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Are stomach temperature recorders a useful tool for determining feeding activity?

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Abstract: Despite a number of limitations, stomach temperature recorders are still commonly used to determine feeding activity in free-ranging marine predators. In this regard, it is important to improve the detection rate of these systems by, for instance, increasing the probability that a cold prey touches the sensors. In the present study, we compared the detection rates and mass estimations of water and fish prey ingested by captive king penguins using a two-point temperature recorder (STL) and a single, but large, point recorder (SICUP). Prey items were of different masses (5–45 g) and delivered at different frequencies (high *vs*. low). Ingestions were recorded as precipitous drop followed by an exponential rise (PDER). Overall, 57.9, 56.0 and 70.0% of the ingestions were detected by the SICUP and the upper and lower sensors of the STL, respectively. Our study confirmed that employing two sensors improves the detection of prey ingestion, but the detection of very small prey items remains insufficient and prey items swallowed at short intervals are detected as cumulative ingestion events. Nonetheless, the total mass of food ingested can be estimated with more than 70% confidence.

key words: stomach temperature recorders, feeding activity, seabirds, king penguins, *Aptenodytes patagonicus*

Introduction

Understanding the processes that optimize feeding activity in free-ranging animals is central to ecological studies but it is difficult to determine when food is ingested by wild individuals. In this regard, the recent development of bio-logging (*cf*. Naito, 2004; Ropert-Coudert and Wilson, 2005) has provided researchers with a variety of tools to allude to prey ingestion. In marine endotherms (essentially large seabirds and marine mammals that maintain a near-constant body temperature), temperature recording in the digestive system allows detection of the ingested "cold" prey (*i.e*. whose body temperature is similar to that of the water) *via* sensors placed in the stomach (Wilson *et al*., 1992; Weimerskirch and Wilson, 1992; Pütz and Bost, 1994; Grémillet and Plös, 1994; Hedd *et al*., 1996). The animals are forced to swallow a generally cylindrically shaped data logger with a temperature sensor. Using such design we can detect prey ingestion as well as estimate prey size/mass. Briefly, when a cold prey touches the sensor, the data-logger records a sharp decrease in temperature followed by a slow, gradual rise in temperature as the stomach warms up; such events being termed PDER, *i.e*. a precipituous drop followed by an exponential rise (*sensu* Wilson *et al*., 1992; Grémillet and Plös, 1994; Fig. 1). Moreover, the area under the curve of the PDER has been shown to correlate statistically with the mass of the prey ingested.

Placing the sensor in the stomach, however, may not be a suitable location since the efficiency of detecting ingestion decreases as food covers the sensor during continued feeding (Wilson *et al*., 1995). This problem is exacerbated in penguins since digestion is delayed to preserve food for their chicks (Wilson *et al*., 1989; Peters, 1997; Gauthier-Clerc *et al*., 2000). To address these problems, researchers tried placing the temperature sensors higher in the digestive system, as close as possible to the mouth (Ancel *et al*., 1997; Charrassin *et al*., 2001; Ropert-Coudert *et al*., 2000, 2001), or alternatively, chose to record jaw movements rather than internal temperature (*e.g*. Plötz *et al*., 2001; Wilson *et al*., 2002; Ropert-Coudert *et al*., 2004). Although these two approaches proved more efficient at detecting prey ingestion, they are either invasive (oesophageal temperature recorders) or difficult to manipulate (sensors, cables and magnets that need to be glued onto sensitive tissues), thus placing the subject animal under increased stress. This may explain why stomach temperature recording is still frequently used and regarded as a suitable alternative to these other approaches. This is especially the case when dealing with species that overheat when handled for too long such as gannets (*Morus* spp.) and cormorants (*Phalacrocorax* spp.). For these species, stomach temperature may prove to be the only approach for investigating prey ingestion in wild individuals (*e.g*. Grémillet and Cooper, 1999).

