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Lip-reading in remote subjects: an attempt to quantify and separate ingestion, breathing and vocalisation in free-living animals using penguins as a model

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Abstract A new mandibular sensor is presented here based on the use of a Hall sensor, attached to one mandible, opposite a magnet, attached to the other mandible. Changes in sensor voltage, proportional to magnetic field strength, and thus inter-mandibular angle, are recorded in a logger. This system was tested on seven captive Adélie penguins (*Pygoscelis adeliae*) and three gentoo penguins (*Pygoscelis papua*) during: (1) feeding trials on land, where birds were given known quantities and types of food; and (2) trials in water where birds were allowed to swim and dive freely. In addition, six free-living Magellanic penguins (*Spheniscus magellanicus*) were equipped with the system for single foraging trips. Angular signatures were looked for in instances when both captive and free-living birds might open their beaks, and it was discovered that five major behaviours could be identified: ingestion, breathing, calling, head shaking and preening. Captive feeding trials showed that prey mass could be determined with reasonable accuracy ($r^2=0.92$), and there was some indication that prey type could be resolved if recording frequency were high enough. Vocalisations in Adélie penguins (arc calls) took <0.7 s for mean maximum beak angles of 4.2° (SD 1.3), and were distinguished by their relatively gradual change in beak angle and by their high degree of symmetry. Beak shakings were distinguishable by their short duration (multiple peaks of

<0.5 s) and minimal maximum angle ($<0.5^\circ$). Preening behaviour was apparent due to multiple decreasing peaks (angles $<8^\circ$). Breathing could be subdivided into that during porpoising, where a characteristic double peak in beak angle was recorded, and that during normal surface rests between dives. During porpoising, only the primary peak (mean maximum beak angle 25.1° , SD 4.7) occurred when the bird was out of the water (mean maximum for second peak 5.9° , SD 4.1). During normal surface rests in free-living birds, breaths could be distinguished as a series of beak openings and closures, showing variation in amplitude and frequency according to an apparent recovery from the previous dive and preparation for the subsequent dive to come. The mandibular measuring system presented shows considerable promise for elucidating many hitherto intractable aspects of the behaviour of free-living animals.

Introduction

The necessity for the quantification of ingestion rates in endotherms has been apparent for many years, since studies such as those involving energy flow between systems (Elton 1927), impact on resources (e.g. Lindeman 1942) and optimal foraging decisions (e.g. Krebs 1978) ultimately depend on such data. In species that cannot be observed foraging this is problematic. The case of marine endotherms is a particularly intractable example of this, and consequently a number of workers have been attempting to resolve this by development of logging systems that are attached to free-living animals recording some physical aspect that is related to feeding. To date, systems have involved recording of stomach temperature, since when endotherms feed on ectothermic prey the stomach temperature drops (e.g. Wilson et al. 1992, 1995b; Gales and Renouf 1993; Grémillet and Plös 1994), oesophageal temperature drops (e.g. Ancel et al. 1997) and jaw muscle movement (Bornemann et al. 1992; Plötz et al., in press). All these systems

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have their advantages and disadvantages (see e.g. Wilson et al. 1995b; Ancel et al. 1997; Handrich et al. 1997; Ropert-Coudert et al. 2000), one particular problem being the fine resolution of prey ingestion.

In the present paper, we document preliminary experiments on the use of a system for measuring inter-mandibular angle based on a Hall sensor, for determining magnetic field strength, on one mandible, opposite a magnet, on the other mandible. Movement of one mandible with respect to the other causes a change in magnetic field strength experienced by the sensor so that, after calibration, inter-mandibular angle can be determined. This system was tested on captive and free-living penguins, and not only has potential for determining the frequency with which prey items are ingested but also has potential for helping determine the food mass and prey type ingested, as well as the frequency of vocalisations and some aspects of respiration.

Materials and methods

Technology used

The beak sensors used consisted of a small, rare earth magnet (neodymium boron; Vacuumschmelze, Hanau, Germany), which was used to produce a magnetic field. The strength of this field was detected by a Hall sensor (KSY 10, Siemens) fitted to a logger (DKLOG 600 series, Driesen and Kern, Bad Bramsted, Germany). The loggers had flash RA memories that varied in size between 500 kb and 1.5 Mb and were either hardware configured to record at a frequency of 7 Hz or could be programmed to record at any frequency up to 30 Hz. Both units had 16 bit resolution and were powered by 3.6 V lithium batteries. Loggers were potted in resin (maximum dimensions of 133×19×25 mm) and shaped hydrodynamically following suggestions in Bannasch et al. (1994). The sensor was also potted in resin (minimum dimensions 6×3×2 mm) and linked to a cable (diameters varying between 0.8 and 2.3 mm, length 350 mm), which exited from the front of the device, the exit being properly waterproofed using Guronic (Paul Jordan, Berlin, Germany) around the base of the cable.

In normal deployment, the magnet was glued to one mandible (beak) and the Hall sensor to the other, being careful to orient the sensor so that it directly faced either the south or north pole of the magnet (Fig. 1). In the normal situation, with the mandibles closed, the magnetic field at the sensor was maximal, being recorded as such by the logger. However, when the mandibles were opened the magnetic field strength at the Hall sensor decreased due to increased distance between magnet and sensor, resulting in a drop in voltage recorded by the logger. The relationship between Hall sensor voltage and inter-mandibular distance (or angle) was determined using wooden doweling of known diameter to separate the mandibles, all voltages being subsequently converted into angles for treatment. The logger associated with the Hall sensor was fixed to the mid-line of the birds' backs using tape (Wilson et al. 1997), being careful to ensure that it was placed caudally so as to minimise hydrodynamic drag (Bannasch et al. 1994).

Free-living birds equipped with beak sensors were also fitted with small depth gauges. The units, Lotek time-depth recorder tags (TDRs; LTD 100, Lotek Marine Technologies, St. John's, Newfoundland, Canada) measured 18 mm in diameter×56 mm long were set to record depth (resolution better than 0.3 m) continuously at 1 s intervals in a 1.5 Mb memory. Information was downloaded via interface directly onto a computer at the site. Devices were attached to specially constructed plastic leg rings, tailor-fitted to the birds in question.

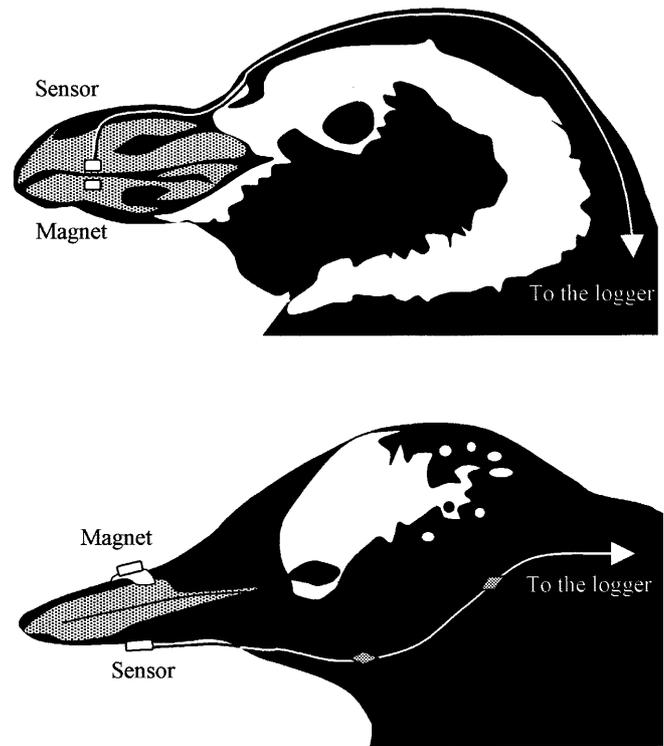


Fig. 1 *Spheniscus magellanicus*, *Pygoscelis adeliae*. Schematic diagram of the manner by which the IMASEN was attached – upper panel: to free-living Magellanic penguins during field trips in Argentina; lower panel: to *Pygoscelis* penguins in captivity in Nagoya, Japan

