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The effect of food temperature on postprandial metabolism in albatrosses

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SUMMARY

Heat generated by the specific dynamic action (SDA) associated with feeding is known to substitute for the thermoregulatory costs of cold-exposed endotherms; however, the effectiveness of this depends on food temperature. When food is cooler than core body temperature, it is warmed by body heat and, consequently, imposes a thermoregulatory challenge to the animal. The degree to which this cost might be 'paid' by SDA depends on the relative timing of food heating and the SDA response. We investigated this phenomenon in two genera of endotherms, *Diomedea* and *Thalassarche* albatrosses, by measuring postprandial metabolic rate following ingestion of food at body temperature (40°C) and cooler (0 and 20°C). This permitted us to estimate potential contributions to food warming by SDA-derived heat, and to observe the effect of cold food on metabolic rate. For meal sizes that were ~20% of body mass, SDA was 4.22±0.37% of assimilated food energy, and potentially contributed 17.9±1.0% and 13.2±2.2% of the required heating energy of food at 0°C for *Diomedea* and *Thalassarche* albatrosses, respectively, and proportionately greater quantities at higher food temperatures. Cold food increased the rate at which postprandial metabolic rate increased to 3.2–4.5 times that associated with food ingested at body temperature. We also found that albatrosses generated heat in excess by more than 50% of the estimated thermostatic heating demand of cold food, a probable consequence of time delays in physiological responses to afferent signals.

Key words: specific dynamic action, postprandial metabolic rate, albatrosses, cold, food, thermoregulation.

INTRODUCTION

Albatrosses (Procellariiformes) are large carnivorous pelagic seabirds having a general affinity for cold and temperate waters (Warham, 1990). Because food is patchily distributed in space and time in the marine environment, albatrosses must fly long distances to satisfy their energy needs. When food is encountered, it is often aggressively contested by other individuals, resulting in gorge feeding of substantial amounts of food in 3–4 min (H.B., M.A.C. and W.A.B., unpublished observations).

In the southern hemisphere, some albatross species forage as far south as the polar pack ice (Weimerskirch et al., 1993), where sea surface temperature (SST) can be below 0°C (National Oceanographic Data Centre 2005). Their diets comprise predominantly marine ectotherms, mainly cephalopods and fish (Warham, 1990; Cherel and Klages, 1998), which are ingested at ambient SST. Meal masses taken by free-flying albatrosses often exceed 20% of body mass (M_b) (Imber and Russ, 1975; Berutti and Harcus, 1978; Clarke et al., 1981; Cooper et al., 1992). As albatrosses are homeothermic endotherms with core temperatures of ~40°C (Warham, 1971), most of their food is sufficiently cold to produce thermoregulatory costs, which reduce the net energy obtained from a given amount of food.

When an endotherm ingests a cold (lower than core temperature) meal, a rise in postprandial metabolic rate (PPMR) will result from warming the cold meal (Wilson and Culik, 1999), from physical activities associated with feeding, and from postfeeding processes termed (alternatively) specific dynamic action (SDA), heat increment of feeding or dietary-induced thermogenesis. SDA (used here) has been studied in a wide array of endothermic vertebrates, including fish (Fitzgibbon et al., 2007), and results in part from the transport of food through the alimentary tract (Masman et al., 1989), but most (>90%) is associated with postdigestive stimulation of cellular protein synthesis (Ricklefs, 1974; Jobling, 1983; Blaxter, 1989; Brown and Cameron, 1991a; Brown and Cameron, 1991b). Because the metabolic heat produced by SDA is known to substitute for thermogenesis in birds exposed to sub-thermoneutral temperatures (Biebach, 1984; Baudinette et al., 1986; Chappell et al., 1997; Masman et al., 1989; Kaseloo and Lovvorn, 2003; Bech and Præsteng, 2004), we considered that SDA-related heat production could also contribute to warming the cold meals from which it was derived.

If SDA is to make a substantial contribution to the cost of warming cold food, the heat generated by SDA must be concurrent with the warming of a meal, which presumably begins immediately after ingestion. This requires food to be quickly processed and for digestion products to be delivered to protein-synthesising tissue within a very short time. To determine SDA and food-temperature effects on metabolic rate (MR) in albatrosses, we measured postprandial MR (PPMR) for meals isothermal to body core temperature (T_b; i.e. with no warming costs). We estimated the relative contributions of SDA and thermogenesis to warming cold meals by predicting the time course of meal warming from a mathematical model, and by measuring PPMR of albatrosses fed cold (0°C and 20°C) meals.

MATERIALS AND METHODS

Experimental animals

We captured free-living Gibson's (*Diomedea gibsoni* Robertson and Warham), wandering (*D. exulans* Linnaeus) and yellow-nosed (*Thalassache carteri* Rothschild) albatrosses at sea off Wollongong,

New South Wales, Australia (32°29′S, 151°50′E) using hand-cast nets as described by Gibson (Gibson, 1967). All of the *Diomedea* were recaptured banded adults of breeding age and all *Thalassarche* were at least 5 years old, as indicated by their adult plumage and primary moult patterns (Brooke, 1981). The Indian yellow-nosed albatross is the smallest of the albatross species and the Gibson's and wandering among the largest. For this study we used one *D. exulans*, seven *D. gibsoni* and seven *T. carteri*. Body mass (fasted) of individuals, was measured with a Pesola spring balance to the nearest 50 g as 2158±113 g (mean ± s.e.m.), range 1850–2300 g, for the yellow-nosed albatross and 6288±237 g, range 5450–7500 g, for the *Diomedea* species. *D. gibsoni* and *D. exulans* are closely related species with virtually identical life histories and for this study were treated as one species (Warham, 1990).

Birds were transferred to the University of Wollongong and held in an air-conditioned facility for up to 4 days; they were returned to sea following PPMR measurements. All aspects of care and handling of birds conformed to the Australian code of practice for the care and use of animals for scientific purposes (Australian National Health and Medical Research Foundation 1999–2004) and had gained approval from the University of Wollongong Animal Ethics Committee (permit no. AE04/11).

