dovekie chicks (Fig. 4), combined with a high energy cost of foraging in adult Dovekies (see next section), may explain the arrest in growth of Dovekie chicks well before attaining adult body mass. At the age of maximum growth and maximum consumption (day 14, Fig. 4), the chicks ingest 5.9 g protein/day (as calculated from composition of their food; Taylor and Konarzewski 1992), and they accumulate 1.7 g lean dry mass (mainly protein) per day (Taylor and Konarzewski 1989). At the same time the amount of fat ingested (4.5 g/day = 178 kJ/day) is sufficient to meet combined costs of maintenance and biosynthesis (188 kJ/day). The dietary surplus of protein may be metabolized to meet maintenance costs, and the energy saved may be stored as fat. At that age growth of chicks is not limited by the amount of energy or by protein delivered by parents. After day 14 further increase in metabolic costs with no increase in energy consumed is accompanied by a slowing down of the rate of increase in body mass, until it reaches zero on day 21 (Fig. 4).

Taking into account the relatively high metabolic rates of Dovekie chicks, it might be expected that the chicks are vulnerable to food shortages (e.g. during inclement weather). In fact, there was significant correlation between several weather parameters and body mass in 1984 chicks at the age of their maximum energy requirements (Konarzewski and Taylor 1989). In 1984 chicks, an obvious reduced rate of increase or even a decline in the relative amount of fat was observed at the beginning of the period of peak energy requirements; also, the fat contents, energy densities, and body masses of older 1984 chicks were significantly lower than in 1986 and 1987 (Fig. 2; Taylor and Konarzewski 1989) resulting in lower total energy deposited in tissues by the age of peak body mass (Fig. 2). All were linked with unfavorable weather in the Hornsund area in 1984. Nevertheless, this does not indicate that Dovekie chicks suffer food shortages, as all individuals measured in the three seasons had a substantial surplus of fat and the interfeed intervals were not unusually long (Taylor and Konarzewski 1989).

Comparison of energy requirements of chick and adult.—High chick energy demands might be expected to contribute to very high energy expenditures of feeding parents. However, the energy delivered to the chick by one parent is only 15% of the energy gathered by the parent to meet both its own and its chick's requirements (Table 3). This calculation is based on the period between days 8 and 21, when the chick is no longer brooded by its parents and is still fed by both parents (Taylor and Konarzewski in prep.). Parents do not share equally in feeding over this time; 64% of meals are delivered to the chick by the female (Taylor and Konarzewski in prep.). The average adult field metabolic rate (FMR) used for calculation included both sexes and was a mean weighted for feeding frequency, as the capture of birds feeding their chicks for FMR determination was proportional to their individual feeding frequency (Gabrielsen et al. 1991). Because there is no difference in food load mass and food composition between sexes (Taylor and Konarzewski in prep.), and adult FMR should be proportional to the number of foraging trips, the ratio should be close to 15% for both sexes.

The proportion of total energy gathered by parents that is delivered to the chick is similar in the other alcid studied, the Least Auklet, and in two species of diving-petrels (Table 3). Roby and Ricklefs (1986) noted that the proportion of energy delivered by European Starlings to their five-chick brood was three to four times higher than that in Least Auklets and diving-

TABLE 3. Proportion of energy gathered by alcids, diving-petrels and European Starlings delivered to their chicks during period of peak chick food demands.[a]

Species	Adult body mass (g)	Brood size	Adult FMR[b] (ml CO_2/ [g h])	Adult energy consumption[c] (kJ/day; *A*)	Food delivered to chicks (kJ/ [adult day]; *B*)	Proportion of energy delivered to chicks (%; 100 *B*/ [*A* + *B*])
1 European Starling (*Sturnus vulgaris*)	76	5	6.18	450	460	50
2 Least Auklet (*Aethia pusilla*)	84	1	6.69	465	97	17
3 South Georgia Diving-Petrel (*Pelecanoides georgicus*)	109	1	6.53	602	123	17
4 Common Diving-Petrel (*P. urinatrix exsul*)	137	1	6.34	723	101	12
5 Dovekie (*Alle alle*)	164	1	6.68	904	162	15
6 Black Guillemot (*Cepphus grylle*)	381	2	3.63	1121	525	32

[a] Sources: (1) Ricklefs and Williams (1984), Westerterp (1973); (2,3,4) Roby and Ricklefs (1986), Roby (1991); (5) Gabrielsen et al. (1991), present study; (6) F. Mehlum, G. W. Gabrielsen and K. A. Nagy (unpubl. data), Asbirk (1979; chicks' food consumption), Cairns (1987; energy density of food).

[b] Field metabolic rates in birds feeding chicks measured by doubly-labeled-water method.

[c] Calculated from FMR, assuming 0.67 energy-assimilation coefficient in European Starlings (Ricklefs and Williams 1984) and 0.77 in all others (Jackson 1986, Davis et al. 1989).

petrels rearing a single chick, although mass-specific field metabolic rates and body masses of all these birds were similar (Table 3). This means that seabirds are less efficient at delivering energy to the nest per unit energy expended. These authors suggested that one-chick broods of auklets and diving-petrels are a consequence of the high energy costs of foraging and transporting chick meals.

The case of the Dovekie supports this supposition, especially as its mass-specific field metabolic rate while feeding chicks is the highest among all birds mentioned above, despite its larger body mass (Table 3). In another study (Gabrielsen et al. 1991), we associated high metabolic costs of adult Dovekies with high costs of flight and their off-shore mode of foraging. Foraging Dovekies are observed as far as 150 km from the colonies (Byrkjedal et al. 1974, Brown 1976, but see Hartley and Fisher 1936). Both auks and diving-petrels utilize their wings for flying and propulsion under water. The latter is associated with strong selection for small wings and very high wing loading (i.e. ratio of body mass to wing area; Warham 1977, Pennycuick 1988), which in turn increases the energy cost of flying. The Black Guillemot, an alcid that usually raises two chicks, is able to collect more food. The proportion of energy delivered to chicks by Black Guillemots is twice that of Dovekies, despite a much larger body mass of the former species (Table 3); the proportion of acquired food that is allocated to a single nestling should decrease with an increase in body mass of the parent (Walsberg 1983). However, Black Guillemots always obtain food for chicks inshore in shallow water (Asbirk 1979, Cairns 1987). The proportion of energy delivered to chicks by Black Guillemots is even higher than that given in Table 3 when calculated using chick food consumption rates reported by Cairns (1987) and/or field metabolic rates of adult birds measured by Gaston et al. (in Roby and Ricklefs 1986). The proportion of energy delivered to chicks by Dovekies is very similar to that in the Least Auklet (higher food consumption in Dovekie chicks is associated with higher consumption in adults; Table 3). However, Least Auklet chicks attain 108% of adult body mass at fledging (Roby and Brink 1986), while Dovekies fledge at only 65 to 70% of adult body mass, although at the same age (Norderhaug 1980, Stempniewicz 1980, Konarzewski and Taylor 1989). This difference in the growth pattern also may be associated with foraging range, as Least Auklets normally forage within 5 to 10 km of the colony (Hunt et al. 1978).

Summarizing, we suggest that the low allocation to chicks of the total food collected by adult Dovekies reflects the adults' high cost of foraging (unproductive time and energy expended to fly between breeding colony and distant foraging areas, combined with high cost of flight itself). In addition, high chick demands at older ages may contribute to the high energy expenditures of adults. This may explain in large part the restriction of Dovekie brood size to one chick and the relatively low chick mass at fledging compared with adult mass.

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Appendix. Parameters of Dovekie chick's energy budget.

Age (days)	Body mass (g)[a]	Energy content (kJ)[b]	Increment in tissue energy (kJ/day)[c]	Resting metabolic rate (kJ/day)[d]
1	21.9	123.6	50.3	24.5
2	26.1	172.4	46.4	30.7
3	31.0	217.4	44.4	44.4
4	36.5	262.1	45.7	62.3
5	42.6	309.4	49.4	82.1
6	49.2	361.3	54.7	102.0
7	56.3	419.1	61.0	120.7
8	63.7	483.4	67.6	137.4
9	71.2	554.2	73.9	151.8
10	78.7	631.1	79.5	163.6
11	85.9	712.9	83.9	173.0
12	92.6	798.5	86.7	180.1
13	98.9	885.8	87.6	185.2
14	104.5	973.1	86.3	188.6
15	109.4	1,058.0	82.8	190.6
16	113.7	1,138.0	76.7	191.6
17	117.3	1,210.7	68.1	191.7
18	120.3	1,273.6	57.0	191.1
19	122.9	1,324.1	43.4	189.9
20	124.9	1,359.9	27.5	188.2
21	126.6	1,378.6	9.4	185.9
22		1,378.2	−10.5	183.1
23		1,357.0	−32.1	179.7
24		1,313.6	−54.9	175.7
25		1,247.0	−78.5	171.2
26		1,156.6	−102.3	166.5
27		1,042.5	−125.8	162.1

[a] Calculated from Richards growth curve

$$W(t) = A/\{1 + \lambda \exp[-k(t - t_i)]\}^{1/\lambda},$$

where A is asymptote, k is growth rate, t is age, t_i is inflection point, and λ is factor determining shape of growth curve. Values were: A of 133.5; k of 0.236; t_i of 8.66; and λ of 1.154.

