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Review

Reconstructing the past using futuristic developments: trends and perspectives in logger technology for penguins

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Abstract: Over the last two decades there has been remarkable progress in the development of sensory systems coupled with loggers that have been attached to free-living marine animals. Increases in sensor resolution, sensor diversity and memory size have been coupled with decreases in unit size. Thus, the periods over which animals have been monitored have increased from hours to months while the sampling frequency has decreased from minutes or seconds to fractions of a second. Four main interrelated trends can be identified. Determination of; (1) animal position in three dimensions, (2) the characteristics of the environment in which the animals operate, (3) animal behaviour and (4) energy management. The elucidation of these trends in penguins is discussed and perspectives given with regard to what is expected in the future.

key words: penguins, data loggers, prey capture, 3 dimensional movement, energy expenditure

Introduction

It is now over 3 decades since the first logging devices were used on free-living air-breathing marine animals (Kooyman, 1966; Kooyman *et al.*, 1971). Earlier units were mechanical and cumbersome (Kooyman, 1966) but demonstrated that remote-sensing devices on free-swimming animals were feasible and that they could deliver some remarkable insights into animal behaviour. Since these first deployments there have been major advances in the development of remote-sensing logging devices for use on air-breathing marine animals. Two factors are particularly important in this respect; (i) the availability of sensors and (ii) development of systems for recording the output of the sensors. During the 1980's and early 1990's, almost all devices used on free-ranging marine animals were concerned with measurement of depth, something that could be conveniently examined by consideration of volumetric changes. Recording methodology ranged from dissolution of water-soluble dyes in air columns (Kooyman *et al.*, 1971; Burger and Wilson, 1988), through autoradiographic tracing of the movement of depth indicators (Wilson and Bain, 1984) to devices that used photographic tracing (Kooyman *et al.*, 1983; Wilson *et al.*, 1989) or tracing using diamond styluses on carbon films (Naito *et al.*, 1990). As enlightening as this methodology was, it was not until the inception of solid-state solutions in devices attached to remote

animals that the rate of development in the field really accelerated. Minute memory chips with low power consumption, which worked with smaller, more animal-friendly batteries, did away with complex analyses of older memory solutions such as films, and data were accessed directly *via* an interface onto the computer. In tandem with massive developments in the solid-state industry, these memory chips have increased in storage capacity, allowing data to be recorded with a resolution of up to 16 bits at higher frequencies for longer periods. Simultaneous development of solid-state sensors by the silicon chip industry now means that many parameters other than dive depth can be measured on free-living animals.

The applications for remote-sensing loggers on free-living marine animals are now so vast that this paper has been restricted to consider only those developments that have been used by the penguin working group in the Institut für Meereskunde in Kiel, Germany. This is not an exercise in self-praise but rather a recognition of the fact that there are so many working groups researching so many different marine animals that to try and cover all their fields of expertise would substantially exceed the space limitations for a single author.

Methods

The work presented here is derived primarily from the use of devices produced by Driesen and Kern GmbH (Bad Bramstedt, Germany), although other companies (*e.g.* Earth and Ocean Technologies, Kiel, Germany) have also been involved as well as Jensen Software Systems (Laboe, Germany) for the necessary software. Major device types and their functions are listed in Table 1. Most work cited comes from recent research on the Magellanic penguins *Spheniscus magellanicus* (body mass *ca.* 4

Table 1. List of the solid-state devices referred to in the paper.

Device	Primary sensors	Primary parameter measured	Typical sampling rate	Optional secondary sensors	Resolution	Memory	Maker	First deployment	Reference
GLS ¹	Light	Location	once per minute	Depth/Temp	8 bit	512 kbyte	Driesen & Kern	1992	Wilson <i>et al.</i> (1992)
Dead Reckoner	Compass Tilt sensor Depth Speed	Location	<4Hz	Temperature Light	up to 16 bit	up to 16 Mbyte	Driesen & Kern	1991	Wilson <i>et al.</i> (1993)
EATL ²	Temperature	Stomach temp	once per 16 s		8 bit	32-64 kbyte	Elkutec	1991	Wilson <i>et al.</i> (1992)
STCUP ³	Temperature	Stomach temp	once per 10 s		8 bit	up to 4 Mbyte	Driesen & Kern	1992	Wilson <i>et al.</i> (1995)
3 d compass	Compass	Activity	30 Hz		8 bit	512 kbyte	Driesen & Kern	1997	Hochscheid and Wilson (1999)
IMASEN ⁴	Hall sensor	Beak movement	10 Hz	Depth/Temp	16 bit	4 or 8 Mbyte	Driesen & Kern	2000	Wilson <i>et al.</i> (2002a)
IMASU ⁵	Hall sensor	Flipper movement	30 Hz	Depth/Temp	16 bit	4 or 8 Mbyte	Driesen & Kern	2001	Wilson and Liebsch (2003)
Cloacal sensor	Hall sensor	Cloaca activity	20 Hz	Hall sensor	16 bit	4 Mbyte	Driesen & Kern	2001	This paper
GPS ⁶	GPS motor	Location	once per minute	Depth/Temp	12 bit	2 Mbyte	Earth & Ocean Technologies	2003	This paper

1 Global location sensor, 2 Einkanalige Automatische Temperatur Logger, 3 Single-channel unit processor, 4 Inter-mandibular angle sensor, 5 Integrating movement assessing sensory unit, 6 Global position sensor.

kg) studied at various sites in Argentina, all work conducted being approved by the relevant authorities. For simplicity, and in order to save space, data presented in this work are primarily derived from single examples and represent an observed general trend. In some examples more extensive work is already published or in press and this is referenced as appropriate. In the newest developments presented, this outlet serves to inform interested parties of work that has yet to be fully analysed and written up in detail.