Thus, it is important to maximise the detection of food ingestion by sensors placed in the stomach of seabirds. Kato *et al*. (1996) previously improved the original design of the cylindrical stomach temperature recorders, which included only one large temperature sensor, by reducing the size of the sensor and implementing a second sensor placed at the opposite end of the cylindrical logger, thus increasing the probability of cold prey touching one of the sensors. They also used sensors of low thermal inertia to increase the probability of detecting small prey. The aim of our study is to compare the efficiency of this two-point temperature recorder with that of a single, but large, point recorder in 1) detecting prey ingestion and 2) accurately determining the mass and/or size of the prey. The efficiency of these two systems was examined in captive king penguins, *Aptenodytes patagonicus*, an extensively-studied top marine predator in the Southern Ocean.

Materials and methods

The study was carried out on a king penguin colony at Baie du Marin, Possession Island, Crozet archipelago (46°25'S, 51°45'E) from the 7th to 15th of March 1996. Two cylindrical stomach temperature data-loggers differing in size, the number of sensors and sampling intervals were employed. The SICUP logger (Single Channel Unit Processor, 69×12 mm, 16 g, Driesen+Kern GmbH, Germany) had one sensor with a relative and absolute accuracy of 0.2°C and 1.0°C, respectively, and sampled temperature every 16 s (*cf*. Wilson *et al*., 1995). Following Wilson *et al*. (1995), the device was introduced into the oesophagus with the device placed so that the sensor entered last, representing the most efficient position to detect feeding events in captive penguins on land. While at sea the stomach of the bird, and thus the logger, adopts various positions due to diving activity, the stomach content density and the proportion of the volume of the stomach occupied by the logger (*cf.* Wilson *et al.*, 1995). The second logger was a cylindrical STL stomach temperature recorder (90×19 mm, 35 g, Little Leonardo, Japan) with one sensor at each end. The top sensor is referred to as the upper sensor, and the bottom sensor as the lower sensor. Each sensor measures the temperature every second with a relative and absolute accuracy of 0.02°C and 0.1°C, respectively (Kato *et al.*, 1996). The temperature sensors of both the STL and SICUP loggers were calibrated in a water bath. There was a 3-fold difference between the initial response speeds of the two devices, the STL responding faster than the SICUP.

The detection rate and ability to estimate the mass of food ingested were examined in seven pairs of late breeding king penguins seen performing courtships and two isolated individuals. Birds were captured one day prior to the experimental feeding session and kept in an enclosure near the colony. On the day of experimentation, both the male and female of a pair were induced to swallow one of the stomach loggers. Devices were attached to a thin nylon line, allowing them to be recovered by pulling gently on the wire at the end of the experiment. Following the experiment, the birds were released in the vicinity of the colony.

During the feeding experiments, we firstly tested the effect of different masses of food items and different frequencies of ingestion on the detection rate of the loggers. When testing the effect of repeated ingestions at high frequencies, birds were induced to sequentially swallow four times 10 g of water or four fish of *ca.* 10 g (average±SD: 10.0±1.4 g), each ingestion being separated by a mean of 0.47±0.7 min. Each high frequency feeding sequence was separated by a mean 34.1±7.7 min. To test the effect of different food masses, birds were alternately given the following: 5, 10, 20, 30, 40 m*l* and 10–15, 15–25, 25–35, 35–45 g of water and fish, respectively. The order in which water and fish were given differed between feeding sessions. Water was employed since it is often used by researchers for calibration purposes (Wilson *et al.*, 1992; Hedd *et al.*, 1996). The range of temperatures of both the fish and water was 4–8°C, *i.e.* the temperature of water masses (from the surface to about 100 m deep) surrounding Possession Island. Each feeding event was separated by an interval of 4–38 min to allow the temperature sensors to warm up again to the original temperature of the stomach.

The water was given through a funnel attached to a soft plastic catheter, and the fish pieces, which were kept in a bucket of seawater, were introduced into the aperture of the birds' oesophagus using wooden chopsticks. If the fish was regurgitated, a second piece of approximately the same weight was immediately given to the bird. Fish and water were weighed to the nearest g using a precision balance. The exact time of prey ingestion (*i.e.* the time when the bird was observed moving its head up and down to push the fish towards the throat) was noted.

