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Feeding behaviour of free-ranging penguins determined by oesophageal temperature

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Sea birds play a major role in marine food webs, and it is important to determine when and how much they feed at sea. A major advance has been made by using the drop in stomach temperature after ingestion of ectothermic prey. This method is less sensitive when birds eat small prey or when the stomach is full. Moreover, in diving birds, independently of food ingestion, there are fluctuations in the lower abdominal temperature during the dives. Using oesophageal temperature, we present here a new method for detecting the timing of prey ingestion in free-ranging sea birds, and, to our knowledge, report the first data obtained on king penguins (*Aptenodytes patagonicus*). In birds ashore, which were hand-fed 2–15 g pieces of fish, all meal ingestions were detected with a sensor in the upper oesophagus. Detection was poorer with sensors at increasing distances from the beak. At sea, slow temperature drops in the upper oesophagus and stomach characterized a diving effect *per se*. For the upper oesophagus only, abrupt temperature variations were superimposed, therefore indicating prey ingestions. We determined the depths at which these occurred. Combining the changes in oesophageal temperatures of marine predators with their diving pattern opens new perspectives for understanding their foraging strategy, and, after validation with concurrent applications of classical techniques of prey survey, for assessing the distribution of their prey.

Keywords: oesophageal temperature; king penguin; ingestion; foraging; diving

1. INTRODUCTION

Marine top predators are major consumers of sea resources and have an important role in the marine ecosystem (Furness 1982; Croxall 1992; Woehler 1995). This concerns especially the birds and marine mammals of the Southern Ocean, which may transfer to the atmosphere as much as 25% of the photosynthetically fixed carbon (Huntley *et al*. 1991). Because these top predators may respond to abiotic variables, there is a considerable potential for using them to study changes in marine resources (Croxall *et al*. 1988; Montevecchi 1993; Guinet *et al*. 1998). Although the animals are not directly observable when at sea, miniaturized technology has given access to certain aspects of their foraging behaviour, such as diving activity (e.g. Kato *et al*. 1996; Peters *et al*. 1998; Davis *et al*. 1999), foraging area (e.g. Jouventin & Weimerskirch 1990; Bost *et al*. 1997) and energetics (e.g. Culik *et al*. 1996; Wilson & Grémillet 1996; Bevan *et al*. 1997; Handrich *et al*. 1997; Grémillet *et al*. 1998). However, a major remaining challenge is the accurate determination of when and how much animals feed while at sea. This is a central question in foraging studies because detecting prey ingestion may give information on prey availability and foraging success.

Until now, the main approach to this problem has been based on records of stomach temperature using remote sensing units (Wilson *et al*. 1992; Grémillet & Plös 1994; Kato *et al*. 1996; Wilson *et al*. 1995, 1998). Feeding can be detected in marine endotherms since most of their prey items are ectothermic organisms that cause a drop of the gastric temperature when ingested. However, the reliability of this method is largely dependent on the type of predator and type of prey (see a review by Wilson *et al*. 1995). Briefly, the likelihood of detecting a prey ingestion with a stomach thermistor decreases with smaller prey size and with the filling of the stomach. Also, recent data have shown that body temperatures of diving sea birds can fluctuate independently of their feeding activity (Culik *et al*. 1996; Wilson & Grémillet 1996; Bevan *et al*. 1997; Handrich *et al*. 1997). Indeed, there is a drop in the lower abdominal temperature during diving which contributes to the long duration of the dives due to the lower oxygen consumption of cooled tissues (Handrich *et al*. 1997).

These considerations led Ancel *et al.* (1997) to test detection of prey ingestion in captive sea birds by measuring their oesophageal temperature. The lumen of the oesophagus is much smaller than the stomach volume and prey do not accumulate in the oesophagus. We have now deployed this promising technique in free-ranging predators. Here we report results of the first measurements of oesophageal temperature in the free-ranging king penguin (*Aptenodytes patagonicus*). This pelagic, deep-diving bird depends on small (2–9 g) schooling fish, the myctophids (Cherel & Ridoux 1992), which form one of