Metabolic rate measurements

To identify thermoneutral temperature ranges for *Diomedea* albatrosses, we continuously measured the metabolic rate of six *D. gibsoni* in a positive pressure open-system respirometer while lowering the chamber temperature from an initial 18°C to 3°C in 1°C steps over a period of 8 h. Five birds showed no MR response to the temperature changes, and one bird increased MR by ~40% when the chamber temperature fell to 6°C. From these results we assumed that chamber temperatures of ~14°C that we intended to use for a range of metabolic rate studies were albatross thermoneutral. As our intention was to simply identify a thermoneutral temperature range for other measurements, we did not extend this study.

We used two negative pressure open-system respirometers as described by Hill (Hill, 1972) to determine rates of oxygen consumption. Measurements were carried out at chamber temperatures of 14±1°C (thermoneutral for albatrosses) and air-flow rates of 20–30 standard litres per minute (s.l.p.m.). Flow rates were monitored by either a Hastings HFM201 100 s.l.p.m. mass flowmeter or a Singer DTM115 slide valve flowmeter modified to give a flow-related pulsed voltage output. At these temperatures we anticipated that albatrosses confined in chambers might suffer thermal stress if unable to readily dispose of postprandial heat output. Accordingly, the chambers were large enough to permit birds to assume resting postures and were provided with cool (13–14°C) fresh running water to allow metabolic heat dissipation *via* their immersed feet. This feature also eliminated soiling of plumage by faeces, which were released in copious amounts after a meal.

Of the 15 birds used in the study, six were measured at three meal temperatures and the remainder at two, as detailed in Table 1. PPMR measurements were recorded at meal temperatures (T_f) of 0°C, 20°C or 40°C. Repeated measurements on individuals were made on successive days and birds were fasted overnight before each measurement session. All measurements were made in daylight hours, corresponding to the active phase of the albatross circadian cycle.

To determine resting metabolic rate (RMR) and assess handling effects, we placed birds in chambers 1–2 h prior to feeding. At the end of this period birds were removed from the chambers, force fed meals of ~20% of body weight of chopped cuttlefish (*Sepia apama* Gray) and returned to the chambers, a process requiring usually less than 2 min. Feeding was simply a matter of holding the bill and gape open, covering the glottis and dropping in the cuttlefish pieces, which, being well mixed with mucus, slipped readily into the proventriculus. Birds were then returned to the chambers and metabolic rates were measured until PPMR returned to RMR levels, a period of 10–12 h. Food was weighed with an Ohaus model E1F110 balance (Nanikon, Switzerland) to the nearest 0.1 g.

Table 1. Relationship between numbers of each species used in this study and the multiple food temperatures at which PPMR measurements were made

Species	0, 20, 40°C	0, 20°C	0, 40°C	20, 40°C
T. carteri	5	1	–	1
D. gibsoni	1	–	5	1
D. exulans	–	1	–	–

PPMR, postprandial metabolic rate.

Excurrent air samples, scrubbed of moisture and CO_2, were drawn through either an Applied Electrochemistry S3A (Pittsburgh, PA, USA) or a Sable Systems FC1 oxygen analyser (Las Vegas, NV, USA) at a rate of ~200 ml min^{-1}. Oxygen analysers were referenced to ambient air for 4 min in each 30 min period, using a Sable Systems Mutliplexer V2.0, to account for baseline drift. Chamber temperatures and oxygen readings were sampled at 2 s intervals using a DataTaker DT500 data logger (Melbourne, Victoria, Australia). Warthog LabHelper software (www.warthog.ucr.edu) on a Macintosh computer acquired data and controlled gas-sample switching.

Determination of SDA and the thermoregulatory component of postprandial metabolism

We define PPMR simply as the MR after a meal is consumed and this will be elevated above RMR by SDA and food heating costs. As we need to refer specifically to the elevation in PPMR following a meal we define elevated PPMR ($PPMR_e$) as:

$$PPMR_e = \int_{t_0}^{t_f} PPMR(t) - RMR\,dt ,$$

where t_f–t_0 is the period for which PPMR(t)–RMR>0.

Because food that is isothermal to a bird's core temperature does not directly perturb its thermal homeostasis, we assumed that SDA would be the only cause of elevation of PPMR following ingestion of food heated to core temperature (T_f=40°C) in quiescent birds. PPMR has the potential to include an activity component, but by using quiescent birds and adjusting the data for any observed activity (as described below), we assumed that we had eliminated this factor. We accordingly determined SDA as the integrated difference between PPMR and RMR over the period of postfeeding MR elevation. That is:

$$SDA = PPMR_e \text{ for } T_f = 40°C . \quad (1)$$

We further assumed that the difference in $PPMR_e$ between isothermal (T_f=40°C) and cold meals reflected the thermoregulatory cost of food warming and calculated these costs as follows:

$$\text{Thermoregulatory component of PPMR} = PPMR_e - SDA . \quad (2)$$

In this study we expressed both SDA (PPMR measured at T_f=40°C) and $PPMR_e$ measured at T_f=0 and 20°C as a percentage of the energy assimilated (AE_n) from a meal. From concurrent studies we determined AE_n for *Diomedea* albatrosses as 81.8% (H.B.,

M. Richardson, A. Watson and W.A.B., unpublished data) and assumed that this value applies equally to *Thalassarche* albatrosses.

Not all birds tolerated a long session enclosed in a chamber, as indicated by restlessness and elevated MR. Intolerant birds were removed from chambers once restlessness was observed and data from these sessions were not used. All other birds used were generally quiescent, but exhibited infrequent short bursts of activity associated with posture changes, scratching, etc., with corresponding increases in MR. The data acquired within these periods of activity were amended by interpolating between average MR values that occurred before and after a given activity period.

