Measuring foraging activity in a deep-diving bird: comparing wiggles, oesophageal temperatures and beak-opening angles as proxies of feeding

Nicolas Hanuise[1,2,*], Charles-André Bost[1], William Huin[1], Arnaud Auber[2], Lewis G. Halsey[3] and Yves Handrich[2]

[1]Centre d'Études Biologiques de Chizé, CEBC–CNRS UPR 1934, F-79360, Villiers en Bois, France, [2]Institut Pluridisciplinaire Hubert Curien (IPHC), UMR 7178 CNRS-ULP, Département Ecologie, Physiologie et Ethologie (DEPE), 23 rue Becquerel, F-67087 Strasbourg cedex 2, France and [3]Department of Life Sciences, Roehampton University, Holybourne Avenue, London W15 4JD, UK

*Author for correspondence (n.hanuise@gmail.com)

SUMMARY

Quantification of prey consumption by marine predators is key to understanding the organisation of ecosystems. This especially concerns penguins, which are major consumers of southern food webs. As direct observation of their feeding activity is not possible, several indirect methods have been developed that take advantage of miniaturised data logging technology, most commonly: detection of (i) anomalies in diving profiles (wiggles), (ii) drops in oesophageal temperature and (iii) the opening of mouth parts (recorded with a Hall sensor). In the present study, we used these three techniques to compare their validity and obtain information about the feeding activity of two free-ranging king penguins (*Aptenodytes patagonicus*). Crucially, and for the first time, two types of beak-opening events were identified. Type A was believed to correspond to failed prey-capture attempts and type B to successful attempts, because, in nearly all cases, only type B was followed by a drop in oesophageal temperature. The number of beak-opening events, oesophageal temperature drops and wiggles per dive were all correlated. However, for a given dive, the number of wiggles and oesophageal temperature drops were lower than the number of beak-opening events. Our results suggest that recording beak opening is a very accurate method for detecting prey ingestions by diving seabirds at a fine scale. However, these advantages are counterbalanced by the difficulty, and hence potential adverse effects, of instrumenting birds with the necessary sensor/magnet, which is in contrast to the less accurate but more practicable methods of measuring dive profiles or, to a lesser extent, oesophageal temperature.

Key words: diving, foraging, Hall sensor, ingestion, king penguin, oesophageal temperature, wiggle.

INTRODUCTION

The determination of food consumption by marine predators is key to understanding the organisation of marine ecosystems (Croxall, 1987). Invaluable information for furthering our knowledge of energy flows and foraging strategies in relation to environmental features is obtained through the quantification of prey ingestion (Wilson et al., 1992). Seabirds are important consumers of sea resources (Brooke, 2004) and thus play a pivotal role in marine environments. However, knowledge of their feeding success in terms of consumption rate and prey mass is still limited. Direct observation of their feeding activity is rarely possible, particularly for diving species. Nevertheless, modern miniaturised technology now provides several methods for estimating the number and timing of ingestions (Ropert-Coudert and Wilson, 2005). As marine endotherms mainly feed on ectothermic prey, recording of stomach (Weimerskirch and Wilson, 1992) or oesophageal (Ancel et al., 1997; Charrassin et al., 2001; Ropert-Coudert et al., 2001) temperatures allows detection of temperature drops when prey are ingested (hereafter termed the 'oesophageal technique'). More recently, measurements of jaw motion (Plotz et al., 2001) or of inter-mandibular angle, by means of a Hall sensor (hereafter the 'Hall technique') (Fossette et al., 2008; Hochscheid et al., 2005; Wilson et al., 2002) have been used to recognise feeding events. Alternatively, accelerometers can be fixed onto the head or the jaw to detect such behaviour (Viviant et al., 2009). At the temporal scale of a dive or dive bout, anomalies in dive profiles called 'wiggles'

(Bost et al., 2007) (the 'wiggles technique') or modifications in wing stroke frequency during aerial flight (Sato et al., 2008), measured by accelerometers, have been linked to feeding success and mass gain, respectively. Finally, the use of video recorders allows association between a particular dive pattern and feeding events (Madden et al., 2008).

