evolution and 100 replications for maximum likelihood. Shape parameters for the gamma distribution were estimated from minimum length trees[26] and were 0.32 (mtDNA), 0.59 (vWF) and 0.52 (A2AB).

Divergence times. 12S rRNA transversions accumulated linearly as far back as the eutherian–metatherian split[24]. Nine independent cladogenic events were selected based on 12S rRNA sequence availability and paleostratigraphic data[10,24,30] (for example, *Rattus* to *Mus* (14 Myr); *Sus* to *Tayassu* (45 Myr); ruminants to Cetacea (60 Myr); *Erinaceus* to Metatheria (130 Myr)). Relative rates were calculated in reference to xenarthrans. Tamura–Nei transversion distances (transversions only) were adjusted for relative rate differences[30] against the xenarthran standard. Rate-adjusted estimates of sequence divergence were regressed against paleostratigraphic divergence estimates for each of the nine calibration points (origin forced through zero; $r^2 = 0.97$; $P = 0.0000002$). The resulting equation (divergence time (in Myr) = sequence divergence/0.00063) was used to estimate interordinal divergence times after making similar adjustments for relative rates. Additional details will be presented elsewhere (M.S., manuscript in preparation).

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Hypothermia in foraging king penguins

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The ability to dive for long periods increases with body size[1], but relative to the best human divers, marine birds and mammals of similar or even smaller size are outstanding performers. Most trained human divers can reach a little over 100 m in a single-breath dive lasting for 4 min (ref. 2), but king and emperor penguins (weighing about 12 and 30 kg, respectively) can dive to depths of 304 and 534 m for as long as 7.5 and 15.8 min, respectively[3–5]. On the basis of their assumed metabolic rates, up to half of the dive durations were believed to exceed the aerobic dive limit, which is the time of submergence before all the oxygen stored in the body has been used up[4,6,7]. But in penguins and many diving mammals[7,8], the short surface intervals between dives are not consistent with the recovery times associated with a switch to anaerobic metabolism[4]. We show here that the abdominal temperature of king penguins may fall to as low as 11 °C during sustained deep diving. As these temperatures may be 10 to 20 °C below stomach temperature, cold ingested food cannot be the only cause of abdominal cooling. Thus, the slower metabolism of cooler tissues resulting from physiological adjustments associated with diving *per se*, could at least partly explain why penguins and possibly marine mammals can dive for such long durations.

King penguins are pelagic predators. To obtain food for their chicks, the parents forage at sea up to the subantarctic or polar frontal zones, 300–1,000 km away from their breeding colony[9,10]. They essentially rely on myctophid fish, of which most are captured in daytime at 150–300 m depths[11]. As sea temperatures there are 4 °C or lower, their stomachs are cooled by ingested prey[12,13]. In freely foraging king penguins, which normally have a body temperature of 38 °C on land, stomach temperatures as low as 19 °C have been reported[11,14]. There is a 2–4 °C fall in body temperature during free diving activity in seals[15,16] and birds[17–19] and it has been suggested that a slight reduction in body temperature during diving might enhance aerobic diving time[6,15,17,18]. The cold food that antarctic animals eat could contribute to this hypothermia[14,20–22], or the aerobic dive limit (ADL) of penguins might be prolonged by a process of temperature-induced metabolic suppression that is independent of stomach cooling.

To investigate these possibilities, the separate influences of feeding and diving on the abdominal temperatures of foraging animals have to be determined. It is important to obtain simultaneous measurements of the temperatures inside and outside the stomach while the animals are freely diving, so that the extent of the temperature changes in relation to diving and feeding activity during the course of a foraging trip can be found. We therefore implanted three data loggers into each of 12 free-ranging king penguins (see Methods). The data loggers (Fig. 1) measured the temperature of each bird at the top (T_{abtop}) and bottom (T_{abbot}) of the abdomen, as well as inside the stomach (T_{stom}). Hydrostatic pressure was also recorded to monitor the diving behaviour. Both the upper-abdominal and stomach loggers measured the full range of temperatures; the lower-abdominal device recorded temperatures