PPMR rise time

As the respirometer chambers were opened for a short period to remove and feed the birds, the chamber steady-state gas mixture was replaced to a large extent by ambient air. After the birds were replaced and the chambers sealed, the observed rates of rise in PPMR (see Fig. 2) were therefore less than actual rates due to dilution of the chamber gas mixture. To correct for this effect, we used nitrogen to determine respirometer chamber dynamic volume and to derive the chamber time constant (τ_c) over the range of flow rates used for this study. The chamber response function was of the form $A(t)=A\exp(-t/\tau_c)$, where t is elapsed time and A is the initial nitrogen fraction of the chamber gas. We estimated the value of τ_c (in min) from:

$$\tau_c = \frac{V_d}{4.98F} , \quad (3)$$

where V_d is chamber dynamic volume (in litres) and F is flow rate (in s.l.p.m.).

Actual PPMR rise times were estimated from observed values using the inverse of the chamber response function. PPMR rise times measured were reduced by 2–3% after correction for the chamber response.

Measurement of physical properties of *S. apama*

For this study we required values for specific heat, density and thermal conductance of *S. apama* tissue, and for measurements of these properties we used tissue samples from coarsely minced and homogenised whole animals. Single samples only from each of 10 animals were used for measurements of density and specific heat, and from seven animals for thermal conductance.

Specific heat of wet tissue samples, weighed to the nearest 10 mg, was determined by cooling samples of ~200 g to ~0°C and measuring the temperature change when these were added to water at ~27°C in a Gallenkamp CBA-301 adiabatic calorimeter (Loughborough, UK). Calibrated standard thermometers accurate to 0.005°C were used for all temperature measurements.

Specific heat of cuttlefish (C_v) was then determined from:

$$C_v = \delta T C_h / M_c , \quad (4)$$

where C_h is the specific heat of water, δT is the observed temperature change in calorimeter water content and M_c is cuttlefish mass. We used 4.15 J g^{-1} as the value for C_h.

Volumes of cuttlefish samples (~200 g) were determined using water displacement at 20°C and density (ρ) was then estimated from:

$$\rho = M_c / V_h , \quad (5)$$

where V_h is water volume displaced.

To determine thermal conductivity (K_t) we placed cuttlefish tissue columns of 5 cm length and 1 cm^2 square cross-sectional area within a polyurethane foam shell with 3 cm deep walls. Bead thermistors

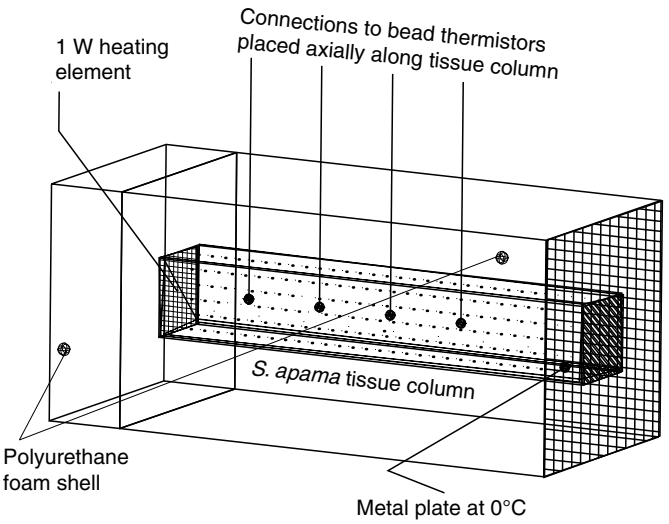

Fig. 1. Configuration used to measure thermal conductance of *S. apama* tissue (not to scale).

were inserted into and along the axis of the tissue columns at 1 cm intervals. These were pre-calibrated against a standard mercury thermometer and capable of measuring temperature with an accuracy of <0.1°C. One end of the column was clamped to 0°C and 1 W of power applied to the other using a 1 cm^2 square resistive grid. Current and voltage values, 1 A at 1 V, applied to this grid were regulated to within 0.1% of nominal values. The measurement configuration is shown (not to scale) in Fig. 1.

Following application of power, temperature rise along the column was sampled at 1 min intervals using a Sable Systems Universal Interface and Sable Datacan application software resident on an IBM-C PC. Thermal conductivity of the cuttlefish tissue was determined from the mean of the temperature drop (δT in °K) over the second 1 cm length of the column after steady-state conditions were observed to exist using (for unit cross-section and length):

$$K_t = \text{power} / \delta T , \quad (6)$$

where power is 1 W.

Differences between temperature drops over the second and third 1 cm lengths of the column were used to estimate loss of heat through the boundaries of the column. This was <1% and was ignored.

A Mettler PM400 electronic balance (Toledo, OH, USA) was used for all mass measurements.

Data analysis

We used Warthog Lab Analyst software (www.warthog.ucr.edu) to calculate and evaluate oxygen consumption ($\dot{V}_{O_2}$, in ml min^{-1}) and used:

$$\dot{V}_{O_2} = F(F_{I_{O_2}} - F_{E_{O_2}}) / (1 - F_{E_{O_2}}) , \quad (7)$$

where F is flow rate (ml min^{-1} s.l.p.m.) and $F_{I_{O_2}}$ and $F_{E_{O_2}}$ are the fractional incurrent and excurrent O_2 concentrations ($F_{I_{O_2}}$ was 0.2095 and $F_{E_{O_2}}$ was always >0.204) (Hill, 1972).

Microsoft Excel and WinSTAT were used for data analysis, descriptive statistics and ANOVA. All percentage data were arcsine square-root transformed to satisfy the requirements of parametric analyses (Zar, 1998). Unless stated otherwise, all values are presented as means ± 1 s.e.m. Measurements at either two or three food temperatures were made on all birds used in this study, necessitating repeated measures ANOVA testing of some results.

Thermal modelling of an ingested meal

A cold meal ingested by an albatross is under pressure laterally from elastic proventricular walls and vertically from meal weight. As a consequence, the food tends to form a bolus, which can be readily determined by palpation of the proventriculus. The bolus can be approximated in shape by a sphere. If the body core is assumed to be adiabatic and maintained at ~40°C, and if the food bolus is assumed to be isotropic and radially isothermal, then the transfer of heat from body core to the meal can be approximated by a simplified form of the general heat equation. The form and general solution of this equation for the time averaged temperature rise of the bolus is derived below. We used Eqn 11 to predict the average temperature rise over time of an ingested cold meal, subject to the above assumptions.