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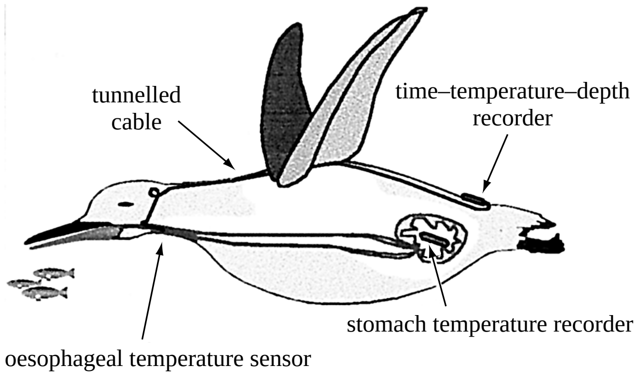

Figure 1. View of a king penguin showing the location of equipment deployed on free-ranging individuals. Cables were tunnelled under the skin from the oesophagus to a logger unit taped onto the feathers, recording dive depth and oesophageal temperature. A second logger recorded the stomach temperature.

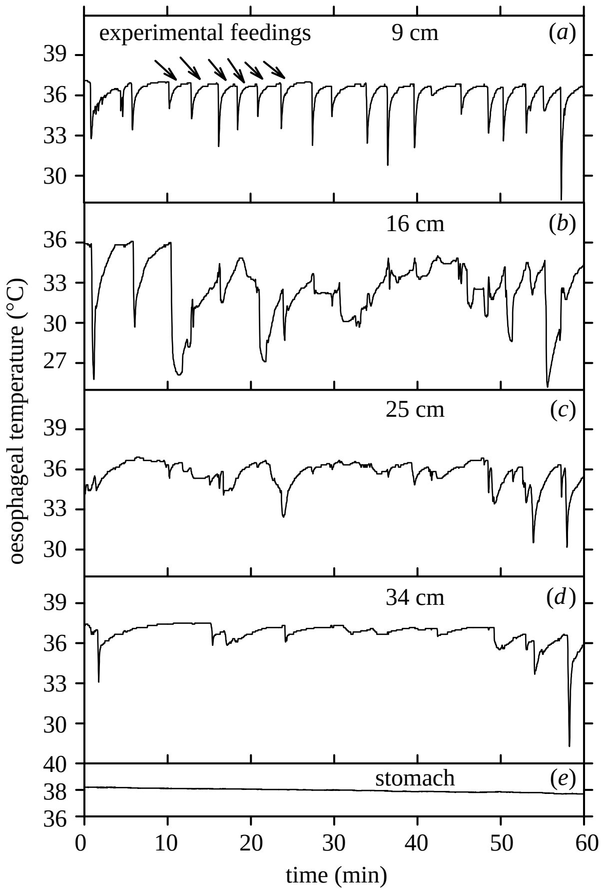

Figure 2. Changes in temperature as a result of the ingestion of 20 fish pieces recorded by four thermistors located in the oesophagus of a captive king penguin. The thermistors were located at 9, 16, 25 and 34 cm from the beak (sensor *a*, *b*, *c* and *d*, respectively) and in the stomach (*e*). Fish temperature was 8 °C and the mass of each piece was about 9 g.

the most important food resources of the Southern Ocean (Sabourenkov 1991; Pakhomov *et al.* 1996). The aims of the present work were (i) to validate this method in captive penguins, and (ii) to assess the feeding activity at sea of free-ranging birds by measuring their oesophageal temperature.

2. MATERIAL AND METHODS

The study was carried out at Possession Island, Crozet Archipelago, Southern Indian Ocean (46°25′ S, 51°45′ E) at the 'Grande Manchotière' colony of king penguins (40 000 breeding pairs; Weimerskirch *et al.* 1992) during the 1996 and 1997 breeding seasons.

(a) *Temperature sensors and time–depth recorders*

Data loggers used to monitor stomach temperature (in captive birds), oesophageal temperature, and dive depth in the 0–200 m range were manufactured by the Little Leonardo Co. (Tokyo, Japan) and had 1–2 Mb of flash memory. In captive birds, oesophageal temperatures were measured by a four-channel temperature logger linked to an oesophageal probe with four thermistors; the logging unit was housed in an aluminium cylinder (8 bits; 90 mm × 14 mm diameter; resolution 0.1 °C); stomach temperatures were recorded by a cylindrical two-channel logger (12 bits; 90 mm × 19 mm diameter; resolution 0.02 °C; accuracy 0.1 °C).

