

## SEASONAL HYPOTHERMIA IN A LARGE MIGRATING BIRD: SAVING ENERGY FOR FAT DEPOSITION?

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*Accepted 17 January; published on WWW 15 March 2001*

### Summary

We have tested the hypothesis that a large (2 kg) migratory bird, such as the barnacle goose *Branta leucopsis*, becomes hypothermic before its autumn migration, when food is not scarce, but when it is necessary to conserve and/or store energy in the form of fat. Abdominal temperature ( $T_{ab}$ ) was measured in wild geese using an implanted data logger. Commencing a few days before and continuing until approximately 20 days after the start of their autumn migration, mean daily  $T_{ab}$  fell progressively by 4.4 °C. Thus, it is suggested that, rather than increasing the rate of pre-migratory fattening, the energy saved as a result of this hypothermia reduces the rate at which fat is used and thus enables its more rapid replacement following and, possibly during, migration. The

energy saved may also be used for the replacement of non-fat tissues such as the locomotory muscles and gastrointestinal tract. These observations are the first of their kind from birds in their natural environment and, together with other data, demonstrate that hypothermia in endotherms is not necessarily related to extremely low environmental temperature, to shortage of food or to the resting phase of the daily cycle. The data also highlight the relationship between hypothermia and fat deposition over extended periods in relatively large, endothermic animals and may have some relevance to obesity in humans.

Key words: relaxed homeothermy, migration, barnacle goose, *Branta leucopsis*, obesity, hypothermia.

### Introduction

Whatever the selective pressures that led to the evolution of endothermy in birds and mammals (Hayes and Garland, 1995), endothermy carries with it a high metabolic cost. Even at the same body temperature (38–40 °C), a vertebrate ectotherm has a metabolic rate some 10–20% of that of a similar-sized bird or mammal and, at a body temperature of 10 °C, its metabolic rate may be only 1% of that of the endotherms (Bennett and Ruben, 1979). As has been pointed out (Golley, 1968; McNeill and Lawton, 1970), the energy consumed by the processes associated with the maintenance of a high body temperature in endotherms could have been devoted to growth or reproduction. There are times, when environmental temperature is extremely low and/or food is scarce, that a number of species of small endotherm reduce their metabolic rate and body temperature on a daily or seasonal basis (Nedergaard and Cannon, 1990; Reinertsen, 1996). There are two different responses to these conditions (Prinzinger et al., 1991; Reinertsen, 1996): (i) daily torpor or seasonal hibernation, during which the body temperature falls to such a low level that the animal becomes lethargic and is not easily aroused, and (ii) controlled hypothermia during the resting phase (night-time, for diurnally active animals), when body temperature drops by only a few degrees and can be readily restored to the normal level.

It is known that larger birds, such as pigeons, will become

progressively more hypothermic at night if they are deprived of food (Graf et al., 1989). It has also been suggested that some species of hummingbird enter torpor at night just prior to migration, not because of a shortage of food but to save on the energy cost of thermoregulation and, thus, to conserve fat for their migratory flights (Carpenter and Hixon, 1988). On the basis of data from laboratory experiments, it has even been suggested that, for some species of small (<20 g) migratory birds, hypothermia over several weeks may enable these animals to devote more energy to fat deposition than would otherwise be the case if they remained euthermic (Merkel, 1958). It is possible, therefore, that wild migratory birds become hypothermic just before their migration, when food is not scarce but when the necessity to conserve and/or store energy in the form of fat is of overriding importance.

One such bird is the barnacle goose *Branta leucopsis*, which breeds in the summer on Spitsbergen (77–80°N), the largest island in the Svalbard Archipelago. Towards the end of September, the geese set out on their long migration to their wintering grounds near Caerlaverock, in the Solway Firth, southern Scotland (55°N). Many of them stop at Bear Island (Bjørnøya) for a few days after leaving Spitsbergen and, until recently, it was thought that they flew non-stop from there directly to their wintering grounds, a distance of 2500–3000 km (Owen and Gullestad, 1984). However, it is

now known that the birds fly along the coast of Norway and make a number of short stops (Butler and Woakes, 1998). Even so, for some of the geese at least, the stops are so short that, from the perspective of taking on fuel, they appear to perform migrations that are effectively non-stop (Butler et al., 1998). The geese may, therefore, have to deposit sufficient fat stores before their migration to complete the journey to their wintering grounds. An estimate of the amount of fat deposited before migration has been obtained from two groups of geese. One of the groups was about to leave its breeding area at an old mining town called Ny-Ålesund (79°N) towards the end of August. The other group was just about to set off on its migration from a more southerly location on Spitsbergen (Hornsund, 77°N), approximately 24 days later. The former group had a mean body mass of 1.82 kg, of which 16 g was triglycerides, whereas the latter group had a mean body mass of 2.30 kg, of which 433 g was triglycerides (Butler et al., 1998).