Results and discussion

Over recent years, there have been four major thrusts in describing the biology of penguins by the working group in Kiel. These are: (i) determination of animal location, (ii) determination of the environmental conditions at the locations, (iii) animal behaviour as a function of locality and (iv) energy management (acquisition and expenditure). These will be briefly considered below.

Determination of animal location

Three systems have been used to determine penguin location, these being Global Locating Systems (GLS, also termed geolocation) (Wilson *et al.*, 1992a; Hill, 1994), Global Positioning Systems (GPS) and dead reckoning (Wilson *et al.*, 1988, 1993). GLS technology stores the values for light intensity at regular intervals for extended periods (days to months) so as to determine the time of dawn and dusk according to some standard time zone and then uses geographically-linked changes in day length and the time of local noon as a function of Julian day to determine geographic position (Wilson *et al.*, 1992a; Hill, 1994). Errors in position determined by this method are high (of the order of tens of kilometres) and position can only be determined twice per 24 h cycle (Welch and Eveson, 1999). However, in view of the size of the logging units, this system can be deployed for long periods, such as during overwinter periods (Wilson *et al.*, 1998a, b) with reduced chances of incurring aberrant device-induced behaviour.

GPS technology was recently used for the first time on free-living seabirds (Weimerskirch *et al.*, 2002) and has now been successfully used on Magellanic penguins breeding on Peninsula Valdes, Argentina (Fig. 1). This technology gives bird position to within a few metres but currently has a high power consumption during operation which limits its use. It cannot operate underwater and can thus only give positional information when the penguin is at the surface. It is, however, the most accurate tool yet developed for determining seabird location.

Dead-reckoning technology uses vectors to calculate the 3 dimensional route taken by a swimming penguin from the measurement of bird speed, heading and depth (Wilson *et al.*, 1988, 1993; *cf.* Davis *et al.*, 1999; Mitani *et al.*, 2003). Although relative positional information can be obtained at intervals of fractions of a second, the methodology is subject to drift due to currents so that calculated position tends to drift away from true position over time (Wilson *et al.*, 2002a). This can now be corrected by using dead-reckoning in tandem with a GPS so that points at the surface can be located by the GPS while the dead-reckoner can be used to determine the movements of the penguin underwater.

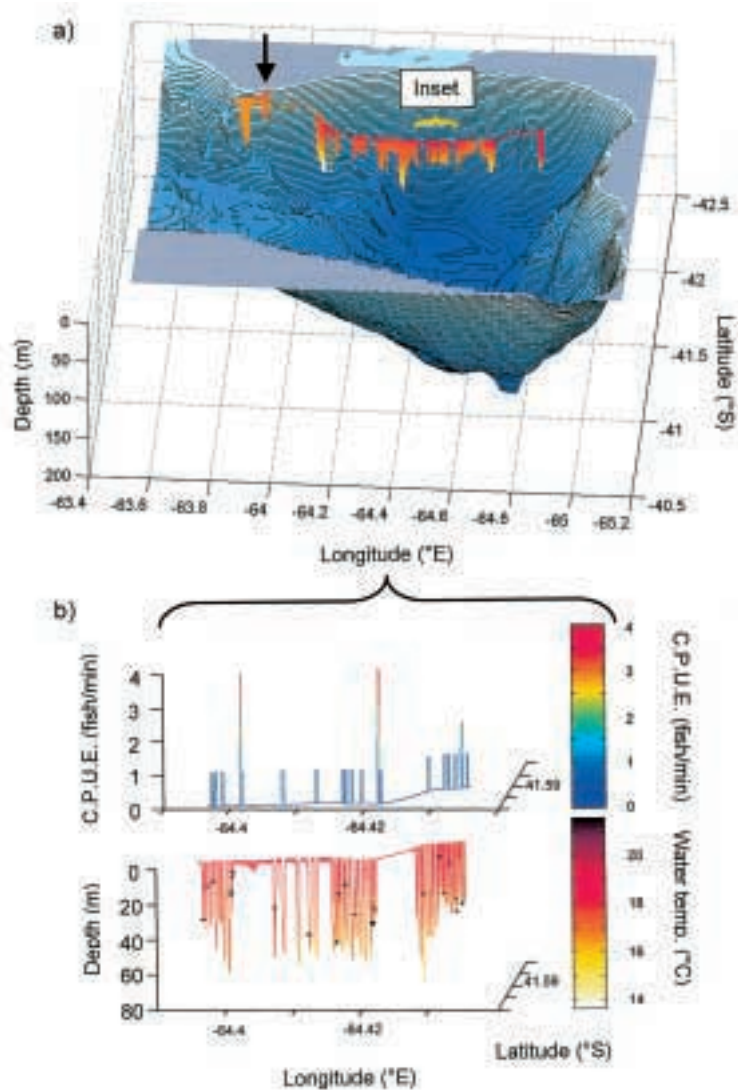


Fig. 1. (a) Movement of a Magellanic penguin at sea for over 36 hours (Jan 2003) as determined by an attached GPS combined with depth transducer. The bird was foraging for two chicks from the penguin colony at San Lorenzo, Peninsula Valdes, Argentina (see start of track indicated by the arrow). Maximum depth within the San Matthias Gulf is *ca.* 200 m. Water temperature, as measured by the unit on the bird, is indicated by the colour of the track. The contour lines show 5 m depth intervals.