In free-ranging birds, oesophageal temperature and dive depth in the 0–200 m range were measured by a cylindrical three-channel logger (12 bits; 90 mm × 20 mm diameter and *ca.* 50 g; temperature and depth resolution 0.02 °C and 0.1 m, respectively). Cylindrical oesophageal thermistors (5 mm × 3 mm) were plastic coated, and had an accuracy of 0.3 °C. Each thermistor was linked to the central unit by a 0.5–1 m electric cable (diameter 1.2 mm). Stomach temperatures were recorded by a cylindrical logger (Driesen and Kern GmbH, Bad Bramstedt, Germany; 8 bits; 105 mm × 16 mm diameter and *ca.* 80 g; resolution 0.1 °C; 0.25 Mb memory). The thermal time-constant of oesophageal sensors (3.2 s) was nine and 14 times shorter than for the stomach sensors used in captive and free-ranging birds, respectively. Dive depth in the 200–500 m range was measured by an MK5 time–depth recorder (Wildlife Computers (Redmond, WA, USA); 65 mm × 38 mm × 15 mm and *ca.* 50 g; 2 m resolution; 0.5 Mb memory).

(b) *Feeding captive birds*

We first examined the temperature changes in the oesophagus and the stomach in response to ingestion of meals of known size and temperature in five non-breeding adults. Each bird was induced to swallow a stomach sensor (1 s sampling interval) attached to a thin plastic line (used to remove the unit after the experiment). The four-channel temperature logger (2 s sampling interval) was then taped onto the back feathers and the bird was induced to swallow the oesophageal probe. Care was taken to reduce handling stress. The oesophageal probe consisted of a 30 cm flexible plastic tube, diameter 0.7 cm, with four regularly spaced thermistors. In the oesophagus, the sensors were at 9, 16, 25 and 34 cm from the beak junction (sensors *a*, *b*, *c* and *d*, respectively). The birds were kept in a fenced enclosure for 30 min to allow the thermistors to reach body temperature. A total of 220 fish pieces (mass and temperature ranges 1.6–14.7 g and 0.5–9 °C, respectively), simulating the temperature and the size of the prey usually caught by king penguins (Cherel & Ridoux 1992), were hand-fed to them at 2–6 min intervals, during sessions lasting, on average, 100 min.

Table 1. *Foraging characteristics of three king penguins equipped with data loggers monitoring their oesophageal temperature and diving behaviour, in early February 1997 at Crozet Archipelago*

(The birds were at the brood stage. A dive was considered as successful when at least one ingestion was detected. Means are ± s.e.).

	foraging dates (1997)	duration of oeso-phageal record (days)	stomach content at the bird's return (kg)	oeso-phageal tempera-ture range (°C)	total no. prey ingestions (RTD ⩾ 0.06° Cs^{-1})	mean no. prey ingestions day^{-1}	mean no dives > 30 m day^{-1}	mean no. ingestions per dive		per cent successful dives	
								⩽ 30 m	> 30 m	⩽ 30 m	> 30 m
bird 1	31/01–10/02	6.3	1	18.9–38.8	1407	187 ± 82	48 ± 12	0.031 ± 0.004	3.94 ± 0.19	3	79
bird 2	01/02–12/02	7.5	1	18.0–38.3	2342	301 ± 121	82 ± 16	0.017 ± 0.004	3.67 ± 0.14	2	75
bird 3	08/02–22/02	6.1	0.5	19.4–39.1	580	91 ± 38	57 ± 11	0.014 ± 0.005	1.55 ± 0.14	1	40

(c) *Equipping free-ranging birds*

Seven birds at the brood stage were surgically implanted under halothane anaesthesia with an intraluminal oesophageal temperature sensor and a tracheal temperature sensor at 6–10 cm from the beak junction. The cables of the sensors were fixed with absorbable suture threads onto the external walls of the oesophagus and trachea, at 15 mm and 5 mm from the sensors, respectively. The body of the unit (2 s sampling interval) was attached externally onto the lower back with the cables tunnelled up to the upper oesophagus and the trachea (see figure 1). The tunnellization was performed using a special sterile stainless steel tube. Cutaneous wounds were closed using absorbable suture threads. The transcutaneous transition was protected and anchored by a non-absorbable suture thread. Six out of the seven penguins were induced to swallow a stomach temperature sensor (16 s sampling interval). Four out of the seven individuals were implanted with an MK5 recorder in the abdominal cavity as described by Handrich *et al.* (1997). Dive depths were sampled every 4 s. The work was performed in a shelter within the colony site and the birds were thereafter returned to their breeding spot. There, using a portable enclosure, they were protected from neighbours and predators until full recovery from the anaesthesia. All equipment was removed under anaesthesia after the birds returned and the individuals were released in apparently good condition. None of the birds implanted with thermistors showed infection. Moreover, all continued to breed (chick brooding) after the removal of the equipment. The procedure complied with current laws of the French authorities: Authorization of the Ministère de l'Agriculture et de la Forêt (no. 04196) followed by approbation of the surgical protocol by the Ethics Committee of the French Institute for Polar Research. In this study, we will report on oesophageal and stomachal temperatures and diving behaviour.