Penguins are among the most important predators of the Southern Ocean, representing up to 90% of the avian biomass in this region (Woehler, 1995), and can represent relatively tractable bio-indicators (Bost et al., 2008). Thus, quantification of their prey consumption is of particular importance for understanding the impact of top predators on marine resources (Guinet et al., 1996) and in using them to monitor changes in the marine environment (Halsey et al., 2008). King penguins (*Aptenodytes patagonicus*, Miller 1778) are a difficult species in terms of quantifying feeding behaviour as not only do they feed on small, mesopelagic fish (Cherel and Ridoux, 1992) but they do so at great depths that can damage instruments [typically between 150 and 300 m (Charrassin et al., 2002)], and they also undertake foraging trips of high duration, placing further constraints on the data loggers (Bost et al., 1997). The ingestion of small prey makes the detection of temperature drops by an oesophageal probe difficult, and, in king penguins, the problems with this technique are further exacerbated, first, because of changes in their body temperatures during deep diving activity (Handrich et al., 1997) and, second, owing to the invasiveness of implanting a probe in the oesophagus. The use of a Hall sensor on the beak can

also be problematic owing to the invasive nature of the instrumentation. Several studies have investigated the feeding behaviour of penguin species, mainly by recording dive profiles (to discern wiggles), oesophageal temperatures (Charrassin et al., 2001) or, more recently, beak-opening events (Wilson et al., 2002). The first two techniques have been applied to king penguins. However, little is known about the relative accuracy and sensitivity of these different methods.

In the present study, we compare, in free-ranging king penguins, these three methods for recording feeding ingestions to assess their accuracy. The penguins were instrumented simultaneously with time-depth recorders, oesophageal temperature sensors and Hall sensors. Unfortunately, owing to technical failures and potential adverse effects of the instrumentation, data were obtained only for two birds. Our objectives were: (1) to obtain the first beak-opening data for king penguins and (2) to compare the accuracy of this technique with that of the two techniques previously used for quantifying feeding behaviour in this species.

MATERIALS AND METHODS
Study birds and equipment
The study was conducted on Possession Island, Crozet Archipelago (46.4°S, 51.8°E), located in the South Indian Ocean, during the austral summer from February to March 2006. The studied king penguins were breeders at La Baie du Marin, a colony of approximately 16,000 breeding pairs (Delord et al., 2004). The capture, release and handling procedures received the approval of the ethics committee of the French Polar Institute (IPEV) and of the French Environment Ministry. Six breeding male king penguins were captured while brooding a young chick (1–10 days old). A portable enclosure was placed in the colony to protect the territory of each bird during their instrumentation with an external data logger and both oesophageal temperature and Hall sensors (see details below) (Fig. 1). Captured birds were immediately anaesthetised to reduce stress and ease their instrumentation. The equipped birds, still anaesthetised, were replaced together with a warm dummy egg within the colony, surrounded by the portable enclosure. After full recovery from the anaesthetic (less than 4h later), the enclosure was removed and the chick was replaced under the bird (see Froget et al., 2004). The capture occurred 2 days after the beginning of their shift and thus allowed sufficient recovery time after anaesthesia. The penguins undertook a foraging trip at sea 7–8 days later, after exchanging the chick with their mate. Upon their return to the colony 5–22 days later, the birds were recaptured and the loggers and sensors removed.

Data loggers
SMAD data loggers (DEPE-IPHC, J. P. Gendner, Strasbourg, France; 80×25×10 mm, 54 g) were attached externally to the lower back of each animal to minimise hydrodynamic drag (Bannasch et al., 1994). These loggers incorporate a hydrostatic pressure sensor measuring water depth, which is recorded at 1 Hz. The beak sensors consisted of a small magnet, which thus produced a magnetic field, and a Hall sensor that detected its strength (Wilson et al., 2002) and was connected to the logger by means of a cable. When the beak was closed, the distance between the magnet and the sensor was minimal (less than 0.5 mm), and thus the magnetic field experienced by the sensor was maximised. Conversely, beak-opening movements led to an increased distance between the magnet and the sensor, which in turn resulted in a decrease in the magnetic field experienced by the sensor. The magnets were glued to the lateral surface of the upper beak, whereas the Hall sensors were attached to the lateral surface of the lower beak, directly facing the magnets (Fig. 1). The
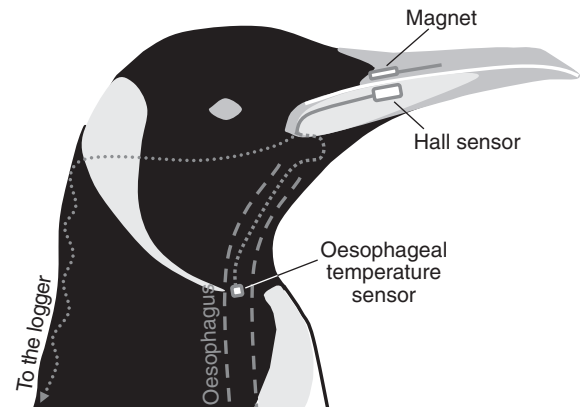