The data presented here were gathered as part of a wider study on migration. They have been analysed to test the hypothesis that a relatively large (approximately 2 kg body mass) migratory bird, the barnacle goose, becomes hypothermic before its autumn migration from its breeding area in the high Arctic to its wintering grounds in southern Scotland, i.e. during the period of pre-migratory fat deposition. The data were recorded by implanting data loggers that store information on temperature and heart rate (Woakes et al., 1995) into the abdominal cavities of adult geese at their summer breeding site. The birds were recaptured the following year, and the loggers were recovered. A brief account of some of these data has been presented elsewhere (Butler and Woakes, 2000).

### Materials and methods

The study was performed at Ny-Ålesund, which is situated in the high Arctic (79°N, 12°E) on the western coast of the island of Spitsbergen, Norway, during the summers of 1995 and 1996. This old mining town now accommodates a number of national research facilities, including those of the Norsk Polarinstittut and the Natural Environmental Research Council of the UK. Non-flying birds were captured in corral nets during the post-breeding moult, between approximately the last 2 weeks of July and the first week of August. Each year, heart rate and temperature data loggers (HRTDLs) were implanted into six non-breeding birds and five or six successful breeding birds of either sex. The following year, up to eight of the birds were recaptured during the same period and the HRTDLs removed. In total, 14 of the 23 data loggers were retrieved, 10 of which contained usable data.

Both implantation and removal of the loggers were performed under general anaesthesia (Butler et al., 1998). Briefly, the birds were anaesthetised with halothane (Zeneca; 2–3% halothane in 75% air/25% O<sub>2</sub>). The incision area was washed with chlorhexidine solution, which also served to deflect the feathers. The sterilised data logger, together with

the attached electrocardiogram leads, was implanted into the abdominal cavity *via* mid-line incisions in the skin and body wall, and the time accurately noted. One electrocardiogram lead was placed anteriorly, close to the heart, and the other was positioned more posteriorly in the abdominal cavity. The temperature sensor is accommodated within the body of the logger and was, therefore, situated within the abdominal cavity. An antibiotic powder was dusted into the wound area, and a long-acting antibiotic (Terramycin LA, Pfizer) was injected intramuscularly. The birds were allowed to recover fully from the anaesthetic before being released. Upon recapture of the geese the following year, the loggers were removed and the data downloaded for further analysis (for further details, see Butler et al., 1998). Data loggers were also implanted into three captive, adult barnacle geese at the University of Birmingham, and recordings were made during August, September and the first 3 weeks of October 1998.

The unencapsulated HRTDLs were 55 mm×25 mm×7 mm in size and weighed 25 g with the electrocardiogram leads. Before implantation, they were encapsulated in a waterproof layer of wax and a biocompatible layer of silicone rubber. They measured heart rate by counting heart beats over a 1 min period and storing each count in memory (128 kbytes). Temperature was measured by the integral sensor and stored every 4 min. This gave a recording period of approximately 70 days. The data loggers were programmed with an initial recording delay of 15 days following implantation and began to store data at approximately the middle of August, 5–6 weeks before the birds set off on the migration to their wintering grounds in the Solway Firth, southern Scotland. Logging continued for approximately 10 weeks. In one goose, the sampling period of the implanted logger was twice that given above, so in this bird logging continued for approximately 20 weeks (see Fig. 2).

The start of migration was determined by identifying from the pattern of flight durations, as indicated by high heart rates (see Fig. 1), when the flight from Spitsbergen to Bear Island or to the northern coast of Norway occurred (Butler and Woakes, 1998). Heart rate and temperature were markedly lower during darkness (see Fig. 1), and this was used to delineate the periods of daylight and night-time for the calculation of the relevant mean values of temperature. For each day, hourly means were also calculated, and the minimum hourly mean was selected.