[b] From the 1986–1987 curve in Figure 2.

[c] For example, value for day 15 calculated as day 15.5 minus day 14.5

[d] From curve in Figure 3.

Paper VI

Energy Expenditure by Black Guillemots (*Cepphus grylle*) During Chick-Rearing

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Abstract.—We used the doubly-labeled water technique to measure the field metabolic rate (FMR) of free-ranging adult Black Guillemots (*Cepphus grylle*) during the chick-rearing period. The FMR was 3.63 ± 0.74 ml CO_2 g^{-1} h^{-1}, equivalent to a daily energy expenditure of 860 ± 175 kJ d^{-1}. The FMR was 3.17 times the resting metabolic rate (RMR) measured in a previous study at the same locality. This FMR/RMR ratio is below the maximum sustained working level (4 x basal metabolic rate) proposed earlier for birds in general. In contrast to most alcid species, the Black Guillemot has a brood of two and is an inshore forager during the breeding season. Because of high costs of flight, offshore feeding would implicate an FMR in excess of 4 x BMR in this species. During chick rearing, adult Black Guillemots must consume ca. 232 g of fresh fish per day (61 % of its body mass) in order to maintain constant body mass. *Received 10 June 1992, accepted 11 February 1993.*

Key words.—Arctic, Black Guillemots, *Cepphus grylle*, daily energy expenditure, doubly-labeled water, field metabolic rate, food consumption, seabird energetics.

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Most alcid species normally feed offshore during the breeding season. However, the Black Guillemot (*Cepphus grylle*), like its two Northern Pacific congeners, the Pigeon Guillemot (*C. columba*) and Spectacled Guillemot (*C. carbo*), is mainly an inshore feeder during the breeding season. Two-egg clutches are common in these species and the young are fed in the nest by their parents until fully grown at an age of 30-40 days. Four other Pacific alcids (*Synthliboramphus* spp.) produce two-egg clutches, but their chicks are fully precocial. All remaining alcids produce single-egg clutches. In these species, chicks of the larger murre species (*Uria* spp.) and Razorbill (*Alca torda*) fledge when they are only 15-35 % of adult body mass (Gaston 1985a). The early-fledging strategy adopted by these species is believed to result from the inability of adults to provide enough food for their growing young (Ydenberg 1989).

Brood size in alcids is probably determined by the number of young that parents can feed (Nettleship 1972, Lloyd 1977, Harris 1978, Summers and Drent 1979, Birkhead and Harris 1985). It is a generally accepted theory that there is a trade-off between reproductive investment and adult survival in birds (Stearns 1976, 1977); i.e., a high energy expenditure in raising a two-chick brood may reduce the life expectancy of the parents. Asbirk (1979) found that adult Black Guillemots raising 1-2 chicks had significantly lower survival rate than adults laying two eggs but raising no chicks. However, he did not find a significant difference in adult survival between those raising one chick and those raising two chicks. Daily energy expenditure (DEE) is a measure of the investment in reproduction by breeding birds. Drent and Daan (1980) suggested that there is a certain "maximum sustained working level" for adult birds feeding young, and indicated that this level is about four times the basal metabolic rate (BMR). New information is now available for several seabird species which supports this hypothesis of a maximum sustained effort of about 4 x BMR (Gabrielsen *et al.* 1991), although some studies have shown that breeding seabirds exceed this metabolic intensity (Peterson *et al.* 1990).

The Black Guillemot is a common seabird in the European arctic region, including the Svalbard area (Mehlum 1989). It breeds all along the coasts of the archipelago and is an important avian predator on fish in coastal waters. Because the Black Guillemot differs from other palearctic alcids in producing a two-egg clutch, it represents an opportunity to compare its energetic investment in reproduction with alcids rearing a single chick. In this inshore feeder, the higher energy demand of rearing a two-chick brood may be compensated for by less energetic investment in flight between foraging areas and colonies. Black Guillemots are known to forage within a few kilometers of the breeding colonies (Cairns 1987a,b). The energetic cost of flapping flight is high (reviewed in Ellis 1984) and, compared to other seabirds of similar mass, alcids have reduced wing span and wing area (Pennycuick 1987). Thus, we believe that long distance foraging by alcids raising two-chick broods such as the Black Guillemot may be too energy demanding and may exceed their maximum sustainable working level.

In this paper, we measure the field metabolic rate of adult Black Guillemots during chick rearing and estimate the daily food consumption required to maintain energy balance in these birds. We also investigate the hypothesis that Black Guillemots are restricted energetically in their foraging range and that this has influenced their breeding strategy.

METHODS

Field studies were conducted during the periods 20-24 July 1985 and 16-22 July 1987 at a small island, Juttaholmen, in Kongsfjorden, Svalbard (79 °N. 12 °E, where 30 - 40 pairs of Black Guillemots breed. The climate is high arctic with maximum air temperatures in July. The mean ambient air temperatures during the two field seasons were 7.8 °C (range 5.0 - 13.5 °C) in 1985, and 6.1 °C (range 3.8 - 10.6 °C) in 1987. Precipitation averaged 0.3 and 2.4 mm/d^{-1} and wind speed 2.8 ms^{-1} and 3.0 ms^{-1}, respectively, in the two periods.

Most birds were caught in mist nets or with a net gun (Coda Enterprises) during flights to and from the nest. Some birds were caught by hand in the nest cavity. All of the birds we studied were breeding and had young aged less than 10 days.

We measured field metabolic rate (CO_2 production) and water flux of free-ranging birds by applying the doubly-labeled water (DLW) technique (Lifson and McClintock 1966, Nagy 1980, Nagy and Costa 1980). One or both members of breeding pairs were used in the measurements, although their sex was not determined. A total of 11 measurement periods with 9 different individuals was successful. Doubly-labeled water, containing 97.11 atom % excess oxygen-18 and 0.4 mCi of tritium, was injected into the pectoral muscle. In the 1985 experiments, 1.10 ml of water was injected and, in 1987, 1.28 ml was injected into each bird. The birds were weighed to ± 5g using a Pesola spring balance. After injection, they were kept in cloth bags for 1 h to allow the isotopes to equilibrate completely with body fluids (Degen *et al.* 1981, Williams and Nagy 1984) prior to collection of an initial blood sample. Each bird was marked on the white wing patch with an individual color and pattern using India ink. The experimental birds were recaptured within 1-3 days (two of the birds were recaptured twice). Initial and final blood samples (each 0.2 ml) were taken from a femoral vein.

The blood samples were flame-sealed in heparinized microhematocrit capillary tubes, and later vacuum-distilled to obtain pure water. Analyses of isotope levels were conducted using liquid scintillation spectrometry (for tritium) and proton activation analysis (for oxygen-18; Wood *et al.* 1975). On the basis of isotope levels, the rates of CO_2 production were calculated by using Eq. 2 in Nagy (1980), and water flux rates by using Eq. 4 in Nagy and Costa (1980). Body water volumes were estimated at initial capture from dilution of injected oxygen-18 (Nagy 1980). Water volumes at the time of recapture were calculated as initial fractional water content multiplied by body mass at recapture.

Field metabolic rates (FMR's) were converted from units of CO_2 production to units of energy (Joules) by using the factor 25.95 J ml CO_2^{-1}. This factor was calculated from the chemical composition of polar cod (*Boreogadus saida*) caught in July (77 % water, 5 % fat, 15 % protein, and 3 % ash; Brekke 1989) and using the energy equivalents for fat and protein from Schmidt-Nielsen (1983: 179) and RQ = 0.72 (Gabrielsen *et al.* 1988). We assumed that the total proportion of dietary fat and protein assimilated were the same as their proportions in the diet. According to Williams and Prints' (1986) review of DLW validation studies, the mean error of this method ranged between -4.9 and + 6.5 %.

Food Consumption

We estimated field food consumption from FMR in the following way: (1) we assumed that the only prey species eaten was polar cod; (2) with an energy content of 4.9 kJ g^{-1} wet mass (21.9 kJ g^{-1} dry mass; Brekke 1989); (3) and an assimilation efficiency of 75 % (Brekke 1989). Brekke's (1989) values are taken from feeding experiments with Thick-billed Murres (*Uria lomvia*) eating polar cod. We assumed that the assimilation efficiency for Black Guillemots eating the same food was similar. Therefore, Black Guillemots should obtain 3.7 kJ metabolizable energy per gram of fresh polar cod.

RESULTS

Field Metabolic Rate

The mean body mass of the experimental birds was 380 ± 20 g (Table 1). The field metabolic rate of free-ranging

Table 1. Rates of body mass change, field metabolism (FMR), water flux, and total body water (TBW) of chick-rearing Black Guillemots.

