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Antennae on transmitters on penguins: balancing energy budgets on the high wire

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Summary

The effect of externally mounted antennae on the energetics of penguins was studied by mounting various antennae on a transducer fixed to a model Magellanic penguin *Spheniscus magellanicus* to determine drag, run at speeds of up to 2 m s^{-1} in a swim canal. For rigid antennae set perpendicular to the water flow, measured drag increased with increasing swim speed. Increasing antenna length (for lengths between 100 and 200 mm) or diameter (for diameters between 1 and 4 mm) resulted in accelerating increased drag as a function of both antenna length and diameter. Where antennae were positioned at acute angles to the water flow, drag was markedly reduced, as was drag at higher speeds in flexible antennae. These results were incorporated in a model on the foraging energetics of free-living Magellanic penguins using data (on swim speeds, intervals between prey encounters, amount ingested per patch and dive durations) derived from previously published work and from a field study conducted on birds from a colony at Punta Norte, Argentina, using data loggers. The field work indicated that free-living birds have a foraging efficiency (net energy gain/net energy loss) of about 2.5. The model predicted that birds equipped with the largest rigid external antennae tested (200 mm × 3 mm diameter), set perpendicular to water flow, increased energy expenditure at normal swim speeds of 1.77 m s^{-1} by 79% and at prey capture speeds of 2.25 m s^{-1} by 147%, and ultimately led to a foraging efficiency that was about 5 times less than that of unequipped birds. Highly flexible antennae were shown to reduce this effect considerably. Deleterious antenna-induced effects are predicted to be particularly critical in penguins that have to travel fast to capture prey. Possible measures taken by the birds to increase foraging efficiency could include reduced travelling speed and selection of smaller prey types. Suggestions are made as to how antenna-induced drag might be minimized for future studies on marine diving animals.

Key words: penguin, *Spheniscus magellanicus*, external antennae, drag, energy expenditure, foraging efficiency.

Introduction

Determination of the movements of vertebrates was revolutionized by the concept of telemetry (e.g. Kenward, 1987), whereby animal position could be determined by using receivers to triangulate on an energy-emitting unit attached to the study animal. Since its inception, telemetry has become highly refined, and is now used on fully aquatic animals such as fish in accoustic telemetry (e.g. Bagley and Priede, 1996), on terrestrial and semi-terrestrial animals, such as mammals, in VHF telemetry (Kenward, 1987) and even on widely ranging vertebrates, such as birds, in satellite tracking telemetry (e.g. Jouventin and Weimerskirch, 1990). In order that signals emitted by the unit carried by the animal can be effectively transmitted, the telemeter must usually have an antenna. Although these antennae have a minimal volume, they are sometimes of considerable length and could potentially affect the wellbeing of the carrier animal (Wanless et al., 1988; Phillips et al., 2003).

The effect of inappropriately shaped animal-carried systems is particularly important in marine animals (e.g. Bannasch et al., 1994; Culik et al., 1994a,b; Watson and Granger, 1998) because the drag caused by moving non-streamlined units through the dense medium, i.e. water, leads to substantial increases in energy expenditure. Following streamlining suggestions by Bannasch et al. (1994), many researchers working with telemetric devices on diving marine endotherms shape their units accordingly but have, to date, essentially ignored the potentially detrimental effect that antennae might have.

In this work we assess the drag incurred by marine endotherms carrying telemetric units with antennae as a function of the size and properties of the antennae. The results of this work are then put into context by examining the behaviour of free-living Magellanic penguins and, using a

simple energetics model, by considering the extent to which this behaviour might be altered in birds having to carry antennae on telemeters. Finally, we consider how antennae might be constructed so as to minimize their deleterious effects on their carrier animals.

Materials and methods

Laboratory studies

The drag caused by antennae was assessed using a pressure transducer to sense the drag experienced by various antennae attached to a model of a swimming penguin and moved through the water at different speeds.