(b) Enlargement of a section of the trace shown in (a) (marked as 'inset') showing individual dives in more detail. Water temperature is shown by colour in the lower trace and prey capture (see later) shown as individual dots. The upper trace shows the calculated catch per unit effort (CPUE; prey items per minute underwater) for the same period.

Environmental conditions at the animal location

Knowledge of animal location is most useful if the environmental conditions at that location are known. Aside from the standard satellite imagery methodology, which only

gives information of conditions at the sea surface, loggers attached to the animals can provide data on abiotic parameters such as temperature (*e.g.* Boyd *et al.*, 2001; Fig. 1), salinity (*e.g.* Lydersen *et al.*, 2002) and light (Wilson *et al.*, 2002a) down the water column.

Biotic parameters, such as prey density, can also be alluded to using loggers to record animal foraging success in relation to foraging effort so as to derive a Catch per Unit Effort (CPUE) index (Wilson, 1992; Wilson *et al.*, 1994) (Fig. 1b). Effort can be relatively easily derived in diving animals by simply determining the time spent underwater (Wilson *et al.*, 1994) using a conventional time depth recorder (TDR). Determination of 'catch' has proved more problematic. In the past, stomach temperature (Table 1) has been used as a measure of foraging success since this drops when marine endotherms ingest ectothermic prey (Wilson *et al.*, 1992b; Gales and Renouf, 1993; Hedd *et al.*, 1996) although this system is subject to numerous errors (Wilson *et al.*, 1995; Ropert-Coudert *et al.*, 2000a). Measurement of oesophageal temperature (Ancel *et al.*, 1997; Ropert-Coudert *et al.*, 2000a, b) appears more reliable but is rather disturbing for the equipped animals (see details in Ropert-Coudert *et al.*, 2001). More recently, very promising results on rates of prey ingestion have been gained by use of an inter-mandibular angle sensor (IMASEN—Table 1), which uses a Hall sensor, located on one half of the penguin bill, to measure magnetic field strength from a minute magnet, located on the opposing bill half. When the beak is opened, as is the case during ingestion, the magnetic field perceived by the sensor decreases (for details see Wilson *et al.*, 2002b). If the relationship between beak angle and perceived magnetic field strength is calibrated and the logger set to record at high frequencies (*e.g.* 10 Hz and higher), ingestion of prey produces a characteristic pattern of beak angle over time which varies in form slightly according to prey type (Wilson *et al.*, 2002b). Integration of the beak angle over time enables calculation of the approximate mass of the prey ingested (Wilson *et al.*, 2002b). Calculated CPUEs for Magellanic penguins are highly variable according to region and indicate the degree of patchiness of the prey (Fig. 2) as well as alluding to prey size distribution (Fig. 2) as a function of area (Fig. 1b; *cf.* Wilson *et al.*, 1994).

Animal behaviour

Many particular behaviours can be recognised by looking at changes in animal orientation, as determined by a three-dimensionally operating compass-tilt system, such as is used in the dead-reckoner (see above) (*cf.* Hochscheid and Wilson, 1999), set to record at high frequencies (> 2 Hz), because many activities involve changes (or not) in body posture in a particular sequence over time. Otherwise, much can be learned about penguin foraging strategies by looking at movement over a variety of scales using the dead-reckoner. Work on Adélie *Pygoscelis adeliae* and Magellanic penguins shows that foraging tracks may be broadly broken down into three types of movement; (i) virtually straight line travel, when birds commute from one area to another, (ii) meandering, where birds search for prey and (iii) prey capture, where the described route shows the pursuit of prey and the strategies used to capture particular prey types (Wilson, 2002; Fig. 3).

Energy management

Central to successful foraging is the concept of energy management and this falls into two major categories (i) energy acquisition and (ii) energy expenditure/use.