Fig. 1. Schematic diagram of the attachment of oesophageal temperature and beak-opening sensors to king penguins. For five penguins, the cable running from the beak to the logger was tunnelled under the skin, whereas, in the sixth bird (E1), it was sewn on the skin.

relationship between sensor output (mV) and beak-opening angle was determined during anaesthesia by using a wooden tube to separate the mandibles and determining a stable beak-opening angle (0 to ~30 deg) during several seconds. Despite high coefficients of determination (R^2>0.92), because a number of factors compromised the calibrations obtained, we decided to analyse beak-opening events in terms of output signal rather than convert those values into angles. The aforementioned factors, in decreasing order of effect, were: (1) the exponentially decreasing relationship between output and angle, prohibiting accurate measurement for angles >10 deg, (2) substantial variations of the relationship linked with lateral movements of the mandibles, and (3) a small shift of the baseline with depth and temperature. The signal of the Hall sensor was recorded during two daily sessions of 3 h at a frequency of 16 Hz, to ensure that data across the entirety of the foraging trip were recorded onto the 16 Mbyte memory card encased within the logger. The oesophageal temperature sensor (time constant: 4 s) was introduced into the buccal cavity through an incision under the chin, performed under anaesthesia (Fig. 1), suspended at 7–8 cm below the beak junction and connected to the logger by means of a cable. The cable was set to run subcutaneously from the logger to the Hall and temperature sensors. To minimise difficulties elongating the neck during prey capture, the cable was inserted while the neck was in full extension, and a surgical stitch was made at both extremities. On one of the six birds (E1), we fixed the cable externally with a loop and with stitches made every centimetre (Fig. 1). Oesophageal temperature was continuously recorded at a frequency of 2 Hz.

Data analysis
Once the loggers were recovered, the data were extracted and analysed using purpose-written computer programs in Matlab 6.0 (The MathWorks, Natick, MA, USA). Dives with maximum depths greater than 50 m ('deep' dives) were included in the analysis as they are considered to represent the majority of foraging dives of king penguins (Charrassin et al., 2002). Dive analysis was conducted following the recommendations of Halsey and colleagues (Halsey et al., 2007). Wiggles are particular short-term patterns in the dive profile, with a 'zigzag' shape, and accurately defined by Halsey and colleagues (Halsey et al., 2007) as an increase in depth followed by a decrease in depth and then another increase in depth.
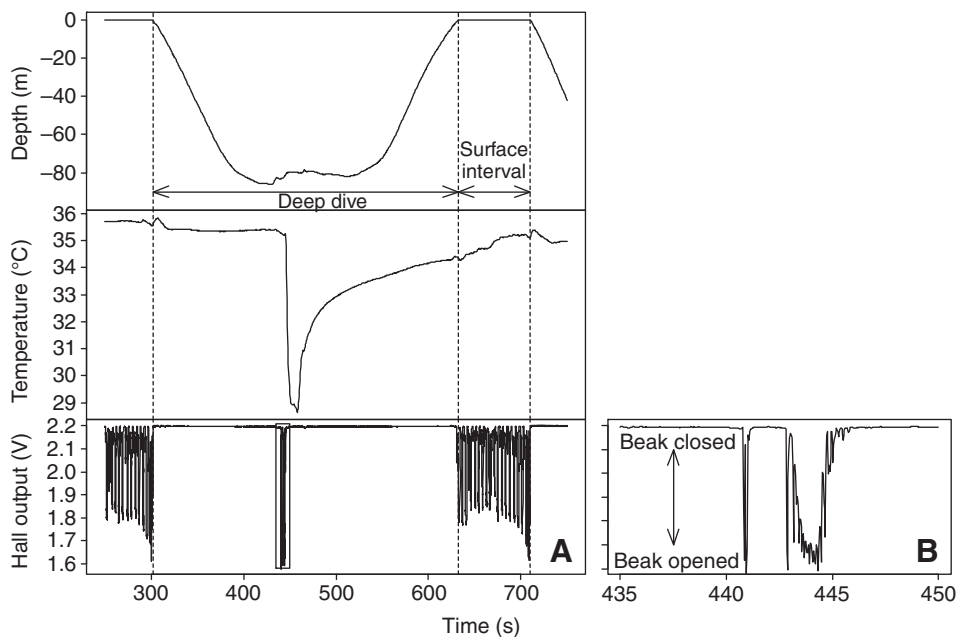
Fig. 2. (A) Data recorded during a deep dive and the subsequent surface interval of a king penguin, 'H1', showing variations of depth (top), oesophageal temperature (middle) and Hall output signal (bottom) against time. (B) Detail of the Hall output signal corresponding to two Hall events that occurred during the dive. Dashed lines indicate the beginning and end of dives and the subsequent surface interval.