(d) *Data analysis*

Data were downloaded and analysed using Jensen System Software programs (Laboe, Germany) and custom-made Foxbase programs. In the stomach and the oesophagus, the expected temperature signal following ingestion of a cold prey item by endotherms is a 'precipitous drop' of the sensor temperature followed by an 'exponential rise' to the body value (PDER). The PDER reflects the cooling and rewarming of the sensor after contact with the cold item (Wilson *et al.* 1992, 1995). However, because temperature changes in divers may reflect either prey ingestion (PDER) or non-feeding events (i.e. temperature changes due to diving *per se*) (Handrich *et al.* 1997), we examined in detail at-sea temperature drops to identify feeding and non-feeding events. For this, we compared the oesophageal temperature drops for the two main categories of dives previously observed in king penguins (Kooyman *et al.* 1992; Charrassin *et al.* 1998; Pütz *et al.* 1998): shallow (⩽30 m) and deep (> 30 m) dives. Means are given ± s.e.

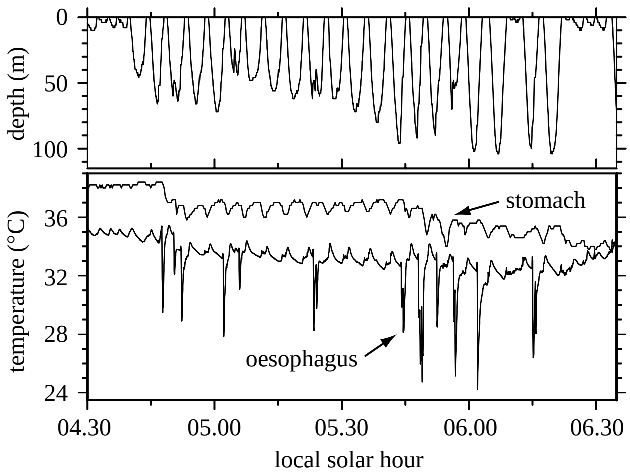

Figure 3. Changes in upper oesophageal and stomach temperatures in relation to dive depth in a king penguin foraging at Crozet Archipelago during 2 h.

3. RESULTS

(a) *Experimental feedings*

All 220 items fed to the penguins were detected (temperature drop ⩾0.3 °C) by sensor *a*, except for five meals that were not swallowed. The proportion of events showing a PDER at the upper sensor (*a*) was 20% (range 0–61%, $n = 9$ feeding sessions). Non-PDER events (i.e. either a non-precipitous drop (slower drop) or a slow rise) reflected a chaotic passage of the prey over the sensor. Indeed, based on the behaviour of the birds, they often did not swallow the food at once, sometimes alternately trying to regurgitate and swallow the food. We assume this does not occur in a free-ranging feeding bird. The response to ingestion was best in the upper thermistor, and with increasing distance from the beak, detection of the prey was less certain (figure 2). Ingestions were not detected by the stomach sensor although the temperature dropped from 38.2 to 37.7 °C during that period (figure 2). The progression velocity of prey items between the sensors *a* and *b*, *b* and *c*, and *c* and *d* averaged