Work on captive penguins

A total of seven captive Adélie penguins (*Pygoscelis adeliae*) and three gentoo penguins (*Pygoscelis papua*) was fitted with the immediate mandibular angle sensor (IMASEN) at the Nagoya Public Aquarium in Japan on 13 and 14 March 2000. For this application, magnets (3×6 mm diam.) were attached to the dorsal surface of the upper beaks, at the point where the feathering began, using cyanoacrylate glue (Loctite) and holding the magnet in place initially with waterproof tape until such time as the glue had bonded. The sensor was then glued in a similar manner to the lower beak, again on the feathering, at a point opposite that of the magnet. For this short-term deployment (no bird was left with the system in place for > 3 h), the cable was set to run under the jaw line and over onto the back, being held in place by attaching it to a few feathers using waterproof tape (Fig. 1 – lower diagram). The logger itself was held in place using tape and an attachment methodology similar, though less extensive, to that documented in Wilson et al. (1997).

Two of the equipped Adélie penguins were then released within the penguin exhibit at Nagoya Public Aquarium, an area consisting of some 25 m² of snow and ice landscape and a pool of 21×4×2.2 m. Air temperatures were of the order of –2°C, while water temperatures were 6.4°C. The birds were allowed to move freely and soon entered the water with the other birds (there were 95 penguins in the exhibit at the time, consisting of six emperor (*Aptenodytes forsteri*), 49 gentoo, 8 chinstrap (*Pygoscelis antarctica*) and 32 Adélie penguins. At this time birds were filmed using a digital video camera, recording 30 images per second and synchronised exactly with the loggers, the time being displayed on the recorded image. Additional comments were also made acoustically on the tape. During the periods in and out of the water, careful documentation was made of all activities that might be associated with beak opening, such as breathing after dives, calling, etc.

After feeding had ceased and the birds settled down again on land, they were recaptured and the sensors calibrated by holding

pieces of wood of known diameter in the beak at a defined distance from the articulation, while the loggers continued recording the Hall sensor outputs. Units were then removed, and data downloaded onto computer by connection with an appropriate interface. Subsequent inspection of the video film allowed us to identify the exact times when prey were ingested or when birds breathed, preened or called, and to isolate these events from the data recorded by the loggers.

After equipment with the beak sensors (see above), five other Adélie penguins and three gentoo penguins were sequentially offered prey of different sizes and shapes on land. Prey types offered were: Antarctic krill (ca. 40 mm long with an approximate mass of 0.6 g), first-year sandlance (*Ammodytes personatus*) (ca. 80 mm long with an approximate mass of 2 g), second-year sandlance (ca. 230 mm long with an approximate mass of 60 g), capelin (*Mallotus villosus*, ca. 160 mm long with an approximate mass of 30 g) and greenling (*Hexagrammos azonus*, 230 mm long with an approximate mass of 160 g). In approximately 20% of the cases, a number of body morphometric parameters were taken, these being fish fork length (L) (or total body length in krill), body depth at 0.25, 0.5 and 0.75 L and body width at 0.25, 0.5 and 0.75 L. As in the birds fed in the water, the birds were filmed continuously during the feeding process and at that time the sensors were calibrated.

Work on free-living penguins

The field work was conducted between 24 November and 15 December 2000 at two sites: Cabo Virgenes (52°24'S; 68°26'W), a large Magellanic penguin (*Spheniscus magellanicus*) colony (ca. 160,000 birds) abutting the Straits of Magellan; and Isla Cormoran (49°17'S; 67°43'W), a colony of some 40,000 birds at Bahia San Julian. All equipped birds were breeding and tending for chicks at the time. Penguins were equipped with devices in two phases. Firstly, at Cabo Virgenes, potentially deleterious effects of the magnet (cf. Gudmundsson and Sandberg 2000) were examined by equipping a total of five birds only with magnets. These (3×2×1 mm) were glued, using two-component epoxy, to the upper beak, about 20 mm from the tip laterally, and left in place for at least one foraging trip. Having ascertained that no differences were apparent between these and control birds, a single bird was equipped. Here, the magnet was attached as described above, but, in addition, a Hall sensor (as part of an IMASEN) was glued, with epoxy, to the lower beak. The cable leading to the logger (0.8 mm diam.) was run between the feathers underneath the head to the nape of the neck before running directly down to the logger placed on the bird's back (Fig. 1 – upper diagram). The logger was attached using tape, as described in Wilson et al. (1997), to the bird's lower back, and the cable was held in place underneath the feathers by gluing single feathers on either side of the cable together using a spot of Loctite. This created a bridge under which the cable could move freely if the bird extended its neck.

Five other Magellanic penguins were also equipped with IMASENs. These birds were both at San Julian (two birds) and Cabo Virgenes (three birds) and differed from the captive birds in that the magnet was attached to the lower beak (laterally and about 20 mm from the tip), while the Hall sensor was attached (laterally) to the upper beak (Fig. 1 – upper diagram). The cable was glued with epoxy to the dorsal surface of the beak, being covered with a thin film of glue and lightly marked with indelible marker so as to accord better with the original colours of the bill. The cable was then run between the feathers directly over the head and down the back to the loggers taped in place on the lower back. Again, glue bridges were made so that the cable could not be seen and would allow the bird to move without being hindered. For periods of up to 30 min, the equipped birds were observed to determine whether there was any evidence that the animals were stressed by or attempting to remove the units. Units were recovered after birds returned from one foraging trip.

All loggers deployed on Magellanic penguins were set to record data at a frequency of 10 Hz, giving a maximum recording life of about 28 h before the memory was full.

Results

Captive penguins on land

No equipped bird appeared to be obviously and extensively irritated by the beak sensor, although the cable linking the Hall sensor to the logger located on the birds' backs was quite thick (2.3 mm diam.). During an interval when no people were present in the pen, one of the birds fed on land pecked briefly at the logger (at the point where the cable exited) and a single bird in the water preened the same area intensively for > 10 s. Other than this, all birds behaved in a manner that appeared to be identical to that of other birds in the exhibit. Nine of the birds equipped with beak sensors fed on the prey items provided, while one bird (an Adélie penguin fed by hand on land) refused to feed. The bird that ate most on land was an Adélie (Adélie "BL"); it ingested a total of 21 prey items, ranging in size from krill weighing 0.5 g to sandlance weighing 240 g during three separate feeding sessions. These three sessions will be considered in detail below. Adélie "BL" also attempted to swallow two greenling, weighing 225 and 230 g, respectively, but rejected these after having tried to ingest them for over 30 s. A further three items were spat out, apparently because their orientation in the beak was inappropriate for ingestion. In all birds, prey ingestion events ($n=108$) always produced marked changes in Hall sensor voltage, which, when transformed into a beak angle on the basis of calibrations (e.g. Fig. 2), manifested themselves as radical departures from the norm (Fig. 3a).