The time rate of change of temperature distribution in a three-dimensional body [$\nu(r,t)$] given by the general heat equation (see Carslaw and Jaeger, 1959; Churchill, 1963) is:

$$\frac{\partial \nu}{\partial t} = \kappa \nabla^2 \nu ,$$

where ∇^2 is the Laplacian operator, and thermal diffusivity κ is:

$$\kappa = \frac{K_t}{\rho C_v} , \quad (8)$$

where K_t, ρ and C_v are thermal conductivity, density and specific heat, respectively.

Expressed in spherical coordinates, where the sphere is isotropic and radially isothermal, it can be reduced to:

$$\frac{\partial \nu}{\partial t} = \kappa \left\{ 1 \Big/ r \left[\frac{\partial}{\partial r} \left(r^2 \frac{\partial \nu}{\partial r} \right) \right] \right\} ,$$

where the variables t and r represent time and radius, respectively. This can be expanded to:

$$\frac{\partial \nu}{\partial t} = \kappa \left(\frac{\partial^2 \nu}{\partial r^2} + \frac{2 \partial \nu}{r \partial r} \right)$$

and letting $u=\nu r$, for a sphere of radius R_f, this reduces to:

$$\frac{\partial u}{\partial t} = \kappa \frac{\partial^2 u}{\partial r^2} \quad (9)$$

for $t>0$ and $0<r<R_f$. With boundary conditions for $\nu(r,t)$ of:

$$\nu(0,0) = T_f$$
$$\nu(R_f,0) = \nu(r,\infty) = T_b$$
$$\nu(0,\infty) = T_b .$$

The solution of Eqn 4 for u throughout a sphere of radius R_f is:

$$u = T_b + \frac{2R_f (T_b - T_f)}{\pi r} \sum_{N=1}^{\infty} \frac{(-1)^{N+1}}{N} \exp\left(-\frac{N^2}{\tau} t \right) \sin \frac{N \pi r}{R_f} , \quad (10)$$

where T_b and T_f are body and meal temperatures, respectively. The time averaged temperature of the sphere, $<\nu>$, which is most relevant, is given by:

$$<\nu> = (T_b - T_f) - \frac{6(T_b - T_f)}{R_f \sqrt{\pi}} \sum_{N=1}^{\infty} \frac{1}{N^2} \exp\left(-\frac{N^2 t}{\tau} \right) , \quad (11)$$

where the thermal time constant τ is given by:

$$\tau = \frac{R_f^2}{\kappa \pi^2} , \quad (12)$$

and the meal bolus radius R_f is given by:

$$R_f = \left(\frac{3M_f}{4\pi\rho} \right)^{\frac{1}{3}} , \quad (13)$$

and M_f is meal mass.

Eqn 11 is the general solution for the time-averaged temperature rise in a spherical meal bolus and has the form of a rapidly converging series of inverted decaying exponential terms. Four terms are adequate and it is readily determined that (i) the effects of higher order terms ($N>1$) have effectively ended after 2τ and (ii) the meal average temperature will have attained 86.5% of its final value after 2τ, and effectively 100% of its final value after 4τ.

Solutions for Eqns 8, 11, 12 and 13 use the values of the physical properties of *S. apama* tissue that we measured as described previously in this section. Meal bolus radius was found from meal mass using Eqn 13. By applying this model to each meal mass fed to a given albatross, we could predict the amount of heat energy required to raise a meal to T_b. By measuring $\dot{V}_{O_2}$ over the 4τ period after feeding we could then determine the amount of heat energy delivered from SDA following this meal. From concurrent studies (H.B., M.A.C. and W.A.B., unpublished data) we found *S. apama* to have a high protein content (Table 2), and for oxygen consumption we used a thermal equivalence of 20.1 kJ ml^{-1} O_2, which corresponds to a respiratory quotient (RQ) of 0.85 for a protein substrate.

We estimated the energy cost of heating a cold meal (H_m) from:

$$H_m = C_v M_f \delta T , \quad (14)$$

where C_v is specific heat, M_f is meal mass and $\delta T = T_b - T_f$.

Among other environmental factors, model precision is dependent on the shape of the food bolus. Any variation from truly spherical will reduce food warming rate, and predictions are therefore essentially first-order approximations.

RESULTS

Specific heat, density and thermal conductivity of *S. apama* tissue

Values measured are listed in Table 2. We found these to be comparable to values found for cuttlefish and other cephalopods (unidentified species) (Rahman 1995; Saiwarun et al., 2001). Also listed in Table 2 are values for energy density and protein content, determined from concurrent studies (H.B., M.A.C. and W.A.B., unpublished data).

Table 2. The physical properties of *S. apama* tissue with values measured in the current study

Property	Value (means ± s.e.m.)	*N*
Density (kg m^{-3})	1037±13.0	10
Specific heat (J g^{-1} °C^{-1})	3.56±0.02	10
Thermal conductivity (W m^{-1} K^{-1})	0.0050±0.0002	7
Wet energy density (kJ g^{-1})*	3.53±0.10	10
Protein content (% dry mass)*	77.00±0.02	30

The above values are required to model the thermal behaviour of a meal bolus within an albatross proventriculus and to predict the energy required to raise a cold meal to body core temperature (T_b). H.B., M.A.C. and W.A.B., unpublished data.

Table 3. Albatrosses have a rapid thermogenic response to cold meals

Genera	Meal temperature (°C)	*N*	$PPMR_{max}$ (kJ kg^{-1} day^{-1})	PPMR rise time (min)	dMR/dt_0 (W kg^{-1} min^{-1})
Thalassarche	0	5	453.1±35.5	14.0±1.5	0.32±0.04
	20	5	306±72	13.2±1.0	0.32±0.04
	40	6	293.3±75.7	57.0±4.2	0.10±0.03
Diomedea	0	6	851±48	13.4±2.0	0.75±0.08
	20	2	923±15	17.6±3.1	0.86±0.20
	40	6	756±59	73.9±10.3	0.17±0.03

In comparison to values measured at 40°C (food temperature, $T_f=T_b$), maximum PPMR ($PPMR_{max}$) is greater and PPMR rise times are less for albatrosses fed cold meals. Measured values (means ± s.e.m.) for these variables are given here for albatrosses fed meals at 0°C, 20°C and 40°C. dMR/dt_0, initial rate of change of MR.