The penguin model was constructed from fibreglass and derived from a cast of a dead *Spheniscus* penguin [original body mass 3.7 kg; mean body mass of Magellanic penguins = 4.0 kg (Williams, 1995); body dimensions without wings and with head retracted in the swimming position 57 cm×14 cm×12 cm]. Such a static, hard-bodied model cannot properly emulate the water flow characteristics over a real, soft penguin body, particularly since features such as feather properties may be responsible for substantial drag reduction (e.g. see Carpenter et al., 2000; Gad-el-Hak, 2002). We thus consider that the proportional drag values obtained by this approach will tend to be more than those actually incurred on a real penguin. However, in order to maintain water flow over the model as accurately as possible, an original penguin skull, complete with beak, was incorporated in the head, this being covered, as appropriate, with fibreglass. The body was supported by a stainless steel rod contiguous with the ends of the flippers and running away from the longitudinal axis of the body at 90°. This rod was clamped in plastic vanes running parallel to the body longitudinal axis so that the penguin could be held firmly in position underwater within a swim canal. These vanes were 1.3 cm thick and spaced 90 cm apart so that they minimally influenced water flow over the model penguin. The canal had dimensions of 20 m×1 m×1 m and was filled with freshwater at *ca*. 20°C. The plastic vanes were connected to a vehicle located on top of the canal on rails running the length of the system so that the penguin model could be driven through the water from one end to the other at a speed regulated by a computer. The speed was programmed so that the penguin model experienced a gentle acceleration phase over the first 3 m before the final speed was reached, which was maintained over most of the length of the canal until shortly before the end when the vehicle decelerated to zero over ca. 2 m. Speed values selected were from 0 to 2 m s^{-1} in 0.25 m s^{-1} increments and were accurate to within 3%.

The unit constructed to sense the drag experienced by antennae (Fig. 1) consisted of a quarter disc (radius 15 mm×10 mm thick) pivoted about what would be the complete disc's centre. A steel rod with a screw thread was attached to the quarter disc in line with one of the edges of the radii so that it projected directly away from the pivot. A cork bung was screwed onto this rod and could be moved up and down the length of the rod so that the bung–pivot distance could be exactly defined. The cork bung rested against the active membrane of a medium-separated pressure transducer (measurement range 0–6×10^5 Pa; Sensortechnik, Munich, Germany), located between rails to allow the transducer to be moved to any specified distance from the pivot directly in line with the steel rod, and orientated to face the bung directly. Three screw holes were turned into the quarter disc on the outside edge of what would have been the circumference of the full disc so that they were at angles of 90, 67.5 and 45° to the steel rod. All antennae to be tested conformed in size roughly to antennae used by PTT and VHF transmitters provided by a number of companies. These antennae were attached at their base to a screw, which fitted any one of the screw holes in the quarter disc outside edge so that the angle between antenna and steel rod could be correspondingly defined precisely as either 90, 67.5 or 45°. The unit was placed on the penguin model so that base of the attached antenna was exactly in line with the contours of the penguin's body, the quarter disc, pivot, bung and associated transducer being located within the body and away from the main current flow over the penguin. With an antenna screwed in place, when the penguin model moved forward through the water, drag acting on the antenna from the front exerted a force which acted, *via* the pivot, on the bung located on the steel rod causing it to exert pressure on the transducer.

The transducer readings were stored in a two-channel logger (IRDA series, Driesen and Kern GmbH, Bad Bramsted,