Prey ingestions were determined from oesophageal temperature records based on criteria defined in previous work (Charrassin et al., 2001). Temperature drops with a rate of decrease $\geq 0.06°C\,s^{-1}$ were assumed to indicate cooling by cold prey (Charrassin et al., 2001) and thus termed 'feeding drops', whereas drops not exceeding the threshold (95% of the total) are believed to reflect tissue cooling due to diving *per se*. Deviations of the Hall sensor output from the baseline, caused by the beak opening and so-called 'Hall events', were automatically detected.

Statistical analysis

Statistical analyses were performed using R 2.9 software (R Development Core Team, 2009). Statistical tests were first performed separately for each bird, and, when similar results were produced, the data were then pooled. Normally distributed data are described by the means ± one standard deviation (s.d.), whereas skewed data are described by the median and interquartile (i.q.) range.

RESULTS
Recorded data

The six equipped penguins left the colony after exchanging the chick with their partner. The six loggers were removed 7 to 23 days later. Two loggers failed after less than 1 day at sea. Complete data recorded by four loggers showed that two birds did not perform deep foraging dives and appeared not to have travelled far from the colony. Finally, we obtained foraging data for only two birds (E1 and H1), the former having been equipped with an external cable (bird E1). Three of the six equipped birds were successful in the subsequent chick exchange with their mate and at rearing the chick until at least the crèche stage. The presented data correspond to two foraging trips of 9 and 7 days, during which both penguins performed dives of depths and durations similar to those of birds fitted with depth recorders only (Table 1). Beak-opening and oesophageal temperature were simultaneously recorded during a total of 96 h, during which both penguins performed a total of 496 deep dives. Totals of 1023 wiggles, 1370 feeding drops and 3047 Hall events occurred during these dives (Table 2, Fig. 2).

Types of Hall events

Hall events were detected both during dives and during surface intervals between dives. The following results refer to the 3047 events detected during dives as it is these that might be associated with feeding activity.

The distribution of both the duration and the area under the curve of Hall events (AUC, defined as the area between the baseline and the output signal) was bimodal (Fig. 3). This enabled the distinction between short- (<1.25 s, N=640) and long-duration Hall events (median=2.3 s, i.q. range: 1.9–2.9 s, N=2407), and small (<7 V s, N=582) and large Hall events (median=25 V s, i.q. range: 16–44 V s, N=2465).

We also classified Hall events into types A and B. Type A Hall events (Hall-A events) were defined by a single, quick decrease of the signal followed by a quick increase, returning to the baseline (Fig. 4A), corresponding to a quick opening–closing event, ending with complete closure of the beak. Type B Hall events (Hall-B events) were defined as demonstrating an initial decrease and increase of the signal, similar to Hall-A events – however, without

Table 1. Characteristics of diving behaviour of two male king penguins during foraging trips away from the colony

Characteristic	Bird H1	Bird E1
Foraging trip duration (days)	9	7
Total number of dives	2070	1720
Number of deep dives	323	650
Mean ± s.d. maximum depth (m)	136±31	117±30
Maximum depth (m)	218	184

Table 2. Characteristics of feeding behaviour of two male king penguins at sea during periods when the Hall signal (relating to beak opening) was being recorded

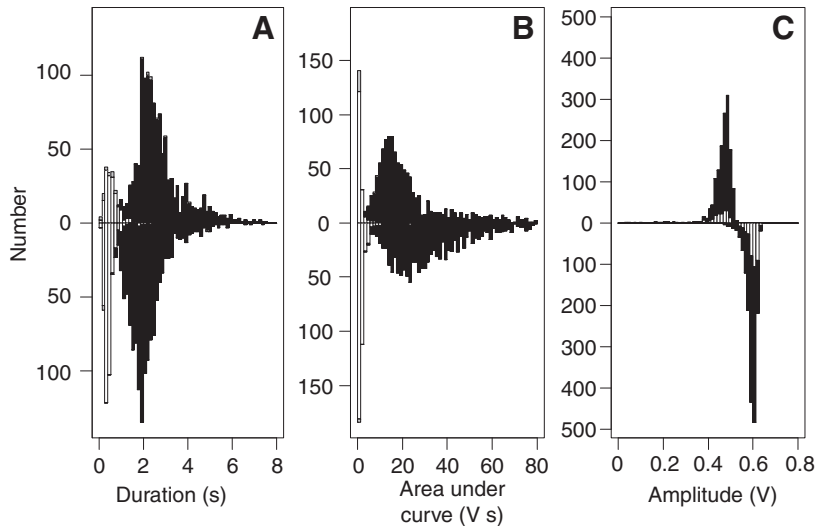| Characteristic	Bird H1	Bird E1	Total
Duration of Hall sensor recording (h)	42	54	96
Number of deep dives	164	332	496
Number of Hall events recorded	1643	1404	3047
Number of feeding drops	655	715	1370