Values are given as means ± S.E.M.

### Results

Data were obtained from a total of 10 birds, five during each year, with a mean mass at the time the HRTDLs were implanted of 1.89 kg. The five geese from 1995 (mean mass at time of implantation of HRTDLs, 1.87±0.08 kg) began their migratory flights, on average, on 25 September, while those from 1996 (mean mass at time of implantation of HRTDLs, 1.91±0.07 kg), began theirs, on average, on 18 September.

Fig. 1A shows the complete record of heart rate ( $\dot{f}_H$ ) and abdominal temperature ( $T_{ab}$ ) from one of the geese, with the

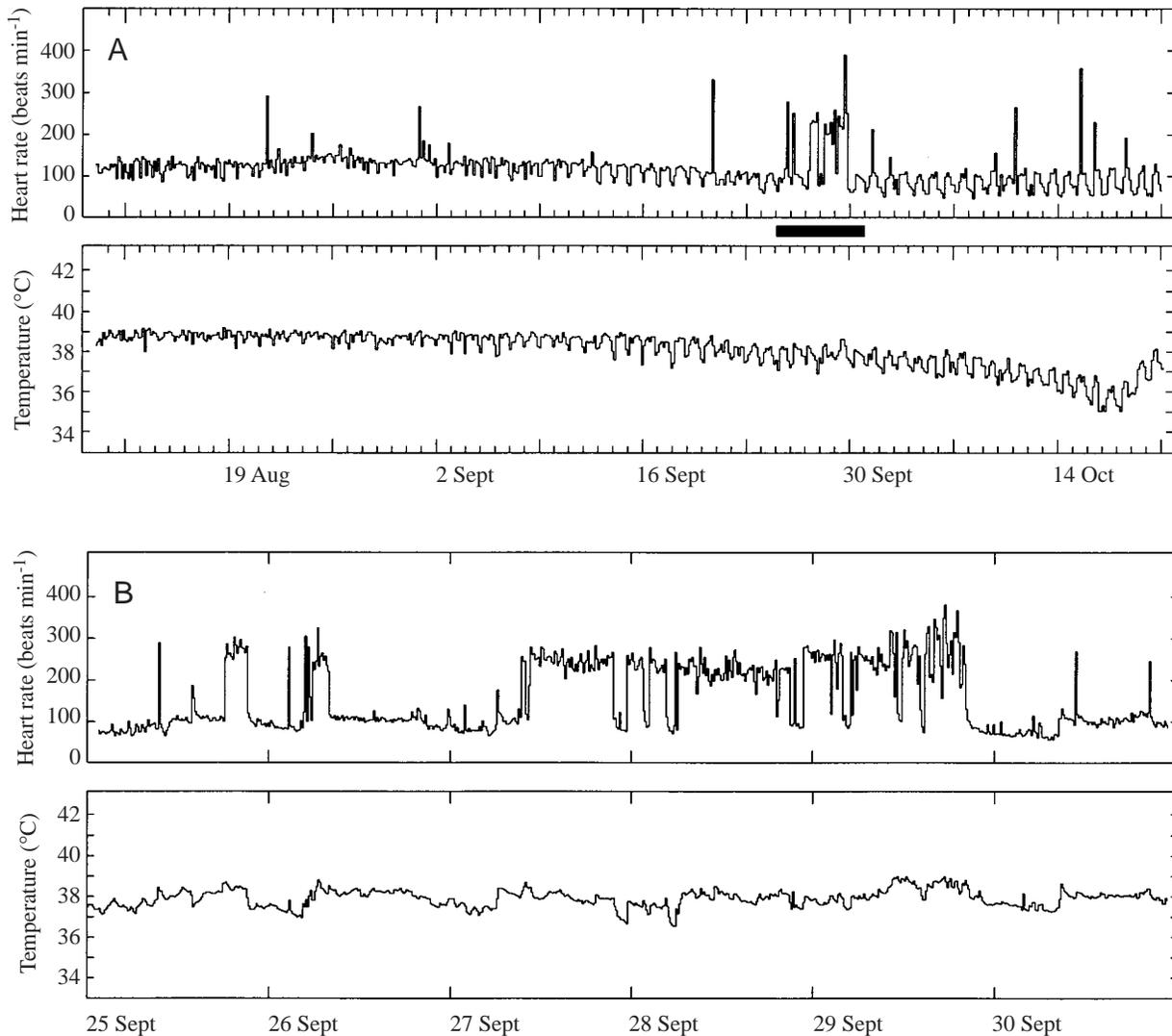


Fig. 1. Original traces of heart rate and abdominal temperature from a male barnacle goose (body mass 1.98 kg at the time of implantation of the data logger in July 1995) before, during and after its autumn migration. (A) Traces of complete recordings over a period of 10 weeks showing a period of 6 days (black bar) that includes the migratory flights (indicated by periods of high heart rate). (B) Expansion of the 6 day period indicated by the black bar in A.

migratory period expanded in Fig. 1B. Until the end of August, the birds were exposed to continuous daylight and there were relatively small variations in non-flight  $f_H$  and in  $T_{ab}$ . By the end of August, as darkness returned to the high Arctic, there was a clear diurnal variation in  $T_{ab}$ , and the daily (24 h) mean was  $40.7 \pm 0.5^\circ\text{C}$  ( $N=10$  birds). As well as the increasing diurnal variation in the traces as the nights became longer, there was