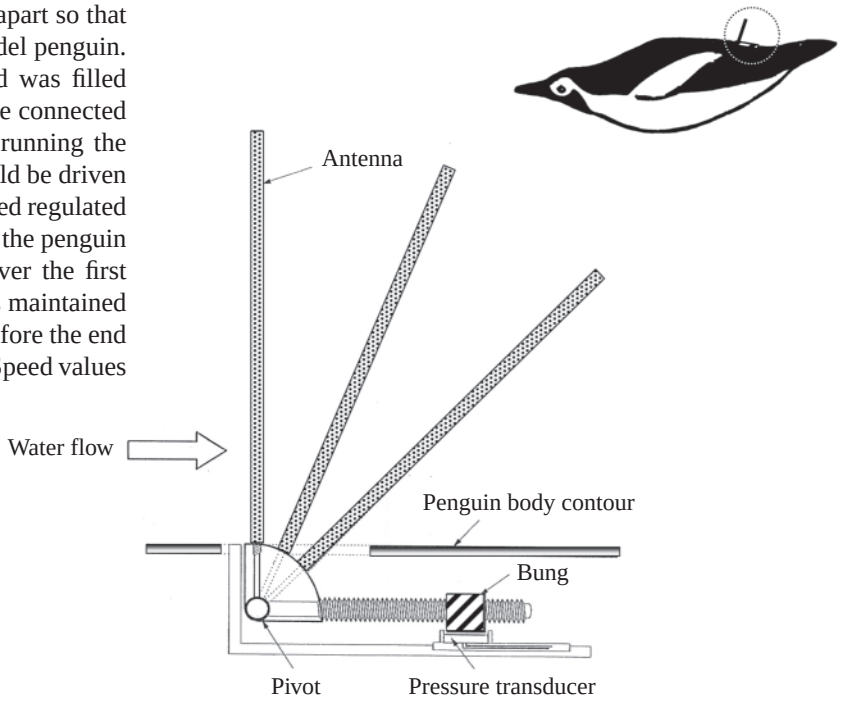

Fig. 1. Schematic diagram of the system used for measuring antenna drag showing details of the relationship between antenna and pressure transducer and the attachment of the measuring system to the penguin model (inset).

Germany), which recorded pressure and temperature continuously at 2 s intervals with 16-bit resolution in a 512 kbyte memory. The temperature sensor was used to compensate for temperature-dependent variability in pressure reading over and above that already corrected by the transducer manufacturers. Independent tests on the quality of the pressure transducer readings showed that it was good to better than 100 Pa. The logger was powered by a 3.6 V battery and the unit was started and data were accessed by an infra-red interface *via* computer.

Tests were conducted with the penguin, complete with pressure-sensitive unit, moving along the canal at defined speeds with no antenna (as the control) and with antennae of diameters of 1, 2, 3 and 4 mm and lengths of 100, 150 and 200 mm. We used two basic types: (i) essentially rigid antennae, although all antennae of this type did bend to some degree, and (ii) highly flexible (wound) antennae. These were considerably more flexible than PTT-type antennae usually used to our knowledge, but were selected to demonstrate the extent to which flexible antennae might be useful in reducing drag.

The pressure measured by the transducer during the various runs was calibrated for the torque incurred due to drag by mounting the unit in air so that the steel screw to which the bung was attached was exactly vertical and an antenna (length 200 mm, diameter 3 mm) fitted so that it was perpendicular to the screw, parallel to the ground and above the steel rod. Weights were hung on the antenna at defined positions and the pressure registered by the transducer, derived from the bung, was recorded by the logger. Calculations enabled us to derive the relationship between recorded pressure and torque.

Field studies

Field work was conducted between September 1996 and December 1997 on Magellanic penguins *Spheniscus magellanicus* Forster at Punta Norte colony (42°05′S, 63°52′W, Peninsula Valdes, Chubut, Argentina). Breeding birds were equipped with data loggers (DK 600 series, Driesen and Kern GmbH, Bad Bramstedt, Germany), fitted using tape (Wilson et al., 1997) to the lower back, as suggested by Bannasch et al. (1994) to minimize drag. 25 devices in total were attached to birds tending the nests and left in place for 1–60 days, during which time the birds went to sea to forage. When they returned, the units were removed and the birds replaced on the nest where they continued with breeding activities. Data were accessed from the units by using a computer and a RS 232 interface.

The devices were potted in resin, had maximum dimensions of 140 mm×58 mm×25 mm, weighed 160 g in air and were hydrodynamically shaped. Previous experiments using Adélie penguins *Pygoscelis adeliae* wearing these devices in a swim canal where oxygen consumption was continuously monitored suggested that energy consumption in birds swimming at 'normal' speeds of 2.1 m s^{-1} was some 6% higher with the units than without (Culik et al., 1994b).

