

SHORT COMMUNICATION

CAN WE DETERMINE WHEN MARINE ENDOTHERMS FEED? A CASE STUDY WITH SEABIRDS

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The foraging ecology of marine endotherms was, until recently, obscure because most species spend the greater part of their life at sea where they are difficult to observe. However, advances in solid state technology have made it possible to develop units that can be attached to animals to give information on movements (e.g. Jouventin and Weimerskirch, 1990; Wilson *et al.* 1991) or activity (e.g. Ponganis *et al.* 1991; Thompson *et al.* 1991) while animals are at sea. Information on the prey consumed may be obtained by stomach lavage techniques (e.g. Wilson, 1984). Assessment of stomach contents allows researchers to determine prey types but not when prey were ingested. To build up a more comprehensive picture of foraging activity of marine endotherms a unit is needed to record information on prey ingestion.

We conceived such a unit to record stomach temperature. Since the body temperature of almost all marine endotherm prey is considerably lower than that of the predators, stomach temperature should drop following ingestion. The unit was built and tested under laboratory conditions simulating endotherm stomachs, and on captive African penguins (*Spheniscus demersus* L.) and free-living wandering albatrosses (*Diomedea exulans* L.).

The unit designed to detect and record temperature changes within the stomach [the Einkanalige Automatische Temperatur Logger (EATL): Elkutec Electronic GmbH, D-8057 Eching, Germany] was controlled by a single chip microprocessor (87C51) linked to a quartz clock and a static RAM memory chip with a 32 kilobyte capacity. Measurement intervals were programmed *via* a computer with an associated interface to be 8, 16 or 32 s, with a maximum recording duration of 12 days before the memory was filled. The unit was powered by a 6 V lithium battery

Key words: stomach temperature sensor, marine endotherms, wandering albatross, prey capture, *Diomedea exulans*.