Detailed examination of the changes in beak angle during prey ingestion showed that the general pattern was for the angle to gradually increase to a maximum (within a time range of between 0.3 and 3.0 s) before decreasing again (Fig. 3b). Over-sized prey were held in

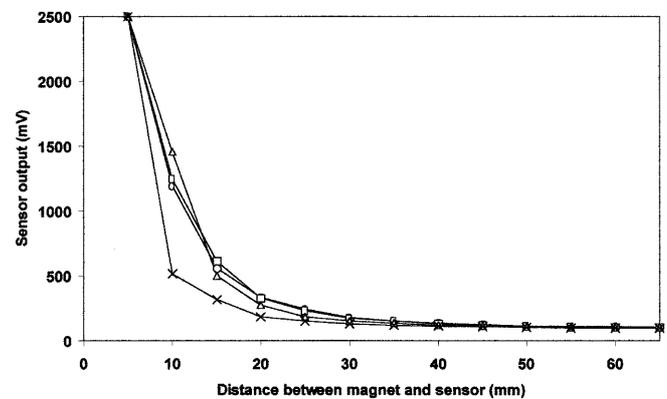


Fig. 2 *Pygoscelis adeliae*. Relationship between voltage produced by a Hall sensor and distance between sensor and magnet for a system in which the North pole of the magnet lies directly parallel to the sensor (line with circles) and in which the North pole of the magnet lies at various angles to the sensor; 30° (line with squares), 45° (line with triangles) and 60° (line with crosses). The value of 2,500 mV shows full scale deflection by the sensor

the buccal cavity for extended periods, during which time birds attempted to swallow them in a series of gulps while the beak was opened to facilitate ingestion. These gulps were clearly visible as changes in beak angle recorded by the logger (Fig. 3c).

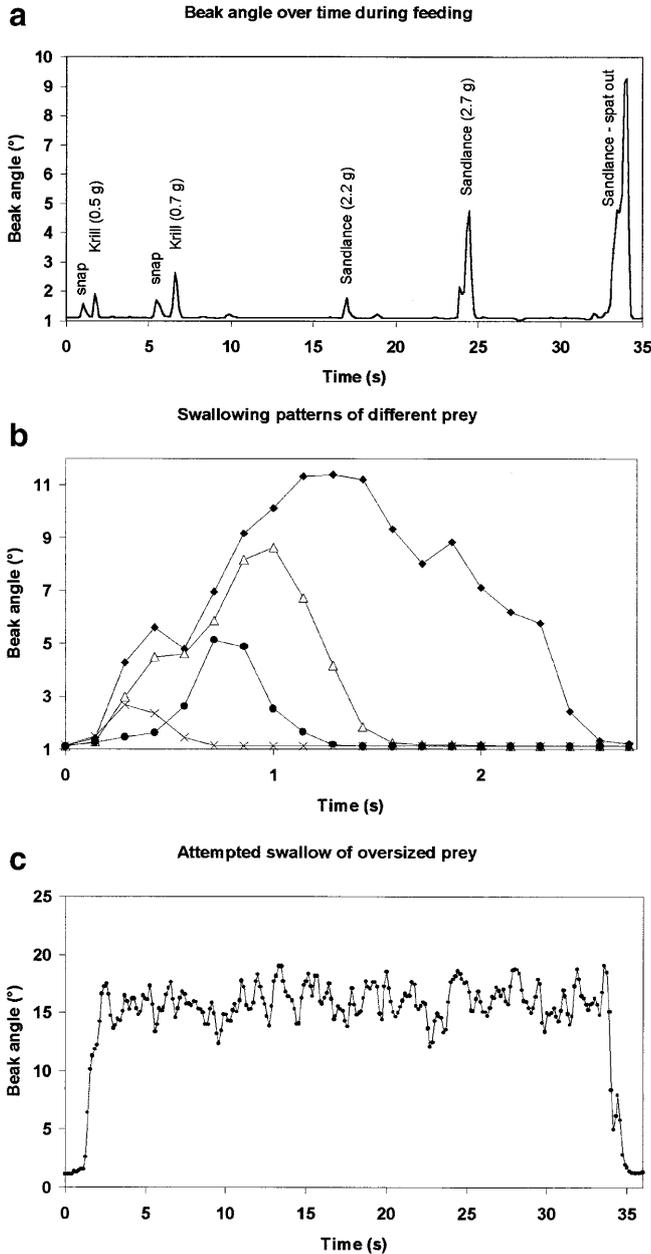


Fig. 3a–c *Pygoscelis adeliae*. **a** Example of data on the inter-mandibular angle (*beak angle*) from a captive Adélie penguin being fed by hand on sandlance and krill. **b** Examples of changes in beak angle in a captive Adélie penguin over time as a function of prey type and size. *Line with crosses* shows ingestion of krill (0.7 g); *lines with circles, triangles and diamonds* show first-year sandlance (3.2 g), capelin (40 g) and second-year sandlance (65 g), respectively. Recording frequency of the IMASEN was 7 Hz. **c** Example of beak angle from an Adélie penguin attempting to swallow a greenling weighing 225 g. Gulps are apparent as irregular peaks. This fish was rejected after the bird had attempted to swallow it for some 33 s. Recording frequency was 7 Hz

During recording of beak angles at high frequencies (25 Hz), the high temporal resolution made it apparent that particular prey types produced particular patterns of bill angles over time, brought about by the necessity of swallowing differently shaped prey. For example, gentoo penguins swallowing large (ca. 170 g, 230 mm long) greenling invariably made an initial snap at the prey, after which they rested for between 1 and 2 s before opening the beak further to let the widest part of the fish pass the rictus; subsequently the beak was slowly closed during obvious gulping movements (Fig. 4). Eel-shaped sandlance (ca. 80 g, 240 mm long), however, were swallowed without an obvious initial snap, although there was a period of almost 1 s while the head and anterior part of the fish were swallowed; after this period the rest of the body was ingested with repetitive

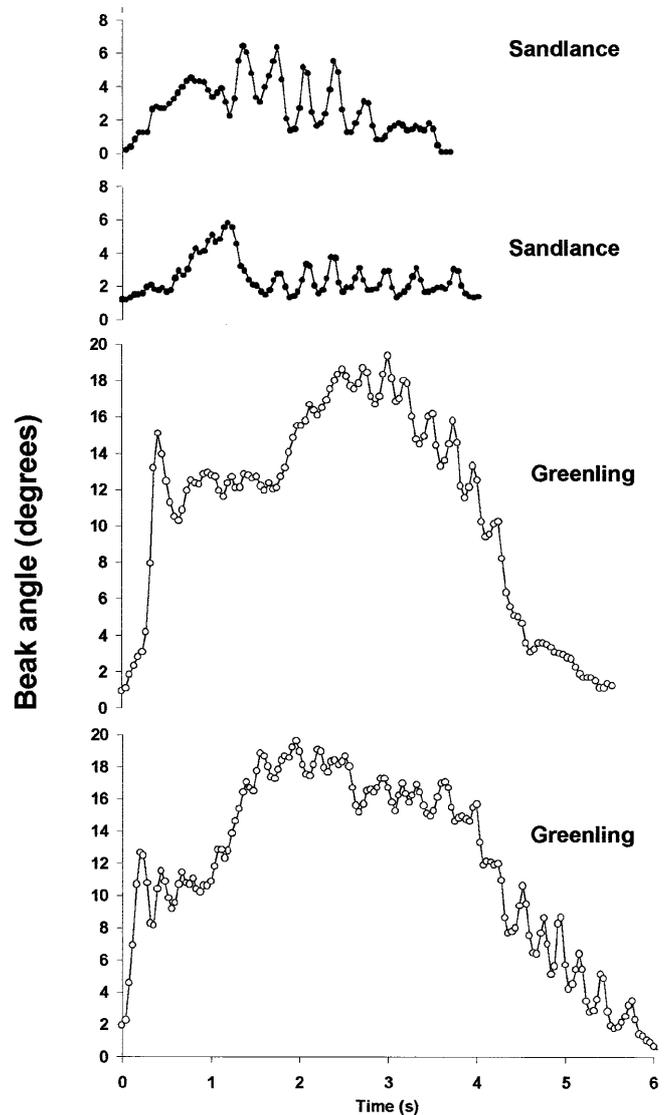


Fig. 4 *Pygoscelis papua*. Characteristic patterns in beak angle over time in gentoo penguins ingesting prey of different shapes. *Closed circles* refer to data obtained while the birds were swallowing sandlance; *open circles* refer to greenling. Recording frequency was 25 Hz