only below 22.7 °C (see Methods and Fig. 2). Before the birds went to sea, upper-abdominal and stomach temperatures did not differ significantly, remaining at the mean value (± s.d.) of 37.5 ± 0.4 °C ($n = 8$ birds). Once the birds were at sea, the stomach temperature was significantly higher between diving bouts than when the birds were ashore (38.3 ± 0.4 °C; $n = 8$), and systematically higher (0.5 ± 0.03 °C; $n = 7$, $P < 0.05$) than the upper-abdomen temperature. In contrast, both upper-abdominal and stomach temperatures fell during foraging dives. The lowest temperature recorded during a bout of deep diving ($n = 52$ for dives deeper than 50 m) ranged from 18.2–37.0 °C in the stomach and 25.8–37.1 °C in the upper abdomen ($n = 7$ birds). At any given time, the difference between these two temperatures could be as much as 12 °C. Surprisingly, this difference could be either positive or negative (Fig. 3A). Furthermore, T_{abbot} was also recorded (that is, it fell below 22.7 °C) during prolonged (>3 h) deep diving (Fig. 2). From ten data sets available, these very low temperatures occurred during 11% of the time of the overall foraging trip in 7 of the 10 penguins, with 83% of the total duration of these events being during the last two days of foraging. When recorded, temperature in the lower abdomen was always lower than the other two temperatures, the difference ranging between 2.9 and 20.1 °C. It was at least 2 °C below stomach temperature. Thus, whereas most previous studies have attributed the decreases in either stomach[14,20] or abdominal[21,22] temperatures to the ingestion of cold prey, our results show that the lower abdomen

is cooled not just by the contents of the stomach but also by other mechanisms (Fig. 3A).

The stomach of the king penguin is divided into two distinct regions, each with a different morphology and thermal insulation (Fig. 1). The lower part, the gizzard, is muscular, well perfused, and well insulated from the abdominal cavity by a thick (1–2 cm) layer of abdominal fat. In contrast, the upper part, the proventriculus, has a thin wall and is in direct contact with the upper abdominal cavity. At the start of a foraging trip, the gizzard is empty, so any ingestion is easily detected[13]; it can be assumed that the stomach temperature at this time is that of the whole stomach and that there is no substantial temperature gradient within the stomach (Fig. 3B). The temperature in the upper abdomen then decreases by ~1 °C during the first bout of shallow diving, although there is no evidence of any ingestion (event a in Fig. 3B).

A similarly slight temperature decrease has been reported in the dorsal aortic blood of a freely diving Weddell seal[15] (*Leptonychotes weddellii*), which was explained by a reflex decrease in the perfusion of peripheral and/or inactive muscle tissues that caused a reduction in metabolic rate[15]. This idea is supported by data from prolonged deep-diving bouts performed by king penguins. At this stage, a change in stomach temperature was observed for all diving events. This phenomenon has been previously described[13] and was attributed to the movement of the stomach recorder through different strata of food at different temperatures. However, the temperatures
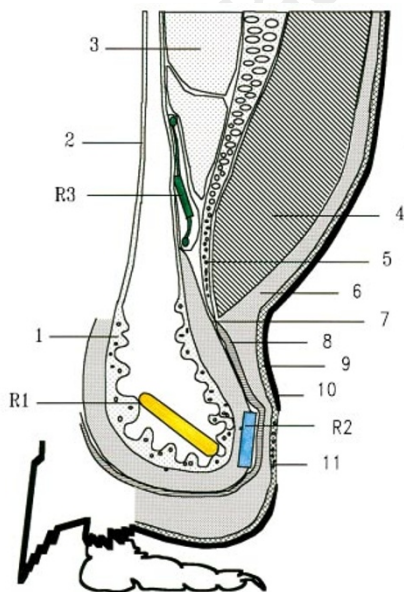

