

## HEAT INCREMENT OF FEEDING IN BRÜNNICH'S GUILLEMOT *URIA LOMVIA*

P. A. J. HAWKINS<sup>1</sup>, P. J. BUTLER<sup>1,\*</sup>, A. J. WOAKES<sup>1</sup> AND G. W. GABRIELSEN<sup>2</sup>

<sup>1</sup>University of Birmingham, School of Biological Sciences, Edgbaston, Birmingham, B15 2TT, UK and <sup>2</sup>Norsk Polarinstitutt, Storgata 25A, Box 399, N-9001 Tromsø, Norway

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### Summary

The rate of oxygen consumption ( $\dot{V}_{O_2}$ ), respiratory quotient (RQ) and deep body temperature ( $T_B$ ) were recorded during a single, voluntary ingestion of Arctic cod *Boreogadus saida* (mean mass  $18.9 \pm 1.1$  g, S.E.M.,  $N=13$ ) by five postabsorptive Brünnich's guillemots (thick-billed murre, *Uria lomvia*). The birds were resting in air within their thermoneutral zone, and the fish were refrigerated to 0–2°C. The rate of oxygen consumption increased by a factor of 1.4 during the first few minutes after ingestion, but there was no significant change in  $T_B$ . Mean rate of oxygen consumption returned to preingestive levels 85 min after the birds ate the fish. The telemetered temperature of one fish reached  $T_B$  within 20 min. This suggests that the persistent elevation in  $\dot{V}_{O_2}$  over the next hour corresponded to the obligatory component of the heat increment of

feeding (HIF) and was not related to heating the fish. Abdominal temperature increases after diving bouts in free-ranging common guillemots (common murre, *Uria aalge*) are possibly achieved through the HIF, since meals are processed at sea. Of the increase in  $\dot{V}_{O_2}$  measured in the laboratory, it is calculated that 30% is required to heat the fish, while 70% is due to the HIF. In free-ranging birds, the excess heat provided by the HIF could contribute 6% of the daily energy expenditure. This suggests that the HIF augments heat production in *Uria* spp. and thus reduces the energetic cost of thermoregulation.

Key words: oxygen consumption, temperature, respiratory quotient, guillemot, *Uria lomvia*, heat increment of feeding, sea bird, metabolism, alcid, thermoregulation.

### Introduction

The increase in resting metabolic rate that accompanies the processes of digestion and assimilation of food by animals is commonly referred to as specific dynamic action (SDA, named by Rubner, 1885; Deuel, 1927) or the heat increment of feeding (HIF, MacArthur and Campbell, 1994). It is considered to comprise an obligatory component, i.e. the energetic cost of converting food to its primary storage forms (Krieger, 1978), and a facultative component, an adaptive mechanism that dissipates extra calories as heat (Lusk, 1919; Simonson and DeFronzo, 1990).

Wilson and Culik (1991) considered that the facultative component included the cost of heating the meal and that the postingestive heat production could prevent deleterious falls in body core temperature. They tested this hypothesis in the Adélie penguin (*Pygoscelis adeliae*) by feeding the birds hot (37°C) and cold (0°C) water and krill. They found that there was no elevation in the postingestive rate of oxygen consumption ( $\dot{V}_{O_2}$ ) when the penguins were fed hot krill or hot water, although it rose rapidly to four times resting levels when they were fed either cold krill or cold water (300 g of each, at 0°C). There was therefore no evidence for the HIF – all energy expenditure above the standard metabolic rate (SMR) was

attributed to the energetic cost of heating the meal (Wilson and Culik, 1991).

In contrast to the results of Wilson and Culik (1991), the HIF was evident in Adélie penguin chicks fed krill warmed to adult body temperature (so that there were no heating costs) during a subsequent study by Janes and Chappell (1995), and other workers consider that the HIF is beneficial in assisting thermoregulation in homeotherms (Šimek, 1975, 1976; Costa and Kooyman, 1984; Baudinette *et al.* 1986; MacArthur and Campbell, 1994; Markussen *et al.* 1994). In particular, Šimek (1975) noted that the HIF increased  $\dot{V}_{O_2}$  by 40% in the golden hamster when the environmental temperature was 30°C, but that the increase was only 7.7% at 10°C. This suggested that much of the postprandial excess heat was 'diverted' to a thermoregulatory function at the lower temperature (Šimek, 1975). Croll and McLaren (1993) measured  $\dot{V}_{O_2}$  before and after feeding in Brünnich's guillemot *Uria lomvia* and suggested that the HIF may be beneficial to this species in providing a supplementary heat source. Despite these possible energetic savings, Croll and McLaren (1993) stated that it may also be costly for the bird to heat its food (Wilson and Culik, 1991).