Fig. 3. Distribution of (A) durations, (B) areas under the curves and (C) amplitudes of Hall events recorded in two king penguins while diving at depth. Data are presented on both sides of a horizontal line at zero, with each side corresponding to a particular king penguin (above: E1, below: H1). Open bars indicate type A Hall events, black bars indicate type B Hall events (see Fig. 4), and grey bars indicate other Hall events. To avoid compression of the graphs due to a low incidence of events of very large duration and areas-under-curve, durations greater than 8 s and areas-under-curve larger than 80 V s are not shown.

a return to the baseline (phase 1) and followed by repeated waves (Fig. 4B) corresponding to a quick opening–closing event with incomplete closure of the beak, and finishing with oscillatory movements of the mandibles. In a typical Hall-B event, the second part of the signal occurred in two phases: (i) the upper values recorded during the oscillations progressively decreased to a minimal value and then increased again to reach the baseline (phase 2); (ii) thereafter the waves originated from the baseline (phase 3).

Based on this criterion, we identified 519 Hall-A and 2498 Hall-B events, and the 30 remaining events were termed as 'others' (Fig. 3). For both birds, the duration and AUC of Hall-A events were significantly lower than that of Hall-B events (median duration: 0.44 and 2.25 s, W=6960, P<0.001; median AUC: 1.1 and 25.4 V.s, W=5827, P<0.001) (Table 3). The first and second peaks of the bimodal distributions of the duration and AUC of Hall events usually (>95%) corresponded to Hall-A and Hall-B events, respectively (Fig. 3A,B).

Comparing Hall events with oesophageal temperature drops
The number of feeding drops per dive correlated with the total number of Hall events per dive (r=0.89, P<0.001) and with the number of Hall-B events per dive (Fig. 5A, r=0.91, P<0.001). However, the number of feeding drops per dive was significantly lower than the number of Hall-B events per dive (feeding drops: 4.4±3.8, Hall-B: 8.2±4.6, P<0.001). There were no dives either without any Hall-B event or with only Hall-A events that showed

an oesophageal temperature drop (N=200). Dives with a single Hall-B event had a mean of 0.97 feeding drop (N=60).

The ratio of feeding drops relative to Hall-B events tended towards 1 when the duration between two successive Hall-B events increased (r=0.65, P<0.001) and reached a plateau for an interval of approximately 10 s. For dives with durations between Hall-B events longer or shorter than 10 s, the ratio of feeding drops per Hall-B event was 0.91 (N=528) and 0.41 (N=577), respectively. This is mainly because the duration of feeding drops is longer than that of Hall-B events (Fig. 6). Thus, when considering all dives within which the durations between Hall events were longer than 10 s, it is possible to assess each individual Hall event in terms of whether it is temporally related to a feeding drop. In these cases, three out of 26 Hall-A events were followed by a temperature drop, two of them (7.7%) exceeding the 0.06°C s^{-1} threshold and thus being detected as feeding drops. Conversely, the 528 Hall-B events were followed by a temperature drop, 29 of them (5.5%) not exceeding the threshold and thus not being detected as feeding drops. Feeding drops following a Hall-B event had the following characteristics: starting 2.1±1.6 s (mean ± s.d.) after the beginning of the corresponding Hall event, with a duration of 8.2±3.1 s, an amplitude of 3.2±1.0°C and a slope of 0.4±0.1°C s^{-1}.