gulping motions, during which beak angle changed little (Fig. 4). In keeping with prey shape and size, the Adélie penguin “BL” took longer overall to swallow heavier prey ($Time = 0.028Mass + 1.16$, $r^2 = 0.75$, $F = 47.6$, $P < 0.0001$) (Fig. 5a) and also required more time to swallow longer prey ($Time = 0.01Length + 0.5$, $r^2 = 0.85$, $F = 88.0$, $P < 0.0001$) (Fig. 5b). Maximum beak angle was also greater for heavier ($Angle = 0.136Mass + 3.31$, $r^2 = 0.82$, $F = 71.2$, $P < 0.0001$) (Fig. 5c) and longer prey items ($Angle = 0.47Length + 0.43$, $r^2 = 0.81$, $F = 69.6$, $P < 0.0001$) (Fig. 5d). Overall, the best indicator of prey mass was the integral of the area under the beak angle curve over time ($Integral = 1.36Mass + 2.5$, $r^2 = 0.92$, $F = 185.1$, $P < 0.0001$), although there was considerable scatter around the line of best fit for the small prey items (Fig. 6).

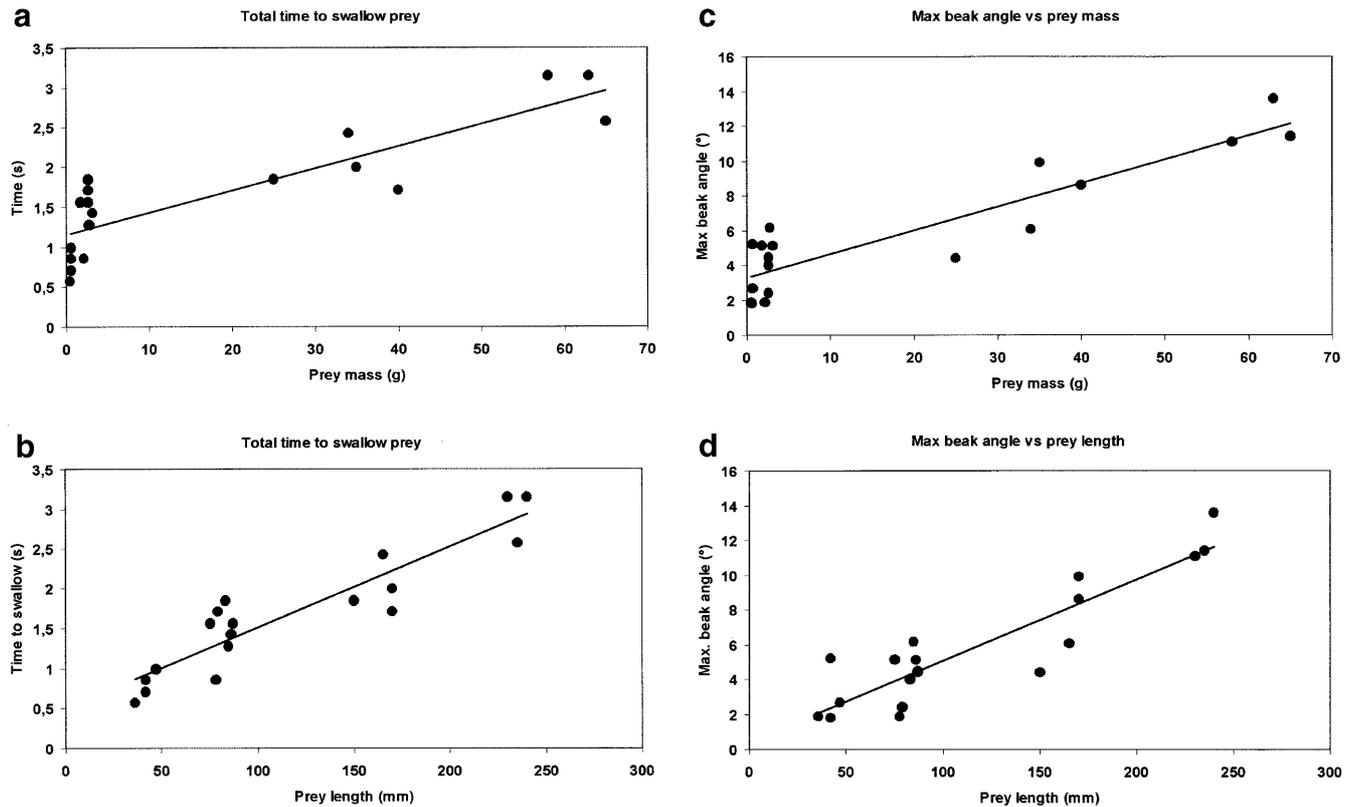
Other than for ingestion purposes, birds opened their beaks for four other reasons: (1) to vocalise (the “arc” call, cf. Ainley 1983), when, in Adélie penguins, beak angles were up to a maximum of ca. 6° (mean = 4.2° , SD 1.34, $n = 7$), but these events were characterised by being short (< 0.7 s) and were symmetrical (Fig. 7a). In gentoo penguins, calls were much more extended and took the form of braying. Here, beak angles could extend to up to 20° for several seconds. (2) Birds also occasionally shook their heads, possibly to remove liquid from salt glands. Here beak angles were minimal, being opened $< 0.5^\circ$ above the norm (ca. 1.5°) (Fig. 7b). (3) Birds also opened their beaks to preen. Preening birds had a clear beak-opening pattern, consisting of rapid bill openings (up to values of 8°) followed by

slower closings. Peaks in bill openings consisted of series with decreasing maximum values (Fig. 8a). (4) Finally, birds also opened their beaks to breathe. This happened once in the bird fed on land and will be covered in more detail below in connection with swimming and diving birds.

Captive penguins in water

Penguins in the tank engaged in two major activities that involved beak opening: preening (see above) and diving. Patterns of breathing between dives were either normal breathing during rests of ca. 3 s at the surface, or, more usually, brief forays into the air, where birds exchanged gases during porpoising. During porpoising, beak openings associated with breathing left a characteristic pattern consisting of a single, virtually symmetrical, high peak, lasting for about 0.4 s, the entire time that the birds’ beaks were out of the water (Fig. 8b). Mean beak angle at this time was 25.1° (SD 4.7, $n = 46$). This first peak was invariably followed by a second, similar,

Fig. 5a–d *Pygoscelis adeliae*. For data obtained by a particularly voracious feeder, Adélie penguin “BL”, the relationship between total time spent in prey swallowing and **a** prey mass, **b** prey length; and the relationship between maximum beak angle and **c** prey mass, **d** prey length. Two prey items which the bird caught improperly and was forced to juggle with extensively before swallowing, and one taken when the bird was so full at the end of the feeding session that it was unable to close its beak, have been omitted. Recording frequency of the IMASEN was 7 Hz