		Body mass						
Bird no.	No. of chicks	Mean mass (g)	Mass change (% d^{-1})	Measurement intervals Days (d)	FMR ml CO_2 $g^{-1}h^{-1}$	Water flux in ml H_2O $kg^{-1}d^{-1}$	Water flux out ml H_2O $kg^{-1}d^{-1}$	TBW (% of) mass)
1985								
505	2	410	+0.42	2.92	3.14	649	647	71.5
524	1	400	-0.60	2.10	4.04	702	705	71.1
526	2	385	+0.65	2.00	3.69	548	544	68.1
529	2	390	-0.86	2.97	3.51	498	503	68.2
534	1	330	-1.76	-1.72	4.68	865	877	73.7
1987								
511	2	375	-5.85	1.00	3.30	409	433	69.8
529	2	390	-4.54	1.13	3.71	143	174	68.1
529	2	390	+4.72	1.03	4.46	890	858	69.8
545	2	355	-0.26	1.06	2.12	623	625	69.7
547	2	390	-4.54	1.08	4.28	325	356	69.9
547	2	380	-1.28	1.03	3.01	468	477	69.9
Mean		380	-1.26	3.63	3.63	566	554	70.0
s.d.		20	2.94	0.76	0.75	223	210	1.7

breeding Black Guillemots averaged 3.63 ± 0.74 ml CO_2 g^{-1} h^{-1}, equivalent to a DEE of 860 ± 175 kJ d^{-1}. This is 23 % higher than the DEE predicted (701 kJ d^{-1}) using Kendeigh *et al.*'s (1977) equation for non-passeriform birds at 0 °C. Our value is 9.7 % higher than Gaston's (1985b) calculated DEE from time budgets and Kendeigh *et al.*'s (1977) allometric equations for energy expenditure for different activities. However, Gaston's estimates are for birds with 5 % lower body mass than the Svalbard birds. In a previous study (Gabrielsen *et al.* 1988), we determined the resting metabolic rate (RMR) of adult Black Guillemots during the breeding season to be 1.15 ml CO_2 g^{-1} h^{-1} (RQ=0.72). The FMR is 3.17 times this RMR value. Although eight of the 11 birds lost body mass during the measuring intervals, the overall mass loss was small (-1.26 ± 2.94 % per day; Table 1), and did not differ significantly from zero (P>0.05, t = -1.42).

Water flux rates were high, the influx averaged 556 ± 223 and outflux 564 ± 210 ml $kg^{-1}d^{-1}$, respectively. Total body water content averaged 70 % of body mass. Thus, the water influx and outflux rates were equivalent to 79 and 81 % of the total body water mass per day, respectively.

Food Consumption

For an individual Black Guillemot maintaining constant body mass, the metabolized food has to provide all the DEE of 860 kJ d^{-1}. With polar cod as the only food source, this means that the bird must consume 232 g of fresh fish per day or 61 % of its body mass.

Feeding rate can also be calculated from its associated water influx rate. A mass of 232 g polar cod, at 77 % water content, contains 179 ml water. Metabolically-produced water from oxidation of assimilated protein and fat, would provide an additional 0.128 ml water g^{-1} fresh fish (conversion factors from Schmidt-Nielsen 1983), or 30 ml for the Black Guillemot's daily food consumption. Thus, the total water yield should be 209 ml d^{-1}. This is almost identical to the water influx rate (210 ml d^{-1}) obtained by the DLW method. This comparison suggests that the feeding rate estimated from energy expenditure is reasonable and that Black Guillemots consumed little or no seawater while foraging.

DISCUSSION

Gabrielsen *et al.* (1988) have argued that their values of RMR are comparable

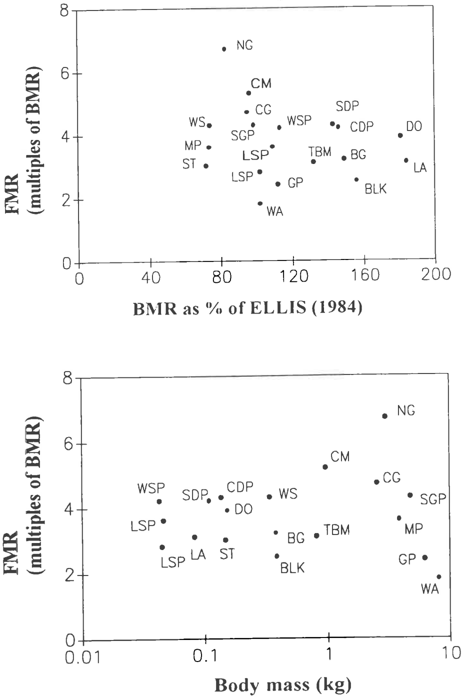

Figure 1. Field metabolic rates (FMR) for free-living seabirds during the chick rearing period represented as multiples of basal metabolic rates (BMR): a) as % of predicted values using the equation given by Ellis (1984), b) versus body mass. FMR's were obtained by using doubly labeled water and BMR's from respirometry. Species codes: BG = Black Guillemot *Cepphus grylle*, BLK = Black-legged Kittiwake *Rissa tridactyla*, CDP = Common Diving Petrel *Pelecanoides urinatrix*, CG = Cape Gannet *Morus capensis*, CM = Common Murre *Uria aalge*, DO- Dovekie *Alle alle*, GP = Gentoo Penguin *Pygoscelis papua*, LA = Least Auklet *Aethia pusilla*, LSP = Leach's Storm-petrel *Oceanodroma leucorhoa*, MP = Macaroni Penguin *Eudyptes chrysolophus*, NG = Northern Gannet *Sula bassana*, SDP = South Georgian Diving Petrel *Pelecanoides georgicus*, SGP = Southern Giant Petrel *Macronectes giganteus*, ST = Sooty Tern *Sterna fuscata*, TBM = Thick-billed Murre *Uria lomvia*, WA = Wandering Albatross *Diomedea exulans*, WS = Wedge-tailed Shearwater *Puffinus pacificus*, WSP = Wilson's Storm-petrel *Oceanites oceanicus*. (See Appendix for references)

to values termed BMR in the literature because thay were obtained in a similar manner. Our value of 3.17 x RMR is well within the 4 x BMR level of "the maximum sustained working level" proposed by Drent and Daan (1980). The Black Guillemot has a ratio of FMR/BMR similar to the Thick-billed Murre, but lower than in the Dovekie (*Alle alle*). FMR/BMR ratios for different seabirds are summarized in Fig. 1. All but two species in Fig. 1, the Northern Gannet (*Sula bassana*) and the Common Murre (*Uria aalge*), are close to 4 x BMR or lower. The high FMR/BMR ratio in these two species might be related to their lower BMR levels (Fig. 1a) compared to the expected values from the allometric equation for seabirds given by Ellis (1984). Some of the scatter in Fig. 1a and Fig. 1b is probably due to the fact that BMR and FMR were not determined in the same individuals. Differences in body mass between birds used for FMR and BMR measurements, respectively, would also have a slight influence on the FMR/BMR ratio. A possible explanation of the low BMR obtained in some species might be the use of different methods of measuring oxygen consumption. Fig. 2 shows that, in experiments using closed-circuit respirometry, the BMR was generally lower (on a body mass basis) than in experiments where open-circuit respirometry was applied. The highest FMR/BMR ratios (Northern Gannet and Common Murre) were obtained from calculations using closed-circuit respirometry. Ineffectiveness of the CO_2 absorbent in closed-circuit systems might be a source of error which should be investigated.

Flight is an energetically expensive activity, especially for species with high wing

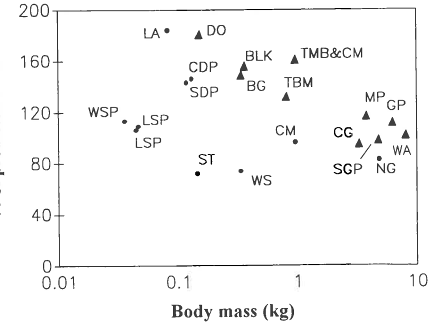

Figure 2. Basal metabolic rate (BMR) as % of predicted values using the equation given by Ellis (1984) versus body mass, for seabirds studied using open-circuit respirometry (triangles) and closed-circuit respirometry (filled circles). (See Fig. 1 for species codes).

loading such as the Black Guillemot. No experimental data on flight costs are available for alcids, but Flint and Nagy (1984) reported the flight cost of Sooty Terns (*Sterna fuscata*) at 4.8 x BMR, and Birt-Friesen *et al.* (1989) measured the flight costs in the Northern Gannet at 11.3 x BMR. Gaston (1985b) used the allometric equation given by Kendeigh *et al.* (1977) to estimate the flight cost of the Thick-billed Murre at 11.3 x BMR. Our data on the FMR/RMR ratio in the Black Guillemot suggests that this species would have an energy expenditure well above 4 x BMR if it fed in offshore areas during chick rearing with the same delivery frequency and size of chick meals. We may illustrate this with the following calculations: If we increase the flight distance between the colony and the foraging area by 25 km and assume a flight speed of 50 km h^{-1} during 9 foraging trips per day (Cairns 1987a), then the birds have to spent about nine more hours flying per day. If we assume that the metabolic rate is 3.17 x BMR during 15 hours and 11.3 x BMR during nine hours of the day spent for additional flying, then the integrated daily energy expenditure would be 6.2 x BMR. The number of foraging trips needed for feeding the Black Guillemot's two-chick brood is significantly higher than the 1-2 trips per day made by long distance foragers with one-chick broods, such as the Thick-billed Murre (Gaston 1985b). Thus, the energy expenditure associated with offshore foraging in a species such as the Black Guillemot rearing a two-chick brood would be very high compared to inshore foraging, as long as inshore prey is abundant.