also a clear reduction in daylight  $T_{ab}$  from around the middle of September (Fig. 1), or 7 days before the start of migration (Fig. 3). Only during the second half of October, well after the completion of the migration in most birds (Fig. 1), did daylight  $T_{ab}$  begin to increase back towards the value seen 2 months earlier (Fig. 2).

The data from all 10 wild birds, aligned to the start of migration, are shown in Fig. 3, and some of the mean values  $\pm$  S.E.M. are given in Table 1. It can be seen that the night-time

values of  $T_{ab}$  decrease over time to a greater extent than the daytime values, giving a daily variation of up to  $2^\circ\text{C}$ . This means that the mean daily (24 h) value of  $T_{ab}$  is progressively more influenced by the night-time value, not just because it falls by a greater extent, but because the duration of night-time becomes progressively longer. Thus, if the data are aligned to the day when the minimum temperatures were reached by each bird, mean daylight  $T_{ab}$  fell to  $36.9 \pm 0.5^\circ\text{C}$ , while mean  $T_{ab}$  at night decreased to  $35.1 \pm 0.5^\circ\text{C}$ . The result is that the lowest mean daily (24 h) value of  $T_{ab}$  was  $35.9 \pm 0.5^\circ\text{C}$ , which gives a significant ( $P < 0.001$ ) reduction in mean 24 h  $T_{ab}$  of  $4.8 \pm 0.4^\circ\text{C}$  from the value recorded at the end of August (see above). In the three captive birds in Birmingham, the mean 24 h  $T_{ab}$  fell significantly ( $P < 0.05$ ) by  $1.8 \pm 0.4^\circ\text{C}$  during the recording period.