The data loggers recorded data up to a maximum of 2 Mb on 6 channels, each with 16 bit resolution, on swim speed, dive depth, swim direction (2 channels; see Hochscheid and Wilson, 1999), light intensity and temperature. Only two channels were of primary importance for this work, these being swim speed and dive depth. Speed was sensed by a differential pressure sensor linked to a Prandl tube projecting from the body of the device. These units were calibrated on the model penguin in the canal for speeds up to 2 m s^{-1} (the maximum allowed by the system). Speeds could be resolved to better than 0.1 m s^{-1}. Dive depth was sensed by a pressure transducer (range 0–10^6 Pa) reacting to hydrostatic pressure and, after calibration, was found to be good to better than 0.1 m.

Eight penguins were also given stomach temperature sensors inserted inside fish, which were then given to the birds to swallow (Wilson et al., 1995). These units (Pillbox series; Driesen and Kern GmbH) consisted of a small logger (maximum dimensions: 18 mm diameter × 85 mm length) enclosed within a titanium turned housing. Temperature was measured with 8 bit resolution in a 128 kbyte memory. After calibration in a water bath, temperature could be determined to 0.1°C. Following Wilson et al. (1998), the units were equipped with a spring crown, which reduced the likelihood that they would be spontaneously regurgitated. In addition, one end of the titanium cylinder was fitted with a strong rare-earth magnet. After birds containing stomach temperature sensors had returned from at least one foraging trip, the units were recovered by inserting a magnetic grab at the end of a silicon tube down the oesophagus. The grab locked onto the rare-earth magnet on the titanium housing and the complete system could be withdrawn (Wilson and Kierspel, 1998). Data from the loggers were accessed by a computer linked to a RS232 interface. Feeding behaviour of the birds was indicated by sudden temperature drops. The time at which prey were ingested can be determined by assessing the exact time of the drop and a measure of the mass ingested can be derived by calculating the area under the asymptote. This is possible after calibrations experiments where captive birds containing a temperature sensor are given prey fish of known mass and temperature so that the relationship between the area under the asymptote and the fish mass can be ascertained (for details, see Wilson et al., 1995). This information was calculated using the programme FEEDINT (Jensen Software Systems, Laboe, Germany).

Results

Laboratory studies

Calibration of sensor

Calibration of the pressure transducer against specific torques applied to a perpendicular antenna showed a very clear positive linear relationship (Fig. 2) between torque M and recorded pressure p (in Pa) so that:

$$p = 269804.56 \times M - 316.25 , \quad (1)$$

(r^2=0.9995) where the units of the constant of proportionality are m^{-3}.

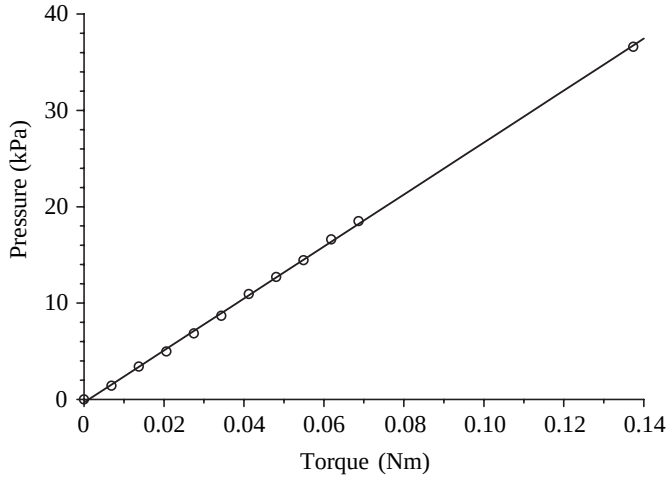

Fig. 2. Relationship between pressure measured by the drag measurement system shown in Fig. 1 and the torque calculated by hanging known weights at specific distances from the fulcrum (see text).