Figure 1 Sagittal view of the abdominal region of a king penguin showing the location of three recorders: R1, time/temperature recorder located in the stomach; R2, time/temperature/depth recorder implanted in the abdominal fat of the lower abdomen, with an external thermistor placed against the stomach wall; R3, time/temperature/heart rate recorder implanted under the sternum and against the stomach wall in the upper abdomen. Parts of the penguin's body indicated are: (1) muscular wall of the gizzard; (2) thin wall of the proventriculus; (3) liver lobes; (4) pectoral muscles; (5) sternum; (6) subcutaneous adipose layer; (7) abdominal and visceral fat deposits; (8) external and internal oblique muscles; (9) skin; (10) feathers; (11) well perfused brood patch.
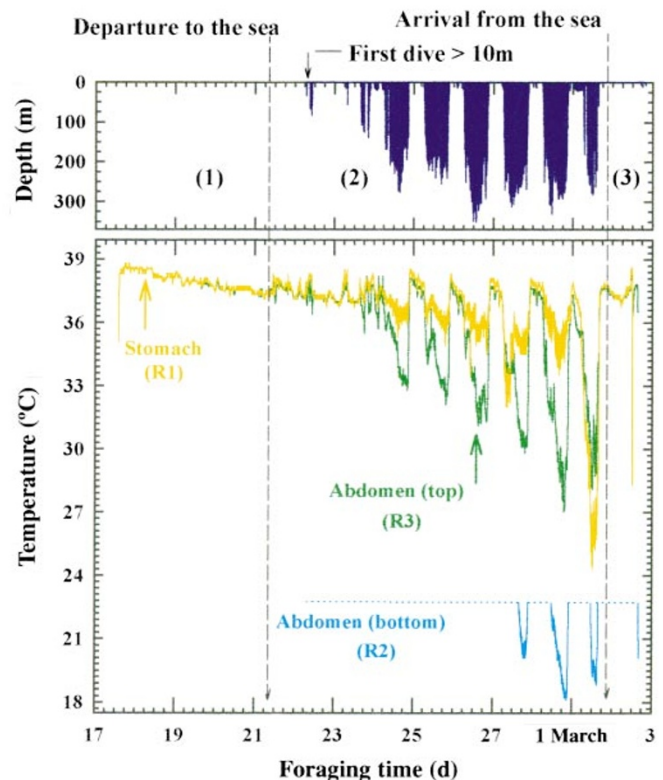

Figure 2 Typical data obtained from a single bird corresponding to: (1) the end of the brooding shift (range, 5–10 d; mean ± s.d.: 7.3 ± 1.9, $n = 12$); (2) the foraging trip (range 5.1–10.2 d; mean, 7.5 ± 1.6); (3) the beginning of the following brooding shift (less than 36 h). The typically gradual decrease in stomach temperature (T_{stom}) is shown over the 2–5 d following implantation, as well as the further periodic decreases in both T_{stom} and upper-abdominal temperature (T_{abtop}) which were synchronized with diving bouts. In the example shown here, the lower-abdominal temperature (T_{abbot}) fell below 22.7 °C (the upper limit of the range of R2) in the three last diving bouts, reaching values as low as 18.1 °C.
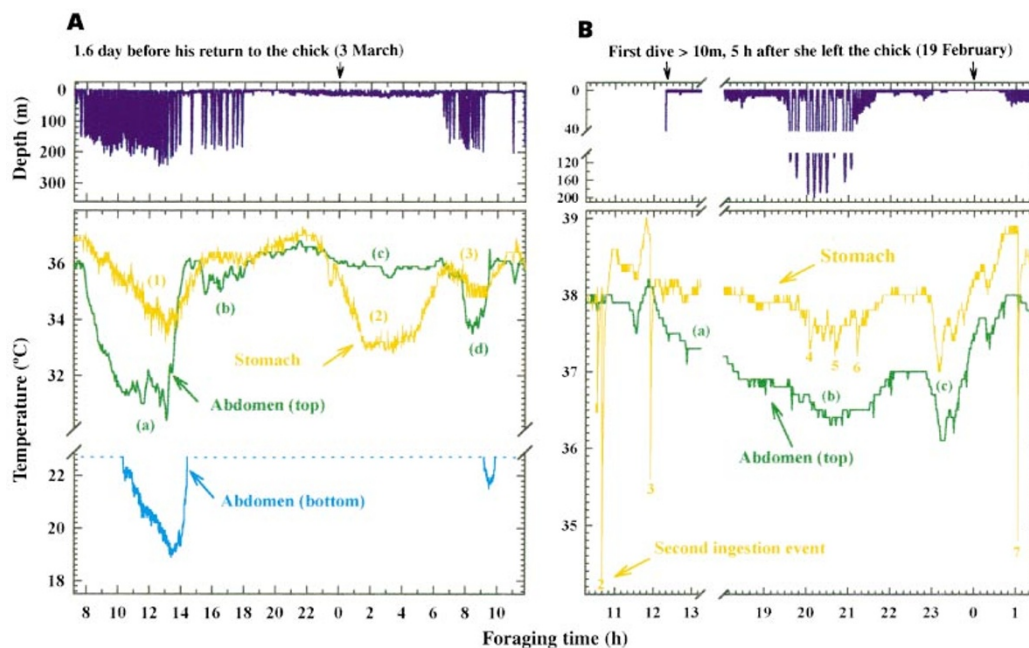
Figure 3 A, Representative changes of the three recorded temperatures during different diving activity two days before the end of the foraging trip (bird N departed on 21 February at 08:02 h for 10.5 d of foraging), showing the temporal changes in temperature that occur inside the abdominal cavity. At any given time, temperatures could differ by more than 15 °C. There is a relationship between the reduction in T_{abtop} and diving behaviour, with slight decreases during periods of shallow diving (**c**) and larger decreases during deep diving bouts (**a**, **b**, **d**). Although T_{abtop} may be several degrees lower than T_{stom} (1 is for T_{stom}, a is for T_{abtop}) the source of cooling could still be the ingested food because large thermal differences exist in the stomach (see text). Note that, during the resting phase preceding shallow dives, T_{stom} is still higher than T_{abtop}, which might indicate local heat production during digestion. When temperature data are available for the bottom part of the abdomen (when T_{abbot} is below 22.7 °C) as shown here in two diving bouts, these events roughly parallel T_{abtop}, with a slight delay, even during the rewarming phase. **B**, Representative changes in body temperature of a king penguin at sea 5 h after leaving the chick (bird K departed on 18 February at 06:49 h for 8.0 d of foraging). At this stage, the stomach is empty and any ingestion of food or water is detected by a typical precipitous fall in T_{stom} (ingestion events 1 to 7; ref. 13). Although there was no ingestion during the 8 h preceding the first deep-diving bout, T_{abtop} progressively decreased by more than 1 °C, suggesting that this decline is due to diving *per se*. The further decrease of T_{abtop} during a deep diving bout (event **b**) could be partly due to ingestion (events 4–6). However, the transient drop in both T_{stom} and T_{abtop} preceding the rewarming phase (event **c**), which routinely occurs during a surface phase, argues for a mechanism independent of feeding.