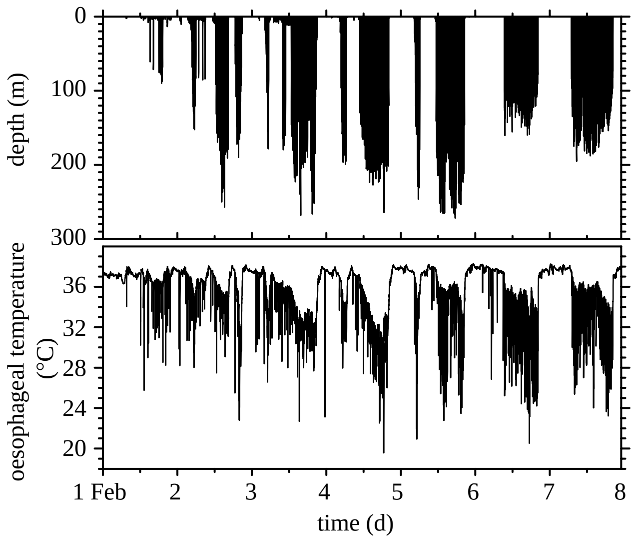

Figure 4. Changes in upper oesophageal temperature in relation to dive depth in a king penguin foraging at Crozet Archipelago during seven days after departure from the colony. The total trip duration was 11 days.

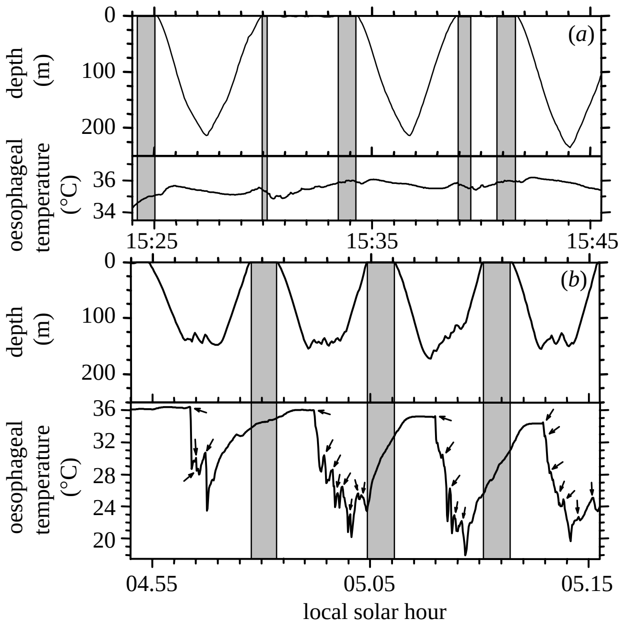

Figure 5. Changes in upper oesophageal temperature in relation to dive depth indicating non-feeding dives (*a*) and feeding dives (*b*) in a foraging king penguin. Arrows indicate prey ingestion. Grey boxes show periods spent at the surface.

0.6 ± 0.03 ($n = 38$), 0.3 ± 0.08 ($n = 4$) and $0.5 \pm 0.1\,\mathrm{cm\,s^{-1}}$ ($n = 4$), respectively.

(b) *Prey ingestion and diving behaviour in free-ranging penguins*

Out of the seven birds equipped, four remained at sea for 11.9 ± 0.9 days on average (range 10.1–14.5 days). The stomach content upon return was sampled using the water off-loading technique (Wilson 1984). It ranged from 0.5 to 1 kg. One bird spent 1.5 days at sea. Two individuals stayed in the colony. Out of the four birds which went to sea with a stomach recorder, two lost the recorder by regurgitation of the unit at sea, and two had retained it when they came back. Continuous oesophageal temperature records lasting six to seven days were obtained from three birds, and a total of 4900 dives from 1–291 m depth were recorded simultaneously (table 1).

As shown in figure 3, both stomach and oesophageal temperatures showed slow and regular variations which coincided with the dives. However, for oesophageal temperature, large and rapid drops, which were not seen for stomach temperature, were superimposed on these variations. Only when numerous rapid drops in oesophageal temperature occurred did stomach temperature decrease further. During the intensive diving that king penguins make during their foraging trips at sea (see figure 4), their drops in oesophageal temperature did reach as much as 13.3 °C. Still, dives with only minor changes in oesophageal temperature (figure 5*a*) contrasted with dives with large variations in oesophageal temperature (figure 5*b*).

For the 650 ± 60 temperature drops $\geqslant 0.02$ °C recorded on average per day for each of the three birds ($n = 19$ days), two groups of temperature drops were characterized according to their amplitude and duration (figure 6). The first group corresponded to slow drops, showing a small amplitude (1–2 °C or below) and lasting for up to 3 min. Based on their rate of temperature decrease (RTD, defined as the amplitude of the temperature drop divided by the drop duration), slow drops accounted for most of those occurring during shallow dives (95% of drops had an RTD $< 0.06\,^{\circ}\mathrm{C\,s^{-1}}$) but were also observed during deep dives (figure 6). They corresponded to the cyclic variations already described in figure 3, which, occurring in relation to the dives, reflect the tissue cooling due to diving *per se* (Handrich *et al.* 1997).