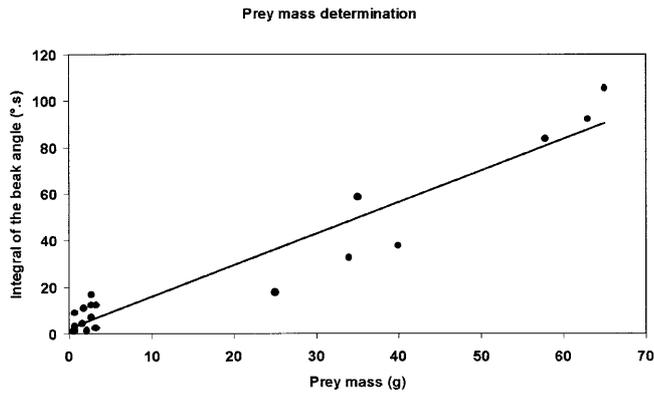


Fig. 6 *Pygoscelis adeliae*. Relationship between the integral of the area under the beak angle curve during prey ingestion and prey mass for an Adélie penguin (“BL”; see Fig. 5) feeding on prey from a variety of species (see “Materials and methods”)

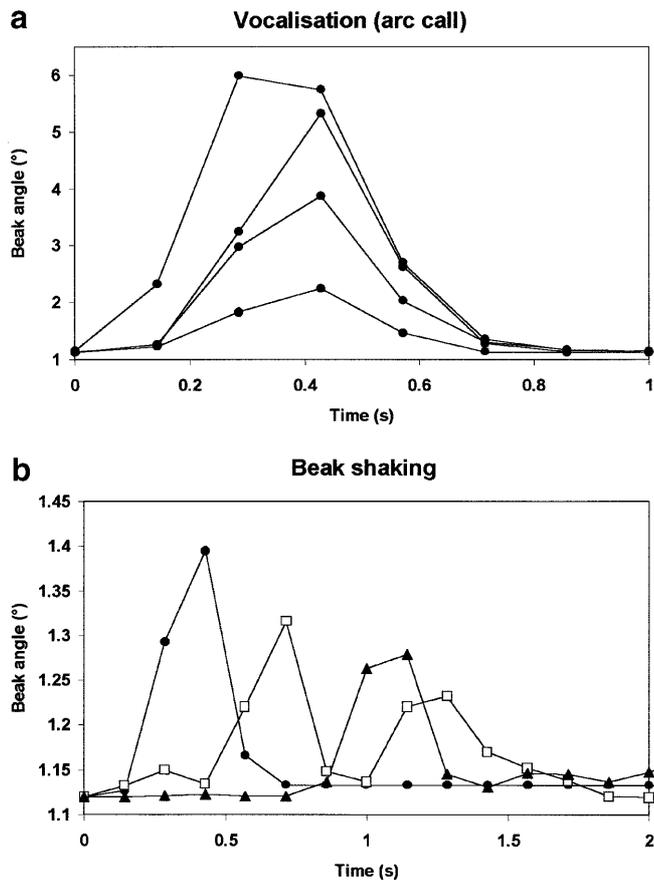


Fig. 7a,b *Pygoscelis adeliae*. **a** Changes in beak angle over time in Adélie penguins executing arc calls. **b** Changes in beak angle over time in Adélie penguins engaged in bill shaking. For ease of interpretation, the different events have been given different symbols. Both diagrams in this figure are derived from data recorded at 7 Hz

though smaller peak (mean = 5.9°, SD 4.1), when the bird’s head was underwater (Fig. 8b). During continuous porpoising behaviour there was no significant relationship between dive duration and the extent of

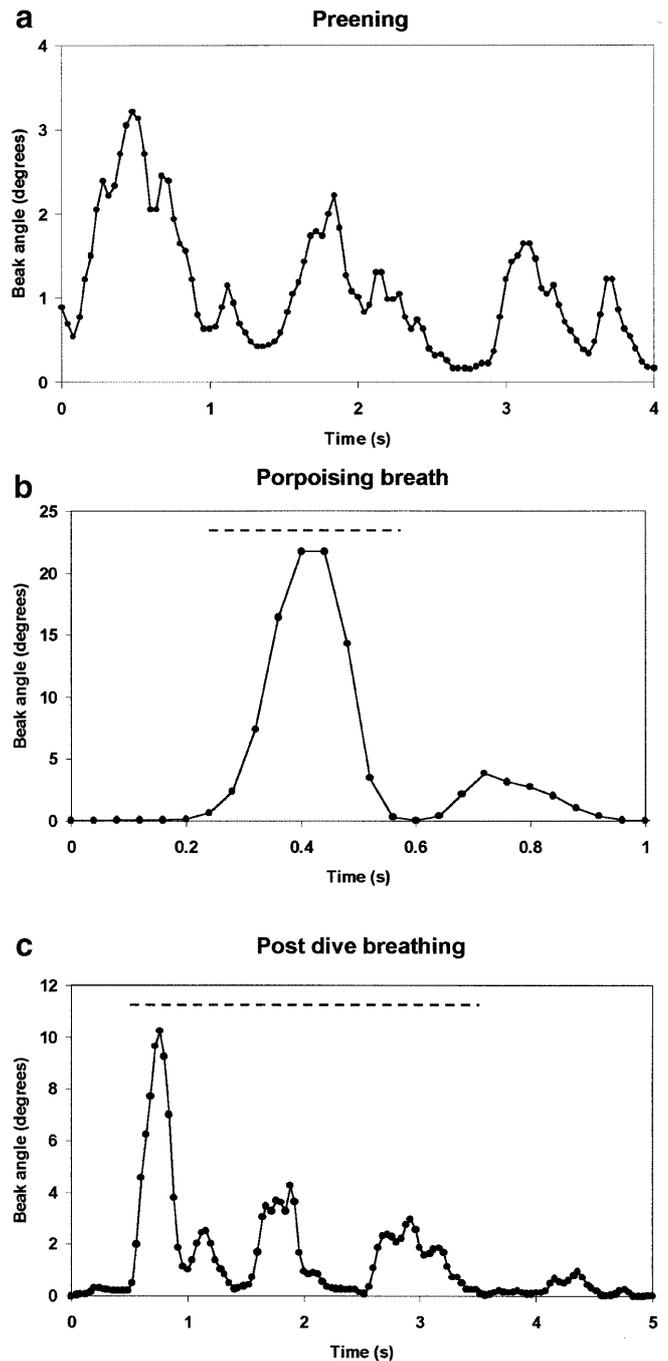


Fig. 8a–c *Pygoscelis adeliae*. **a** Changes in beak angle over time in a preening Adélie penguin in a tank. The logging unit was set to record at 25 Hz. **b** Changes in beak angle over time in a captive Adélie penguin during a period when the bird exited the water to breathe (*dashed line*) during porpoising. The logging unit was set to record at 25 Hz. **c** Change in beak angle over time in a captive Adélie penguin during a 3 s rest period at the surface (*dashed line*) between dives. The logging unit was set to record at 25 Hz

beak opening in the subsequent breathing event ($r^2 = 0.00$, $F = 0.2$, $P = 0.65$), although there was a weak, but significant, relationship between the extent of beak opening and the following dive duration according to $beakangle = 0.19 \times diveduration + 22.5$ ($r^2 = 0.1$,

$F = 5.16$, $df = 44$, $P < 0.05$). In the limited cases where we observed normal breathing at the surface between dives ($n = 5$), the individual breaths could be identified in the changing beak angles, which took on a distinct wave form (Fig. 8c, cf. Fig. 8b), with these waves being apparent as a series of decreasing peaks. Breaths taken in this manner had a cycle that was approximately twice as long as the breaths taken during porpoising, when time in the air was limited, although maximum beak angles were lower (cf. Fig. 8b,c). Following immersion, a smaller peak was observed, similar to that displayed after porpoising breaths (Fig. 8c).

Free-living penguins

No equipped Magellanic penguin was observed to be stressed by the beak sensors and at no time were they observed to peck at the unit while on land. Despite this, a bird equipped with the beak system at Cabo Virgenes during 1999 returned after 24 h having removed the magnet, the Hall sensor, the cable and the logger. The original glue was also found to be inadequate in this regard and was changed for another type (Devcon) in the following deployments.