Fig. 3 also indicates that four birds arrived in Scotland

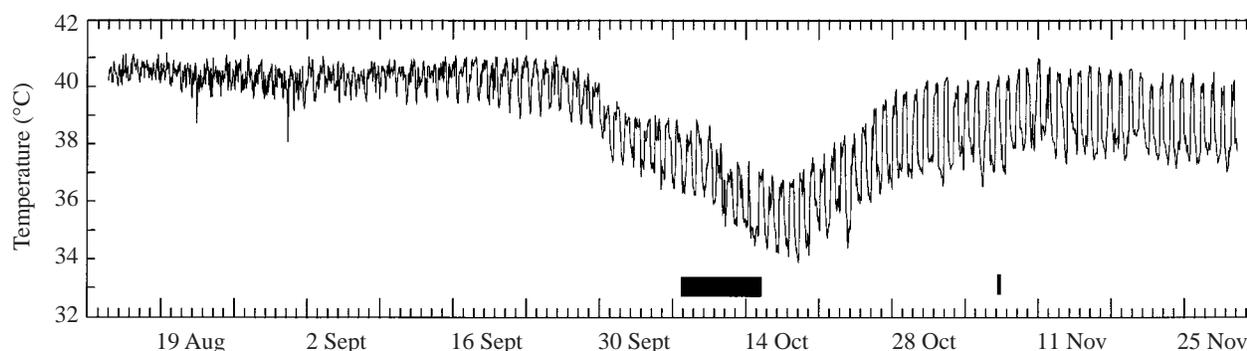


Fig. 2. Original trace of abdominal temperature from a male barnacle goose (body mass 2.07 kg at the time of implantation of the data logger in July 1995) over a period of 16 weeks showing the recovery of the daylight value back towards its pre-migratory level. A longer recording period was available for this bird because the sampling periods were doubled (for further details, see Materials and methods). The black bars indicate periods of migratory flight. It appears that this individual spent over 3 weeks in northern Scotland from the middle of October before flying on to Caerlaverock.

Table 1. Mean abdominal temperatures of wild barnacle geese before, during and after their autumn migrations in 1995 and 1996

Day relative to start of migration	Abdominal temperature (°C)			
	24 h mean	Daylight mean	Night-time mean	Minimum hourly mean
-20	40.7±0.5 (10)	40.7±0.5 (9)	40.1±0.5 (10)	39.5±0.6 (9)
-7	40.3±0.5 (10)	40.6±0.5 (10)	39.3±0.5 (10)	38.9±0.5 (10)
-5	40.1±0.6 (10)	40.4±0.6 (10)	39.2±0.5 (10)	38.7±0.5 (10)
-2	39.5±0.6 (10)	40.1±0.7 (9)	38.8±0.7 (9)	38.0±0.6 (10)
-1	39.2±0.6 (10)	39.3±0.8 (7)	38.0±0.6 (7)	38.0±0.6 (10)
0	39.0±0.6 (10)	39.0±1.2 (4)	37.4±0.9 (4)	37.7±0.6 (10)
2	38.9±0.7 (10)	40.1±1.0 (5)	38.2±0.7 (7)	37.4±0.7 (10)
20	37.1±0.6 (10)	38.2±0.6 (10)	36.0±0.5 (10)	35.5±0.5 (10)

Values are means ± S.E.M. (*N*).

The data have been aligned to the start of migration (day 0).

Long periods of flight make identification of day/night transitions impossible.

For further details, see caption to Fig. 3.

within a few days and, in terms of refuelling, had effectively flown non-stop (Butler et al., 1998), while three birds arrived several days later than the others. The latter was probably related to the presence of strong southerly winds while the birds were in southern Norway (Butler and Woakes, 1998).