The other group included large (up to 13.3 °C) and short (< 30 s) drops, which occurred mainly during deep dives (figure 6). During deep dives, 50% of these drops had an RTD greater than $0.06\,^{\circ}\mathrm{C\,s^{-1}}$. Because such rapid drops were much shorter than the duration of the dives during which they occurred, they indicate cooling by cold prey. Fast temperature drops (RTD $\geqslant 0.06\,^{\circ}\mathrm{C\,s^{-1}}$) were therefore assumed to reflect prey ingestion. Feeding events inferred from oesophageal temperature are shown in figure 5*b*.

(c) *Feeding frequency and feeding depth*

The number of ingestions per day varied from 95 to 300 among the birds, and the number of ingestions per shallow dive ($\leqslant$30 m) was much smaller than for deep dives (table 1). Bird 3 apparently experienced a much lower foraging success than the others. Feeding depths were obtained from the dive profiles recorded simultaneously with oesophageal temperature. In bird 2, prey ingestions occurred mainly between 80 and 170 m, where 70% of ingestions were detected (figure 7). During diving, 5 ± 3, 41 ± 2 and 54 ± 5% of prey ingestions took place during the descent, bottom and ascent parts of the dives, respectively ($n = 3$ birds, and 4200 dives > 70 m).

4. DISCUSSION

This study is based on the assessment of oesophageal temperature of free-ranging diving birds as a new

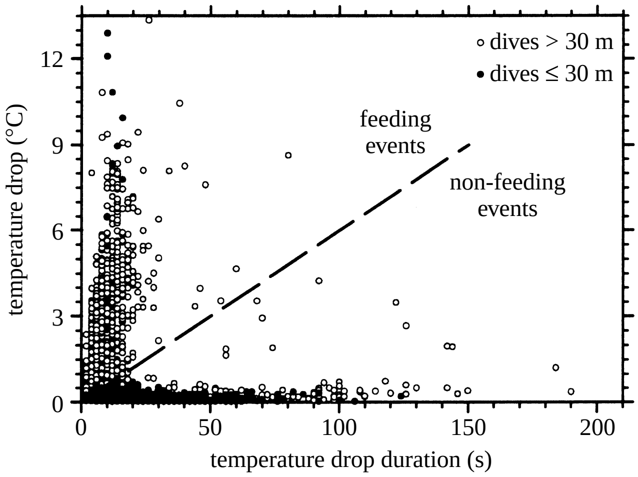

Figure 6. Relationships between amplitude and duration of temperature drops in the upper oesophagus recorded in a king penguin during shallow dives ($\leqslant 30$ m; $n = 1951$ drops) and deep dives (> 30 m; $n = 2450$ drops). The dashed line indicates the rate of temperature decrease above which temperature drops were considered as reflecting prey ingestion (0.06 °C s^{-1}, see § 3). The period covered six foraging days.

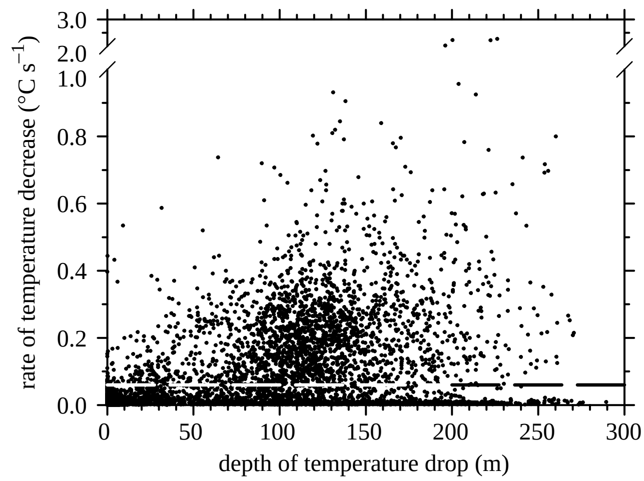

Figure 7. Depths at which temperature drops of the upper oesophagus occurred in a king penguin foraging for 7.5 days ($n = 6209$ drops $\geqslant 0.02$ °C). Considering that a rate of temperature decrease $\geqslant 0.06$ °C s^{-1} (dashed line) indicates feeding, most prey ingestion occurred at depths from about 80 to 170 m.

method for detection of food ingestion. Our technique allows detection of ingestion of prey items as small as myctophid fish in relation to depth.