The present study aimed to investigate the effects on  $\dot{V}_{O_2}$

\*To whom reprint requests should be addressed.

under non-active conditions of the voluntary ingestion of a single fish by Brünnich's guillemots. Although the HIF has been examined previously in piscivorous birds (Wilson and Culik, 1991; Croll and McLaren, 1993; Janes and Chappell, 1995), the present study differs in that  $\dot{V}_{O_2}$  was monitored continuously before, during and after ingestion, and in that the fish was eaten voluntarily. The temperature of the ingested fish and the birds' deep body temperature ( $T_B$ ) were measured telemetrically to examine heating time and the effect of the cold ingesta on thermoregulation. Only one fish was placed in the respirometer box in the experiments described here because it could not be guaranteed that the birds would eat several fish at once. It might have been possible to force-feed the guillemots (see Wilson and Culik, 1991; Janes and Chappell, 1995), but this could have induced undesirable metabolic changes due to stress and handling effects.

Brünnich's guillemots eat a variety of foods including crustaceans, molluscs and annelids besides species of fish (Lønne and Gabrielsen, 1992; Mehlum and Gabrielsen, 1993), and the proportions of these dietary components vary seasonally (Mehlum and Gabrielsen, 1993). The fish chosen for the present study was the Arctic cod *Boreogadus saida*, which is frequently eaten by guillemots and fed to their young (Lønne and Gabrielsen, 1992; Mehlum and Gabrielsen, 1993). The calorific values and assimilation efficiency of this fish are also known (Brekke and Gabrielsen, 1994). However, any contribution from the HIF to thermoregulatory costs may differ among prey species and within the same prey species at different times of the year, as the body composition of all fish varies throughout the year (Brekke and Gabrielsen, 1994; Montevecchi and Piatt, 1994).

### Materials and methods

The experimental work was carried out during June and July 1995 at the Research Station of the Norwegian Polar Research Institute, Ny-Ålesund (79°N), Svalbard, Norway. Five Brünnich's guillemots *Uria lomvia* L. were captured from breeding cliffs at Krykkjefjellet (Kittiwake Mountain), Kongsfjorden, Norway, using a noose pole with a nylon snare. As the birds were required for several days, only non-breeding birds were taken. The breeding status of each captured bird was carefully checked by examining the chest and abdomen to determine whether a brood patch was present. Any brooding birds caught accidentally were immediately released and returned to their ledges within minutes. In the laboratory, on the day of capture, each bird had a pulse-interval modulated radiotransmitter, which transmitted  $T_B$ , of mass 6.5 g (Butler and Woakes, 1989) implanted into the abdominal cavity. The transmitters were calibrated in a waterbath before and after use in each bird and were accurate to 0.08 °C.

Surgical operations were performed while the birds were under halothane anaesthesia (1–2% Fluothane, ICI Ltd, in a 3:1 O<sub>2</sub>:air mixture) and using sterile procedures. The abdominal feathers were soaked in chlorhexidine solution (0.05%) and deflected before an incision was made. It was

necessary to make the incision to the left of the base of the sternum, as the cloaca is close to the caudal tip of the sternum in this species. The transmitters were placed deep into the abdominal cavity and sutured in place. The wounds were dressed with Woundcare powder (Animalcare Ltd, York), and antibiotic (tetracycline, 0.1 ml kg<sup>-1</sup>) and analgesic (Temgesic, 0.1 ml kg<sup>-1</sup>) were administered intramuscularly. Following recovery from the anaesthesia, the birds were housed individually in 1 m × 1 m × 0.8 m outdoor cages. The cages were protected from the rain by sheets of polythene. Mesh floors were necessary to allow faecal matter to fall through so that feather contamination was reduced. The birds were housed singly to prevent any escaping while one was being caught, but could see one another at all times. They were given Arctic cod to eat and sea water to drink *ad libitum*. Mean outside air temperature ( $T_a$ ) was 7.0 ± 0.9 °C (S.E.M., N=13) during the experimental period and was monitored using a copper-constantan thermocouple connected to a digital thermometer (Fluke 2168A).

All experiments took place at least 4 days after the transmitters had been implanted. Each bird was placed in an acrylic respirometer, 30 cm × 30 cm × 40 cm high, housed in a wooden box outside the laboratory. The box measured 1 m × 1 m × 1 m and was 1.2 m above the ground. The front of the box was open, but was covered by black cloth pinned securely in place while experiments were in progress. A video camera (Sony) was positioned inside the box so that the entire floor of the respirometer was visible, and the image was relayed to a monitor (Hitachi) inside the laboratory. The signal from the transmitter was passed from a receiver (Sharp FX-213AO) to a purpose-built decoder that displayed the mean pulse frequency, which varied with the temperature. The pulse frequencies were recorded on a two-channel cassette recorder (Superscope CD-320), the other channel of which was used to comment on the bird's activities and to record time checks.