Effect of antenna length

The transducer indicated that for essentially rigid antennae of variable length, pressure rose gradually for swim speeds up to about 1 m s^{-1} (Fig. 3A). After this, pressure rose rapidly with increasing swim speed, the effect being most apparent with longer antennae. For example, with the 200 mm antenna, the pressure rose by a factor of about 10.2 at speeds between 1.0 and 2.0 m s^{-1} whereas with the 100 mm antenna it rose by a factor of about 7 (Fig. 3A). The point of inflection appeared to occur at lower speeds with longer antennae (Fig. 3A).

Effect of antenna angle

The angles at which essentially rigid antennae of fixed length and diameter were mounted with respect to water flow affected recorded pressure substantially. Again, at low speeds, recorded pressure increased only slowly with increasing speed until ca. 1 m s^{-1} (Fig. 3A), but subsequently recorded pressure increased much more rapidly, being most apparent at the least acute angles. For example, the 200 mm long antenna set perpendicular to water flow increased drag between speeds of 1.0 and 2.0 m s^{-1} by a factor of 10.2 but only increased drag by a factor of 7.7 over the same speed range when set at an angle of 45° to water flow (Fig. 3A). The point of inflection occurred at lower speeds in the least acute angles (Fig. 3A).

Effect of antenna flexibility

Although the pressure recorded by the transducer increased with increasing speed for flexible antennae, the form of the increase was sigmoid (Fig. 3B). This feature was apparent even for antennae set at acute angles to the direction of water flow. Unlike the case with primarily rigid antennae, it appeared that increases in pressure were not systematic with antenna length; the pressure increase recorded with the 150 mm long antenna was markedly less than that recorded for both the 200 mm and the 100 mm long antennae. This arose because, although the material used for the antennae in the tests was the same, there were substantial differences in the flexibility, presumably due to minute differences in the way the springs were wound. This affected the recorded pressure changes and demonstrated the extent to which antenna flexibility may be important in drag considerations.

Effect of antenna diameter

Recorded pressure for rigid antennae of fixed length increased substantially with increasing antenna diameter (Fig. 4). For example, the pressure recorded for a 200 mm