(a) *Implantation of oesophageal probes in free-ranging penguins*

Four birds went to sea and showed normal foraging behaviour as judged by dive depth and food brought to the chick (Kooyman *et al.* 1992; Charrassin *et al.* 1998; Pütz *et al.* 1998). Why two birds stayed at the colony is unclear. However, recent work (Y. Le Maho, unpublished data) suggests that the passage of the cables in the neck may particularly disturb some individuals. Accordingly, future work with data transmission to the logger unit rather than a cable connection may solve the issue. However, implantation of the sensor in the oesophagus eliminates the possibility of losing the logger by regurgitation as can occur for stomach sensors (this study; Wilson *et al.* 1998).

(b) *Relevance of oesophageal probe for detecting small prey ingestions*

Since all experimental feedings gave a detectable response, we conclude that our system is sensitive enough for small-sized prey items. The low thermal inertia of the small sensor accounts for its good sensitivity (Ancel *et al.* 1997). Such a small size reduces the probability of contact with prey but is counterbalanced by the small cross-sectional area of the oesophagus. Prey items were less often detected with increasing distances from the beak, and detection was almost impossible in the stomach of captive penguins. However, prey detection in the stomach could be less reliable in our captive individuals than in free-ranging birds, since movements during diving may continually change the sensor position in the stomach (Wilson *et al.* 1995) thereby favouring contact with prey. Progression of food items is faster in the upper part of the oesophagus. This lessens the time between prey ingestion and prey–sensor contact, and favours detection by reduced warming of the prey. Prey ingestion is then easier to distinguish from physiological changes due to diving (Handrich *et al.* 1997) if the probe is located in the upper oesophagus rather than deeper in the body (e.g. in the stomach). Based on the 0.6 cm s^{-1} displacement of prey items in the upper oesophagus found in captive birds, the delay for reaching a sensor located 9 cm from the beak is 15 s. Such a short interval allows a quasi real-time detection of food ingestion.

(c) *Detecting prey ingestion in free-ranging penguins*

King penguins feed on patchily distributed mesopelagic fish (Adams & Klages 1987; Cherel & Ridoux 1992; Olsson & North 1997). Oesophageal temperatures recorded in free-ranging birds showed large variations (> 13 °C) that indicated feeding events and feeding depths when combined with dive profiles. The typical fast, short and precipitous temperature drops clearly indicate prey ingestions, as opposed to the slow temperature variations corresponding to the tissue cooling due to physiological responses to diving (Handrich *et al.* 1997). Furthermore, these prey ingestions were confirmed, as the rapid temperature drops mainly occurred during deep dives (exclusively performed during daylight by king penguins; see figure 4; Kooyman *et al.* 1992; Charrassin *et al.* 1998; Pütz *et al.* 1998), which correspond to the depths where myctophids concentrate during the day (Zasel'sliy *et al.* 1985; Duhamel 1998).

Based on a penguin's average vertical velocity during diving of 1.3 m s^{-1} (Pütz *et al.* 1998) and with an ingestion–detection delay of 15 s, the accuracy of depth where ingestion occurs is *ca.* 20 m, i.e. 10% of the dive depth if the bird reaches 200 m. Being validated with concurrent application of a classical technique, such as hydroacoustic prey survey, or net trawl, this method may provide a unique means to assess the prey distribution over depth. For instance, one of the three birds fed mainly at 80–170 m, where it probably encountered dense prey patches. Using average prey mass of king penguins (7.4 and 1.7 g for the two main prey species, in proportions of 75 and 15% of the diet, respectively; Cherel & Ridoux 1992), the daily mass of fish ingested by birds 1 and 2 was *ca*. 1.6 kg and was 0.6 kg for bird 3. These values are comparable with those ranges found in studies based on energetics (Kooyman *et al*. 1992) and argue for the reliability of our method.

In conclusion, measurement of oesophageal temperature appears to be a promising tool for detecting prey ingestion by marine predators. Beside new information on the feeding ecology of these predators, an interesting perspective is their use to infer the prey distribution at depth, in particular for small schooling fish difficult to detect by conventional methods, but which are key marine resources in the Southern Ocean.

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