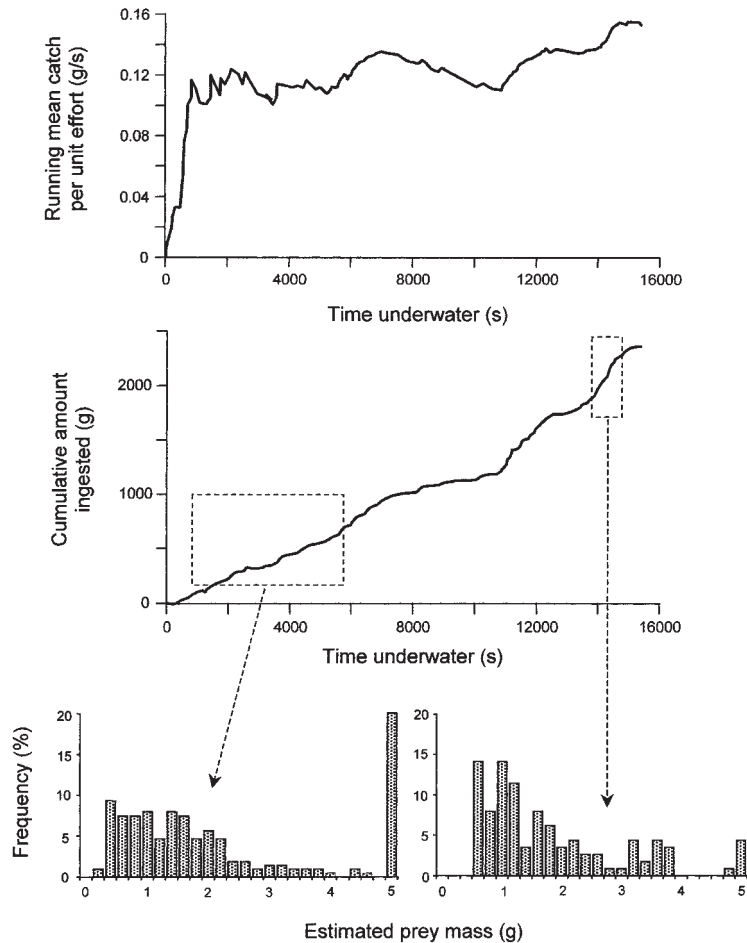


Fig. 2. Prey ingested by a particularly successful, single Magellanic penguin breeding at Cabo Virgenes, Santa Cruz, Argentina during a foraging trip lasting *ca.* 10 h. The prey ingested were determined using an IMASEN which measured beak angle at 10 Hz. Prey mass was determined using the integral of the beak angle over time during prey swallowing (for details see Wilson *et al.*, 2002). The central graph shows the cumulative amount ingested over time underwater, the gradient of which is a measure of the catch per unit effort (CPUE) (upper graph). Two sections of the prey caught over time are highlighted (boxes in the central graph) to show how the frequency distributions of prey masses vary according to time (space).

Energy acquisition:

Energy acquisition occurs via feeding and this can be well documented by IMASEN technology (see above). However, use of this technology shows that Magellanic penguins, at least, apparently consume much more than was previously thought (*e.g.* Fig. 2) (*cf.* Croxall, 1987). It is unlikely that major errors occur in the determination of how much penguins eat since beak opening underwater that does not lead to ingestion shows a different pattern to that during actual feeding (Wilson, 2003a). Current consumption estimates for penguins are based, among other things, on assimilation efficiencies determined for birds in captivity (*cf.*

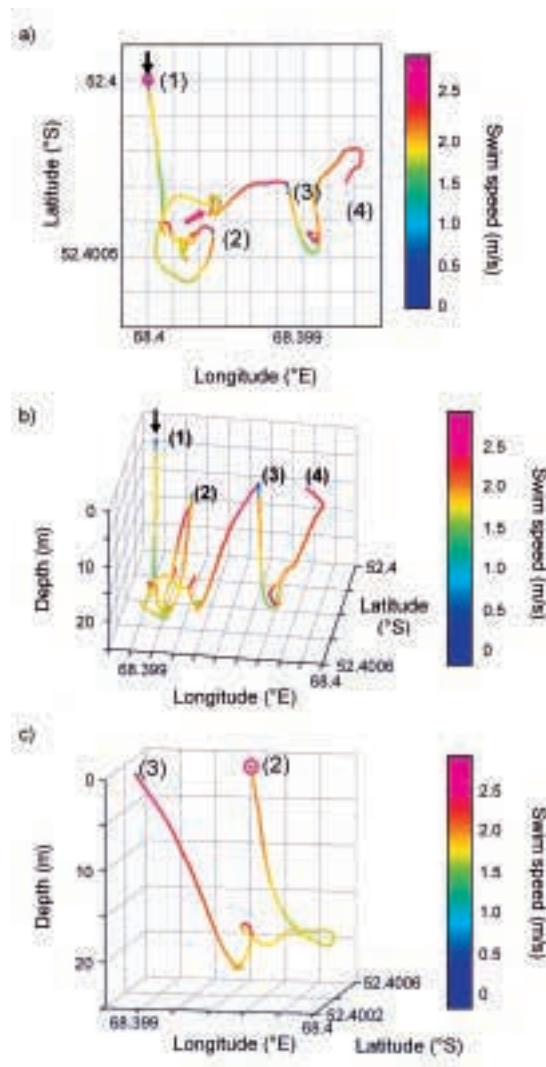


Fig. 3. Three dimensional representation of the route taken by a Magellanic penguin foraging for sardines near the Cabo Virgenes colony in Santa Cruz, Argentina. The upper figure (a) shows the position of the bird during three dives (starting at the arrow) as seen from directly above (surface periods denoted by numbers) while the middle figure (b) shows the same three dives taken from an angled northern perspective. Swim speed during the dives is shown by the colour and data are shown on a second by second basis. Prey pursuit and capture is exemplified by tight, erratic turning behaviour at the bottom of dives with highly variable speed (*cf.* Fig. 3c which shows the second dive in the series). Note between the end position of the first dive (at position (2)) and the prey capture behaviour (between position (2) and (3)), that the bird executed a large circle (evident in the bottom left hand corner of Fig. 3a). This is assumed to be prey searching behaviour where the penguin attempted to relocate the shoal exploited in the previous dive. The supposed movement of the shoal between the time the penguin had left it and then relocated it is shown by the pink arrow in Fig. 3a.