outside the stomach show similar changes (Fig. 4) and may instead be attributed to reflex adjustments in blood perfusion that are associated with diving *per se*[23,24].

The cooling of less well perfused tissues during descent and the redistribution of blood of different temperatures during ascent[23] would explain these observations. This means that the monitoring of stomach temperature in marine birds, which has proved useful for detecting prey ingestion events[12,13], should be re-evaluated in terms of diving hypothermia for calculating the mass of prey ingested by diving species.

As the diving bouts continue, the stomach temperature recorder (located in the gizzard[13]) is progressively surrounded by more food, and the sensor becomes unable to detect single ingestion events[13]. When sufficient food has been ingested to fill the proventriculus, a thermal gradient may develop between this cooled compartment and the warmed gizzard[25]. At this stage, the upper abdomen close to the proventriculus was often at a lower temperature than the stomach and this could, at least partly, be attributed to cooling from the proventriculus (event a in Fig. 3A). Ingested food could then contribute to the cooling of the core temperature close to the liver, while the digestive (thermogenic) process continues in the lower gizzard. As this lower part of the stomach is well insulated, the temperature here can be 20 °C higher than that in the lower abdomen, even though the sensors are only 5 cm apart. Towards the end of the foraging trips, however, the temperature in the stomach may progressively decrease and become less than that in the lower abdomen (Fig. 2, event 2 and 3A). This could result from a slowing down in the processes of digestion and assimilation by the foraging penguin, and from the storage of cold food for the chick.