The data obtained were downloaded onto a computer and analysed using Jensen System Software (J. Lage, Feldstraße 85, 2300 Kiel 1, Germany). Detection of a feeding event was considered when a precipitous drop in the temperature signal followed by an exponential rise, *i.e.* a PDER event, was observed as described by Wilson *et al.* (1992, 1995; Fig. 1). Three signal categories were determined following prey ingestion:

1) No feeding event detected ("Not Detected"): no effective decrease in temperature around the time the prey was swallowed.

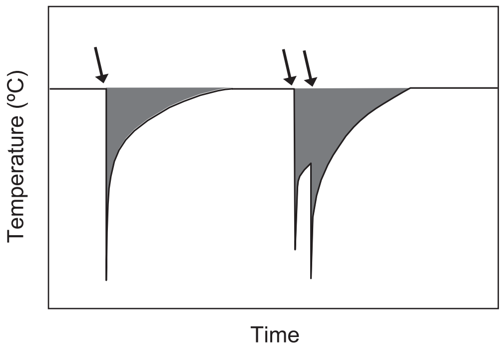

Fig. 1. Theoretical curve depicting the evolution of the internal temperature recorded using a data-logger in the stomach of endothermic species on ingestion of cold prey (indicated by arrows). Contact between the temperature sensor and prey leads to an abrupt drop in the temperature followed by a gradual rise corresponding to re-warming of the stomach back to baseline (PDER event, *sensu* Grémillet and Plös, 1994). On the left of the graph, a single prey item was swallowed leading to a single PDER, while on the right two prey items were swallowed quickly one after the other leading to a single PDER event with 2 abrupt temperature drops (see text for definition).

2) A single feeding event detected ("Single"): a decrease in the temperature followed by an exponential rise and subsequent return to the initial baseline temperature (Fig. 1).
3) Multiple feeding events that could not be isolated from each other: multiple ingestions corresponding to a single precipitous temperature drop (hereafter referred to as 'cumulative ingestion', Fig. 1).

The software used for analysis automatically calculated the numerical value of the area between the drop in temperature–corresponding to the contact point between the cold water or fish item and the sensor–and the exponential rise–when the metabolic activity of the bird warms up the stomach–until the stomach temperature approximately reaches its initial value. The area of the PDER is linearly related to the energy, E, invested to warm the food (Wilson *et al.*, 1992):

$$\text{Area} = k \times E,$$

where k is a constant.
E is also related to the mass of food ingested, M, as follows:

$$E = M \times SH \times (T_a – T_p),$$

where SH is the heat conductivity of the prey in $J°C^{-1}g^{-1}$, T_a is the temperature of the asymptote (*i.e.* the resting stomach temperature) and T_p is the temperature of the prey (both in °C). Values of fish heat conductivity were assumed to be similar to the water heat conductivity, which is equal to 4.17 $J°C^{-1}g^{-1}$, as the temperature of the water or fish ingested was the same as that of the local sea surface (Pütz and Bost, 1994).

Thus, the relationship between prey mass and the area of the PDER is expressed by the following linear equation:

$$\text{Area} = K \times M \times DT,$$

where $K=k\times SH$ in $J°C^{-1}g^{-1}$; and $DT=(T_a-T_p)$ in °C.

Statistical tests were conducted using Systat (SAS Institute Inc., USA, version 10). Differences were considered significant if $P<0.05$. Values are presented as means±standard deviation (unless stated otherwise). Because of the small number of points used for each individual (1–3), data were pooled, although doing so meant that there was a slight risk of pseudo replication. Simple linear regression was used to highlight trends.

Results

A total of 207 prey items (105 water and 102 fish) was fed to the 16 king penguins during the 15 days of the experiment. Of these, 117 (64 water and 53 fish) and 90 items (41 water and 49 fish) were used in the mass effect and frequency effect tests, respectively. Overall, birds equipped with the STL ingested 56 water samples and 44 fish pieces, while those equipped with the SICUP logger ingested 58 water samples and 49 fish pieces. Of the 107 items (water plus fish) fed to the birds equipped with the SICUP logger, 57.9% was detected, while the upper and lower sensors of the STL logger detected 70.0 and 56.0% of the items, respectively.

