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

Geir Wing Gabrielsen,[1,3] Jan R. E. Taylor,[2]
Marek Konarzewski,[2] and Fridtjof Mehlum[1]
[1]*The Norwegian Polar Research Institute, P.O. Box 158, N-1330 Oslo Lufthavn, Norway, and*
[2]*Institute of Biology, University of Warsaw, Branch in Bialystok, Swierkowa 20B,*
P.O. Box 109, 15-950 Bialystok, Poland

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 $O_2 \cdot g^{-1} \cdot h^{-1} \cdot °C^{-1}$, 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-

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 × 70 μl) 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:

body water (ml) = 7.70 + 0.589 (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
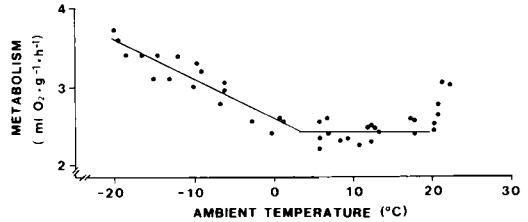

Fig. 1. Oxygen consumption rates of Dovekies at different ambient temperatures.

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).

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 $y = 2.61 - 0.05x$ ($y =$ 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 $O_2 \cdot g^{-1} \cdot h^{-1} \cdot$ °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 ($\pm$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:

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

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		Water influx rate (ml/day)	Metabolic rate		Measure- ment period (days)	Age of chicks (days)
Bird No.[a]	Mean (g)	Change (g/day)		(ml $CO_2 \cdot g^{-1} \cdot h^{-1}$)	kJ/day		
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/cm²; 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%

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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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