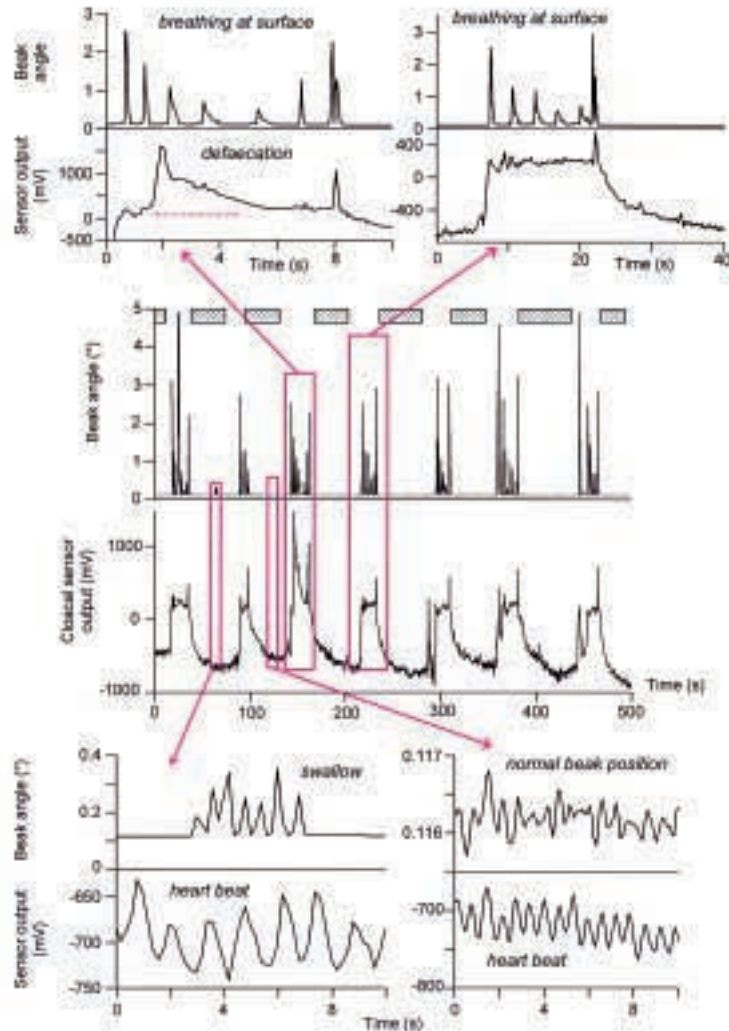


Fig. 4. Output of IMASEN and cloacal sensor, both recording at 10 Hz, over 500 s for a Magellanic penguin diving at sea. The central figure shows the outputs from both sensors (the IMASEN data have been converted to beak angle) for the whole time period considered. Periods when the bird was underwater are shown by the dotted boxes at the top of the central figure. Periods at the surface are characterized by breathing (shown by the opening and closure of the beak, Wilson *et al.*, 2003; for more detail in single inter-dive periods at the surface see the figures at the top left and right) while changes in the tail angle with respect to the body associated with diving and being at the surface are readily apparent. Note that defaecation is shown by a marked peak in the cloacal sensor output although the short peak at the onset of diving (a feature that is consistent prior to all dives) is presumably due to some tail movement (top left figure). The two figures at the bottom show (left) a period when the bird swallowed underwater (but without prey ingestion) — note minimal changes in beak angle) and (left and right) rhythmicity picked up by the cloacal sensor which is likely to be heart rate. Note that the beak also shows is similar, though slightly offset, rhythmicity in angle (bottom right). Note that all behavioural components alluded to here (swallowing, defaecation etc.) were ascertained by following equipped birds in captivity prior to field trials.

Jackson *et al.*, 1987; Jackson, 1992). However, assimilation efficiency is likely to be based on the transit time of the food in the gut so that high rates of ingestion by birds at sea may be accompanied by correspondingly rapid transit times and reduced digestive efficiency. Such a premise is tenable if the net energy gain by birds feeding in this way exceeds those that digest according to the currently accepted scenario. In order to examine the rate of digestion, a Hall sensor-magnet based system similar to the IMASEN was constructed for use on penguin cloacas. This cloacal sensor was tested on captive Magellanic penguins before being used on free-living birds in tandem with the IMASEN during January 2003. Although the correct functioning of the system is critically dependent on the precise positioning of the sensor, defaecation can be determined (Fig. 4). Work is underway to examine the extent to which this system can help answer the question related to the speed and efficiency of digestion.

Energy use:

Optimal foraging literature purports that there is selection pressure for animals to operate so as to minimize energy expenditure whilst maximizing energy gain (Pyke *et al.*, 1977; Krebs and Davis, 1993) ultimately in order to maximize the net energy gain (Perry and Pianka, 1997). Thus, examination of indices related to energy expenditure can allow us to determine the extent to which penguins adhere to this. Two basic complementary lines are being pursued here; determination of movement, because movement requires energy, and determination of the rates of air inspired, because this should be related to oxygen requirements.