The air flow through the respirometer was maintained at 51 min<sup>-1</sup> (Charles Austen pump) and was measured using a flowmeter (Bronkhurst Hi-Tec EI-Flow mass flowmeter/controller) that displayed the flow corrected to STPD (273 K and 101.3 kPa). Oxygen and CO<sub>2</sub> concentrations in the air leaving the respirometer were measured using an oxygen analyser (Applied Electrochemistry, Inc., S-3A) and carbon dioxide analyser (Leybold-Heraeus, Binos-1) respectively. The delay between air leaving the respirometer and arriving at the instruments was calculated by dividing the total volume of the sampling vessels and Drierite columns by the flow rate of 51 min<sup>-1</sup> and was found to be 21.0 s for the CO<sub>2</sub> analyser and 18.4 s for the O<sub>2</sub> analyser. These delay times were taken into account when calculating  $\dot{V}_{O_2}$  and  $\dot{V}_{CO_2}$  and relating them to feeding events, although they do not include the time constant of the respirometer box itself, which was calculated to be 7.2 min. The CO<sub>2</sub> level within the respirometer box was kept below 0.5% during experiments, although it occasionally rose above this level when the bird was first put in. The rate of oxygen consumption was calculated according to equation 1d of Withers (1977):

$$\dot{V}_{O_2} = \frac{(\dot{V}_{out} - \dot{V}_A - \dot{V}_{EWL})(F_{IO_2} - F_{EO_2})}{1 - (1 - RQ)F_{EO_2}}, \quad (1)$$

where  $\dot{V}_{O_2}$  is the rate of oxygen consumption (in  $\text{ml min}^{-1}$  STPD) (all gas volumes are corrected to STPD: 273 K and 101.3 kPa),  $\dot{V}_{out}$  is the rate of air flow out of the box,  $\dot{V}_A$  is the flow rate due to ambient water vapour,  $\dot{V}_{EWL}$  is the rate of evaporative water loss by the animal,  $F_{IO_2}$  is the the fractional concentration of oxygen entering the chamber and  $F_{EO_2}$  is the the fractional concentration of oxygen leaving the chamber. As the gas was dried before analysis,  $\dot{V}_A = \dot{V}_{EWL} = 0$  (equation 2 in Culik *et al.* 1990). RQ was set at 0.7 (calculated from previous measurements made myself using the same birds, when testing the set-up). Nitrogen dilution tests (Fedak *et al.* 1981) showed that there were no leaks and that the accuracy of the system was within 2%. The rate of carbon dioxide production  $\dot{V}_{CO_2}$  was calculated according to Withers (1977) and equation 3 in Culik *et al.* (1990):

$$\dot{V}_{CO_2} = \frac{\dot{V}_{out}(F_{ECO_2} - F_{ICO_2})}{1 + (1 - 1/RQ)F_{ECO_2}}, \quad (2)$$

where  $F_{ICO_2}$  is the fractional concentration of carbon dioxide entering the chamber and  $F_{ECO_2}$  is the fractional concentration of carbon dioxide leaving the chamber.

Each bird was fasted overnight or for at least 6 h before experiments began, although sea water was always available. Following its fast, the bird was weighed (mean mass  $0.82 \pm 0.03$  kg, S.E.M.,  $N=5$ ) and placed in the respirometer box, then left for at least 2 h or until the measured levels of  $O_2$  and  $CO_2$  leaving the box appeared to be constant. The bird's behaviour was observed on the video monitor; all the birds quickly settled down once the black cloth had been pinned in place and lay or stood quietly. Resting  $\dot{V}_{O_2}$  was calculated over a 10 min period during this resting sequence, while the birds were postabsorptive and resting at temperatures within their thermoneutral zone (TNZ) and before the fish was introduced into the respirometer.

When each bird was settled, an Arctic cod (refrigerated at  $0-2^\circ\text{C}$  to approximate seawater temperature) was weighed and quickly put into the respirometer box through the door. The black cloth was pinned back and the bird's behaviour was

monitored before and after it ate the fish. At least 10 min elapsed between adding the fish and the bird eating it, and resting  $\dot{V}_{O_2}$  was calculated again during the 10 min immediately before the fish was eaten. As  $\dot{V}_{O_2}$  increased when the birds stood upright (see below), data from birds which remained standing after eating were excluded from the subsequent analysis. Results are presented from birds which stood while swallowing, but rested immediately afterwards, either sitting right down or leaning slightly upright on the side of the box. Rates of oxygen consumption and carbon dioxide production were calculated every 2.5 min for 3 h after consumption of each fish. When the experiments planned for each bird had been completed, the transmitters were removed, using the sterile procedure described above, and the birds were released back into the colony the following day.