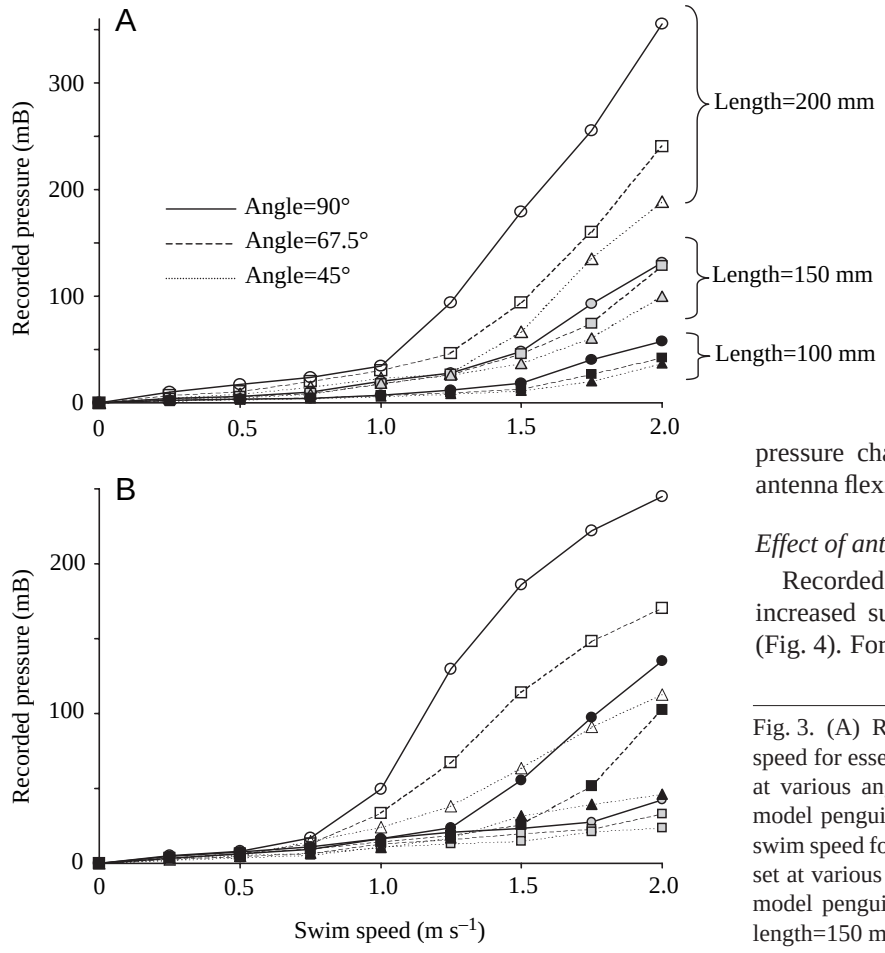

Fig. 3. (A) Relationship between recorded pressure and swim speed for essentially rigid antennae of various dimensions and set at various angles to the direction of water flow mounted on a model penguin. (B) Relationship between recorded pressure and swim speed for highly flexible antennae of various dimensions and set at various angles to the direction of water flow mounted on a model penguin. White symbols, length=200 mm; grey symbols, length=150 mm; black symbols, length=100 mm.

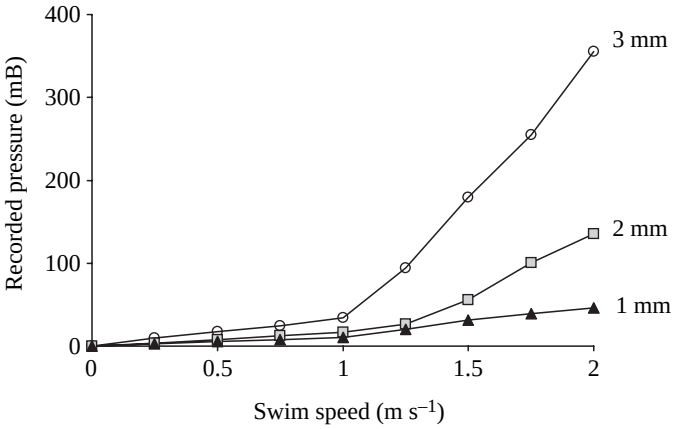

Fig. 4. Relationship between recorded pressure and swim speed for rigid antennae (length 200 mm and set at an angle of 90° to water flow) with differing diameters mounted on a model penguin.

antenna with a diameter of 3 mm at 2 m s^{-1} was about 230% higher than that for a 2 mm diameter antenna and about 770% higher than for a 1 mm diameter antenna. It was notable that, although we attempted to use rigid antennae, the cases with small diameter were observed to bend somewhat at higher speeds. As in the case of antenna length, increases in pressure with increasing speed were slight up to ca. 1 m s^{-1} whereupon, with further increasing speeds, they increased much more rapidly (Fig. 4). The point of inflection occurred at lower speeds for antennae of greater diameter.

Field studies

Swim speeds and time underwater

Birds equipped with external loggers generally swam at speeds calculated to be between 1.5 and 3 m s^{-1}. There was, however, consistent, marked reduction in swim speeds during the first part of all foraging trips, which corresponded to periods of travel from the breeding colony to the foraging site (for a discussion, see e.g. Wilson and Wilson, 1990). If these periods are excluded (to facilitate later calculations; see below), the mean swim speed of Magellanic penguins was 2.3±0.88 m s^{-1} (mean ± S.D., *N*=8302 from nine birds). Modal swim speed was 2.2 m s^{-1} (Fig. 5A). Close examination of individual dives showed that, during foraging, swim speed generally varied between 1.8 and 2.8 m s^{-1}, increasing markedly during particular dives (Fig. 5B). We interpreted this increase in speed to be due to periods of prey pursuit, as documented by Wilson et al. (2002). Assuming this to be the case, the mean number of consecutive dives where birds exploited a patch was 2.74±2.84 (mean ± S.D., *N*=302), although the frequency distribution of this was not normal (Fig. 6). During periods of prey exploitation, birds spent a total of 83% of their time underwater, 17% being spent resting between dives. During periods when prey were apparently not being exploited birds spent 76% of their time underwater and 24% of their time resting between dives.