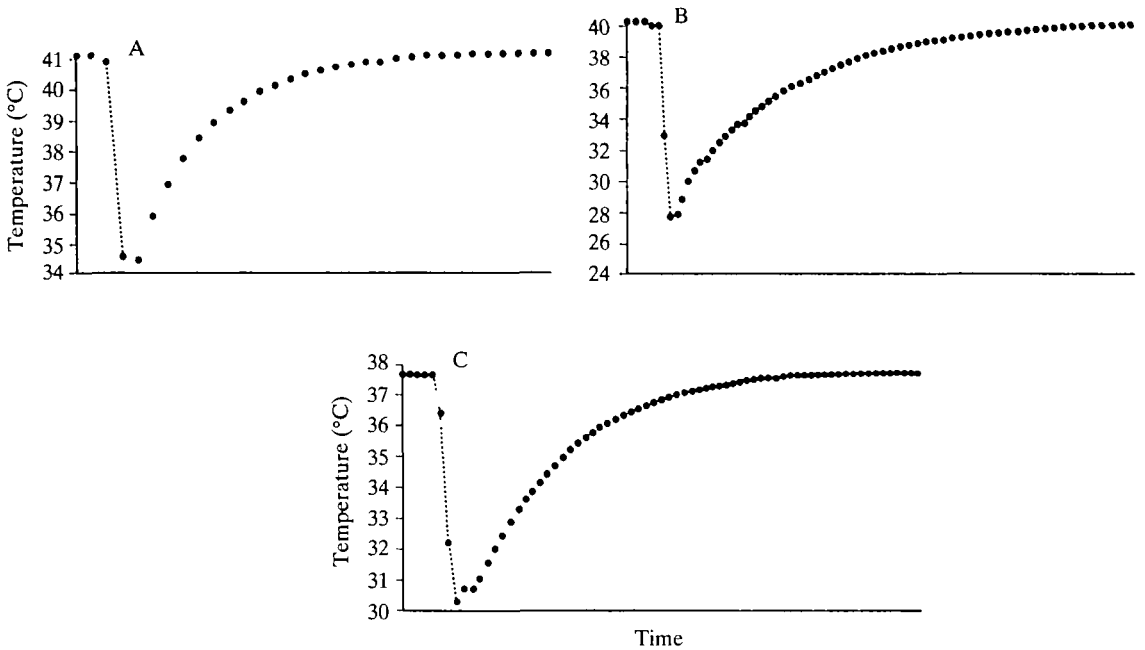


Fig. 1. Typical changes in temperature recorded by the EATLs as a function of recording time for devices in (A) a balloon in a water bath with 50 cm³ of water at 15°C added (time interval between recorded values=16 s), (B) an African penguin with 50 cm³ water at 14.5°C added (time interval between recorded values=16 s) and (C) a wandering albatross with a prey estimated to weigh 175 g at 6°C ingested (time interval between recorded values=32 s).

and housed within titanium (100 mm×25 mm diameter) or aluminium (90 mm×25 mm diameter) cylinders sealed by threaded lids fitted with O-rings. EATLs ready for deployment weighed about 60 g (aluminium housing) or 100 g (titanium housings) and were tested watertight to 700 m. The EATL temperature sensor (with relative and absolute accuracies better than 0.1°C and 0.8°C, respectively, within the range 20–45°C) was placed flush with the inside of the protective housing so that temperature changes incurred anywhere on the metal capsule would be conducted to the sensor. This meant that, rather than measuring the temperature of a highly specific local site, the EATL measured a temperature averaged over the whole of the housing. Recorded data were accessed by computer and stored on diskette for analysis.

To simulate the stomach of a seabird in the laboratory we immersed a balloon in a 10 l water bath set at 40°C. Temperature changes, such as those hypothesized to occur when seabirds swallow prey, were brought about by introducing known quantities of water or fish at various temperatures into the balloon. Changes in balloon content temperature were monitored with an EATL. After the addition of cold material into the balloon an EATL typically recorded a precipitous drop in temperature followed by an exponential rise (Fig. 1). The integral of the curve

below the asymptote (40°C) was directly proportional to the energy (E) needed to heat the cold material to asymptotic temperatures i.e. $E = SH_i \times M_i \times (T_{\text{asympt}} - T_i)$, where SH_i is the specific heat of the substance ingested, M_i is the mass added to the balloon and T_{asympt} and T_i are the temperatures of the asymptote and the material added, respectively (Fig. 1).

We used African penguins to examine the effects of ingestion on stomach temperature in seabirds. Four penguins were captured from a non-breeding group at Dassen Island ($33^{\circ}25'S$, $18^{\circ}05'E$) at 11:00 h on 21 June 1991 and housed in a large wicker basket for 1 h before each was induced to swallow an EATL. The birds were then left for a further 2 h before being given 50 cm^3 of sea water at 14.5°C (ambient seawater temperature for this species) *via* a plastic catheter directly into the stomach (Wilson, 1984). One hour later the birds were given an additional 100 cm^3 of sea water and 1 h after that the birds were given a further 200 cm^3 of sea water. EATLs were recovered about 18 h later. One bird had regurgitated its device and the others were recovered by stomach pumping (Wilson, 1984). EATLs within African penguin stomachs showed temperature changes very similar in form to those obtained by EATLs within the simulated stomach when cold water was added (Fig. 1). Precipitous drops in temperature after the addition of water were followed by exponential rises. However, the integrals of the curves below the asymptote were not directly proportional to $4.17M_i(T_{\text{asympt}} - T_i)$ (Fig. 2). Instead, the integrals were lower than expected,