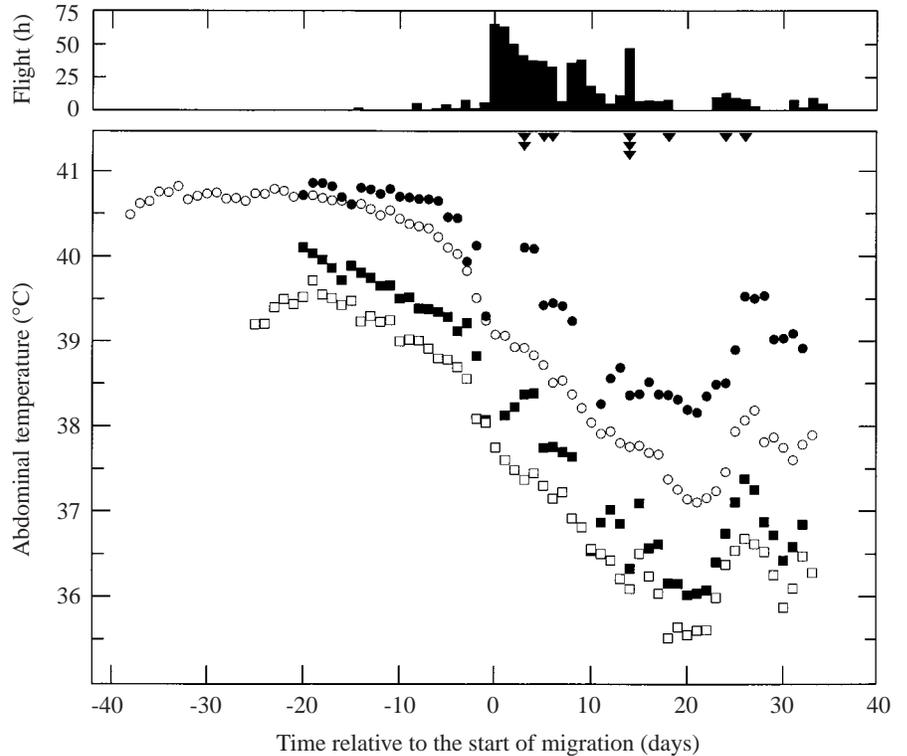
### Discussion

The data from the present study are the first of their kind from birds in their natural environment. However, the significance of the progressive reduction in  $T_{ab}$  is not easy to assess. If the period of hypothermia is taken from the time that the daylight and mean 24 h  $T_{ab}$  values began to show a clear decline (i.e. 7 days before the start of migration, Fig. 3) to the time that the minimum value of the 24 h mean  $T_{ab}$  is reached (21 days after the start of migration, Fig. 3), this gives a total duration of 28 days. Seven days before the start of migration, mean 24 h  $T_{ab}$  was 40.3±0.5 °C (Table 1), while the lowest value reached was 35.9 °C (see Results). This gives a mean

change in 24 h  $T_{ab}$  of 4.4 °C. If it is assumed that the whole goose experiences the same reduction in body temperature ( $T_b$ ) as we have measured for the abdominal cavity and if the apparent  $Q_{10}$  (Heldmaier and Ruf, 1992) is between 2.5 and 3 then, other things remaining equal, the metabolic rate of the geese would be between 34 and 39% lower at the end of the period of progressive hypothermia than at the beginning.

Assuming a linear reduction in  $T_b$  over a period of hypothermia (Fig. 3) and a resting metabolic rate for euthermic barnacle geese of 4.4 J s<sup>-1</sup> kg<sup>-1</sup> (S. Ward, C. M. Bishop, A. J. Woakes and P. J. Butler, unpublished data), then the average saving in energy expenditure over the 28-day period of hypothermia for a resting 2.0 kg goose would be between 3619 and 4151 kJ. If the energy density of fat is 39 kJ g<sup>-1</sup> (Weathers, 1996), this amount of energy would represent between 93 and 106 g of fat. This compares with the 430 g of fat estimated to be used by a 2.3 kg barnacle goose during its migration from Svalbard to southern Scotland (Butler et al., 1998). In the light of the above calculation relating to the possible reduction in

Fig. 3. Mean values of abdominal temperature from 10 barnacle geese before, during and after their autumn migration. Five geese (mean mass at time of implantation of data loggers,  $1.87 \pm 0.08$  kg) were from 1995 and, on average, began their migratory flights on 25 September. Five geese (mean mass at time of implantation of data loggers,  $1.91 \pm 0.07$  kg) were from 1996 and, on average, began their migratory flights on 18 September. The data from the 2 years have been aligned to the start of migration. The amplitudes of the standard errors for a selection of the data points are indicated in Table 1. Filled circles, daylight mean; open circles, 24 h mean; filled squares, night-time mean; open squares, minimum hourly mean. The solid histogram at the top indicates the total number of hours flown each day by all the birds. Also indicated are the arrival times of the birds in Scotland (filled arrowheads). For further details, see text.



metabolic rate at the end of the period of hypothermia, it is relevant to note that Battley et al. (Battley et al., 2000) reported a 32% reduction in mass-specific basal metabolic rate in great knots (*Calidris tenuirostris*) following their migration from northwestern Australia to eastern China. It would be interesting to know whether these birds exhibit hypothermia associated with this migration.

In the present study, mean daylight  $T_{ab}$  only began to decline a few days before migration and the decline continued for approximately 3 weeks after the start of migration. Thus, the proposed energy saving resulting from this hypothermia did not coincide with the deposition of fat prior to migration (thus rejecting our original hypothesis), but rather with its utilisation during the migratory period and with its replacement following migration. Following migration, there is an increase in the abdominal index (an indicator of the total fat content of the bird) of barnacle geese over a period that coincides with the period of hypothermia described in the present study (Owen, 1981). Of course, those birds from the Ny-Ålesund population that arrive in Scotland several days later than the others (Fig. 3) may begin to refeed before they arrive at their wintering grounds. However, there is growing evidence that birds not only replace at least some of the fat used during the migratory period, but also that tissue protein catabolised during migration must be replaced (Klaassen et al., 1997). It was estimated that barnacle geese use approximately 130 g of tissue protein during their migration from Svalbard to Scotland, but that the flight muscles would only account for approximately 80 g of this (Butler et al., 1998). The remainder is probably provided by the visceral tissues such as the gastro-intestinal tract and liver