Rates of change and rise times of PPMR

Air exchange during the period that metabolic chambers were open to feed the birds meant that we had to estimate (as explained in Materials and methods, above) rather than measure the true metabolic responses after the chambers were closed. However, it is clear that the initial rate of increase in PPMR was much greater when albatrosses were fed cold compared with isothermal meals. PPMR increased linearly towards a maximum value ($PPMR_{max}$) at a rate of 0.75±0.08 W kg^{-1} min^{-1} in *Diomedea* albatrosses fed meals at 0°C and 0.86±0.20 W kg^{-1} min^{-1} for meals at 20°C. In contrast, PPMR of albatrosses fed similar-sized meals at 40°C increased at a rate of only 0.17±0.03 W kg^{-1} min^{-1}. Mean initial rates of change of PPMR (dMR/dt_0) were 4.4–5 times greater at meal temperatures of 0°C and 20°C than at 40°C (Table 3), and PPMR rise times, the time between attaining 10% and 90% of $PPMR_{max}$, were 18–24% of the 40°C value. These differences are readily apparent when comparing PPMR profiles measured at meal temperatures of 0°C and 40°C in Fig. 2, for an individual *D. gibsoni*.

After meals at 0°C and 20°C the PPMR responses of *Thalassarche* albatrosses, while of lower peak values, were similar to those of the larger *Diomedea*, rising relatively quickly and linearly (Table 3) to $PPMR_{max}$. Mean dMR/dt_0 values were 3.2 times greater and rise times were 23–24.5% of those measured for meal temperatures of 40°C. These cold meal rise times were not significantly different between the genera (t=2.36, P>0.1) or between meal temperatures of 0°C and 20°C (t=0.72, P>0.4).

PPMR and SDA

Observed PPMR increased to levels exceeding RMR within 10 min after animals were fed cold meals and in excess of 20 min for meals at 40°C. PPMR typically attained a peak ($PPMR_{max}$) within several hours and then gradually returned to RMR over a period of 10–12 h (Fig. 2). Mean $PPMR_e$, integrated over the period of elevation and expressed as a percentage of energy assimilated (AE_n), is given in Table 4 for the three meal temperatures used in this study, and individual values are displayed in Fig. 3. Based on meals of *S. apama*, these values represent 4.22±0.37% of AE_n, or 5.07±0.45% of gross energy intake (GEI).

As we measured PPMR of albatross individuals at either two or three meal temperatures, we performed repeated measures ANOVAs for mass-specific $PPMR_e$ values at the meal temperatures used. $PPMR_e$ differed significantly between all meal temperatures examined (30.35>F>115.4, 0.002>P>0.0002), but there were no significant differences in $PPMR_e$ between individuals ingesting food at a given food temperature (0.65<F<6.06, 0.64>P>0.08).

Between genera there were found no significant differences in mass-specific $PPMR_e$ at each of the meal temperatures (0.40<F<0.47, 0.79<P<0.82).

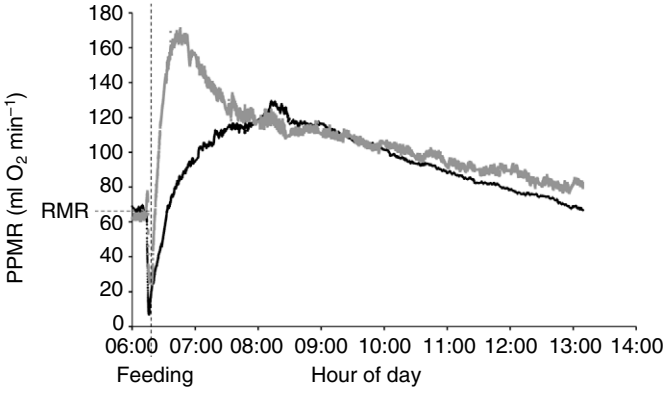

Fig. 2. Cold food stimulates a rapid increase in PPMR. Here for a *D. gibsoni* individual the time course of postprandial metabolic rate (PPMR) after a cold meal (food temperature, T_f=0°C, grey) is compared with that of PPMR after a similar sized meal at T_f=40°C (black). RMR is the resting metabolic rate prior to feeding, and opening the chamber at feeding time causes the apparent rapid fall in MR from an inrush of ambient air. As a result, measured PPMR rise times require correction for respirometer chamber characteristics and for this individual are estimated to be ~2.2% less than those shown.

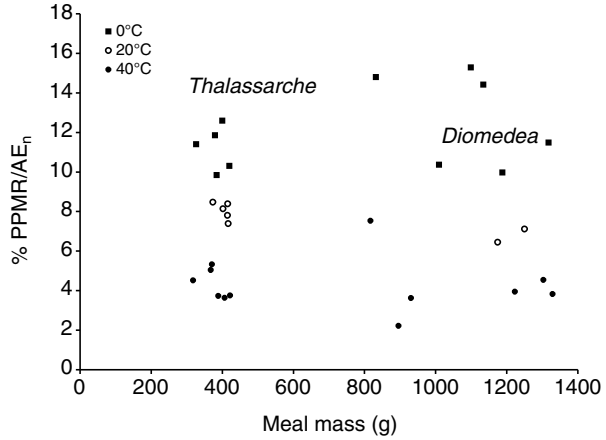

Fig. 3. Cold meals elevate PPMR above specific dynamic action (SDA). SDA is PPMR from meals at body temperature, T_b (T_f=40°C). Meals at lower temperatures include a thermogenic component that is dependent on food temperature. PPMR here is given as a percentage of energy assimilation efficiency (AE_n) to show the significant decrease in net energy gain from cold food.