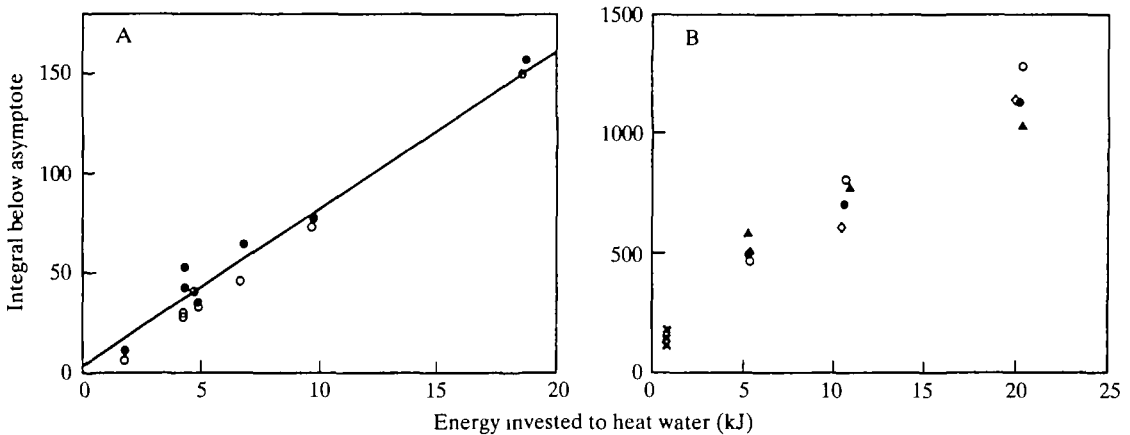


Fig. 2. (A) Relationship between the integral of the temperature drop below the asymptote and the energy (E) needed to heat an added water mass to asymptotic temperatures in a simulated stomach in a water bath. The regression is best fitted by $\text{INT} = 7.96E + 2.51$ ($r^2 = 0.94$, $P < 0.00001$). Different symbols indicate different EATLs in the water bath. (B) Relationship between the integral of the temperature drop below the asymptote and the energy needed to heat an added water mass ($50\text{--}200\text{ cm}^3$) in captive African penguins, as determined by EATLs (see text). Different symbols indicate different individual penguins. The crosses, however, indicate the values obtained by heating the EATLs to asymptotic temperatures immediately following ingestion.

particularly when 100 and 200 cm³ of water were ingested. This is presumably because some of this water was voided from the stomach into the intestine before it reached asymptotic temperature. We observed a very high liquid fraction in the faeces within 10 min of water ingestion.

Six wandering albatross nests were kept under observation at 5–15 min intervals from before sunrise to last light (a period of approximately 11.5 h) from 13 April to 1 May at Marion Island (46°54'S, 37°45'E). Arrivals and departures of adults attending nests were recorded to the nearest 15 min or to the nearest minute if actually observed. The nests contained downy chicks, approximately 25–55 days old. Following changeovers at the nests, the incumbent brooding or guarding birds were caught a few minutes after the arrival from the sea of their mates and induced to swallow an EATL. Nests were then kept under continual observation until birds with EATLs had flown out to sea, when the times were recorded to the nearest minute, as were the times when the EATLs were initiated and also swallowed.

When the birds containing EATLs returned to their nests after their foraging trips they were captured and induced to regurgitate their stomach contents of food and EATL by multiple stomach flushing (Wilson, 1984; Ryan and Jackson, 1986; Gales, 1987). Approximately 5–7 l of lukewarm water was used at each flushing until only clear water emerged. Experimental birds were released at their nest site. The data on recovered EATLs were then transferred to computer and the EATLs reset for deployment.

EATLs were deployed six times and successfully recovered from two birds after their return from a foraging trip. One EATL was regurgitated by a bird beside its nest before it departed. Three EATLs were not recovered after stomach flushing the birds up to three times and were presumed to have been regurgitated at sea. The length of foraging trip for all birds that went to sea carrying EATLs was 80.1 ± 43.3 h (s.d., $N=5$). This is not significantly different from that for birds not carrying EATLs, which have foraging trips lasting 122.6 ± 62.4 h (s.d., $N=9$, $t=1.34$, $P>0.05$) (data from Adams *et al.* 1986, for wandering albatrosses at the same locality and at the same time of year).