Some temperature transmitters had been constructed which were small enough to ingest (Mackay, 1970). Unfortunately, only one of these was still functioning when the time came to use them. It was pushed down a fish's oesophagus deep into the widest part of the body, and this fish was used in one of the trials. The signal from this transmitter was passed from a receiver directly to the second channel of the cassette recorder without passing through the decoder.

As it was not possible to obtain an equal number of samples from each bird, the data were analysed non-parametrically. For each variable ( $\dot{V}_{O_2}$ ,  $\dot{V}_{CO_2}$ , RQ and  $T_B$ ), a Wilcoxon paired test was performed to evaluate whether the maximum level attained after eating the fish was a true increase at the 5% level over resting values.

## Results

Data from ingestion events during which the guillemots remained standing were discarded, since  $\dot{V}_{O_2}$  measured when the birds stood up and remained standing for several minutes increased by a mean factor of  $1.07 \pm 0.03$  ( $N=5$ ). After these data had been rejected, results were obtained from 13 experiments, using five different birds. Although the statistical analysis was performed using 13 pairs of results in each case, Figs 1, 2 and 3 depict mean values ( $N=13$ ) over time and Table 1 gives the weighted as well as the overall mean values.

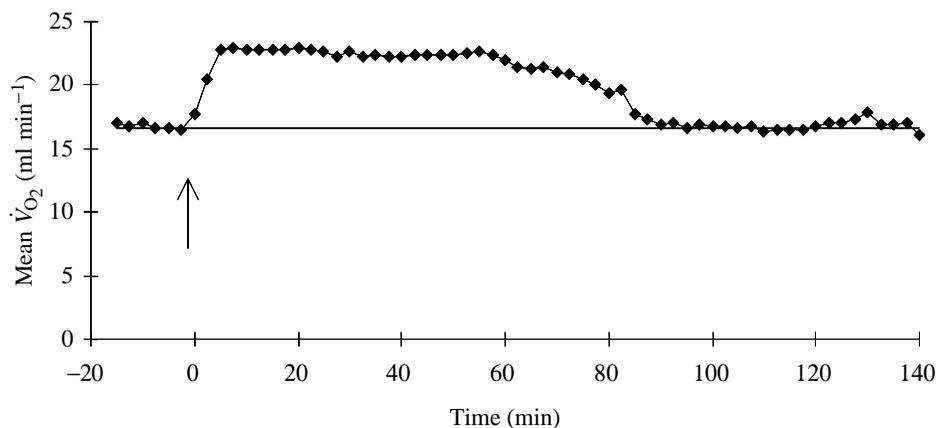
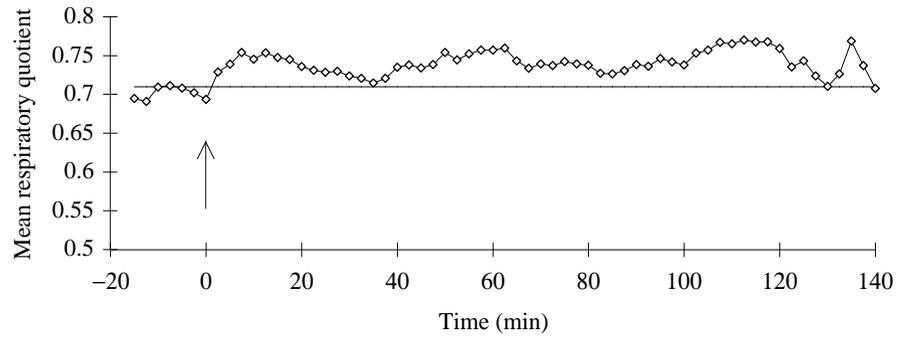


Fig. 1. Mean rate of oxygen consumption ( $\dot{V}_{O_2}$ ) during ingestion of an Arctic cod by *Uria lomvia*. The fish (mean mass  $18.9 \pm 1.1$  g, mean  $\pm$  S.E.M.,  $N=13$ ) were refrigerated to the approximate temperature of sea water ( $0-2^\circ\text{C}$ ). They were voluntarily ingested by the birds at time 0, indicated by an arrow. Each data point represents the mean of 13 values of  $\dot{V}_{O_2}$  obtained from the five birds. The horizontal line represents mean resting  $\dot{V}_{O_2}$  ( $16.22 \text{ ml min}^{-1}$ ).

Fig. 2. Mean respiratory quotient (RQ) during ingestion of an Arctic cod by *Uria lomvia*. Each data point represents the mean of 13 values of  $\dot{V}_{O_2}$  obtained from the five birds. The horizontal line represents mean resting RQ (0.71). Other details as in Fig. 1.