Ingestions and wiggles
The number of feeding drops and the number of Hall-B events per dive correlated with the number of wiggles per dive (Fig. 5B,C, r=0.56 and r=0.57, respectively, both P<0.001). The number of
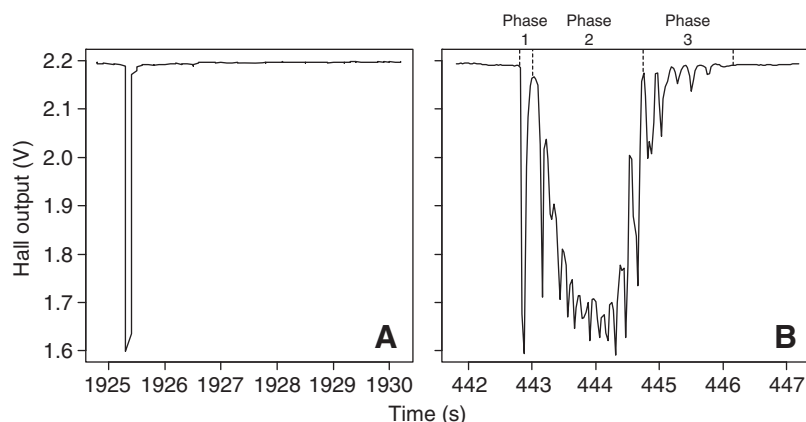

Fig. 4. Characteristic patterns in beak-opening over time for (A) type A Hall events (quick, single decrease of the signal, returning to the baseline), and (B) type B Hall events (type A-like phase without return to the baseline, followed by oscillations).

Table 3. Characteristics of Hall events of two male king penguins during foraging trips away from their colony (median and i.q. range)

Characteristic	Bird H1	Bird E1	Total
Number of Hall events	1643	1404	3047
Duration of Hall events (s)	1.8 (1.1–2.4)	2.4 (1.9–3.0)	2.1 (1.4–2.7)
Area under the curve (V s)	25 (12–41)	17 (11–30)	21 (11–38)
Amplitude (mV)	598 (584–608)	474 (450–490)	554 (477–599)
Number of Hall-A events	354	165	519
Duration of Hall-A events (s)	0.4 (0.3–0.5)	0.5 (0.4–0.7)	0.4 (0.3–0.6)
Area under the curve (V s)	1.3 (0.8–2.2)	0.8 (0.5–1.4)	1.1 (0.6–1.9)
Amplitude (mV)	603 (592–614)	462 (436–481)	592 (483–610)
Number of Hall-B events	1285	1213	2498
Duration of Hall-B events (s)	2.1 (1.6–2.5)	2.5 (2.1–3.2)	2.3 (1.8–2.8)
Area under the curve (V s)	31 (21–48)	19 (13–35)	25 (16–43)
Amplitude (mV)	596 (582–606)	476 (455–491)	530 (478–597)

wiggles per dive was not significantly different from the number of feeding drops per dive (wiggles: 4.1±2.9, drops: 4.4±3.8, $P=0.19$). However, it was lower than the number of Hall-B events (Hall-B: 8.2±4.6, $P<0.001$). A total of 79.7% of all the detected feeding drops occurred within a wiggle, with a mean number of 1.42±1.02 feeding drops per wiggle. The amplitude and duration of wiggles with
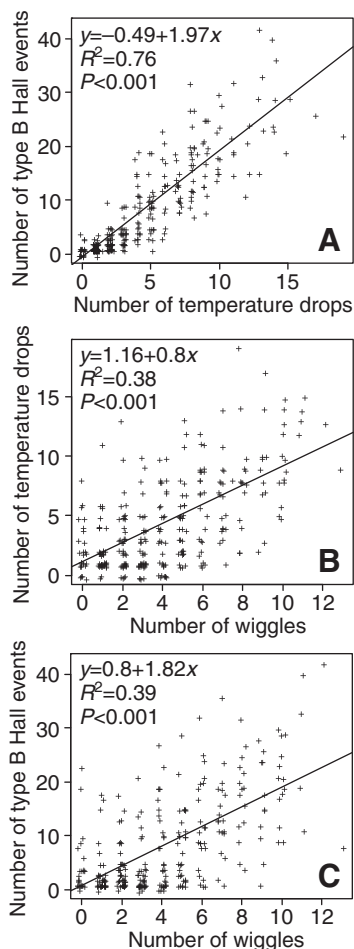

Fig. 5. Relationships between (A) the number of feeding drops per dive and the number of type B Hall events per dive, (B) the number of wiggles per dive and the number of feeding drops per dive, and (C) the number of wiggles per dive and the number of type B Hall events per dive.

feeding drops was not significantly different from wiggles without ingestions (2.9 m, 15.3 s vs 8.8 m, 21.1 s, both $P>0.15$).

DISCUSSION

Here, we have presented the first simultaneous data recordings of dive profile wiggles, oesophageal temperatures and beak openings in a diving animal – three methods used to gain detailed information on feeding activity. Furthermore, these measures have been compared to obtain some understanding of the accuracy of each as a proxy for prey capture events.