We monitored 132.3 h of stomach temperatures (14 879 readings) comprising 32.9 h when birds were on, or near, the nest and 99.4 h when the birds were at sea (Fig. 3). Two types of temperature fluctuation could be easily distinguished by consideration of the rate of temperature change. (1) Short-term temperature changes (STTC), where the maximum change between any two adjacent readings (at 32 s intervals) never exceeded 0.1°C and temperature changes typically followed a sine wave form of 90–270° for a descent and 270–450° for an ascent (Fig. 3). Careful watch of the albatrosses on land showed that the onset of flight coincided with an increase in stomach temperature following the STTC form (Fig. 3). (2) Precipitous drops with exponential rises (PDER events) (Fig. 3). During the temperature decrease phase the minimum temperature decrease always exceeded 0.3°C between adjacent readings and decreases as high as 5°C were recorded. These PDER events were very similar in form to our feeding events simulated in the laboratory (Figs 1 and 3).

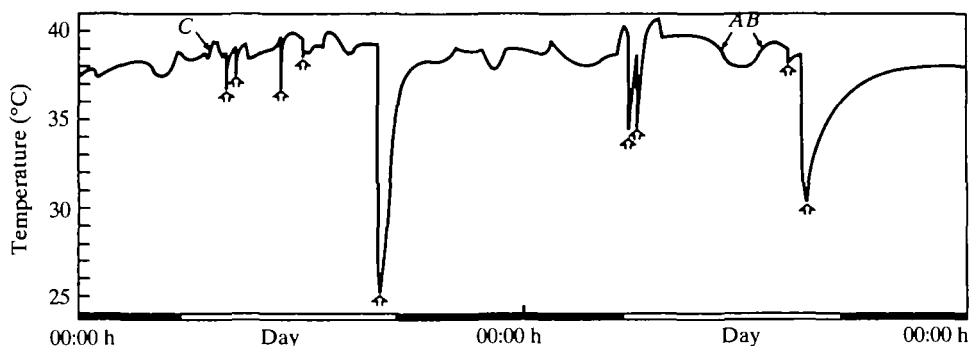


Fig. 3. Stomach temperatures from a section of a foraging trip recorded in a free-living wandering albatross by an EATL. Arrows *A* and *B* show STTC (see text) and arrow *C* marks the time at which the bird took flight. Ingestion events are shown as open vertical arrows.

Assuming that the PDER events are indicative of water or prey ingestion (no PDER events were recorded when the birds were on land), 20 primary ingestion events occurred during the time both albatrosses were at sea. During three PDER events, after particularly low stomach temperatures had been reached, five further small drops occurred during the recovery phase, suggesting that 25 ingestion events actually occurred. These additional ingestion events are not considered as separate in future calculations since we had no clear asymptote to use for our integrations. We estimate, however, that all these five ingestion events represented prey items weighing only a few grams.

Overall, it would appear that assessment of the changes in temperature of marine endotherm stomachs enables us to deduce much about the activity of the animal. A seabird's stomach is placed close to its core so that, in the absence of ingested prey, stomach temperature should be close to core temperature. Measurement of stomach temperature in endotherms may serve to indicate endogenous rhythms (e.g. Cooper, 1979), provided the data set is large enough and STTC and PDER events can be filtered out.

Muscular activity produces heat that must be dissipated if an unacceptable rise in core temperature is not to be incurred (Paladino and King, 1984). To achieve this, various lower temperature zones in the body may become more irrigated with blood to increase their temperature. We observed an increase in stomach temperature which coincided with the initiation of flight for an albatross that had previously been resting on land. It is thus likely that the STTCs apparent in our results are derived from changes in bird activity. Major activities for albatrosses on land may be resting and walking. Two major activities for albatrosses at sea would be flight, at an estimated energetic cost of $2.35 \times$ basal metabolic rate, and resting on the water's surface, at an estimated energetic cost of between basal metabolic rate and $1.83 \times$ basal metabolic rate (Adams *et al.* 1986). The essentially bimodal nature of the STTC in our results for birds at sea may be due to these two

activities. More direct observations of birds equipped with EATLs are needed to clarify this.