Our measurements of field metabolic rate (3.63 ml CO_2 g^{-1} h^{-1}) in chick- rearing Black Guillemots in Kongsfjorden may be compared with our previous study of chick-rearing Black-legged Kittiwakes (*Rissa tridactyla*) at Hopen Island (76° 30′ N) (Gabrielsen et al. 1987). The Black-legged Kittiwakes and Black Guillemots had similar body masses. By averaging the FMR values obtained in Black-legged Kittiwakes for individuals attending the nest and those out at sea foraging, we calculated an integrated FMR of 3.24 ml CO_2 g^{-1} h^{-1}.

Our study on Black Guillemots was made in the early part (first 10 days) of the chick-rearing period. The exact age of the chicks was unknown, but the majority of the chicks was 5-10 days old. Cairns (1987a) reported that the number of feeds delivered to Black Guillemot chicks per day did not vary significantly with chick age (2-34 days), while the total amount of energy delivered to the chicks increased with age through increases in food loads carried. On this basis, and on the assumption that the incrase of FMR caused by increased food loads over short distances is negligible, we conclude that our FMR measurements of the adults may be representative of the whole chick-rearing period. Gaston and Nettleship (1981) came to the same conclusion in their study of Thick-billed Murre.

In Gaston's (1985b) model, a chick-rearing Black Gulillemot would have a DEE of 1.4 times a hypothetical non-breeder. If these birds maintain constant body mass, the additional energy expenditure due to rearing chicks would require a 40% increase in food consumption.

We estimated that a Black Guillemot consumed 61% of its body mass per day during chick rearing. This is less that the ca. 82% reported for the similar-sized Black-legged Kittiwake (Gablielsen *et al.* 1987) which fed offshore from Hopen Island, Svalbard. On the other hand, the much smaller Dovekie was reported to consume about 80% of its body mass per day (Gablielsen *et al.* 1991). Our estimate of food consumption in the Black Guillemot is based upon the assumption that the diet consists exclusively of polar cod. However, the diet of Black Guillemots in the Svalbard area is varied, comprising several species of invertebrates, as well as fish (Hartley and Fisher 1936, Løvenskiold 1964, Lydersen *et al.* 1989, Mehlum and Gabrielsen, unpubl. data). In our study colony, we have observed adults bringing polar cod, sculpin (Cottidae) and blennies (Blennioidea) to their young. If the energy content of different food items varied, this would influence our estimate of the total amount of food needed to balance energy expeditures. Cairns (1987a), however, found no significant difference in energy content between polar cod, three species of blennies, and one species of sculpin taken by Black Guillemots in Canada. His mean value was 21.4 kJ g^{-1} dry mass which is close to Brekke's (1989) value of 21.9 kJ g^{-1} used in our calculations. Energy content of arctic crustaceans is similar. In February/March the pelagic amphipod *Parathemisto libellula* and the krill *Thysanoessa inermis* found in seabird stomachs in the northern Barents Sea had a mean energy content of 19.9 (n = 4) and 23.0 (n = 5) kJ g^{-1} dry mass, respectively (Gabrielsen, Lønne and Mehlum, unpubl. data). A sensitivity analysis of our estimate of food consumption shows that a 5 % higher energy content in the food would implicate a reduced food requirement by only 11 g fresh mass, or 3 % of Black Guillemot body mass. We therefore believe that our estimate of food consumption is representative of a mixed diet consisting of polar cod, various benthic fishes, and crustaceans.

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Appendix. Species and references referred to in Figure 1.

Species	Reference	
	BMR	FMR
Black Guillemot, *Cepphus grylle*,	Gabrielsen *et al.* 1988	This study
Black-legged Kittiwake, *Rissa tridactyla*	Gabrielsen *et al.* 1988	Gabrielsen *et al.* 1987
Cape Gannet, *Morus capensis*	Adams *et al.* 1991	Adams *et al.* 1991
Common Diving Petrel, *Pelecanoides urinatrix*	Roby and Ricklefs 1986	Roby and Ricklefs 1986
	Johnson and West 1975.	

Appendix. Continued

Species	Reference	
	BMR	FMR
Common Murre, *Uria aalge*	Cairns *et al.* 1990	Cairns *et al.* 1990
Dovekie, *Alle alle*	Gabrielsen *et al.* 1988	Gabrielsen *et al.* 1991
Gentoo Penguin, *Pygoscelis papua*	Brown 1984	Davis *et al.* 1989
Leach's Storm-petrel, *Oceanodroma leucorhoa*	Ricklefs *et al.* 1986 Montevecchi *et al.* 1992	Ricklefs *et al.* 1986
Least Auklet, *Aethia pusilla*	Roby and Ricklefs 1986	Roby and Ricklefs 1986
Macaroni Penguin, *Eudyptes chrysolophus*	Brown 1984	Davis *et al.* 1989
Northern Gannet, *Sula bassana*	Birt-Friesen *et al.* 1989	Birt-Friesen *et al.* 1989
South Georgian Diving Petrel, *Pelecanoides georgicus*	Roby and Ricklefs 1986	Roby and Ricklefs 1986
Sooty Tern, *Sterna fuscata*	MacMillen *et al.* 1977	Flint and Nagy 1984
Southern Giant Petrel, *Macronectes giganteus*	Adams and Brown 1984	Nagy 1987
Thick-billed Murre, *Uria lomvia*	Johnson and West 1974, Gabrielsen *et al.* 1988	E. Flint pers. comm.
Wandering Albatross, *Diomedea exulans*	Adams and Brown 1984	Adams *et al.* 1986
Wedge-tailed Shearwater, *Puffinus pacificus*	Ellis 1984	Ellis 1984
Wilson's Storm-petrel, *Oceanites oceanius*	Obst *et al.* 1987	Obst *et al.* 1987

Paper VII

Energy expenditure of breeding Common Murres

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Abstract

The doubly labeled water (DLW) method was used to measure CO_2 production and food consumption in Common Murres (Uria aalge) (mean body mass 1025 ± 53 g) throughout the chick rearing period (3 to 20-day-old chicks) on Hornøya in northern Norway. Field metabolic rate (FMR) of foraging birds averaged 3.34 ml $CO_2 \cdot g^{-1} \cdot h^{-1}$, or a daily energy expenditure (DEE) of 2200 $kJ \cdot day^{-1}$. This is 3.8 times the resting metabolic rate (RMR), measured in the laboratory to be 0.88 ml $CO_2 \cdot g^{-1} h^{-1}$ or 580 $kJ \cdot day^{-1}$. FMRs of breeding Common murres varied widely among individuals and among days (range 959-3954 $kJ \cdot day^{-1}$). This is equivalent to a variation in the FMR/RMR ratio from 1.7 to 6.8, which suggests that breeding Common Murres have a flexible energy budget and that they can adjust their foraging behaviour in response to changes in food abundance. There was a significant positive correlation ($p<0.005$) between FMR and the time at sea. The high and variable FMR is probably associated with a high cost of flying and diving in Common Murres.

The mean daily change in body mass of each bird studied was 38 ± 21 g. Assuming that body fat is the main energy resource (minimum 17 g and maximum 59 g) and based on a minimum FMR of 959 $kJ \cdot day^{-1}$ breeding Common Murres may rely on these resources for an average of 1.5 days (minimum 16 h and maximum 2.4 days) without feeding. The average rate of food consumption by adult Common Murres, calculated on the basis of the chemical composition and digestibility of capelin (Mallotus villosus) and sandlance (Ammodytes sp.) was 440 g fresh matter per bird every

day. This food consumption is equal to 43 % of body mass per day. The water influx rate (WIR) was highly positively correlated with changes in body mass ($p<0.0001$), indicating that Common Murres digest as much food as possible at sea before returning to the colony. The population of 1400 pairs of Common Murres on Hornøya is estimated to consume a total of 27 580 kg of prey during 20 days of chick rearing.

Introduction

The seabird breeding populations in the Barents Sea and the northern parts of the Norwegian Sea are among the largest in the world (Anker-Nilssen and Barrett 1991), and Common Murres (Uria aalge) are an important species in the seabird communities in this region. They breed colonially in groups of hundreds to thousands of birds along the coast of northern Norway.

In order to determine the energy flow through seabird populations or communities, it is important to determine the energy requirements of individuals. The resting metabolic rate (RMR) and field metabolic rate (FMR) of seabirds breeding in the north are high when compared with tropical and temperate species (Roby and Ricklefs 1986; Obst et al. 1987; Gabrielsen et al. 1987, 1988, 1991).

Cairns et al. (1987) hypothesized that breeding Common Murres have flexible time budgets which are adjusted to changes in fish availability. Burger and Piatt (1990) found that breeding Common Murres spent more time at sea in response to poor feeding conditions. This change in feeding behaviour resulted in a constant provisioning and did not affect growth and survival of the chick. Monaghan et al. (1993), studying the foraging behavior of breeding Common Murres in two years of radically different levels of food abundance, also found that birds spent more time at sea in a poor year compared to a good year. However, these birds spent five times as much time diving in the poor year than in the good year. According to their calculation, the energy expenditure was twice as great in the poor year compared with the good year. Breeding Common Murres seem to have flexible time budgets, but whether they also have flexible energy budgets was one of the main questions addressed in the present study.