Table 4. $PPMR_e$ is negatively correlated with food temperature, demonstrating energy costs incurred that are additional to SDA and associated with cold meals

	0°C	20°C	40°C
Diomedea	12.72±0.97 (*N*=6)	8.04±0.20 (*N*=2)	4.28±0.72 (*N*=6)
Thalassarche	11.20±0.50 (*N*=5)	6.78±0.33 (*N*=5)	4.30±0.30 (*N*=6)
Pooled	11.96±0.60 (*N*=11)	7.66±0.29 (*N*=7)	4.22±0.37 (*N*=12)

Generic and pooled results for elevated PPMR ($PPMR_e$) from *Thalassarche* and *Diomedea* albatrosses at three meal temperatures are given here as AE_n% (true energy assimilation efficiency, means ± s.e.m.).

Metabolic response to feeding and its contribution to meal warming

The metabolic heat production associated with SDA over 4τ for the various sized meals fed to *Diomedea* and *Thalassarche* albatrosses is contrasted in Fig. 4 with the predicted energy needed to warm 0°C meals to T_b (based on Eqn 12). The difference between these two values represents the amount of thermoregulatory energy that individual albatrosses must generate to warm these meals.

Using measured SDA values and predicted temporal food heating profiles (from Eqn 11) for T_f=0°C, we estimated that the maximum contribution from SDA to the energy demand for warming a 0°C meal, under the conditions of this study and over a time period of 4τ, was 17.9±1.0% (*N*=4) for *Diomedea* and 13.2±2.2% (*N*=5) for *Thalassarche* albatrosses. For T_f=20°C, where food heating requirements are 50% of the T_f=0°C values, we estimated the maximum contribution from SDA to be 40.2±4.2% (*N*=2) for *Diomedea* and 25.7±2.0% (*N*=6) for *Thalassarche* albatrosses. These results are summarised in Table 5.

The meal sizes (~20% of M_b) fed to *Diomedea* and *Thalassarche*, 1090±55 g and 412±18 g, respectively, were significantly different ($P \ll 0.001$) and the estimated SDA contributions to meal warming between genera were significantly different at P=0.012.

Metabolic overcompensation in response to a cold meal

In all cases where $T_f < T_b$, we found that the total thermoregulatory energy expended during the period of PPMR elevation was significantly greater than the amount required to heat a cold meal to T_b levels (Fig. 5; P<0.001 at 0°C and 20°C). This was determined by first subtracting SDA heat production (estimated using the values in Table 4) from the total thermogenesis associated with PPMR (using Eqn 2) and comparing this difference to the energy needed to warm a given mass of food at a particular temperature at feeding to T_b. The extent of this metabolic overcompensation was 63.5±12.4% (*N*=11) at T_f=0°C and 51.0±11.5% (*N*=7) at T_f=20°C, but these values are not significantly different (t=1.75, P>0.23). We found no significant differences between genera (P>0.22).

We checked for correlations between meal temperatures and activity levels for all measurement sessions. All birds were generally quiescent throughout all sessions and any activity that occurred was very brief, sporadic and unrelated to meal temperature.

DISCUSSION

Metabolic responses to cold meals

All albatrosses displayed an immediate rapid increase in PPMR after a cold meal. In contrast, the rate of increase in PPMR was 3.2–5 times less and $PPMR_{max}$ was lower in birds fed meals at T_b (40°C; Fig. 2). MR in the common eider, *Somateria mollissima*, shows a similar rapid increase to oesophageal thermal challenges, indicating the presence of cold sensors in the upper alimentary tract (Mercer, 1989). Signals from these sensors in albatrosses can therefore be expected to initiate thermoregulatory responses to cold meals well before the start of digestion and the onset of SDA-related thermogenesis.

In every case where albatrosses were fed a cold meal, total postprandial heat production exceeded the amount required to raise T_f to T_b, as predicted from Eqn 1. Similar excess thermogenesis has been reported in humans after cold drinks (Boschmann et al., 2003) and Pekin ducks when core temperature was reduced by thermodes implanted in the hypothalamus (Simon-Oppermann et al., 1978). This MR overcompensation is apparently associated with delays in physiological responses to afferent signals, as demonstrated in pigeons *Columba livia* by Østnes and Bech (Østnes and Bech, 1998).

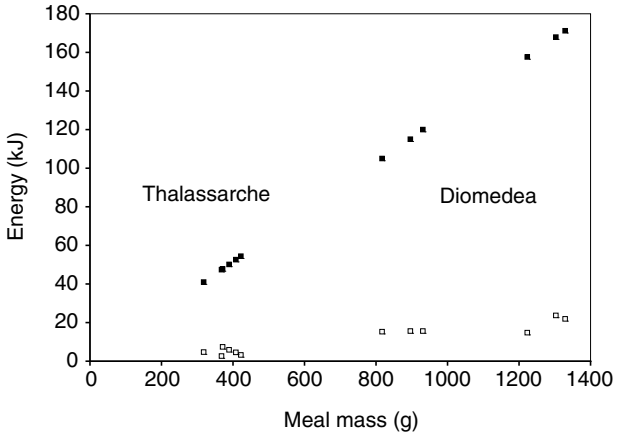

Fig. 4. For *Diomedea* and *Thalassarche* albatrosses, SDA can contribute to the heating cost of cold meals. Here, the measured energy delivered by SDA over a period of 4τ from meals of ~20% of body mass (M_b) at 0°C (□) is compared with estimated total meal heating cost (■).

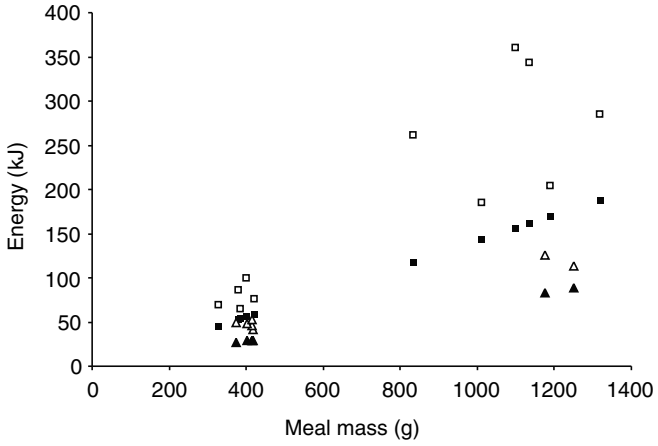

Fig. 5. Energy expended by albatrosses to heat cold meals exceeds the actual heating demand. Here the measured energy expense (□) for *Diomedea* and *Thalassarche* albatrosses in warming meals from 0°C to T_b is compared with energy estimates for this demand (■) and for warming food from 20°C (△ measured expense, ▲ estimated expense). The differences are attributable to an inherent delay in lowering MR after thermal equilibration of body and meal temperatures has occurred.