Effect of ingestion frequency on the detection rate

During the high frequency feeding experiment, none of the prey items were detected as single events; they were either not detected or detected as cumulative ingestion events (Table 1). Water samples were more often detected than fish pieces (all water ingestions were recorded by the two sensors of the STL logger). Although all items were detected as cumulative ingestion events, the upper sensor of the STL logger showed a higher percentage of detection than the SICUP sensor (86.8% *vs.* 61.5%) when both water and fish were considered together.

Effect of prey mass on the detection rate

The percentage of ingestion events detected by the stomach recorders increased with

Table 1. Effect of a high feeding frequency on the detection of cold prey items (water and fish) ingested by captive king penguins (*Aptenodytes patagonicus*) by the single temperature sensor of the SICUP and the two temperature sensors (upper and lower) of the STL. All prey were either not detected or detected as cumulative ingestion events (see text).

Sensor type	Water		Fish	
	Cumulative ingestion event (%)	Not detected (%)	Cumulative ingestion event (%)	Not detected (%)
SICUP	66.7	33.3	57.1	42.9
Upper sensor	100	0	76.2	23.8
Lower sensor	100	0	20	80

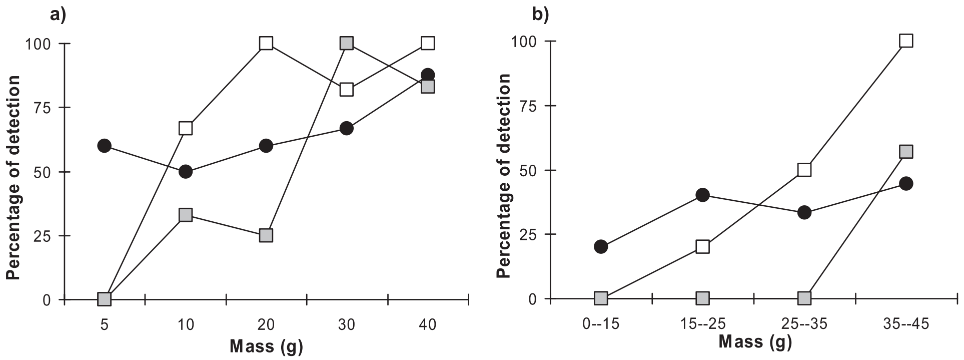

Fig. 2. Percentage of ingestion events detected as a function of the mass of a) water samples and b) fish items using the single temperature sensor of the SICUP (closed circles) and upper (open squares) and lower (grey squares) sensors of the STL stomach temperature recorders.

the mass of the items (Fig. 2). Overall, water samples were detected more often than fish pieces. The upper sensor of the STL logger detected almost all water ingestion of >20 m*l*. In contrast, no fish prey with a mass <15 g (and even <25 g in the case of the lower sensor) was detected by either of the temperature sensors of the STL logger. All categories of fish and water were detected by the SICUP logger, but the percentages of detection for prey >10 g (water) and 25 g (fish) were smaller than those observed with the upper sensor of the STL logger. In other words, the SICUP logger was more efficient at detecting small fish than the STL, but as the size of the fish increased the probability of detection became lower than in the case of the STL logger.

Determination of the mass of prey items

The mass of the prey items ingested was multiplied by the temperature difference between the prey and the resting stomach temperature of the penguin ($M\times DT$). When events were detected as cumulative ingestion events, the masses were added together then this value was plotted against the area under the PDER (see methods) as recorded by the stomach loggers. Overall, the area was a good predictor of the mass of the prey. Each relationship was statistically significant ($P<0.05$) with a coefficient of determination of between 0.78 and 0.95 (Fig. 3). The coefficient of determination was higher for water than fish. The highest coefficient was observed with the lower sensor of the STL logger when birds ingested fish, but the sample size in this particular case was small.