(Karasov and Pinshow, 1998). Thus, the energy saved as a result of the hypothermia may be just as important in replacing tissue protein, such as the gastro-intestinal tract and liver, as it is in reducing the use of fat. However, quantification of the energy cost of replacing protein is not simple because the energy cost of protein synthesis in birds is uncertain (Weathers, 1996) and we have no estimate of the cost of obtaining the raw materials (feeding) for such synthesis.

It is clear that the thermal conditions that the geese experienced after their migration were less severe than those experienced before migration. The mean maximum and minimum air temperatures at Caerlaverock, southern Scotland (the wintering area for the wild geese), during the first 3 weeks of October were  $15.5 \pm 0.5$  and  $9.5 \pm 0.8$  °C, respectively, in 1995 and  $14.1 \pm 0.4$  and  $5.6 \pm 0.8$  °C in 1996 (E. Rees, personal communication). The corresponding values at Longyearbyen, Svalbard (close to areas the geese visit after leaving Ny-Ålesund at the end of August and prior to their migration), during the first 3 weeks of September were  $4.4 \pm 0.4$  and  $0.8 \pm 0.4$  °C, respectively, in 1995 and  $4.7 \pm 0.6$  and  $0.5 \pm 0.6$  °C in 1996.

The data from the present study demonstrate that hypothermia is a more widespread phenomenon among endothermic homeotherms than was previously thought and that it is not necessarily related to extremely low environmental temperatures, to shortage of food or to the resting phase of the daily cycle. We already know that regional hypothermia occurs in some species of marine birds during their foraging (diving) behaviour and may, by causing a reduction in metabolic rate, enable them to remain submerged longer than would otherwise be the case (Handrich et

al., 1997). Hypothermia related to the deposition of fat, with or without non-fat tissues, may not be restricted to birds that migrate. During the same period that the captive geese at Birmingham demonstrated a significant fall in mean 24 h  $T_{ab}$ , a flock of 12 captive barnacle geese in the same location showed a gain in body mass of  $338 \pm 47$  g (G. Froget, J. A. Green and P. J. Butler, unpublished data). It is interesting to note, however, that the degree of hypothermia was much less in the captive birds than in the wild, migrating ones. This may be related to the differences in the light/dark cycles in the two locations and to the fact that the captive birds were not engaged in the process of migration.

It has also been reported that mild hypothermia ( $\Delta T_b$  approximately  $-1$  °C) accompanies obesity in some mammals (Klaus et al., 1998), including humans (Rising et al., 1992). In mammals, there seems to be some relationship between leptin levels, brown adipose tissue, hypothermia and obesity (Pellemounter et al., 1995; Scarpace et al., 1997; Haynes et al., 1997). Unfortunately, the situation is not so clear in birds. There appear to be no data supporting the presence of thermogenic adipose tissue in birds (Saarela et al., 1991; Brigham and Trayhurn, 1994), and even the presence of non-shivering thermogenesis in skeletal muscle appears to be restricted to the young of most species of birds (Barré et al., 1986; Duchamp et al., 1989; Duchamp et al., 1999). However, while the first claim to have cloned the leptin gene in birds (Taouis et al., 1998) has been questioned (Friedman-Einat et al., 1999), Ashwell et al. (Ashwell et al., 1999) have confirmed the presence of a leptin homologue in the liver and adipose tissue of broiler chickens, and they conclude that there may be a relationship between leptin levels and lipid metabolic rate in birds. There is, therefore, much to be learned about the relationship between metabolic rate, body temperature and fat deposition in birds, particularly in adults of those species that naturally undergo large seasonal changes in their fat stores.

This study was funded by the Natural Environmental Research Council of the United Kingdom. We thank Maarten Loonen for his assistance in catching the geese, Geir Wing Gabrielsen for his logistical support and the following for their very helpful comments on an earlier version of the manuscript: Professors Claus Bech and Gerhard Heldmaier and Dr Yvon Le Maho.

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