The remarkable similarity between PDER events achieved using the simulated stomach in the laboratory, the penguins in captivity and the albatrosses in the wild suggests very strongly that PDER events observed in free-living birds represent the ingestion of cold material, either water or prey. Furthermore, these PDER events in free-living birds, as in our laboratory simulation, derive their form from the purely physical process of heating the stomach contents. The stomach represents a metabolically inactive sac at a lower temperature surrounded by an essentially constant-temperature power-producing unit. The rate of heat transfer between the power-producing unit and the inactive sac will depend on the temperature difference between them. The physical conditions defining temperature equilibration after ingestion are highly dependent on this. If we assume that M_s , SH_s , M_p , SH_p and M_n , SH_n are the masses and specific heats of the stomach, the previously swallowed prey and the prey actually being swallowed, respectively, and that T_{Si} is the initial stomach temperature, T_p is the prey temperature in the sea and T_{Sr} is the final stomach temperature, then $T_{Si}(M_s \times SH_s + M_p \times SH_p) + T_n \times M_n \times SH_n = T_{Sr}(M_s \times SH_s + M_p \times SH_p + M_n \times SH_n)$ defines the final stomach temperature. The water equivalent of the stomach and contents, W , is equal to $M_s(SH_s/SH_w) + M_p(SH_p/SH_w) + M_n(SH_n/SH_w)$ after the last prey is swallowed, where SH_w is the specific heat of water.

Suppose that the EATL is separated from the (isothermal) blood supply at temperature T_0 in the stomach walls by a thermal conductance ϕ . The heat flow will be $\phi(T_0 - T)$ and the rate of temperature rise of the stomach contents will be given by:

$$WdT/dt = \phi(T_0 - T).$$

Integrating,

$$T = T_0 - (T_0 - T_{Sr})e^{(-t/\tau)},$$

where $\tau = W/\phi$. This solution is closely matched when temperature changes within the stomach following ingestion are empirically curve-fitted (Fig. 4). In this formulation τ is proportional to W , but the proportionality constant is not readily accessible.

In the case of the albatrosses, the mass ingested at each PDER event can be approximated by the following procedure. The water equivalent of the EATL is determined by assuming that the unit is composed entirely of titanium) (see above). The unit is then placed in a balloon in a water bath and allowed to reach an asymptotic temperature before a known quantity of cold fish is added and the contents of the balloon are again allowed to reach an asymptotic temperature. Regression of the integral of the temperature under the asymptote (INT) *versus* the energy needed to bring the mass added to asymptotic temperature (E) shows the extent to which the assumption that the EATL is composed entirely of titanium is valid. Subsequently, the calculated water equivalent of the EATL can be changed so that the INT value for the EATL lies on the line of best fit for the fish

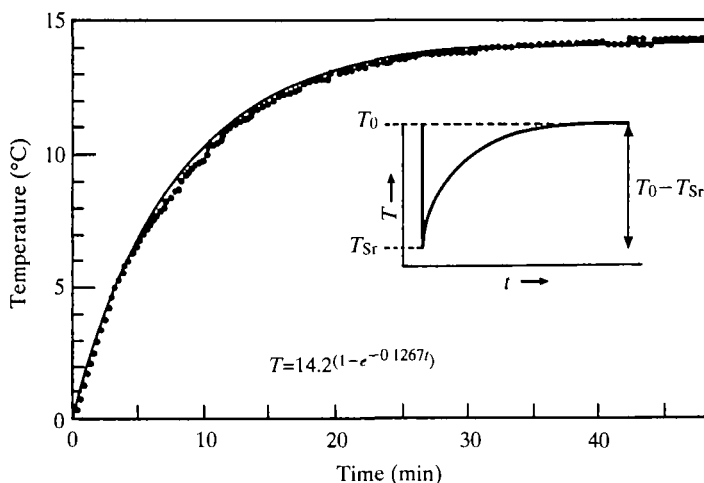


Fig. 4. Changes in stomach temperature (corrected so that asymptote $-\delta T=0$) as a function of time in an African penguin after ingesting 50 cm^3 water at 14.5°C . The relationship has been fitted to an exponential curve to show the agreement between thermodynamic theory and acquired data. Variables are defined in the text.