Feeding behaviour

The stomach temperature loggers showed clearly when birds had ingested food *via* sharp drops in measured temperature (cf. Wilson et al., 1995). However, this pattern was not apparent over the whole foraging period, the latter half showing a slow general temperature drop (Wilson et al.,

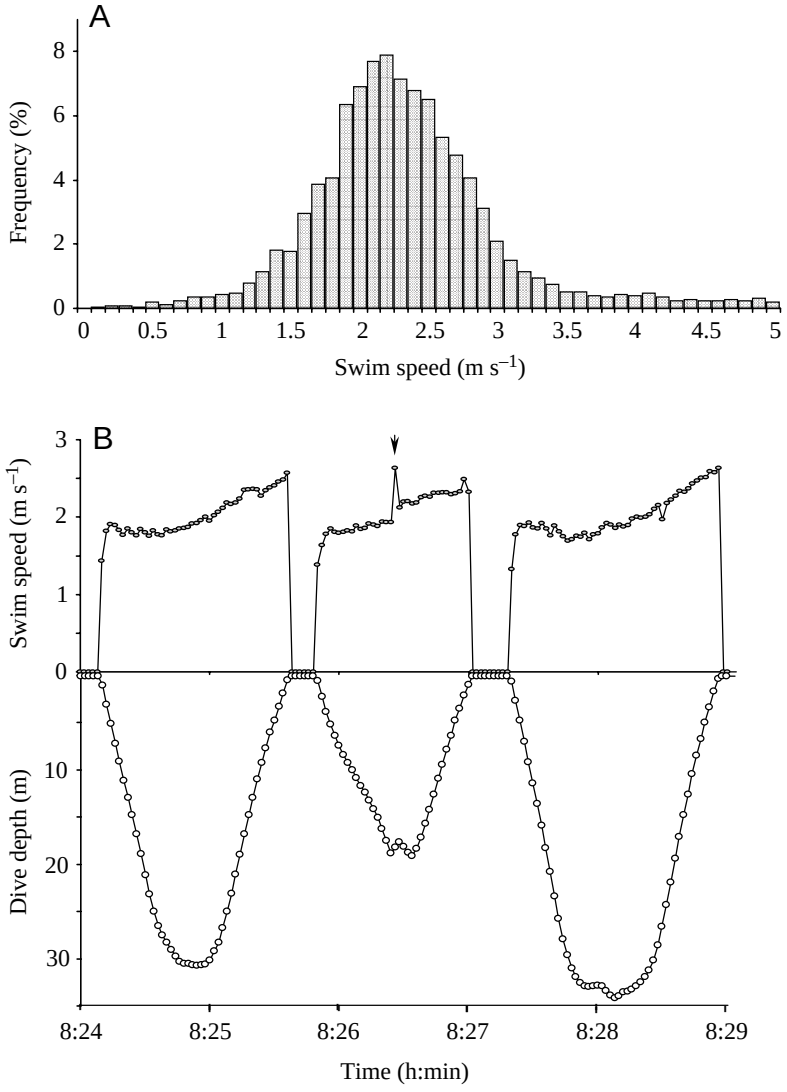

Fig. 5. (A) Frequency distribution of swim speeds used by nine Magellanic penguins swimming from a colony at Punta Norte (*N*=8302). (B) Swim speed and dive depth over three consecutive dives made by a Magellanic penguin foraging from Punta Norte, Argentina. Note that the first and last dives in the series show gradually changing speeds during the dives whereas the second dive shows an abrupt change in speed (marked by an arrow) associated with a similarly abrupt change in depth, which we assume is due to prey capture (see Simeone and Wilson, 2003).