Energy demands upon parent birds are thought to be at a maximum during the chick rearing period (Drent and Daan 1980; Ricklefs 1983). In seabirds, free-living parents use energy at 3-6 times their basal metabolic rate (BMR) or RMR during the breeding period (Birt-Friesen et al. 1989). Based on doubly labeled water (DLW) studies on seabirds, among others, several researchers have hypothesized a daily maximum sustained working level of 4 x RMR during the chick rearing period (Drent and Daan 1980; Ellis 1984). While some DLW studies support such a hypothesis (Roby and Ricklefs 1986, Gabrielsen et al. 1987, 1991; Mehlum et al. 1993), other studies have shown that some seabirds exceed this level (Birt-Friesen et al. 1989; Cairns et al. 1990; Obst and Nagy 1992). In this study, this hypothesis was tested by comparing RMR and FMR measured at the same locality during the same breeding period.

FMRs in seabirds are generally presented as an average throughout the chick rearing period. Only two studies, in which the DLW method was used, have investigated the relationship between adult FMR and age of chicks (Roby and Ricklefs 1986; Gabrielsen et al. 1991). In both these studies, adult FMR was independent of the chicks' age. One would expect adult energy expenditure to increase with the age of the chick to meet the increasing energetic demands of the growing chick (Coulson and Pearson 1985). Common Murres as well as Thick-billed Murres (Uria lomvia) have a very high wing loading (Greenewalt 1962) and probably use more energy per unit distance flying than other seabirds (Pennycuick 1987; Croll et al. 1991). One consequence of this is that they are only able to transport chick meals which are less than 1.5% of their body weight (Gaston and Nettleship 1981). In this study, FMR was measured at different chick ages to determine if adult Murres are able to adjust their energy budgets as a result of the increased energy demand of the chick.

Material and methods

Birds

Common Murres breeding on Hornøya in Finnmark ($70^0 22'$N, $31^0 10'$E) were studied on 7-13 July 1990 when approximately 1400 pairs (Anker-Nilssen and Barrett 1991) of Common Murres bred on the island. The chicks were between 3-20 days old when we performed our doubly labeled water study, with one or both parents (n=11) making foraging trips.

Weather

Local weather conditions were measured at Hornøya Fyr (lighthouse), 300 m from the colony. During the study period, the weather was mild with no precipitation and little wind. The mean (± SD) air temperature was 13.1 ± 2.0 ^{0}C, and mean wind speed was 4.1 ± 1.8 m/sec. The ocean surface temperature was 9.5 ± 1.0 ^{0}C. There was continuous (24 h) daylight.

Resting Metabolic Rate

RMRs of 11 adult Common Murres were measured in a field laboratory near the colony. RMR measurements were made during both the day and "night" using the apparatus described by Gabrielsen et al. (1988). A metabolic chamber was placed outside in an open-top wooden box (in which the bird could see only the sky). Metabolism was measured at ambient chamber temperatures which varied between 10-20 ^{0}C.

We measured air flow (3.5 to 4.0 $l \cdot min^{-1}$) with a mass flow meter (Model F-201C-FA, Hi-Tec) connected to a readout (Model

5611-EA, Hi-Tec). Oxygen consumption and CO_2 production were measured with an Applied Electrochemistry oxygen analyzer (S-3A) and a Leybold-Heraeus (BINOS 1) CO_2 analyzer. Temperature in the metabolic chamber was measured with thermocouples connected to a Fluke thermometer. Body temperatures were not measured during metabolism trials, but were measured separately after each experiment, using a small thermocouple inserted 2-3 cm into the cloaca. Birds were habituated to the metabolic chamber, by introducing them into the chamber 3 times before the first measurements were made 12 h after the capture in the colony. Each bird was measured two times. At each ambient temperature, recordings were measured for at least 3 h. Metabolism was measured under full light conditions while the bird was resting. Oxygen consumption (ml $O_2 \cdot g^{-1} \cdot h^{-1}$), CO_2 production (ml $CO_2 \cdot g^{-1} \cdot h^{-1}$), respiratory quotient (RQ), and energy expenditure ($kJ \cdot day^{-1}$) was calculated at standard temperature and pressure (STPD, 0°C, 760 mmHg). When calculating energy expenditure from oxygen consumption a conversion coefficient of 20.08 kJ per liter oxygen was used (Schmidt-Nielsen 1975).

Doubly Labeled Water

Field metabolic rates (FMRs, as CO_2 production) and water flux rates were measured using the DLW method (Lifson and McClintock 1966; Nagy 1980; Nagy and Costa 1980), using the same procedure as described by Gabrielsen et al. (1987), in 11 adult Common Murres caught on the nest. These consisted of 3 pairs and 5 single individuals. Each bird was placed in a nylon bag and carried to the field laboratory.

Birds were injected with 2.5 to 3.0 ml $H_2{}^{18}O$, containing 97.11 atom % oxygen-18 and 0.4 mCi tritium, into the pectoral muscle. The birds were held in a wooden box for 1.0-1.5 h while the isotopes mixed thoroughly in body fluids (Degen et al. 1981; Williams and Nagy 1984). Birds were weighed to the nearest 5 g using a Pesola spring balance. Wing, head and bill lengths were measured to the nearest 1 mm in an attempt to determine the sex in all pairs. Each bird was banded and marked with individual patterns on the breast using felt-tipped pens. Blood samples (5 x 70 μl) were taken from a wing vein. All birds were released in the colony, and they returned to nest-sites within 30 min. Over the next 6 days, they were recaptured, weighed, and sampled, some two and three times. The nest sites were not disturbed but the birds were monitored from a hide continuously for 6 h each day (randomly during both the day and "night") and thereafter visited each 3 h to check if the birds were present. This check frequency was assumed to give representative samples of activity based on previous studies of murres (Burger and Piatt 1990; Furness and Barrett 1985). Two back-ground samples were taken from control birds at the start and at the end of the experimental period. The background for oxygen-18 was 0.2023 atom % and 35 cpm for tritium. Measurements of FMR by DLW become unreliable when the final level of oxygen-18 approaches background. One sample was excluded since the final oxygen-18 enrichment was within 5% of background.

Blood samples were stored in flame-sealed, heparinzed microhematocrit capillary tubes, and were vacuum-distilled to obtain pure water. Isotope levels in water were measured by liquid scintillation spectrometry (for tritium) and proton activation analysis (for oxygen-18) (Wood et al. 1975) by K. A. Nagy (University of California, Los Angeles, California, USA). Rates of CO_2 production were calculated with eq.2 in Nagy (1980), and water flux rates from eq. 4 in Nagy and Costa (1980). Body water volumes at recapture were calculated as the initial fractional water content multiplied by body mass at recapture. Validation studies in the laboratory have shown that DLW measurements of CO_2 production are accurate within 7% (Nagy 1989).

Food consumption

Food samples were collected from adult Common Murres feeding their chicks. For purpose of initial considerations, it was assumed that the food given to the chicks was the same as they ate themselves. During the study, Common Murres fed chicks primarily on capelin (*Mallotus villosus* 53%), sandlance (*Ammodytes* sp. 39%) and herring (*Clupea harengus* 8%; M. Asheim, pers. com.). However, the conversion factors for these diet items should be within 5% of that for capelin, due to similarities in the conversion factors for protein and fat (Schmidt-Nielsen 1975). Field metabolic rates (FMR) were converted from units of CO_2 production to units of energy (J) by using the factor 26.1 $J \cdot ml\ CO_2^{-1}$. This factor was calculated from the chemical composition of capelin (76.2% water, 6.6% fat, 15.2 % protein, 1.9% ash) and sandlance (70.7 % water, 6.7 % fat, 15.0 % protein; Barrett et al. 1987; R.T. Barrett, unpubl. data). Energy equivalents for fat and protein were from Schmidt-Nielsen (1975). In this calculation, it was assumed that the proportions of dietary fat and protein assimilated were the same as their proportions in the diet, and that Common Murres ate only capelin and sandlance during our study. The amount of food an adult Common Murre would have to consume to satisfy its daily energy requirements (as measured with DLW) was calculated from the energy content of food samples and energy assimilation efficiency for capelin and sandlance. Capelin and sandlance contain 26.25 $kJ \cdot g^{-1}$ and 21.35 $kJ \cdot g^{-1}$ dry matter, respectively. Based on feeding experiments of kittiwakes and Thick-billed Murres eating capelin with a fat content of 7%, an assimilation effeciency of 80% was used (Brekke and Gabrielsen, 1994). Thus, with a water content of 76% for capelin and 71% for sandlance, the food contains 6.25 $kJ \cdot g^{-1}$ wet mass, or 5.0 kJ metabolizable energy per gram of fresh matter.

Statistics

Two-tailed t-tests were used to compare means. Results are reported as mean ± SD unless noted otherwise. Analysis of covariance (ANCOVA; Proc. GLM, SAS 1988) were used to simultaneous relate FMR and WIR to the age of chick, time at sea, body mass change and individual variation. In order to test the effect of individuals, I first excluded all data from individuals from which only one measurement was collected (1, 5 and 6). When no such effect of individuals was found, all data were included in further calculations. Body mass change (%/d) were arcsine-transformed for analysis.