regression. This corrected water equivalent can then be used to determine the gradient of the slope (m) of the line in the regression INT versus E in the albatross. This necessitates using the INT value obtained when the bird was first fed the EATL and assumes an intercept of 0. The mass ingested at each subsequent PDER event is then given by $M_i = (\text{INT})/m \times SH_i(T_{\text{asympt}} - T_i)$. For the albatross calculations we have assumed that the prey has a specific heat equivalent to that of water. Based on these calculations, the mean mass of food ingested per feeding event by the two albatrosses carrying EATLs was $204 \pm 278 \text{ g}$ (S.D., $N=20$). In future work, estimates of prey masses ingested can be simplified and made more accurate by feeding the device-carrying bird a prey of known mass at ambient seawater temperatures some minutes after the EATL has been ingested (and has therefore warmed to asymptotic temperature). Subsequently, when the device is recovered after the foraging trip, the integral of the temperature under the asymptote for that particular PDER event can be used to calculate a value for m that is not dependent on the assumptions that the EATL is composed entirely of titanium and the prey entirely of water.

The validity of such calculations in free-living seabirds depends on the capacity of the temperature sensor to average values for the whole of the stomach in cases where stomach churning may be minimal. Even in the absence of stomach churning, temperature changes in one area of the stomach will, however, be transmitted to some extent to other areas of the stomach because of the conductivity of the food (see Wilson and Culik, 1991).

It is unfortunate that studies conducted with EATLs do not allow researchers to differentiate between the ingestion of water and prey. In our study with

albatrosses, most PDER events were probably due to prey ingestion since it is unlikely that wandering albatrosses drink more than small quantities of water when at sea (Adams *et al.* 1986). This is likely to be true of marine endotherms in general. For endotherms living in cold regions, there are good energetic reasons for not drinking more water than absolutely necessary since the specific heat of water is very high and it is metabolically expensive to heat this water to body temperature (Wilson and Culik, 1991).

The utility of a unit to sense and record stomach temperature in marine endotherms automatically so as to give information on prey ingestion is dependent on the unit remaining in the stomach so that it may be retrieved at the end of the foraging trip. To this end, the device must be too large to be voided through the stomach pylorus but at the same time should not be large enough to affect the animal. In addition, the unit should ideally be capable of recording an averaged temperature from within the stomach rather than being influenced by local temperatures, which may be particularly variable in the absence of stomach churning. Our unit was conceived with these points in mind. It is, however, a problem that many seabirds regurgitate indigestible fragments of prey (see Duffy *et al.* 1987) and the EATLs induced 67% of our study animals to do this. More work is needed on the form and density of the EATL as well as on the timing and methods of administration to reduce the incidence of regurgitation. The length of foraging trips for birds that went to sea carrying EATLs was not significantly different to that of birds not carrying devices and there is no indication that birds fitted with EATLs had a chick-rearing performance different from that of non-equipped conspecifics. However, if EATLs do affect foraging performance, it is unlikely that a single deployment per individual will markedly affect the chick in the long term. In future, more comprehensive long-term studies will have to be conducted to assess realistically the changes that EATLs might induce in the behaviour and ecology of the animals carrying them.

Despite these problems, stomach temperature loggers can considerably enhance our knowledge of the ecology of marine endotherms, providing information on the timing of prey capture, the size of prey items, endotherm energetic requirements *via* prey consumption estimates, circadian rhythms and, when suitably calibrated, overall animal activity.

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