Since the first deployments of Hall sensors on the beaks of penguins (Wilson et al., 2002), approximately 15 species have been studied using this technique. Marine predators whose foraging cannot be observed directly, such as turtles (Fossette et al., 2008; Hochscheid et al., 2005; Myers and Hays, 2006), cetaceans (Ropert-Coudert et al., 2002), pinnipeds (Liebsch et al., 2007) and diving birds (Shepard et al., 2010; Simeone and Wilson, 2003; Takahashi et al., 2004; Wilson et al., 2002) are represented in most of these studies (but see Ropert-Coudert et al., 2004), the data from which provided valuable information on prey captures. Of the two penguin species that have been fitted with Hall sensors at sea, the Magellanic penguin *Spheniscus magellanicus* (Simeone and Wilson, 2003; Wilson et al., 2002) and the chinstrap penguin *Pygoscelis antarctica* (Takahashi et al., 2004), both dived to moderate depths (<100 m) and remained for less than 24 h at sea each trip, in contrast with king penguins.

Recording feeding events from beak recorders

Our Hall sensor data were able to identify two clearly distinct types of beak openings considered to be related to feeding activity during deep diving, termed Hall-A and Hall-B events. Most likely, these two behaviours could either correspond to feeding events on two types of prey differing in size or to successful versus unsuccessful capture attempts. At the Crozet Islands in summer, king penguins mainly prey on two small myctophid fish species, *Electrona carlsbergi* and *Krefftichthys anderssoni* (Cherel and Ridoux, 1992). These two types of prey differ in mass and size, with the former being heavier and longer than the latter (Cherel and Ridoux, 1992). Therefore, differences in beak-opening amplitude and duration while penguins ingested these fishes of two different species should be expected. In our study, the distribution of durations and areas under the curve of the beak-opening events is clearly bimodal and, in accordance with the two identified patterns of Hall events, Hall-A and Hall-B. However, as Hall-A events were almost never followed by an oesophageal temperature drop, and as the ranges of mass of
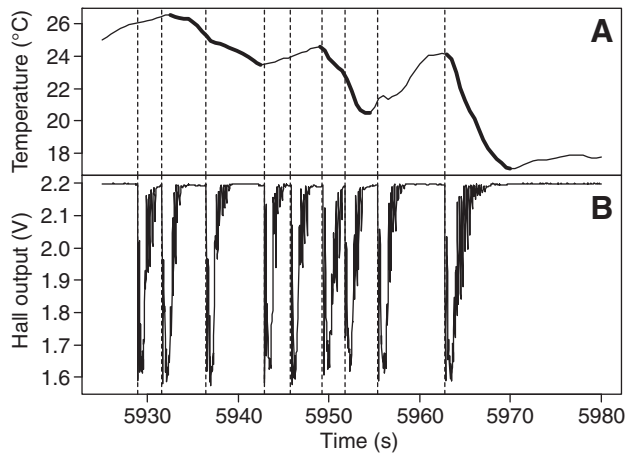
Fig. 6. Differences in the number of detected ingestions assessed with the oesophageal technique (A, three temperature drops, bold lines) compared with the Hall technique (B, nine prey captures, broken lines indicate start time of each event).

Hall-A events virtually never associated with oesophageal temperature drops, strongly indicating that prey are not captured during these behaviours. By contrast, temporally distant Hall-B events were almost always associated with a large and rapid drop in oesophageal temperature, and, on the assumption that king penguins do not swallow water when they fail to capture a prey item, this strongly suggests that a prey item is, or prey are, captured during type B beak openings. However, when Hall-B events occurred within a short time-frame, they did not consistently correspond to the same number of drops in oesophageal temperature (Fig. 6), probably owing to the lag time of the oesophagus and of the temperature probe to recover from the previous temperature drop (Charrassin et al., 2001), thus not detecting the next prey capture. Furthermore, some Hall-B events are associated with subsequent drops in oesophageal temperature not exceeding the threshold and thus not counted as feeding drops. This suggests that oesophageal probes tend to underestimate prey capture rates during periods of high-frequency prey capture. The Hall sensor technique, once beak opening events have been separated into successful and failed prey capture events, has the advantage over the oesophageal temperature technique of a much higher recording resolution able to detail high-frequency events.