Before the fish were eaten,  $\dot{V}_{O_2}$ , RQ and  $T_B$  did not increase significantly above the lowest values recorded before the respirometer door was opened;  $P > 0.2$  in each case (Figs 1–3). The mean mass of fish eaten by the birds was  $18.9 \pm 1.1$  g (S.E.M.,  $N=13$ ).  $\dot{V}_{O_2}$  had increased significantly by a mean factor of 1.4 ( $P=0.01$ ) by 7.5 min after ingestion. It fell steadily over the next hour and was still slightly elevated 85 min after ingestion ( $P=0.04$ ). The area below the curve in Fig. 1 (following the subtraction of resting  $\dot{V}_{O_2}$ ) is 470 ml  $O_2$ .

The pattern of change in  $\dot{V}_{CO_2}$  corresponded closely to the increase recorded in  $\dot{V}_{O_2}$  (results not shown). Mean  $\dot{V}_{CO_2}$  increased by a factor of 1.5, which was a significant increase ( $P=0.001$ ). The rate of carbon dioxide production had not returned to baseline levels 85 min after ingestion ( $P=0.02$ ), as noted for  $\dot{V}_{O_2}$ . Since  $\dot{V}_{CO_2}$  increased slightly more than  $\dot{V}_{O_2}$ , RQ was also significantly elevated above resting levels after ingestion ( $P=0.02$ ; Fig. 2). RQ fluctuated widely throughout the rest of the experimental period.

Body temperature  $T_B$  fell slightly when the birds first ate the fish ( $P=0.02$ ; Fig. 3) and increased above the mean preingestive level of  $39.93^\circ\text{C}$ , reaching the significantly higher temperature of  $40.3^\circ\text{C}$  80 min after the fish had been eaten ( $P < 0.001$ ).

The temperature of an Arctic cod swallowed by one of the birds increased rapidly, reaching  $36.8^\circ\text{C}$  in 7 min (Fig. 4). It

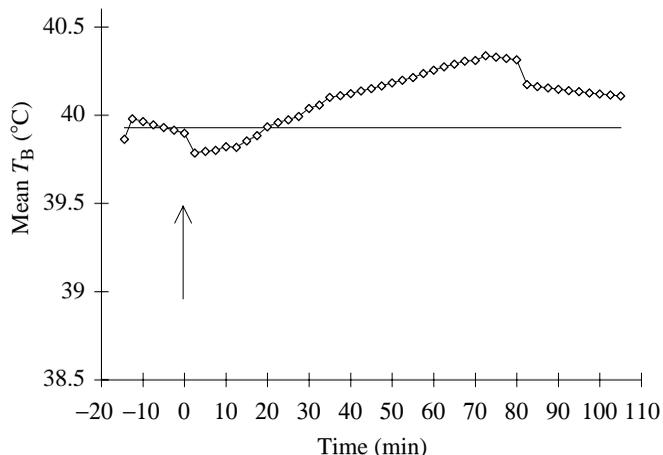


Fig. 3. Mean abdominal temperature ( $T_B$ ) during and after ingestion of an Arctic cod by *Uria lomvia*. Each data point represents the mean of 13 values of  $\dot{V}_{O_2}$  obtained from the five birds. The horizontal line represents mean resting  $T_B$  ( $39.93^\circ\text{C}$ ). Other details as in Fig. 1.

then fell to  $28.1^\circ\text{C}$  over the following 3 min, before rising again, reaching  $40.0^\circ\text{C}$  at 19 min and  $41.1^\circ\text{C}$  at 22 min. Unfortunately, the bird's  $T_B$  transmitter failed during this experiment, so its body temperature immediately after ingestion is not known. The bird retained the transmitter (which had failed 24 h later), so it was not possible to use it again.

### Discussion

The mean weighted resting  $\dot{V}_{O_2}$  of  $16.6 \text{ ml } O_2 \text{ min}^{-1}$  (i.e.  $\dot{V}_{O_2}$  immediately before the birds ate the fish; Fig. 1; Table 1) was similar to the mean values of  $15.2 \text{ ml min}^{-1}$  reported for this species by Gabrielsen *et al.* (1988) and  $16.5 \text{ ml min}^{-1}$  by Croll and McLaren (1993). The lower critical temperature ( $T_c$ ) of *Uria lomvia* is  $+2.0^\circ\text{C}$  in air (Gabrielsen *et al.* 1988), and mean  $T_a$  during the experiments in the present study was  $7.0 \pm 0.9^\circ\text{C}$ . Therefore, the birds were under no thermal stress. The animals were postabsorptive and resting during measurements of resting  $\dot{V}_{O_2}$ , but were exposed to full daylight because the experiments were performed during the Arctic summer. Values for resting  $\dot{V}_{O_2}$  measured in full light during the 'day' (09:00–15:00 h) and 'night' (21:00–03:00 h) are not significantly different in *U. lomvia* living in Svalbard during June and July (Gabrielsen *et al.* 1988), so any effects of diurnal rhythmicity (Aschoff and Pohl, 1970) will be negligible in the present study. The mean resting RQ of 0.71 (Fig. 2; Table 1) is in accordance with the usual assumption that fasting birds are catabolising stored lipid. The mean resting body temperature of  $39.93^\circ\text{C}$  (Fig. 3) was within the range of the mean