Results

Resting metabolic rate

The mean temperature in the metabolic chamber during metabolic trials was 16.1 ^{0}C (± 2.7 ^{0}C). Based on measurements of 6 species of seabird in the high Arctic (Gabrielsen et al. 1988), this should be well within the murres' thermoneutral zone. The body mass of each individual was used when calculating the mass-specific metabolic rate. The mean body mass during the metabolic measurements averaged 913 ± 53 g. Standing birds (1.31 ± 0.04 ml $O_2 \cdot g^{-1} \cdot h^{-1}$; n=9) had a significantly higher mass-specific RMR value than lying birds 1.20 ± 0.03 ml $O_2 \cdot g^{-1} \cdot h^{-1}$; n=12; $p<0.05$), or a 9% difference in RMR level between lying and standing birds. The CO_2 production of a resting, lying bird was 0.88 ml $CO_2 \cdot g^{-1} \cdot h^{-1}$ or 580 $kJ \cdot d^{-1}$. The mean RQ, within the thermoneutral zone, was 0.73 ± 0.01. The mean body temperature of resting lying birds was 39.7 ± 0.5 ^{0}C (n=7).

Body mass

Due to large variation in body size in Common Murres, it was not possible to separate males and females based on measurements of wing, head and bill (M. Asheim and R.T. Barrett, unpubl.). The mean body mass of birds included in the DLW experiment was 1025 ± 53 g (n=22 measurements). This value was used in subsequent calculations. Throughout the experimental period (1 to 3 days for each bird studied), all Common Murres maintained their body mass (the arithmetic average of weight changes) to within 0.25 ± 2.99 $\% \cdot d^{-1}$ (Table 1). Body mass change for each bird averaged 38 ± 21

$g \cdot d^{-1}$) (11 birds).

Field metabolic rate

Of 11 birds used in the DLW experiment, one FMR sample was obtained from 3 birds, two samples from 5 birds and three from 3 birds. Since there was no effect of individuals, all data was included in further calculations. FMRs of free-ranging birds averaged 3.34 ml $CO_2 \cdot g^{-1} \cdot h^{-1}$, or 2200 kJ/day (Table 1). This gives an average FMR/RMR ratio (based on whole body rates of metabolism) of 3.8. There was much variation in body mass, FMR and WIR among individuals and among days (Table 1). When FMR (ml $CO_2 \cdot g^{-1} \cdot h^{-1}$) was related to the age of the chick and time at sea, there was a significant positive correlation between FMR and time at sea ($r^2=0.36$; $p<0.005$; Fig.1);

$$FMR = 1.65 + 0.14\ T \qquad (1)$$

where FMR = ml $CO_2 \cdot g^{-1} \cdot h^{-1}$ and T = time at sea in h/d. The average time at sea was 12 h and 57 min per day (± 3 h 26 min). There was also a weak positive correlation between FMR of adults and age of the chick ($r^2=0.44$, p = 0.12). When age of the chick was used as a covariate in a multiple regression model the explained variance increased from $r^2=36$ to $r^2= 0.44$. This may indicate that adults with older chicks spend slightly more time at sea than adults with small chicks.

Water flux

WIR in Common Murres was 352 ± 138 ml/d (n=22 measurements). When WIR (ml/d) was related to body mass change, age of the chick and time at sea, there was a significant positive correlation between WIR and body mass change ($r^2=0.59$; $p<0.0001$; Fig.2);

$$\mathrm{WIR} = 343 + 61.5\ \mathrm{BWC} \tag{2}$$

where WIR = water influx rate in ml/day and BWC = body weight change (%/d). When the time at sea and the age of the chick were used as covariates in a multiple regression model the explained variance decreased from $r^2=0.59$ to $r^2=48$. This indicate no significant correlation between WIR and age of chick. This is probably due to the large daily variation in WIR. When the mean WIR value was used for each bird, water (food) consumption tended to increase ($p < 0.067$) as the chick grew. However, more samples are needed to show such a relationship.

Body water content during the experimental period averaged 68.5 ± 3.1% of body mass (n=9).

Food consumption

FMR in free-ranging Common Murres averaged 2200 ± 576 kJ/d (Table 1). At a metabolizable energy yield of 5.0 kJ/g fresh mass of food, Common Murres have consumed 440 g fresh food or approximately 43% of their body mass daily. This estimate of feeding rate was checked by calculating the associated water influx rate, and comparing this with the actual influx measured with tritiated water. A mass of 440 g of capelin (76.2% water) and sandlance (70.7 % water), in which the birds are eating 50% of each species, contains 323.2 ml of water. Metabolic water production from oxidation of assimilated proteins and lipids would provide an additional 0.122 ml water per gram fresh food (conversion factors from Schmidt-Nielsen 1975) or 53.7 ml water. This yields a total of 376.9 ml water when consuming 440 g of food, which is about 7% higher than the measured water influx of 351.5 ml water per bird (Table 1). This comparison from energy expenditure is reasonable, and indicates that Common Murres drank little or no sea water while foraging. These calculations also indicate that during the study period adult Common Murres were feeding on the same food items as the chicks as assumed in the methods section.

Discussion

Resting metabolic rate

The resting metabolic rate (RMR) value in the present study was obtained while the bird was at rest (both while standing and lying), in a post-absorptive state and within the thermoneutral zone. I do not claim to have measured true basal metabolic rate (BMR) but these metabolic measurements are comparable to values termed BMR in the literature since they were made in a similar manner.

In the present study, the mass-specific RMR of lying Common Murres was 9% lower than that of standing birds. The mass-specific RMR value was equivalent to RMR values for Common Murres measured at St. Paul Island in Alaska (Gabrielsen et al. 1994; Table 2). Johnson and West (1975), in a metabolic study of captive Common and Thick-billed Murres at Fairbanks, Alaska, obtained RMR values which were 7% and 5% higher respectively, than lying Common Murres measured at Hornøya and at St. Paul Island (Table 2). The mass-specific RMR value of Thick-billed Murres measured at St. Paul Island, Alaska, was similar to that measured on Svalbard (Table 2). These mass-specific RMRs of murres in Alaska, Svalbard and northern Norway are considerably higher (56-61%) than those reported by Cairns et al. (1990) (Table 2) for Common Murres in Newfoundland. Cairns et al. (1990) used a closed-respirometry method described by Ricklefs et al. (1984). The same system was also used on Northern Gannets (Sula bassana) in Newfoundland (Birt-Friesen et al. 1989); they obtained a BMR value which was 85% lower than the BMR value obtained on the same species in Scotland using an open-respirometry system (D.M. Bryant and R.W. Furness, unpubl.). To test the validity of these BMR or RMR values, it will be necessary to carry out a controlled comparison of the open-system used in this study and the closed-respirometry technique used by Cairns et al. (1990) and Birt-Friesen et al. (1989).

The mass-specific RMR value in Common Murres exceeds allometric predictions made for non-passerines by 143-189 % (Lasiewski and Dawson 1967; Aschoff and Pohl 1970), birds in general (Bennett and Harvey 1987) and seabirds (Ellis 1984; Gabrielsen et al., 1994). However, the RMR value is very similar to that predicted from the latitude-corrected equation of Ellis (1984). This equation is based on a pecentage increment (% BMR= 2.02 lat. + 52.3) relative to predictions made from the Lasiewski and Dawson (1967) equation.

The RMR value obtained in this study and earlier BMR or RMR studies of northern seabird species (Scholander et al. 1950; Johnson and West 1976; Gabrielsen et al. 1987, 1988, 1991, 1994; Gabrielsen and Mehlum 1989) confirm findings that seabirds breeding at high latitude have a higher RMR (or BMR) than similar species at low latitudes. The high RMR is consistent with Weathers' (1979) observations that the RMR (or BMR) of high latitude bird species generally exceeds those of warm-climate species.

The high RMR value may also indicate a difference in the adaptation to cold by different seabird species. While Common Murres measured both on Hornøya (70^{0}N) and at St. Paul Island, Alaska (57^{0}N; Gabrielsen et al. 1994), show no latitudial trend in mass-specific RMR there is a strong latitudial trend in RMR in Black-legged Kittiwakes measured at Svalbard (79^0N; Gabrielsen et al. 1988), Hornøya (G.W. Gabrielsen, unpubl.) and at St. Paul Island (Gabrielsen et al. 1994). This may be related to their foraging mode in which Common Murres are better cold adapted than kittiwakes. Common Murres are divers and are thus more exposed to a low sea water temperature than surface-feeding kittiwakes. However, murres are exposed to less variation in temperature since sea water temperatures vary less than air temperatures. While the RMR is the same at different latitudes, the thermal conductance (TC) is lower (they are better insulated) in murres studied in the high Arctic (Johnson and West 1976; Gabrielsen et al. 1988, 1994). Murres therefore appear to have reduced their insulation as the ambient air and sea water temperatures increase with decreasing latitude (Gabrielsen et al. 1994).

Field metabolic rate

Prior to this study, energetic studies of free-living murres have been characterized by small sample sizes (3-4 individuals) and have not taken chick age into account. In this study, the number of measurements has been increased. However, in order to show relationships between the field metabolic rate and the different parameters, the sample size should be increased.