The cause of the decline in body temperature in freely diving endotherms has been debated for over fifty years[1,15,23,26]: it may simply be the result of an increase in blood flow to the periphery which causes increased heat loss[1,26], or there may be a local metabolic depression as a result of reduced blood perfusion[15,23]. These explanations may not be mutually exclusive, at least for breeding king penguins at the beginning of a diving bout. Our results are consistent with the possibility that the king penguin is engaged in an active process of temperature reduction, with the well vascularized brood patch and flippers being effective surfaces for heat loss (Fig. 1). When a diving bout ends and the deep regions of the body gradually rewarm, blood from the active pectoral muscles may be redistributed preferentially to the deeper tissues in order to reduce heat loss from the periphery and to rewarm the core[23]. The question is, would the energy savings from such a regional hypothermia be of overall benefit, considering the cost of rewarming the body? The fact that rewarming occurs while the penguins continue to dive (Figs 2, 4) suggests that the 'waste' heat of exercise[27], rather than shivering thermogenesis, may be used for rewarming. Foraging birds must also travel between prey patches as well as back to the breeding site. 'Waste' heat is therefore readily available during foraging activity and rewarming could occur at little or no extra cost to the birds.
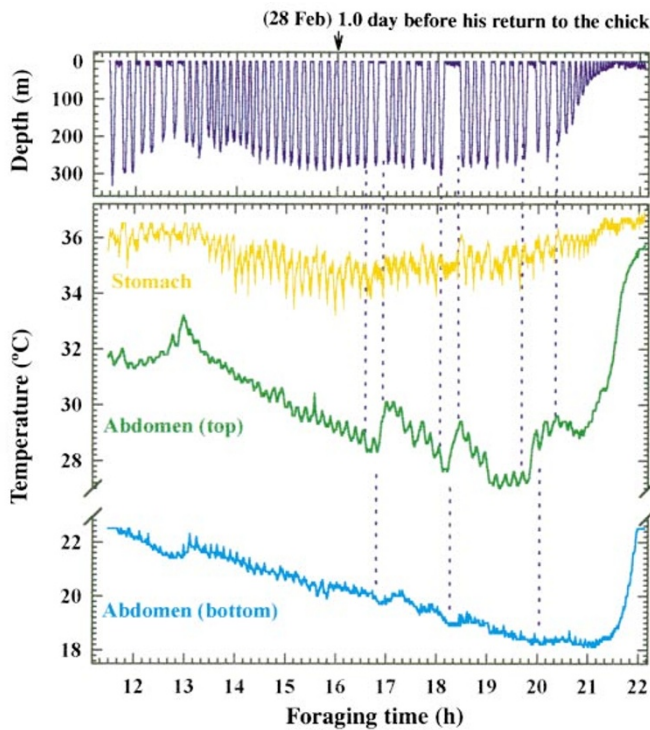
Figure 4 Short-term variations of the three abdominal temperatures near the end of a deep-diving bout and 1 d before the end of the foraging trip (bird O returns to the chick on 01 March at 16:08 h after 8.2 d at sea). There are systematic oscillations of the three temperatures which are clearly associated with individual dives. The synchronization of the three temperatures with diving is not precise, which could be due to physical and electronic delays (sampling interval). Long interdive intervals indicate a tendency for temperatures (particularly T_{abtop}) to fall during a dive and to increase during the time spent at the surface. In all cases, the progressive decrease in temperature is probably due to the fact that the post-dive interval is not long enough to allow for a full recovery. These oscillations and progressive decreases may be due to a diving-induced redistribution of blood at different temperatures from different regions of the body.

Our results show that during deep dives, temperatures in certain body regions of freely foraging penguins can decrease much more dramatically ($>10\,°C$) than in the stomach, which is cooled predominantly by the ingestion of cold prey. These temperature decreases, which would lead to a metabolic depression, might help explain the extraordinary diving performance of king penguins and other marine endotherms. The extent of the metabolic depression caused by the lowered temperatures in diving king penguins might confer upon them a significant overall energetic benefit during their foraging trip, which would be a particular advantage at the time breeding parents need to minimize their own energy expenditure while accumulating food in the stomach for their chicks. This energy saving would also be analogous to that which results from torpid periods in hibernators, despite the cost of arousal[28,29]. Finally, although they are much poorer at diving that penguins, the best human divers rely on voluntary control of automatic processes by using techniques such as yoga[2]; these may induce hypometabolism[30], which, according to our results, is a key process for tolerating an extended breath-hold. □

Methods

Twelve birds (males and females) were equipped two days after the start of their first brooding shift. All chicks were less than 12 d old. The stomach recorder (R1 in Fig. 1) was swallowed before implantation of the lower- and upper-abdominal temperature recorders. R2 and R3, respectively, were implanted under halothane anaesthesia and sutured in place. For R1:

dimensions (d), 105 mm × 16 mm diameter[13]; temperature range (R), 16 to 41 °C; sampling interval (SI), 16 s. For R2: $d = 64\,mm × 38\,mm × 15\,mm$ (Wildlife Computer, Inc.); R, -2.5 to 22.7 °C; SI, 30 s; depth range, 0–500 m; SI, 3 s. For R3: $d = 55\,mm × 24\,mm × 6\,mm$; R, 12–41 °C; SI, 60 s. Sampling of stomach temperature (T_{stom}) started immediately; upper abdominal temperature (T_{abtop}) and hydrostatic pressure sampling started after the first foraging dive that exceeded 10 m. Pressure was recorded from 11 birds. Bottom abdominal temperature (T_{abbot}) was from 10 birds; T_{abtop} was from 8 birds; and T_{stom} was from 8 birds. Data from all four channels were recorded simultaneously in 7 birds. The 12 birds were recaptured 1–2 days after returning to their chicks. Only one failed in brooding after removal of the three recorders. R2 and R3 were removed surgically and R1 by stomach flushing. All thermistors were simultaneously calibrated ($\pm0.2\,°C$) after the experiment.

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