Both birds equipped at San Julian during 1999 returned complete with their systems, but both had bitten through the cable connecting the Hall sensor with the logger at the spot where the cable exited from the logger. We do not believe that the cable snapped due to neck extension since plenty of slack was left in the cable during equipment to allow for this. One of the loggers had no data in it due to unit malfunction, while the second had data for a total of 14 h until the bird bit through the cable. Since the unit was not calibrated on the bird before deployment (see above), it proved impossible to convert observed changes in Hall sensor voltage into beak angle. All three birds equipped at Cabo Virgenes during December 2000 returned with their IMASENs fully intact, having logged data for the full duration of the foraging trips. These birds had fed extensively as evidenced by their protruding stomachs, fresh guano and fed chicks (Table 1).

The Cabo Virgenes birds all showed similar patterns in beak opening activities, which could be best interpreted by reference to the TDRs and known patterns elucidated by studying the birds in captivity. For the following we restrict ourselves to documentation of activities of birds at sea. At this time two major patterns

were apparent: beak openings, which we assumed to be indicative of prey capture and ingestion which always occurred underwater and beak openings due to breathing which occurred at the surface (Fig. 9). Prey ingestion almost invariably took place during the bottom phase of dives, at times when the rate of change of depth became erratic (Fig. 9). Prey ingestion took between 0.8 and 8 s with maximum beak angles ranging between 5° and 16° (cf. Fig. 10). During ingestion the change in beak angles over time showed patterns that were reminiscent of those displayed by the captive penguins (cf. Figs. 3, 4), in having a variable number of peaks that were presumably

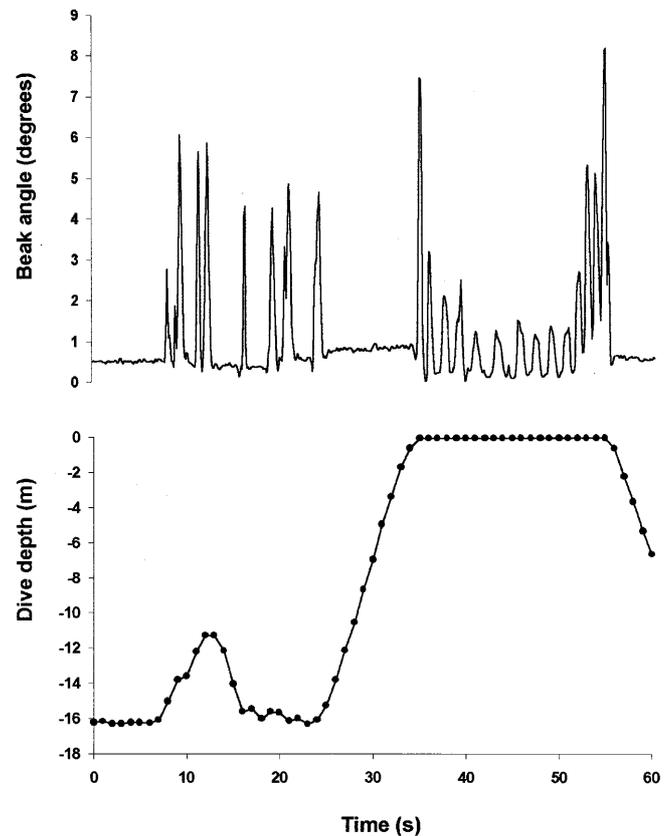


Fig. 9 *Spheniscus magellanicus*. Relationship between beak angle over time and dive depth for a Magellanic penguin foraging near Cabo Virgenes, Argentina, as recorded by an IMASEN logging data at 10 Hz. The lower trace begins with the bottom phase of the dive, showing abrupt changes in depth associated with prey ingestion as evidenced by changes in beak angle (upper trace). The bird then surfaced and engaged in breathing, apparently taking 14 breaths before diving again

Table 1 *Spheniscus magellanicus*. Instrumentation of free-living Magellanic penguins with IMASENs (inter-mandibular angle sensor) and TDRs (time-depth recorders)

Date	Locality	Bird	Hours at sea	Total no. of dives	Hours recorded by IMASEN at sea
Dec 1999	San Julian	George	28	TDR failed	14
		Antje	27	TDR failed	Unit failed
Dec 2000	Cabo Virgenes	Cordola	22.2	880	Unit lost
		Alpha	21.6	951	21.6
		Beta	9.6	365	9.6
		Gamma	23.1	1,706	23.1

due to gulps. Prey, which was often caught in patches, could be captured at rates approaching 1 prey item per second (Fig. 9). During inter-dive periods at the surface, the penguin breathing rhythm could be readily followed by examining changes in beak angle (based on a subsample of 240 dive cycles) (Fig. 11). Immediately upon surfacing, birds apparently inhaled deeply, since the beak was opened by up to 8° over the course of about 0.5 s (that this pattern corresponded to breathing could be ascertained by examining data from an IMASEN-equipped bird on land, which was observed to pant while resting in the sun). Following exhalation, the beak closed almost completely before opening again for the subsequent breath. Typically, the amplitude of beak movement decreased for some seconds following surfacing, while the frequency of ventilation also decreased (Fig. 11). Subsequently, the process was reversed so that both amplitude and frequency increased prior to the next dive. At the end of a dive bout, this increase in amplitude and frequency was not observed, nor was a

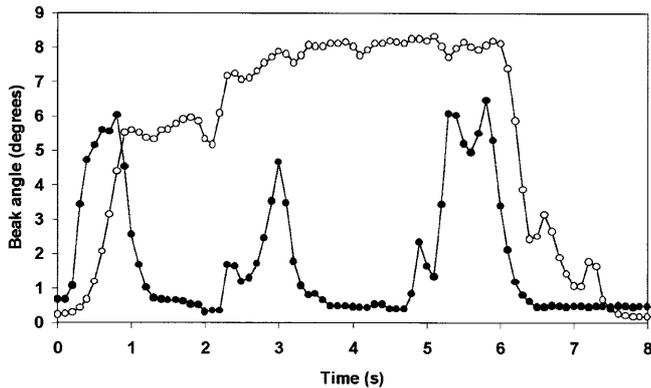


Fig. 10 *Spheniscus magellanicus*. Beak angle in a free-living, foraging Magellanic penguin (see Fig. 9) during putative prey ingestion, as logged by an IMASEN recording at 10 Hz. The data have been pasted together (omitting several seconds of non-ingestion in between swallowing events) to show smaller prey ingested in one, two and three gulps (filled circles) and an apparently larger prey item (open circles) (cf. Fig. 3)

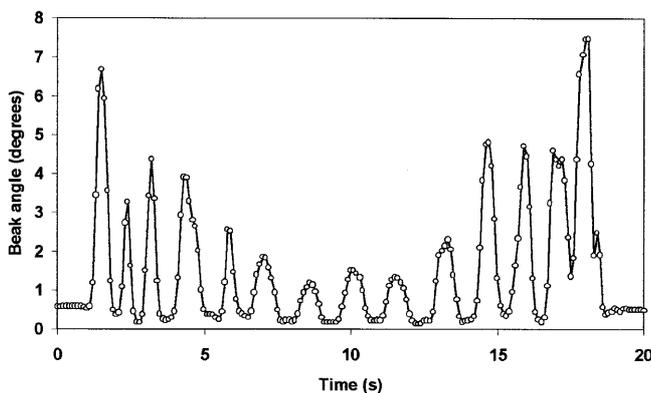


Fig. 11 *Spheniscus magellanicus*. Changes in beak angle over time in a free-living Magellanic penguin during a surface period between dives (see Fig. 9). The IMASEN recorded data at a frequency of 10 Hz

decrease in respiratory amplitude and frequency observed prior to a dive series after an extended period at the surface. In both cases, at this time the bill angle remained stable at a fixed value of about 0.5° .