Table 5. SDA can contribute to the warming cost of cold meals from which it is generated

Genera	0°C	20°C
Diomedea	17.9±1.0	40.2±4.2
Thalassarche	13.2±2.2	25.7±2.0

Values given are those estimated for the percentage contributions to warming meals at 0 and 20°C, and for the meal sizes used and conditions applying in this study. SDA, specific dynamic action.

To prevent their legs from freezing when exposed to sub-zero temperatures for extended periods, pigeons regularly flush their legs and feet with pulses of warm blood. This process, 'cold induced vasodilation', injects corresponding pulses of cold blood into the body core. Each cold pulse triggers an immediate rise in MR, which persists for some time after core temperature has been restored to T_b, thus delivering more heat than required (Johansen and Millard, 1974; Murrish and Guard, 1974; Østnes and Bech, 1998) and offering an explanation for the observed overcompensation.

In this study, as birds were quiescent in the respirometer chambers, activity costs did not contribute to PPMR. Cold meal PPMR therefore had three major components: the thermoregulatory demand of heating cold food, SDA and thermogenic overcompensation.

For any organism an upper limit can be expected in the rate of increase in MR following a thermoregulatory challenge. In the pigeon, the maximum MR value was measured as 1.05 W kg^{-1} min^{-1} (Østnes and Bech, 1998). From the pooled 0°C and 20°C dMR/dt_0 values given in Table 3, we found the equivalent values for *Diomedea* and *Thalassarche* albatrosses (dMR/dt_0) to be 0.78±0.52 and 0.32±0.03 W kg^{-1} min^{-1}, respectively.

It is apparent that thermal signals propagate rapidly through the blood stream (Østnes and Bech, 1998). A body core cooling event is therefore expected to generate a cold front that will propagate throughout the body, rapidly triggering a chain of responses from cold sensors located throughout the vascular system and other sites within the body core (Lin and Simon, 1982; Fruhstorfer and Lindblom, 1983; Simone and Kajander, 1997; Simon, 2000). Conceivably, such a large ensemble of coincident afferent signals will strongly stimulate a marked and rapid thermoregulatory response to counter a drop in core temperature, resulting in the rapid rise in PPMR observed in albatrosses fed cold meals.

Regardless of the physical and neurological bases, the thermoregulatory overcompensation represents an additional cost to processing a cold meal, and consequently reduces the net energy available from a given meal.

SDA measurement

The amount of SDA is known to vary as a function of food type (Blaxter, 1989) and diet energy density (Costa and Kooyman, 1984; Rosen and Trites, 1997), with protein diets producing the greatest effect. Results of SDA measurements in adult birds fed protein meals are listed in Table 6. Kestrels and tawny owls were fed whole mice

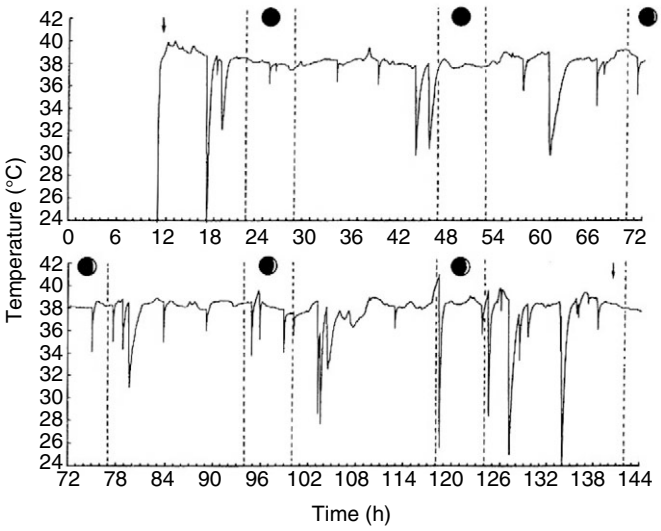

Fig. 6. Warming time of cold food in an albatross' stomach. Shown here are stomach temperature excursions for a wandering albatross *D. exulans* over a 6 day foraging trip in the Southern Ocean, which reflect the influence of sea surface temperature (SST) and meal mass on stomach temperature and meal warming time. On days 1, late 6 and 7, meals were taken in cold water south of the subtropical convergence (STC). On days 2–5, meals were taken from warmer water north of the STC. [Reproduced from Weimerskirch and Wilson (Weimerskirch and Wilson, 1992), by permission from Inter-Research Center, publisher of Marine Ecology Progress Series.]

(Masman et al., 1989; Bech and Præsteng, 2004), and their SDA values would include an activity component associated with food fragmentation, whereas pre-chopped albatross meals were placed directly into the oesophagus. Furthermore, because food temperature was not reported by Masman et al. (Masman et al., 1989), the SDA value they report may include a thermoregulatory component.

Costa and Williams (Costa and Williams, 2000) reviewed SDA studies of adult marine mammals. They reported SDA values ranging from 4.7 to 16.8% of GEI, with the majority of values above 10% GEI. Although we could not verify that any of these studies corrected for food temperature effects, it appears that the $PPMR_e$ values we found for albatrosses fed cold meals were comparable to the 'SDA' values reported for these marine mammals.