A modification of the Hall sensor-magnet system for use on penguin flippers (the integrated movement assessing sensory unit - IMASU; Table 1), rather than on the beak, allows measurement of flipper movement. In this application the magnet is glued to the flipper while the Hall sensor is glued opposite on the body and appropriate calibrations allow the conversion from the Hall sensor output of millivolts into flipper angle with respect to the body (for details see Wilson and Liebsch, 2003). The work done by a swimming penguin is manifest by the flipper beat frequency and the flipper amplitude and both these terms can be conveniently combined in the flipper angular velocity (Wilson and Liebsch, 2003). It is a general sense increased flipper angular velocities are expected to be related to increased energy expenditure although the precise form of the relationship will have to be determined. During

Fig. 5 (opposite). Flipper movements (recorded at 30 Hz) as a function of dive depth (recorded at 5 Hz) and inspired air volume (recorded at 10 Hz) derived from a free-living Magellanic penguin foraging off Cabo Virgenes, Santa Cruz, Argentina combined in an attempt to derive a measure of energy expended using new technology. (a) shows the flipper movement as a function of depth for a single dive to ca. 4 m (derived from the use of a depth gauge in tandem with an IMASU) and (b) shows typical changes in beak angle associated with breathing at the water's surface between dives (Wilson *et al.*, 2003). (c) shows that flipper angular velocity (flipper amplitude X flipper beat frequency; a measure of the work done by the penguin for motion) changes systematically with instantaneous depth, maximum depth of the dive and whether the bird is descending or ascending the water column (each point shown represents a mean from at least 15 dives). The total angle traversed by the flippers during any one typical dive to a specific depth (related to the total energy expended during the dive) (d) can be derived by summing all flipper angular velocities over the time taken for the dive. The total air volume inspired previous to any dive to a specific depth (e) (which must be, in some way, related to energy expenditure during the dive) can be determined by summing the maximum beak amplitudes due to breathing between dives (maximum beak amplitude per breath is linearly related to tidal volume; see Wilson *et al.*, 2003). Finally, the two measures of energy expenditure during a dive; the total angle traversed by the flippers during any dive to a particular depth and the total inspired air volume previous to the depth (see Wilson, 2003a; Wilson *et al.*, 2003) can be regressed against each other to see the extent to which the two measures compare.

the initial part of a dive, flipper beat frequencies and amplitudes are high, but these decrease during the bottom phase and decrease still further as the penguin returns to the surface (Fig. 5; Wilson and Liebsch, 2003; cf. Sato *et al.*, 2002). Flipper angular velocity varies according to both the maximum depth of the dive and the depth at which it is measured. Although during the descent flipper angular velocity decreases, dives terminating at deeper depths have overall higher angular velocities. The situation is reversed during the ascent where flipper angular velocity decreases with decreasing depth but values are higher in dives which terminate at shallower depths (Fig. 5; Wilson and Liebsch, 2003). This situation arises because, although swim speed does not change during the dive (except during prey capture) (Wilson

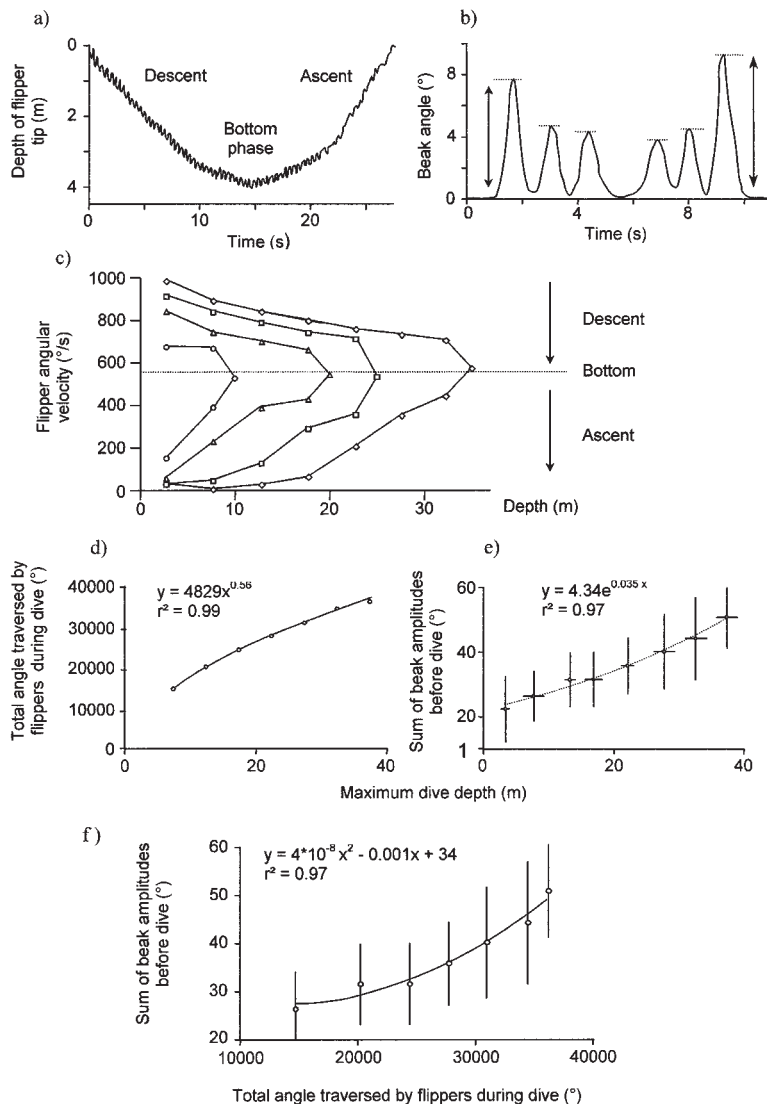


Fig.5

et al., 2002c), birds diving deeper inhale more in the last breath (Wilson, 2003b) and descend the water column at a steeper angle with increasing maximum dive depth (*cf.* Wilson and Peters, 1999). Thus, the higher flipper angular velocity associated with the descent for deep dives reflects birds having to work harder against the higher upthrust (Fig. 5c), the reverse being true for the ascent. Assuming that higher flipper angular velocities are indeed coupled with higher energy expenditure, a measure of the total energy expended over the dive can be gained by integrating the flipper angle velocity over the full dive duration. This can be most conveniently translated as the total angle traversed by the flippers during the dive (Fig. 5d).