Discussion

Device effects and system requirements

Despite the apparent insensitivity of penguins to the IMASEN, in both captivity and the wild, the destruction of the units while the birds were at sea (and not observed) augers otherwise. It is not known how much time and effort the free-living birds actually invested in this process, although the bird equipped at Cabo Virgenes clearly must have spent considerable time in removing the unit (see Wilson et al. 1997). Certainly, equipped penguins do peck at attached devices at sea, even if they do not appear to react to them on land (Wilson and Wilson 1989). In the two cases at San Julian, the results are equivocal. We erred on the side of leniency in equipping birds with very powerful beaks (see Wilson and Duffy 1986) with overly thin cables and suggest that a single powerful bite could have severed the connection, which was enough to render the units useless. Future work with this species will rely on having a more robust cable, although clearly a compromise is needed between having a cable that is thin enough to disturb the bird minimally, but thick enough to resist being severed. Other species may be less problematic.

Some species of birds are known to use the earth's magnetic field for orientation (e.g. Gudmundsson and Sandberg 2000; for review see Wehner et al. 1996), although other species are less affected (Papi et al. 2000), so preliminary tests to determine that animals are unaffected by the magnet are important. Theoretically, the potential effect of a magnet on the relevant receptors could be examined by looking at the drop off in magnetic field strength as a function of distance from the magnet (cf. Fig. 2). Subsequently the magnet could be glued to a site that ensures that the distance between the magnet and the receptors is adequate for the magnetic field to drop below background levels. Such a procedure, however, necessitates that the site of the receptors be known, which is not always the case. In addition, for the unit to be effective, certain physical conditions must be fulfilled; a particular, measurable magnetic field strength is required for detection by the Hall sensor and this is dependent on the distance over which the mandibles are likely to move and the sensitivity of the sensor itself. Extremely sensitive sensors are inappropriate because eventually the strength of the earth's magnetic field will become a significant noise factor. The exponential drop off of Hall sensor voltage with increasing distance between sensor and magnet (Fig. 2) means that maximum resolution is achieved when the mandibles are closed, i.e. the distance between sensor and magnet should be at a minimum. Note also that the rate of change of voltage

with distance between sensor and magnet is also dependent on the angle between magnet and sensor (Fig. 2), so that inappropriate angles also compromise accuracy. Given the variability of animal jaw dimensions, the correct emplacement, size and strength of magnets to be used in a mandibular system will have to be determined on a case-by-case basis.

Care should also be taken to reduce background noise (other than biological) recorded by the system. During our study, in which we glued both magnets and sensors to the feathers of the penguins in captivity, noise was produced due to feather movement, particularly during swimming. Clearly, a directly beak-mounted system would have been better, although such a system is more problematic in Adélie penguins than in many other species, since these birds have a well-feathered bill.

Accuracy with which events can be resolved

The system that we used allowed us to distinguish between a number of different behaviours, these being vocalisations, snaps at prey, prey ingestion and breathing. The ability to distinguish between these is critically dependent on recording interval because the ability to determine absolute maximum beak angles and accurate swallowing times depends directly on sampling interval. Based on data presented in Boyd (1993) and Wilson et al. (1995a), where the accuracy with which the shape and characteristics of dive profiles in marine endotherms was examined as a function of the frequency with which depth was logged, we suggest that, for truly accurate determination of bill opening events, the recording frequency should be a maximum of 10% that of the total duration of the event. This condition was not fulfilled in all parameters examined, notably for vocalisations, bill shaking, prey snaps and ingestion of prey < 3 g, for logging units set to record at a frequency of 7 Hz. This may be partially responsible for the poor correlation between the integral of the beak angle and prey mass for prey items < 5 g. An appropriate recording frequency to monitor all treated events would be 20 Hz, since the shortest of these was about 0.5 s.

During deployment of such mandible sensors on free-living animals, it is desirable that other complementary devices be deployed. Simultaneous deployment of, e.g., depth or speed loggers (for penguins) (see e.g. Bost et al. 1997) gives a context for beak-opening events that makes interpretation much easier. Ultimately, however, correct interpretation of mandibular events in free-living animals will be highly dependent on calibrations done on animals in captivity.

Determination of prey mass

It was a major aim of this preliminary work to examine the potential that this beak sensor system had for determination of the mass of prey ingested. While these

initial results are promising, there is still considerable margin for error. This comes in three major forms. (1) A beak opening event might occur that is not associated with prey capture, but be interpreted as such. Penguins might, for example, call underwater, although this is unlikely. The likelihood that this type of error will be detected will depend, to a large extent, on sampling frequency (see above) and the extent to which specific mandible opening behaviours produce specific signatures. Only extensive work on captive animals will allow accurate assessment of this type of error, which, in any event, is liable to vary greatly between species. (2) Where animals feed on particularly small prey, the system may not allow mass to be determined, except to indicate that the prey are small (Fig. 6). Some penguin species, such as those of the genus *Eudyptes*, feed predominantly on small, swarming Crustacea (for reviews see Croxall and Lishman 1987; Williams 1995), and it is thus expected that these birds would be particularly prone to such errors. (3) In the case of animals feeding on large numbers of live prey, such as is the case here, there may be considerable variability in handling time while the prey is being subdued and/or manoeuvred into position for swallowing (see e.g. Meire 1987). While there will perhaps be a general tendency for larger prey to require more handling time, it is quite conceivable that particular prey types may be less easy to manoeuvre than others of a comparable mass (e.g. Goss-Custard 1977). A potential index of this could be gained by looking at the number and amplitude of the peaks occurring before the maximum peak. One difficulty in this is that there are likely to be differences between captive and free-living animals, as well as differences in beak opening patterns, between birds fed prey underwater and those fed prey on land. Inappropriate snaps at prey by birds on land, a wholly unnatural procedure for penguins, increased the variance around the mass-integral curve. Due to the difficulty in relating mass-specific integrals from birds fed dead prey on land to those taking live prey underwater, we consider that exhaustive treatment of land-derived data is not warranted. In the case of many free-living animals, it may be possible to observe the animal feeding and then correct the jaw movement patterns to accord, although this is unlikely to be the case in penguins. Here, perhaps the best solution would be to stomach pump birds (Wilson 1984) and then examine stomach contents in relation to the last recorded movements of the beak sensor, considering that the last ingested prey are likely to be the least digested and the first recovered during the stomach pumping. Certainly, the first prey items recovered during stomach pumping are generally less digested than those recovered later (Wilson, personal observations).

Determination of prey species

Our study shows that changes in beak angle over time can be used to allude to prey type (presumably deter-

mined by fish form) as well as prey mass. The success of this, however, is critically dependent on sampling interval (cf. Figs. 3b, 4). The higher the sampling rate, the more likely a particular species of prey is to reveal a particular species-specific signature. Features that may prove useful in this regard are: the speed at which the bird opens its mandibles up to the initial point of inflection, the speed up to the point of maximum beak angle, the rate of decrease of angle over time after the maximum has been reached and the overall number of gulps. The number of minor peaks before the major swallowing peak (cf. Figs. 4, 10) may be indicative of prey juggling to get it into position before ingestion (and therefore perhaps a measure of prey tractability), while the number of peaks after the major peak, together with the rate of angular decrease, may give information as to the body shape of the prey (Fig. 4). More data are urgently needed to clarify this under more natural conditions than feeding penguins on land.