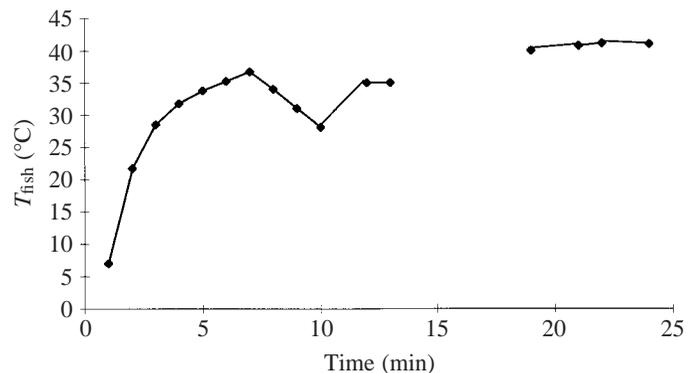


Fig. 4. The temperature recorded by a transmitter within an Arctic cod ( $T_{\text{fish}}$ ) after ingestion by *Uria lomvia*. The fish ( $N=1$ ) was ingested at time 0. The gap in the graph is due to the signal becoming indistinct.

Table 1. Rates of oxygen consumption ( $\dot{V}_{O_2}$ ) and carbon dioxide production ( $\dot{V}_{CO_2}$ ) and respiratory quotient before and after ingestion of Arctic cod by *Uria lomvia*

Bird	$\dot{V}_{O_2}$ (ml min <sup>-1</sup> )			$\dot{V}_{CO_2}$ (ml min <sup>-1</sup> )			RQ		
	Rest	Maximum	$\Delta$	Rest	Maximum	$\Delta$	Rest	Maximum	$\Delta$
1	14.51	22.32	7.81	9.60	16.81	7.22	0.66	0.75	0.09
1	16.77	23.86	7.08	11.06	18.07	7.01	0.66	0.76	0.10
2	19.65	24.71	5.06	14.36	17.77	3.41	0.73	0.72	-0.01
2	17.99	22.18	4.19	12.74	15.87	3.14	0.71	0.72	0.01
2	13.87	23.18	9.31	10.01	17.11	7.10	0.72	0.74	0.02
3	16.14	24.01	7.88	10.47	16.88	6.41	0.65	0.70	0.05
3	13.60	16.68	3.08	9.75	12.15	2.39	0.72	0.73	0.01
3	17.69	23.15	5.45	12.34	15.51	3.17	0.70	0.67	-0.03
3	14.52	22.04	7.52	9.91	16.57	6.66	0.68	0.75	0.07
3	12.78	16.23	3.45	9.48	12.53	3.05	0.74	0.77	0.03
4	15.07	24.67	9.59	11.10	20.27	9.17	0.74	0.82	0.09
4	21.22	32.02	10.80	16.79	27.34	10.55	0.79	0.85	0.06
6	17.10	22.47	5.37	12.13	15.84	3.71	0.71	0.70	0.01
Mean	16.22	22.88	6.66	11.52	17.13	5.61	0.71	0.75	0.04
S.E.M.			0.68			1.17			0.01
Weighted mean	16.60	23.53	6.93	11.83	17.75	5.91	0.71	0.75	0.05
S.E.M.	0.57	1.31	0.89	0.68	1.58	1.14	0.02	0.02	0.02

$\dot{V}_{O_2}$ , rate of oxygen consumption;  $\dot{V}_{CO_2}$ , rate of carbon dioxide production; RQ, respiratory quotient.

Resting values were measured over the 10 min immediately before each bird ate a fish. Maximum values were recorded 7.5 min after ingestion. Data were analysed using the (non-parametric) Wilcoxon test.  $\dot{V}_{O_2}$ ,  $\dot{V}_{CO_2}$  and RQ all increased significantly ( $P=0.01$ ,  $0.001$  and  $0.02$ , respectively).

Weighted means were obtained by calculating mean values for each bird, then taking the mean of those means.  $N$  is therefore 13 for the means and 5 for the weighted means.

$\Delta$ , difference between maximum and resting values.

colonic  $T_B$  of  $39.6 \pm 0.7^\circ\text{C}$  measured directly by Gabrielsen *et al.* (1988;  $P > 0.2$ ).