The mean mass-specific FMR value (3.34 ml $CO_2 \cdot g^{-1} \cdot h^{-1}$) obtained for adults during the chick rearing period on Hornøya was 8 % higher than the mean value (3.18 ml $CO_2 \cdot g^{-1} \cdot h^{-1}$) of Common Murres (4 individuals) measured during the same period at Gull Island, Newfoundland (Cairns et al. 1990; Table 3). Both these

FMR values are 10-40 % higher than the FMR values obtained for Thick-billed Murres in the Pribilofs (2.89 ml $CO_2 \cdot g^{-1} \cdot h^{-1}$; E. Flint, unpubl.) and in the eastern Canadian Arctic (2.37 ml $CO_2 \cdot g^{-1} \cdot h^{-1}$; 3 individuals; Gaston 1985b; Table 3). Since Thick-billed Murres live in colder environments and are better insulated than Common Murres (Johnson and West 1976; Gabrielsen et al. 1988) these findings are consistent with the suggestion that the high FMR in Common Murres is associated with cold stress.

The FMR of Common Murres was 23-134 % above the allometric equations made for birds in general (Kendeigh et al. 1977; Walsberg 1983) and seabirds (Nagy 1987; Birt-Friesen et al. 1989; Nagy and Obst 1991). Birt-Friesen et al.'s (1989) equation for birds breeding in cold water and using flapping flight gave the best prediction for Common Murres.

The high FMR in high-latitude seabirds is explained by the cost of thermoregulation in cold environments and by foraging mode (flying or diving), which is especially expensive in murres. Ellis (1984) proposed a close linkage between RMR and the maximum power output, whereas Roby and Ricklefs (1986) and Gabrielsen et al. (1988) suggested that the birds' physical activity may influence the RMR level. According to Birt-Friesen et al. (1989), auks and diving petrels have an elevated FMR compared to other seabirds because they use their wings both for flying and diving. This contrasts with penguins in which the wing form is optimized for swimming while that of such seabirds as fulmars and Larids is optimized for flying. Since the optimum design for wings differs for flyers and divers one would expect that an intermediate stage would be less effective both in water and air. According to Greenewalt (1962), the wing loading of auks falls within the upper extreme of the range of all flying birds. Of three auk species measured, Common Murres had the highest wing loading (BM=950 g, wing area 0.0544 m^2, 17.5 g/cm^2; Pennycuick 1987). Using Pennycuick's (1989) Program 1 to calculate flight cost, the values for Common Murres, based on body measurements of individuals included in the DLW experiment, were compared to the measurements of FMR and no correlation was found. In this study it was not known how much time is spent and how far the birds flew when foraging at sea. However, since there is a good correlation between FMR and time at sea, the high and variable FMR might be associated with a high cost of flying and diving in Common Murres.

Flexible energy budget

Several recent studies have shown that Common Murres are able to change their foraging behaviour in response to changes in food availability. For instance, Monaghan et al. (1993) found an increase in diving time in years with low food abundance. The increase in foraging effort (increased diving time) resulted in an estimated doubling of energy expenditure. In the present study, times spent flying and diving is unknown, so it is impossible to calculate respective costs. However, based on preliminary heart rate recordings of free ranging Common Murres foraging from Hornøya, using a data logger system (P.J. Butler, T. Woakes and G.W. Gabrielsen, unpubl.), there are indications that the energy cost of diving is high. According to Croxall and

Briggs (1991), 80-95 % of the total daily energy budget is incurred at sea. The diving behaviour data from Common Murres (Cairns et al. 1990; Monaghan et al. 1993; P.J. Butler, T. Woakes and G.W. Gabrielsen, unpubl.) and my energetics data, show that they are able to increase their FMR to 2 to 7 times their RMR during the breeding period. This clearly suggests that breeding Common Murres may be able to adjust their FMR in response to changes in food abundance.

While Common Murres show great flexibility in time and energy budgets, their ability to change their work rate while foraging at sea does not seem to affect breeding success (Monaghan et al. 1993; Uttley et al. 1993). For Common Murres during situations of moderate food abundance, this may indicate that factors such as provisioning rate, chick growth and breeding success which is monitored in the colony may not reflect food availability in the area (Burger and Piatt 1990). Similarly, although there was a good correlation between FMR and time at sea, the latter does not necessarily reflect the parents foraging effort (see Cairns (1987 and 1992)).

Parental energy demand

According to Ricklefs (1983), parental energy demands are at a maximum during the chick rearing period. The working level during this time, described as "the maximum sustainable working level", was suggested to be about 4 X BMR (Drent and Daan 1980). This was later supported with DLW (Roby and Ricklefs 1986; Gabrielsen et al. 1987, 1991; Mehlum et al. 1993). However, studies show that some species exceed this sustainable working level during chick rearing (e.g. Cairns et al. 1990; Birt-Friesen et al. 1989; Obst and Nagy 1992). The FMR/RMR ratio in the present study ranged from 2 to 7, which corroborate that Common Murres can exceed this metabolic ceiling.

Until now, DLW studies of seabirds have been presented as an average FMR throughout the chick rearing period. In two species of diving petrels (Pelecanoides urinatrix and P. georgicus; Roby and Ricklefs 1986) and in Dovekies (Alle alle; Gabrielsen et al. 1991) there was no change in adult FMR with respect to chick age. In adult penguins, the highest energy cost was found at the end of chick growth (Gales and Green 1990). Burger and Piatt (1990) contend that there is a lack of consistent evidence for any increase in parental feeding effort as the chick grows. This seems unusual since the maintenance requirements of Common Murre chicks are thought to increase about six fold while they are in the colony (Coulson and Pearson 1985). In several studies of Common Murres, there was no apparent increase in provisioning rates with increasing chick age (Birkhead 1977; Harris and Wanless 1985). However, Birkhead and Nettleship (1987) found an increase in two seasons among Thick-billed Murres and in one season among Common Murres. Since the growing chicks require more energy as they become older it is expected that the parent bird must use more energy to catch and transport sufficient food to the colony. In the present study a weak correlation (p=0.12) was found between FMR and the chick age, suggesting that adults with older chicks spent slightly more time at sea compared to adults with smaller chicks.

It is suggested that the energy requirements of the chick are small compared to the daily energy expenditure variation of adults. In Common Murres, at the peak of growth, the energy requirements of the chick is only 20% of that of the adults (G.W. Gabrielsen, unpubl.). It may well be that adult Common Murres, with an average FMR/RMR ratio of 3.8, are working at a maximum during chick rearing and that they are unable to provide more food to secure further growth of the chick. This would therefore support the hypothesis that murre chicks fledge at < 30% of adult body mass due to the inability of parents to provide sufficient food to older chicks at the colony (Sealy 1973; Birkhead 1977; Gaston 1985a; Furness and Barrett 1985; Ydenberg 1989).

Body mass change

Croll et al. (1991) found a decrease in body mass in adult Common Murres very soon after hatching, which was interpreted as an adaptation to reduce the energy cost of flight while foraging. It was estimated that the energy saved was eqivalent to 25% of the RMR (or BMR) per day or a 5-10% reduction in the mechanical power required (Croll et al. 1991). Common and Thick-billed Murres studied on Hornøya lost 100 g and 80 g, respectively, from the end of incubation to fledging (M. Asheim, pers. com.). In this study, average body mass was stable throughout the chick rearing period. However, there were large individual and daily variations in body mass (mean 38 ± 21 $g \cdot d^{-1}$). Breeding Common Murres, working at a maximum during chick rearing, will, by processing food and storing excess energy at sea, be energetically more efficient when flying back to the colony than parents returning with full stomaches. Diurnal weight cycles associated with fat deposition have been shown in several species of tits (Parus spp.; Haftorn 1992). In Common Murres, the daily variation in body mass must also be associated with storage and turnover of body fat. While the fat is processed and stored at sea, the reserves can be used for maintenance when the bird is not feeding. Breeding Common Murres with a minimum FMR of 959 $kJ \cdot d^{-1}$ (Table 1) and utilizing body fat as the energy resource (losing an average of 38 $g \cdot d^{-1}$ and a energy eqvivalent of 38.5 $kJ \cdot g^{-1}$) will be able to rely on these resources for an average of 1.5 days (minimum 16 h and maximum 2.4 days) without feeding.

Food consumption

Based on the estimate of food consumption, Common Murres were calculated to consume an average of 43% of their body mass per day during chick rearing. According to Diamond et al. (1986), a high food consumption rate may cause physiological limitations due to digestive bottlenecks in hummingbirds. This means that high food consumption and digestion may also limit their time budget while foraging at sea. In this study, WIR was correlated to body weight change. Since WIR is a measure of the amount of food processed, this indicates that, while at sea, the murres probably spend time feeding themselves and processing the food. In murres a full meal, based on stomach analyses of birds shot at sea just after foraging, weight between 80-100 g (G.W. Gabrielsen, pers. obs.). If the amount of food ingested while foraging at sea is processed randomly in time before the bird is caught and weighed in the colony, one would not expect any correlation between WIR and body weight changes. However, the high correlation between WIR and changes in body weight indicate that Common Murres digest as much as possible at sea before returning to the colony.