The volume of air passing through the lungs during the period at the surface during preparation (Wilson, 2003a) for a dive, which should be related to the oxygen requirements for the dive, can be calculated by examination of the beak angle. The individual breaths during the inter-dive period are apparent as openings and closures of the beak (Fig. 5b; Wilson *et al.*, 2003) and maximum beak angle during inspiration is linearly related to the tidal volume (Wilson *et al.*, 2003). Thus, the total amount of air passing through the respiratory system can be calculated by summing the maximum beak angles for all the breaths that occur during the inter-dive period at the surface and this can be related to the maximum depth of the dive (Fig. 5e) and ultimately even to the total angle traversed by the flippers during the dive (Fig. 5f). In this latter case we have a measure of the energy expended via the work done by the flippers regressed against a measure for the amount of oxygen inhaled, this also being a measure of energy expenditure. Ultimately, it should be possible to calculate the cost of a single flipper beat (under defined circumstances) expressed as a volume of air inhaled. Unfortunately, none of the IMASENSs used on birds in the wild were calibrated for beak angle versus tidal volume as suggested by Wilson *et al.* (2003) so it is not possible to carry the calculation shown here to completion. In the regression of the sum of the beak amplitudes for a specific dive versus the total angle traversed by the flippers during that dive it is notable that the form is non-linear (Fig. 5f). This is ultimately due to the non-linearity in the oxygen saturation curve for birds resting at the surface; even within a single pause at the surface, more oxygen will be extracted from the first than the last breath (Wilson *et al.*, 2003) and this feature will be most apparent in surface pauses of longer durations. Cognisance of the rates of removal of oxygen from the inspired air on a breath by breath basis might help linearize the relationship and perhaps even lead to proper derivation of metabolic rates in relation to mechanical work.

There is extensive literature on the use of bird heart beat frequency (often termed heart rate) as a measure of energy expenditure (*e.g.* Owen, 1969; Butler and Woakes, 1979; Butler, 1993) and it appears that the cloacal sensor described above (Table 1) can be used for this purpose too. One major advantage of the Hall sensor-magnet sensory system is that it is extremely sensitive to minute changes in sensor-magnet distance if the magnetic field strength is appropriate. Examination of data derived from free-living Magellanic penguins shows that the cloacal sensor not only shows a highly regular change in output values associated with breathing, the latter being defined by the IMASEN (Fig. 6), but also a rhythmicity that correlates in frequency well with that expected for penguins of this size (Green *et al.*, 2003) and for Magellanic penguins in particular (Regel, 1997). Interestingly, although the beak angle does not change with each breath when metabolic rates are particularly low (Fig. 6) because enough air can be inspired through the nares (Wilson *et al.*, 2003) the cloacal sensor continues to show breathing patterns (Fig. 6). Examination of the output of the cloacal