The 7% increase in  $\dot{V}_{O_2}$  when the birds stood upright was similar in magnitude to the 9% increase in resting  $\dot{V}_{O_2}$  recorded when the common guillemot stood (Gabrielsen, 1996). However, the behaviour and posture of the birds were closely monitored by video during the feeding experiments to eliminate such postural effects from the analysis. A measurable increase in  $\dot{V}_{O_2}$  has been observed on standing in other birds (Bevan *et al.* 1994, 1995), which illustrates the importance of monitoring behaviour when measurements of resting  $\dot{V}_{O_2}$  are made. As the birds stood momentarily to swallow the fish, a small proportion of the increase in  $\dot{V}_{O_2}$  following feeding will be due to the change in posture. However, the birds stood for 1–2 s only, so the effect should be negligible.

The 40% increase in  $\dot{V}_{O_2}$  that occurred within 7.5 min of the birds eating the fish was accompanied by an increase in RQ. This remained at approximately 0.74 during the rest of the experimental period, which corresponds to the typical value for protein metabolism in uricotelic species (King, 1957). The initial increase could indicate the oxidation of non-fat substrates soon after prey ingestion, possibly to heat the cold food rapidly. The continued high RQ may have been due to the metabolism of non-fat components of the fish, corresponding to the facultative component of the HIF.

There was a slight significant change in  $T_B$  following ingestion of a fish, in contrast to the large decrease in  $T_B$  from

$38.8$  to  $37.1^\circ\text{C}$  when Adélie penguins are fed cold krill (Wilson and Culik, 1991). However, the mean mass of the fish used in the present study was 18.9 g compared with the 300 g of krill which Wilson and Culik (1991) fed their penguins. The common guillemot *Uria aalge* can eat a meal of 80–100 g of fish (Gabrielsen, 1996), which would take longer to heat and perhaps depress  $T_B$  more than the single fish eaten in the present study.

A study on *Uria lomvia* by Croll and McLaren (1993) reported an absorptive  $\dot{V}_{O_2}$  increase of 45% (on water at  $20^\circ\text{C}$ ) when the birds ate voluntarily. These authors discovered that the lower  $T_c$  of the guillemot in water is  $15^\circ\text{C}$  and suggested that the raising of  $\dot{V}_{O_2}$  by the HIF would allow the birds to become thermally neutral in water temperatures of  $10^\circ\text{C}$ , which may either decrease the need to shiver or increase the time between bouts of activity (Croll and McLaren, 1993). The absorptive  $\dot{V}_{O_2}$  was measured (while the birds floated on water) at least 20 min after the cessation of a dive bout, so the food was likely to have been warmed by then (see below).

The temperature transmitter inside one of the fish was heated to  $T_B$  within 20 min (Fig. 4). The drop in temperature between 8 and 10 min suggests that the transmitter came into contact with a colder area of the fish, perhaps due to the muscular action of the stomach. Apart from the transient temperature drop, the rise in temperature closely resembles the typical exponential rise in stomach temperature recorded after ingestion by a variety of species of sea bird (Wilson *et al.* 1992, 1995; Grémillet and Plöös, 1994), harp seals *Phoca groenlandica* (Gales and Renouf, 1993)

and harbour seals *Phoca vitulina* (Hedd *et al.* 1995). When the transmitter reached mean  $T_B$ , either the fish was heated through or the transmitter had come to rest in a heated portion of the fish. Since 50 ml of water at 1 °C was heated to  $T_B$  within 27 min inside the stomach of a chinstrap penguin *Pygoscelis antarctica* (Fig. 10 in Wilson *et al.* 1995), it is possible that the 18.9 g fish had also been heated to  $T_B$  in the guillemot. In this case, the elevated  $\dot{V}_{O_2}$  that persisted for an hour afterwards was not related to heating the meal and may have been due to the HIF as the common guillemot takes 1–2 h to process a full meal of 80–100 g (Brekke and Gabrielsen, 1994).

An Arctic cod of mass 7.7 g has an energetic value of 4.9 kJ g<sup>-1</sup> (Table 3 in Brekke and Gabrielsen, 1994). The mean mass of the fish fed to the birds in the present study was 18.9 g. If the energy density was the same as that of a 7.7 g Arctic cod, the mean energetic content per fish in the present study was 92.6 kJ. If these fish had the same specific heat capacity as water, i.e. 4.17 J g<sup>-1</sup> °C<sup>-1</sup>, then the mean energy required to heat the fish in the present study to the mean  $T_B$  of 39.9 °C would be 3.0 kJ if they were eaten at 2 °C. The energy required to heat the meal therefore accounts for 3.2% of the energy content of the fish. The area below the curve in Fig. 1 of 470 ml O<sub>2</sub>, is equivalent to 9.5 kJ. This is 6.5 kJ more than the cost of heating the fish; therefore, 30% of the increase in  $\dot{V}_{O_2}$  is required to heat the fish, while 70% is due to the HIF.