When these birds have to consume an average of 440 g per day to cover their own requirements and the digestive process take 1-2 hrs for each meal (Brekke and Gabrielsen, 1994), this means they need to spend 4-8 h to digest their own food. In murres, the time spent at sea varies between 47 and 96% of daylight time (Burger and Piatt 1990). On Hornøya, Common Murres spend 54% of their time at sea, which is very similar to the 47% recorded for Thick-billed Murres at the same colony (Furness and Barrett 1985). While at sea, 70-85% of time is probably spent digesting food on the surface (Cairns et al. 1990; Monaghan et al. 1993), a process which thus may ultimately affect their time budgets.

Several factors influence the calculation of food consumption of breeding Murres. While the metabolic efficiency is determined by the fat content in the food (Brekke and Gabrielsen, 1994), the energy density of the food has the greatest effect on the calculation of food consumption. Cairns et al.'s (1987) study of Common Murres in Newfoundland was based on capelin with a lower fat content than those caught around Hornøya, and there the daily average food consumption was 16% higher than in the present study. When presenting population energy requirements it is therefore important to present energy values of different food items.

The Barents and Norwegian Seas are very productive. Capelin, sandlance and herring are three very important constituents of the diet of nearly all seabird species in the area. The diet of Common Murres breeding on Hornøya consists mainly of capelin and sandlance (Furness and Barrett 1985; Barrett and Furness 1990). However, herring is now becoming an important food item during the breeding period (M. Asheim and R.T. Barrett, pers. com.). During the period of this study, adult Common Murres on Hornøya fed their chicks on capelin (53%), sandlance (39%) and herring (8%) (M. Asheim, pers. com.). Assuming adults eat nearly the same as the chick, the present estimate of food consumption by all Common Murres was based on the assumption that they ate only capelin and sandlance. However, since the energy content of sandlance in this study was not significantly different from that of capelin, the calculation of the total amount of food needed should not be influenced.

During 20 days of chick rearing each Common Murres consumed an average of 8.8 kg of food. This include only the needs of the adult and excludes the foods given to the young. Based on the WIR of growing Common Murre chicks, water content of food, and the energy value of food, it was calculated that a 15 day-old chick consumed 105 g fresh food each day (G.W. Gabrielsen, unpubl.). The food requirements of two adults and one chick should total 19.7 kg during 20 days of chick rearing. The consumption by 1400 pairs of Common Murres on Hornøya would thus be 27 580 kg during chick rearing.

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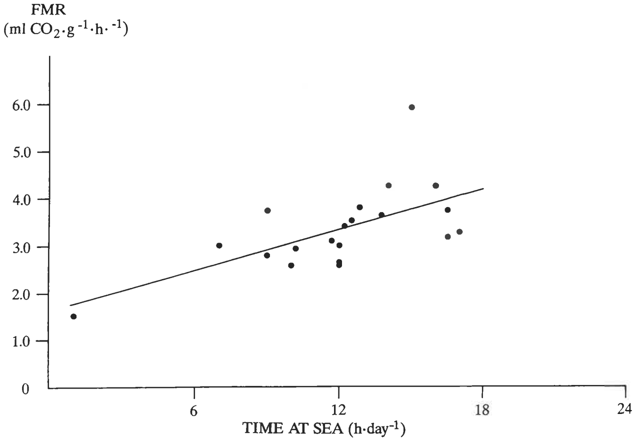

Figure 1.

The relationship between field metabolic rate (FMR) and time (T) at sea (h/d) in breeding Common Murres ($FMR = 1.65 + 0.14\ T$, $r^2 = 0.36$, $P<0.005$).

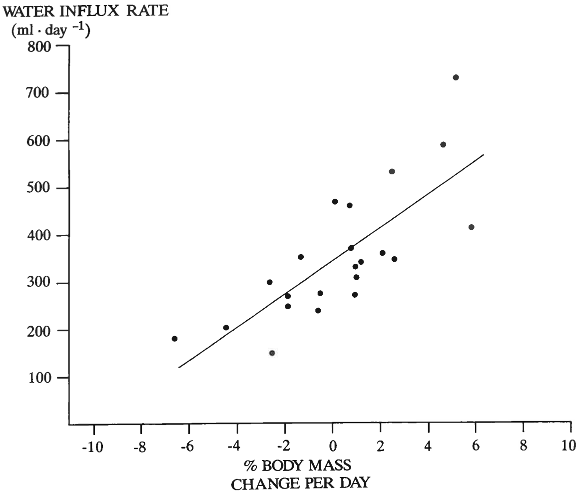

Figure 2.

The relationship between water influx rate (WIR) and body mass change (BMC)(%/d, based on arcsine transformed data) in breeding Common Murres ($WIR = 342.7 + 61.5\ BMC$, $r^2 = 0.59$, $P<0.0001$).

TABLE 1

Field metabolic rate, water influx rate, body mass (mean, change and arcsin transformed) and time at sea of adult Common Murres on Hornøya, 7 - 13 July 1990

Bird No.	Age of chick (days)	Body mass			Field metabolic rate		Water influx rate (ml/day)	At sea h·day^{-1}	Measurement period (days)
		Mean (g)	Change (%/day)	Arcsin (trans)	ml CO_2/g h	kJ/day			
C-1	18	1026.0	5.90	3.38	3.00	1975	413	12.00	1.03
C-2	4	945.5	-1.95	-1.12	3.11	1890	249	11.46	1.03
C-2	5	939.5	0.67	0.38	3.51	2122	460	12.29	1.12
C-3A	5	1089.5	1.00	0.58	3.23	2260	308	17.20	1.01
C-3	7	1085.0	-1.87	-1.07	2.64	1844	273	12.00	0.99
C-4B	13	1010.0	-0.58	-0.33	2.57	1666	240	9.50	1.02
C-4	14	1007.5	0.10	0.05	3.64	2357	469	13.41	1.00
C-5	3	977.5	-2.53	-1.44	1.53	959	150	1.00	1.66
C-6	15	937.0	1.08	0.61	3.19	1923	340	16.34	1.97
C-7C	9	1074.5	0.95	0.54	3.76	2597	333	16.34	1.08
C-7	10	1056.5	-4.45	-2.55	3.73	2534	201	9.07	1.00
C-7	11	1044.0	2.11	1.20	2.92	1959	360	10.19	1.00
C-8B	16	1016.5	4.60	2.64	4.22	2757	588	15.50	1.13
C-8	17	1035.5	-1.36	-0.77	5.94	3954	351	14.53	1.06
C-8	18	1015.5	- 2.71	-1.55	-	-	300	13.55	0.91
C-9	6	1064.0	0.93	0.53	2.80	1911	271	9.07	1.02
C-9	7	1076.5	0.67	0.38	3.77	2611	368	12.43	2.08
C-10A	8	1081.5	- 6.55	-3.76	2.65	1839	183	12.00	1.03
C-10	9	1059.0	2.53	1.44	3.39	2306	349	12.14	1.05
C-10	10	1087.0	2.45	1.40	3.12	2180	530	12.14	1.09
C-11C	9	945.5	- 0.51	-0.29	3.06	1861	273	6.58	1.03
C-11	10	966.0	5.09	2.91	4.26	2642	729	14.30	0.94
Mean		1024.5	0.25	0.14	3.34	2198	352	12.57	1.15
SD		52.6	2.99	1.71	0.86	576	138	3.26	0.32

$^{A, B, C}$ Pairs marked with common letter.

Table 2.

Resting metabolic rate (RMR) of Common (CM) and Thick-billed Murres (TBM) measured at different localities

Species	Body Mass (±SD) (g)	Number of birds	RMR (±SD) (ml $0_2 \cdot g^{-1} \cdot h^{-1}$)	Location	Source
CM	956 (12)	5	1.28 (-)	Fairbanks, Alaska*	Johnson & West 1975
CM	803 (52)	10	1.19 (0.05)	St.Paul Island, Alaska	Gabrielsen et al. 1994
CM	972 (24)	3	0.77 (0.15)	Great Island, Canada	Cairns et al. 1990
CM	913 (53)	11	1.20 (0.03)	Hornøya Island, Norway	This study
TBM	989 (10)	5	1.23 (-)	Fairbanks, Alaska*	Johnson & West 1975
TBM	1090 (59)	11	1.17 (0.05)	St.Paul Island, Alaska	Gabrielsen et al. 1994
TBM	819 (73)	11	1.11 (0.12)	Ny-Ålesund, Norway	Gabrielsen et al. 1988

*Birds captured in the colony at St.Lawrence, Island, Alaska

Table 3.

Field metabolic rate (FMR) of Common (CM) and Thick-billed Murres (TBM) measured at different localities

Species	Body Mass (±SD) (g)	Number of birds	FMR (±SD) (ml $CO_2 \cdot g^{-1} \cdot h^{-1}$)	Location	Source
CM	940 (34)	4	3.18 (0.53)	Gull Island, Canada	Cairns et al.1990
CM	1025 (53)	11	3.34 (0.86)	Hornøya Island, Norway	This study
TBM	936 (-)	3	2.37 (-)	Digges Island, Canada	Gaston 1985b
TBM	820 (-)	8	2.89 (-)	St.Paul Island, Alaska	E. Flint (unpubl.)

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