Effects of logger deployments on the birds
Of the six equipped penguins, we obtained data for only two of them owing both to the effects of logger instrumentation and technical problems with regards to two of the loggers. Two of the instrumented birds might not have foraged because of complications involving the cable running under the skin along the neck and the back. In a previous study using oesophageal temperature sensors, cables were tunnelled in the same manner for seven king penguins, which performed trips of normal duration at sea (Charrassin et al., 2001). However, in the present study, owing to the additional presence of the Hall sensor and associated connections, the cable was larger and more rigid. We believe that the presence of a cable under the skin of the neck, without sufficient flexibility, is the major cause of adverse effects observed in this study, highlighting the importance of other methods to study prey captures. An external fixation to the neck is obviously an alternative solution, but, in the only bird (E1) equipped by this manner, the duration of the foraging trip was still long, and the neck fixations broke at sea (after the memory was full). This method thus remains a technique with a large logistical onus as it requires anaesthetisation of the subject bird, precise fixation of the magnet and the sensor on the mandibles, and fixation of cables from the sensor to the logger on or under the skin. In contrast to the Hall sensor, and, to a lesser extent, the oesophageal temperature sensor, instrumentation of a bird with only a time-depth recorder for quantifying wiggles requires far less manipulation of the subject animal and is also less invasive, in the main because it is 'cable-free'. The main advantage of the wiggles method is its ease of use, the short duration of bird manipulation required to attach the necessary time–depth data logger, and the relatively unobtrusive cable-free nature of the logger attachment.

In summary, the three techniques have their advantages and disadvantages, resulting in a trade-off between the ease of implementation of the method and the accuracy of detecting feeding events.

Future developments
In combination with the use of criteria to dichotomise underwater beak-opening events into those that represent successful prey capture and those that do not, the Hall sensor technique is the most sensitive and accurate of the three methods presented in the current paper for quantifying feeding behaviour and estimating ingestion

the two main species overlap, we propose that Hall-A events might mainly reflect capture attempts without ingestions rather than ingestions of small-sized prey, and that Hall-B events mainly reflect successful capture of prey of various sizes. Indeed, based on the previous work of Charrassin and colleagues (Charrassin et al., 2001), ingestions of small prey of approximately 2 g should induce a feeding drop in the oesophagus. Only a very small number of isolated Hall-A events were followed by temperature drops, which might indicate that occasional instances of Hall-A events represent feeding events on small prey.

Importantly, Hall-B events are rather similar to those described in previous studies on penguins corresponding to prey capture (Wilson et al., 2002), with the following pattern: an initial wide-opening of the beak while the mandibles surround the prey body, a narrowing during the initial snap at the prey, followed by an increase in the beak angle (as the widest part of the fish goes past the rictus) together with gulping behaviour, which continues as the beak angle diminishes to zero. By contrast, Hall-A events comprise simply a quick opening and then closing of the beak as the bird attempts but fails to catch hold of a prey item.

Comparison of the three methods
The present study has confirmed that the number of wiggles occurring in a dive correlates with the number of ingestions, estimated with the Hall sensor or oesophageal temperature techniques. Similar findings have been reported previously in studies comparing just wiggles and feeding drops (Bost et al., 2007) or wiggles and beak-openings (Simeone and Wilson, 2003; Takahashi et al., 2004). However, using wiggles to estimate feeding behaviour appears to be less accurate than either of the two other measures, probably because wiggles integrate the combined effects of prey searching and/or pursuit and/or attempted capture.

Without visual verification, it is of course not possible to validate absolutely the techniques for assessing prey capture. However, the evidence suggests that beak opening is the most accurate technique and close to a 'gold standard' once the data are categorised into Hall-A and Hall-B events. In combination, these two types of beak opening account for the vast majority of all underwater beak opening events, suggesting that, bar a small number of anomalies, underwater beak opening behaviour is dichotomised by the use of a few simple criteria.

rate. However, it is also the most logistically demanding method. Clearly, the ideal technique will be both accurate and non-invasive.

The three proxies of feeding behaviour assessed in the present paper are those that have been widely measured in diving predators; however, the advent of miniaturised accelerometer loggers provides another and as yet relatively untested option, which is particularly exciting as it is another 'cable-free' method. Accelerometers employed to record body or limb posture and the dynamic motion of animals (Shepard et al., 2009) will certainly provide more information on feeding events than can wiggles. Alternatively, accelerometers can be fixed onto the head or the jaw to detect feeding events more directly (Viviant et al., 2009), but this method also requires considerable manipulation of the subject animal, and, as yet, those loggers deployed have been small enough only for use on pinnipeds. In the same manner, development of Hall sensor logging systems small enough to be put on the head of the animal would avoid use of cables and hugely enhance the study of feeding. Finally, quantification of the mass of ingested prey still remains a challenge, which could be approached through measuring the length of prey through the use of appropriate sensors.

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