The field metabolic rate (FMR) of Brünnich's guillemot has been estimated at 2080 kJ day<sup>-1</sup> while feeding chicks (E. N. Flint and G. L. Hunt, unpublished data cited in Brekke and Gabrielsen, 1994). If the assimilation efficiency of Arctic cod during the breeding season is 75% and its energy content is 4.9 kJ g<sup>-1</sup>, a bird feeding on cod alone will require 562 g day<sup>-1</sup> (Brekke and Gabrielsen, 1994, birds studied were incubating when caught). If the seawater temperature was 2 °C, this would cost 89 kJ to heat, i.e. 4.3% of the bird's daily energy requirements. Furthermore, as meals increase in size, the HIF also becomes elevated (Gallivan and Ronald, 1981; Markussen *et al.* 1994; Janes and Chappell, 1995), peak metabolic rate is delayed and persists for longer, and the HIF accounts for less of the gross energy of the diet (Gallivan and Ronald, 1981; Janes and Chappell, 1995). However, if it is assumed that 70% of the increase in metabolic rate after ingesting food is due to the HIF and that 30% is the cost of heating the fish, then the 562 g of fish requiring 89 kJ of energy to heat to  $T_B$  will also provide 208 kJ of excess heat *via* the HIF. This represents 10% of the daily energy expenditure of 2080 kJ (E. N. Flint and G. L. Hunt, unpublished data cited in Brekke and Gabrielsen, 1994). In this example, therefore, 208 kJ of excess heat minus the 89 kJ which the fish cost to heat leaves a net contribution of 119 kJ (5.7% of FMR) to thermoregulation.

In breeding *U. aalge* of mean body mass ( $M_B$ ) 1025 ± 53 g (mean ± S.E.M.,  $N=11$ ), a daily variation in  $M_B$  of 38 ± 21 g is associated with the quick storage and turnover of fat at sea (Gabrielsen, 1996). Processing as much food as possible at sea also reduces wing loading when the guillemots fly back to their chick, carrying a fish for its meal (Gabrielsen, 1996). *U. lomvia* fly more at this time than at any other time and have an

extremely high wing loading, so that even small changes in body mass can have a profound effect on their energy budgets (Croll *et al.* 1991). Further evidence for the digestion of the parents' meals at sea is the observation that birds caught at a breeding colony rarely contained any food material in the foregut (Gaston and Perin, 1993). Although the blood supply to the gut may be interrupted *during* a dive bout (Bevan and Butler, 1992; study on tufted duck *Aythya fuligula*), it will be restored during the processing of the bird's meal at sea, so the birds would then benefit from the HIF. Outside the breeding season, both *Uria* spp. live almost exclusively at sea, so all food processing would occur while floating at the surface. This is similar to the situation in the little penguin *Eudyptula minor*, which spends up to 2 days continuously at sea. If a 1 kg little penguin (while resting on land) eats approximately 100 g of fish,  $\dot{V}_{O_2}$  increases to 1.87 times the resting level (Baudinette *et al.* 1986). These authors concluded that the HIF was important in augmenting heat production (besides shivering and muscular activity). Costa (1988) suggested that such increases in  $\dot{V}_{O_2}$  would decrease an animal's aerobic dive time, yet this may not affect birds that complete the bulk of their digestion before the next bout of diving activity.

Following a diving bout by free-ranging *U. aalge*, mean  $T_B$  rises to 40.1 °C 17 min after a diving bout (P. J. Butler, A. J. Woakes and G. W. Gabrielsen, unpublished observations). It is likely that this increase is assisted by the HIF. A combination of stomach temperature (Wilson *et al.* 1992, 1995), heart rate and  $T_B$  logging could help to test this hypothesis. Although  $T_B$  does not fall significantly during dive bouts by *U. aalge* (P. J. Butler, A. J. Woakes and G. W. Gabrielsen, unpublished observations), additional heat generated by the HIF could still offset the cost of thermoregulation in both *Uria* spp. In the South Georgian shag *Phalacrocorax georgianus*,  $T_B$  falls by a mean 4.9 °C during dive bouts, and it has been suggested that the post-bout increase in  $T_B$  is augmented by the HIF (Bevan *et al.* 1997).

From the results presented here, it appears that the cost of heating fish is not a major metabolic burden for *U. lomvia*. The significance of the HIF in this species is likely to lie in the offsetting of thermoregulatory costs to a bird that spends the majority of its time (over the whole year) in water at temperatures well below its thermoneutral zone (Croll and McLaren, 1993). However, these birds employ a variety of behavioural methods, including preening, shivering and diving, to increase their metabolic rate, and reduce heat loss by withdrawing their legs and feet into feathered areas and keeping their wings out of the water (Croll and McLaren, 1993). Thermal conductance is very low in *U. lomvia* and, in common with all alcids, they are extremely well adapted to life in cold waters (Gabrielsen *et al.* 1988). The optimal timing of the obligatory and facultative components of the HIF is one of a range of adaptations that enable this species to survive and reproduce in an exacting environment.

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