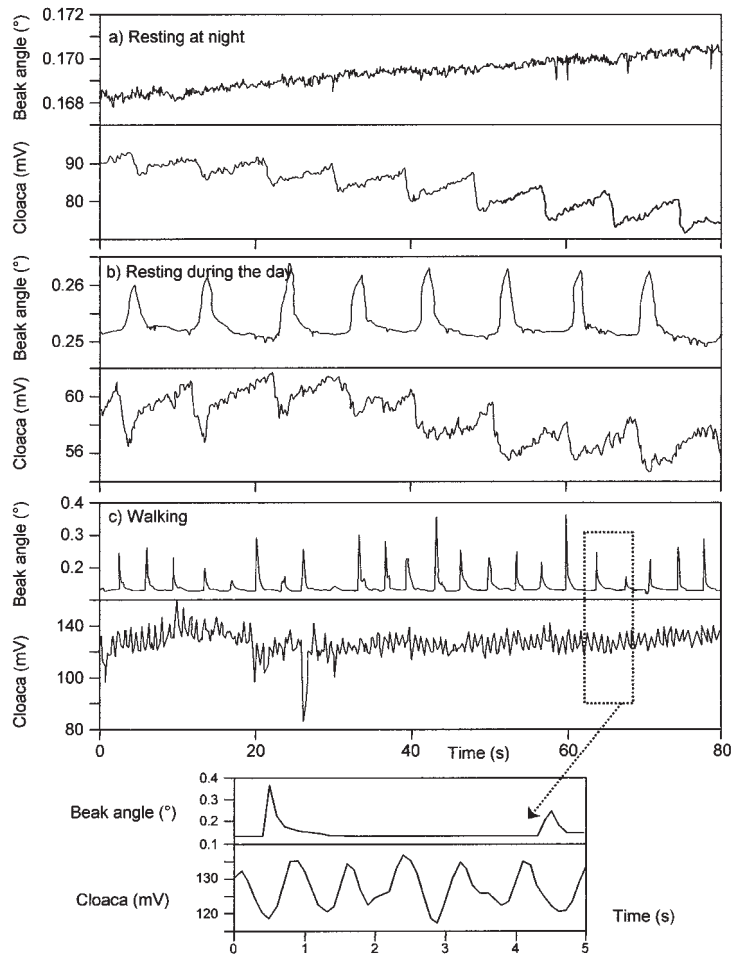


Fig. 6. Beak and cloaca movements during different behaviours on land as determined by a Hall sensor and magnet system recording at 10 Hz (see text) deployed on a Magellanic penguin (the same bird whose beak and cloacal data are shown during diving in Fig. 4). The upper figure (a) shows no apparent change in beak angle during normal breathing while resting at night although breathing patterns are obvious in the cloacal movement. Note here that the bird did slowly, and very slightly, open its beak over the 80 s measurement period and this ties in with a general decrease in voltage from the cloacal sensor. In the centre figure (b) the same bird resting during the day shows distinctive peaks in beak angles (maximum change per breath $< 0.02^\circ$) due to breathing which are mirrored in movement of the cloaca. The lower figure (c) is taken from the same bird during walking and shows greater changes in beak angle per breath (maximum change per breath $< 0.2^\circ$) and a higher respiration frequency than during resting. The inset shows how the cloacal sensor also appears to be giving data on heart rate. Note how the data on breathing frequencies and beak angles compare to those incurred during periods at sea (Fig. 4).

sensor shows that it is subject to noise from a number of sources such as a tail movement during walking (Fig. 6), defaecation (Fig. 4) or sudden tail movements (see periods immediately prior to surfacing (Fig. 4, top)). That the heart beat frequency is not apparent in the surface periods in our data may be due to the set recording frequency of 10 Hz simply being too low.

During diving the heart beat frequency is of the order of 50–70 bpm (Green *et al.*, 2003) which means that the wave form may be reasonably defined by 7 or 8 values (Fig. 4) but foraging penguins undergo substantial tachycardia at the surface where heart beat frequencies reach *ca.* 140 bpm (Green *et al.*, 2003) so that the periodicity will not be apparent. Further work with cloacal sensors recording at least 20 Hz is necessary to confirm this. Despite these misgivings, the cloacal sensor shows much promise as a system for accessing many internal events in free-living animals and its potential use as a system for determining heart beat frequency may partially obviate the rather onerous implantation (*e.g.* Bevan *et al.*, 1995) or subdermal sensory systems (*e.g.* Regel, 1997) used to date.

Future perspectives

There is little doubt that the solid-state industry will continue producing more spectacular sensors and memory chips for some time to come so that remote-sensing technology for free-living animals will be correspondingly more powerful while being further miniaturized. The immediate benefit will be that units will be able to record at higher frequencies for longer periods whilst impeding the carrier less so that units such as the IMASEN and IMASU can be worn for periods extending to perhaps months. Over the last two decades there has been a primary emphasis on elucidating the position of whole animals, be it via depth (*e.g.* Kirkwood and Robertson, 1997) or position (*e.g.* Bost *et al.*, 1997). Now that the use of accurate systems for determination of animal position, such as GPS, has become more commonplace, it is likely that there will be a concentration on body movements such as of the flippers, head and jaws via Hall sensors or perhaps solid-state compasses. Simultaneously-logged information on the environment such as with temperature (Weimerskirch *et al.*, 1995), salinity (Lydersen *et al.*, 2002) or light (Wilson *et al.*, 2002a) coupled with cameras (*e.g.* Davis *et al.*, 1999) will allow the study animals and their precise movements through the waters to be reconstructed and displayed using virtual reality concepts. Such visualization techniques can be combined with on-screen flags to indicate physiological parameters such as heart beat frequency so that ultimately we will finally be able to visualize, in more than 3 dimensions, what our study animals do when they disappear beneath the waves.

Initially, the lack of technology dictated that research on the marine ecology of air-breathing animals be highly focussed on rather narrow aspects, rather than considering the wider perspective. This was particularly the case with regard to depth use. However, the plethora of new systems for studying various aspects of animal behaviour and physiology at sea is now leading to a corresponding multifaceted understanding of these creatures. For example, it has become apparent in penguins that flipper beat frequency and amplitude affect swim speed and energy expenditure but that both these are dependent on depth and the amount of air inhaled prior to diving. Energy expenditure, which is mirrored by heart beat frequency, is also affected by the dive angle. The latter variable determines the time that the penguin spends at the various depths within the water column, and this affects the chances of encountering prey, according to the depth distribution of the prey. Since the amount of oxygen that penguins can take underwater with them is limited by oxygen-bound in the blood and muscles and in the amount inhaled, inappropriate use of energy can result in inefficient foraging and reduced prey capture success. The decision made by the bird as to how fast to swim and how much to inhale as well as to which dive angle should be adopted is critical. This simplified example can already be much more expanded and shows the inter-dependence of the fea-

tures that are being studied today. Definition of the animal hardware (blood oxygen stores, the relationship between energy expenditure and speed under varying conditions of buoyancy, etc.) combined with meticulous study of the associated software (behavioural patterns that are likely to be relatively hardwired but, for reasons of complexity, currently seem inaccessible) should allow us to be more holistic in our approach so that we understand the programmed entity that is the penguin. Understanding based on these principles should allow us to predict what our study animals will do if we are given the environmental conditions to which they might be exposed. This understanding will make our job as guardians of marine systems much easier and is a far cry from the simple observations of yesteryear.

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