Deployment of units in the wild

The enhanced sensitivity of the Hall sensor-based system means that very small changes in beak angle around the fully closed position will be particularly well resolved. This makes a beak angle measuring system, such as proposed here, particularly powerful for deployment in free-living animals. One of the most striking features of this is that it enables detailed studies into breathing as well as feeding patterns of penguins. Selection of an appropriately rapid sampling interval has demonstrated that every breath is apparently recorded. Here, beak angle is likely a measure of air intake rate, so that greater beak angles should indicate more rapid, or extensive, air exchange, because according to Poiseuille's equation the rate of volume flow is proportional to the radius of the aperture to the power of 4. Thus, porpoising birds, which have extremely limited time in the air for gas exchange, can maximise oxygen uptake by having large beak angles. When birds simply rest at the surface for extended periods, beak angles can be less and breath cycles longer (Fig. 8b,c). In this regard it is interesting that captive porpoising penguins do not apparently breathe to recover from dives, but rather to prepare for the next period underwater. In non-porpoising, free-living birds, the decrease in amplitude and frequency in breath extent immediately following dives, however, augers clearly for a recovery from that dive. This is also indicated by the few instances of captive Adélie penguins recovering between dives during rests at the surface. That this should be followed by a reversal of the process preceding the next dive in free-living Magellanic penguins suggests, though, that wild birds also prepare for the exercise to come. Such an observation leads to questions related to the extent to which penguins may determine or predict their performance in dives following appropriate (or not) preparation. The potential to be able to separate recovery from prepara-

tion means that previously unclear patterns in ventilation rates and surface durations between dives (e.g. Le Boeuf et al. 2000, and references therein) can be more rigorously approached. Appropriate calibration of beak angle with gas exchange in a laboratory set up may enhance this process still further.

Although our study on mandibular angles in captive and free-living penguins is preliminary, the concept of the IMASEN may prove useful in enhancing our understanding of a variety of important processes in free-living animals by virtue of the specific signatures in mandibular angles associated with different activities. In the case of penguins we have been able to allude to respiration, ingestion, preening, head shaking and calling. Where patterns are equivocal, units to record other parameters may prove helpful. The precise value of the IMASEN for various study requirements will only be apparent, however, after extensive, systematic work. Finally, the small size of the sensory system and its remarkable sensitivity in determining minute movements mean that researchers might benefit in deploying similar systems to determine bodily movements other than those associated with mandibular activity, such as operculum or fin movement in fish.

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References

- Ainley D (1983) Breeding biology of the Adélie penguins. In: Ainley DG, LeResch RE, Sladen WJL (eds) California Press, London
- Ancel A, Horning M, Kooyman GL (1997) Prey ingestion revealed by oesophagus and stomach temperature recordings in cormorants. *J Exp Biol* 200:149–154
- Bannasch R, Wilson RP, Culik B (1994) Hydrodynamic aspects of design and attachment of a back-mounted device in penguins. *J Exp Biol* 19:83–96
- Bornemann H, Mohr E, Plötz J (1992) Registrierung des Fraßverhaltens beim frei beweglichen Tier am Beispiel der freitauchenden Weddellrobbe (*Leptonychotes weddellii*). *J Vet Med Ser A* 39:228–235
- Bost CA, Georges JY, Guinet C, Cherel Y, Pütz K, Charrassin JB, Handrich Y, Zorn T, Lage J, Le Maho Y (1997) Foraging habitat and food intake of satellite-tracked king penguins during the austral summer at Crozet Archipelago. *Mar Ecol Prog Ser* 150:21–33
- Boyd IL (1993) Selecting sampling frequency for measuring diving behaviour. *Mar Mamm Sci* 9:424–430

- Croxall JP, Lishman GS (1987) The food and feeding ecology of penguins. In: Croxall JP (ed) *Seabirds: feeding ecology and role in marine systems*. Cambridge University Press, Cambridge, pp 101–134
- Elton CS (ed) (1927) *Animal ecology*. Macmillan, New York
- Gales R, Renouf D (1993) Detecting and measuring food and water intake in captive seal using temperature telemetry. *J Wildl Manag* 57:514–519
- Goss-Custard JD (1977) The energetics of prey selection by redshank, *Tringa tringa* (L.), in relation to prey density. *J Anim Ecol* 46:1–19
- Grémillet D, Plös A (1994) The use of stomach temperature records for the calculation of daily food intake in cormorants. *J Exp Biol* 189:105–115
- Gudmundsson GA, Sandberg R (2000) Sanderlings (*Calidris alba*) have a magnetic compass: orientation experiments during spring migration in Iceland. *J Exp Biol* 203:3137–3144
- Handrich Y, Bevan RM, Charrassin JB, Pütz K, Butler PJ, Lage J, Le Maho Y, Woakes AJ (1997) Hypothermia while hunting in a bird diver: the king penguin (*Aptenodytes patagonicus*). *Nature* 388:64–67
- Krebs JR (1978) Optimal foraging: decision rules for predators. In: Krebs JB, Davies NB (eds) *Behavioural ecology: an evolutionary approach*. Blackwell, Oxford, pp 23–63
- Le Boeuf BJ, Crocker DE, Grayson J, Gedamke J, Webbs PM, Blackwell SB, Costa DP (2000) Respiration and heart rate at the surface between dives in northern elephant seals. *J Exp Biol* 203:3265–3274
- Lindeman RL (1942) The trophic dynamic aspects of ecology. *Ecology* 23:399–418
- Meire PM (1987) Foraging behaviour of some wintering waders: prey selection and habitat distribution. In: Kamil AC, Krebs JR, Pulliam HR (eds) *Foraging behaviour*. Plenum, New York, pp 215–238
- Papi F, Luschi P, Åkesson S, Capogrossi S, Hays GC (2000) Open-sea migration of magnetically disturbed sea turtles. *J Exp Biol* 203:3435–3443
- Plötz J, Bornemann H, Knust R, Schröder A, Bester M (in press) Foraging behaviour of Weddell seals, and its implications for the food web ecology of the Antarctic sea ice zone. *Polar Biol*
- Ropert-Coudert Y, Baudat J, Kurita M, Bost CA, Kato A, Le Maho Y, Naito Y (2000) Validation of oesophagus temperature recording for detection of prey ingestion on captive Adélie penguins. *Mar Biol* 137:1105–1110
- Wehner R, Lehrer M, Harvey WR (eds) (1996) *Navigation*. *J Exp Biol* 199:1–261
- Williams TD (1995) *The penguins*. Oxford University Press, Oxford
- Wilson RP (1984) An improved stomach pump for penguins and other seabirds. *J Field Ornithol* 55:109–112
- Wilson RP, Duffy DC (1986) Prey seizing in African penguins *Spheniscus demersus*. *Ardea* 74:211–214
- Wilson RP, Wilson MPT (1989) A peck activity recorder for birds fitted with devices. *J Field Ornithol* 60:104–108
- Wilson RP, Cooper J, Plötz J (1992) Can we determine when marine endotherms feed? A case study with seabirds. *J Exp Biol* 167:267–275
- Wilson RP, Pütz K, Charrassin J-B, Lage J (1995a) Artifacts arising from sampling interval in dive depth studies of marine endotherms. *Polar Biol* 15:575–581
- Wilson RP, Pütz K, Grémillet D, Culik BM, Kierspel M, Regel J, Bost CA, Lage J, Cooper J (1995b) Reliability of stomach temperature changes in determining feeding characteristics of seabirds. *J Exp Biol* 198:1115–1135
- Wilson RP, Pütz K, Peters G, Culik BM, Scolaro JA, Charrassin JB, Ropert-Coudert Y (1997) Long-term attachment of transmitting and recording devices to penguins and other seabirds. *Wildl Soc Bull* 25:101–106