Contribution of SDA to meal warming

We have assumed that SDA for a given food mass and type is independent of food temperature (we can only measure it at T_f=T_b=40°C), and we have found that the rise times of PPMR for food temperatures of 0 and 20°C are comparable, and presumably this also holds for the 0–20°C range. As food at T_f=20°C has a heating demand that is 50% of the T_f=0°C value, the percentage contribution of SDA to food warming at T_f=20°C can therefore be

Table 6. SDA measurement requires quiescent subjects and elimination of food warming costs

Species	Reference	Body mass	Diet	SDA
Kestrel (*Falco tinnunculus*)	1	160–200 g	Whole mice	16.6% AE
Tawny owl (*Strix aluco*)	2	400–700 g	Whole mice	8% GEI
Diomedea and *Thalassarche* albatross	This study	2000–7000 g	Fragmented cuttlefish	4.22±0.37% AE_n (5.07±0.45% GEI)

SDA was found to be lower in albatrosses than in comparative studies where PPMR in protein-fed adult birds of prey included some activity metabolism and possibly some cost of warming food.

AE, apparent energy assimilation efficiency; GEI, gross energy intake. References: 1 (Masman et al., 1989); 2 (Bech and Præsteng, 2004).

expected to be twice that estimated for the lower temperature. Differences between values (listed in Table 5) estimated at T_f=0°C and one-half of those estimated for T_f=20°C were not significant at P=0.3.

Comparison of model predictions with *in vivo* measurements

Weimerskirch and Wilson (Weimerskirch and Wilson, 1992) implanted breeding wandering albatrosses at the Crozet Islands with stomach temperature loggers to identify feeding patterns during their 6–18 day foraging flights over the Southern Ocean. The Crozet Islands lie at 46°25′S, 51°40′E, below the subtropical front (STF) where SST ranges between 6 and 8°C (Smith et al., 2005). Wandering albatrosses from these islands regularly forage north of the STF (Weimerskirch et al., 1993), and recordings from one bird's 6 day trip suggest that this albatross fed below the STF at the extremes of its journey, but moved north of the STF where SST is ~12°C (Smith et al., 2005) at other times. Stomach temperature dropped rapidly after ingestion of cold food and returned to 38–39°C over a consistent time course (Fig. 6). After a particularly large meal, ingested some 60 h into the trip, stomach temperature restoration time was about 4 h (=4τ), and attained 90% of its final value after 2 h (=2τ), suggesting that stomach thermodynamics predicted by our model are comparable with those of free-living albatrosses.

Ecological significance

Albatrosses can be considered energetically frugal animals. Field metabolic rates of foraging/brooding albatrosses with chicks were found to be <2.4 basal metabolic rate (BMR) (Adams et al., 1986; Bevan et al., 1995; Arnould et al., 1996). Their reproductive costs are reduced by raising a single chick over 7–8 month periods in the smaller species and 12 months in the *Diomedea* (Tickell, 1968; Tickell and Pinder, 1975; Thomas et al., 1983; Warham and Sagar, 1998); natal philopatry and lifelong pair bonding minimise many costs associated with breeding. Moult and breeding are mutually exclusive and body moult proceeds very slowly, taking 3–6 years to complete (Tickell, 1968; Brooke, 1981; Prince et al., 1993); and transport costs are typically very low, permitting long-distance foraging at sites very remote from breeding locations (Pennycuick, 1983; Pennycuick, 1987; Weimerskirch et al., 1984; Weimerskirch et al., 2000; Cooper, 1988; Costa and Prince, 1987; Croxall and Prince, 1990). In such a regime, subtle energy gains may result in marginal increases in adult or juvenile survival or in breeding success parameters to which albatross populations have been shown to be very sensitive (Croxall et al., 1990; Robertson, 1991). Accordingly, food temperature may influence the manner in which resources are partitioned between age groups, sexes and species of albatrosses. For example, satellite tracking of wandering albatrosses breeding on the Crozet Islands showed that breeding males generally forage at higher latitudes than females and juvenile birds (Weimerskirch et al., 1993; Weimerskirch et al., 2000).

Male wandering albatrosses are significantly larger (20–27%) than females and juveniles and contribute more resources than females to chick rearing (Tickell, 1968; Weimerskirch et al., 2000; Shaffer et al., 2001). Conceivably, males will take larger meals than females and the greater thermal time constant of the meal boluses will result in lower heating rates and longer digestion times, and extend the time available for SDA heat to contribute to meal warming. This is apparent from the significant difference (P<0.001) between the possible contributions of SDA to meal warming in *Diomedea* and *Thalassarche* albatrosses. Lower convection heat losses from the larger body diameters of males can be expected (Buttemer et al., 1986) and overall males will have thermoregulatory advantages over females and juveniles, making foraging in colder regions more energetically affordable. Conversely, smaller females and juveniles may be restricted to foraging at lower latitudes where the higher SST would lower the energy cost of warming food and would be accompanied by a greater relative contribution of SDA-derived thermogenesis for food warming. Sexual segregation of foraging sites is found in other albatross species, with females consistently foraging at lower latitudes. This has been documented in wandering and grey-headed albatrosses (*Thalassarche chrysostoma*) breeding on Marion Island, grey-headed and black-browed (*T. melanophrys*) albatrosses at South Georgia and Buller's albatrosses (*T. bulleri*) on islands south of New Zealand (Nel et al., 2000; Nel et al., 2002; Phillips et al., 2004; Stahl and Sagar, 2000a; Stahl and Sagar, 2000b).

In conclusion, because *Diomedea* and *Thalassarche* albatrosses forage in southern latitudes where SST is generally at or below 20°C, meals can be expected to provoke a rapid postprandial rise in MR in defence of core temperature. Meal-generated postprandial heat production will consist of three components; the energy demand of warming food, thermogenic overcompensation and SDA. Due to the rapidity of the thermogenic response to cold meals and the significantly lower rate of rise of SDA, SDA will make only a minor contribution to the energy demand of warming cold meals, but this contribution will increase proportionately with increasing food temperature. Studies of some species have found that SDA, which is an unregulated heat source, can be used to offset thermoregulatory costs in endotherms (Costa and Kooyman, 1984; Jensen et al., 1999). Albatross feeding is usually associated with a considerable amount of activity including flight, swimming, and contesting and mechanically processing forage. Thus thermoregulatory costs associated with maintaining body temperature and food warming may be further offset by metabolic heat associated with these activities.

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