Discussion

Stomach temperature recorders have pioneered our ability to examine the feeding activity of free-living endotherms; yet, as our study highlights, these devices have limitations. The main problem is that the detection rate of very small prey items is low, especially when prey are swallowed in an isolated circumstance. However, when small prey items are swallowed sequentially and at a high frequency (<1 min apart), they are likely

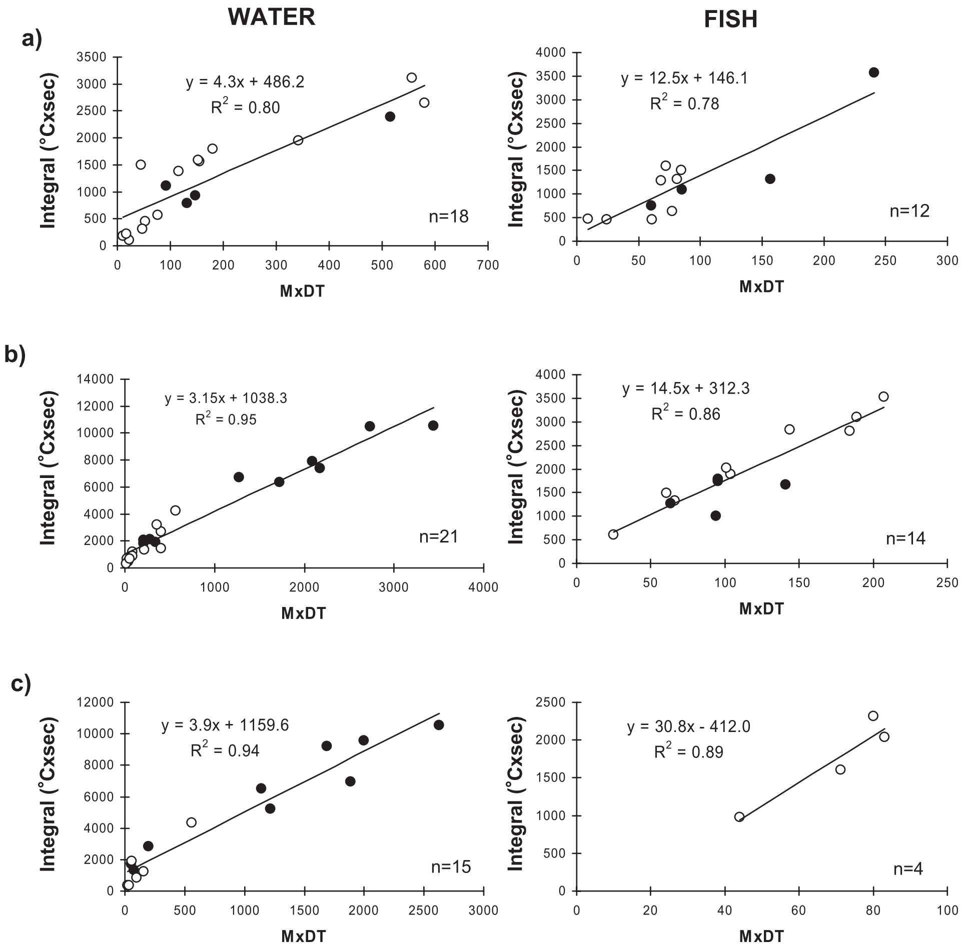

Fig. 3. In a) the SICUP sensor, and b) upper and c) lower sensors of the STL, the area under the curve of the PDER was a good predictor of the mass of the prey ingested—both for water (left graphs) and fish items (right graphs)—when multiplied by the temperature difference between the temperature of the prey and the resting temperature of the captive king penguins stomach (M×DT). Single ingestion (open circles) and cumulative ingestion events (closed circles) are indicated.

to be detected as a cumulative ingestion event. The model species used in this study, king penguin, feed on pelagic fish that are smaller than the prey items used here. For instance, *Electrona carlsbergi*, which ranges from 51.6 to 92.5 mm in length and 1.9 to 12.1 g in mass, and *Kreftichtys andersonii*, which ranges from 23.4 to 70.6 mm in length and 0.1 to 78 g in mass (Cherel and Ridoux, 1992). Furthermore, penguins have to catch their prey at a mean frequency of 25.4 per minute to cover their energetic needs (Pütz and Bost, 1994), which corresponds to one fish every 2.3 s. Similarly, Adélie penguins (*Pygoscelis adeliae*) have also been shown to sequentially swallow small prey items (principally Antarctic krill, *Euphausia superba*) at a high rate, gathering pieces in their mouth before swallowing (Ropert-Coudert *et al.*, 2000). In other words, individual ingestion events by these two species of penguin will not be detected by stomach temperature loggers, but rather will be recorded together in a single event.

Increasing the surface of the sensor would help improve the detection of individual prey, as suggested by the greater percentage of water samples detected in our study. Prey would, thus, have a higher probability of directly touching the sensor, although the logger would consequently occupy a greater volume of the stomach. This was observed in the present study with the SICUP logger, the entire surface of which is titanium and conducts heat. This, together with the poor sensitivity and low sampling rate, explains why the SICUP was occasionally able to detect the smallest of all prey, although the overall probability of detection remained low. In contrast, the STL has a smaller sensor surface, which makes it more sensitive to smaller prey but reduces the probability of contact. With regard to the STL logger, our study confirmed that the higher the temperature sensor is placed in the stomach cavity, the greater the likelihood of detection of prey ingestion. Although the lower sensor had a very limited capacity to detect feeding events, a stomach temperature recorder with two opposing sensors appears a useful improvement of the original design, since the logger may turn upside-down in the stomach of diving birds (*cf.* Wilson *et al.*, 1995). Thus, as suggested by Wilson *et al.* (1995) and Kato *et al.* (1996), a second sensor would improve the detection of prey ingestion.

Nonetheless, although the number of prey items ingested may have been underestimated, the total mass of the detected food ingested could be estimated with more than 70% confidence using:

$$M = \text{Area}/(k \times DT),$$

where Area is the area under the curve of the PDER and DT is the temperature difference between the minimum temperature reached during the temperature drop and the resting temperature level (see methods).

Note that the detection efficiency also improves when the sampling interval decreases and the temperature response time of the sensor increases. The efficiency of the upper sensor of the STL logger in detecting a single event may have been due to a great extent to its sampling interval of 1 s compared to that of the SICUP (16 s). A greater sampling frequency means that each event is detected as a single event. Similarly, a high sampling frequency may improve the reliability of the mass estimations, since the PDERs would then be described with much more accuracy.

In light of the above, it is therefore not surprising that the water samples were detected with greater efficiency than the fish items. Water spreads in the stomach cavity, hence increasing the probability of touching a sensor. In addition, although we assumed here that the water and fish prey had the same heat conductivity, this may not be completely realistic. Such a difference could thus explain the greater detection of water samples compared to fish items. Consequently, using water to calibrate stomach recorders, as is occasionally done, may not lead to an accurate estimate of the detection capacity of these devices. We therefore recommend that calibration using fish prey, in a range of sizes and masses, usually preyed upon by the study subject be conducted prior to free-ranging deployment of stomach temperature recorders.

In conclusion, stomach temperature recorders, despite having several limitations and being unable to detect high frequency ingestions of small prey, can provide reliable quantitative estimates of the amount of food ingested over time. Thus, they appear a useful tool for ecological studies. Further experiments should be conducted on birds with a full stomach (the present study was performed on non-breeding birds with almost empty stomachs) to determine the efficiency of two-point temperature recorder in detecting prey ingestion. Note that stomach temperature recorders are often regurgitated spontaneously on land or at sea; nevertheless, the use of an anchor system (*cf.* Wilson *et al.*, 1998) has proved useful in retaining the logger in the stomach for substantial periods of time. Anchor systems could also potentially avoid the logger turning upside-down, enhancing the detection rate of individual small prey.

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