1995). This pattern is due to food ingestion and digestion for the foraging adult during the initial phase of the foraging trip followed by a period where food is ingested for the chick, this process necessitating that digestion be stopped (see Peters, 1998; Gauthier-Clerc et al., 2000). Calculation of both the timing of food ingestion as well as the mass ingested is inaccurate for this latter period (Wilson et al., 1995; Peters, 1998). Thus, our results regarding feeding frequency and masses are only presented for the initial period of the foraging trip.

The mean mass of food ingested per ingestion event was 53.3±67.7 g (mean ± S.D., *N*=65); however, the frequency distribution of the masses was not normal, with smaller amounts being ingested most often (Fig. 6). The mean time between patch encounters was 47.5±74.7 min (mean ± S.D., *N*=60) although this was not normally distributed either (Fig. 7). Generally, prey patches were encountered within 10 min of each other although there were three occasions in excess of 2 h when prey were not encountered (Fig. 7). Since the birds carrying stomach temperature loggers were not simultaneously equipped with external loggers, we could not be sure that, in these cases, the penguins were actively foraging and we suspect that the birds rested (cf. Wilson and Peters, 1999). If these data are excluded, the mean search time between prey patches becomes 36.3±33.3 min (mean ± S.D., *N*=57).

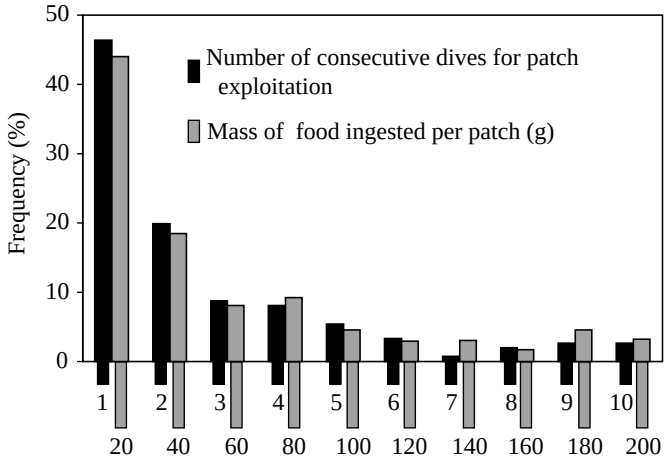

Fig. 6. Frequency distribution of the number of consecutive dives (black bars; *N*=302) where Magellanic penguins (*N*=25) foraging from Punta Norte, Argentina, were considered to be exploiting a prey patch (this being defined by higher swim speeds; see text) and the frequency distribution of the amounts of estimated food ingested per patch for Magellanic penguins (grey bars; *N*=4 birds for 65 patches) foraging from Punta Norte, Argentina. Note that these two data sets were not derived from the same birds (see text).

Discussion

Animals equipped with external devices may behave aberrantly for a number of different reasons and there are many publications to this effect (see e.g. Calvo and Furness, 1992, and refs therein). These have been grouped into three categories by Wilson and Culik (1992). (i) 'Psychological' problems, such as repeated manifestation of a particular behaviour that normally does not appear, or only does so at a much lower frequency. Excessive preening or repeated attempts to remove the device may be classified under this heading (e.g. Wilson et al., 1991). (ii) Physical inability to engage in particular behaviours due to device effects, e.g. penguins might not be able to swim as fast or dive as deep with devices as without (e.g. Wilson, 1989), with consequent repercussions on prey capture ability. (iii) Changed energetics, whereby maintenance of physically 'normal' behaviour by device-equipped animals results in higher energy expenditure, which compromises their ability to forage and ultimately to survive.

Changes under the 'psychological' category can only be considered on a species-by-species basis, so that no general rules can be derived (see e.g. Calvo and Furness, 1992, and references therein). Physical disabilities can be determined to some extent by examination of animals in captivity (e.g. Heath, 1987), although their consequences are often difficult to quantify. Changed energetics can be accessed by careful gas respirometry studies (e.g. Culik et al., 1994b) or by doubly labelled water studies (e.g. Gales et al., 1990) and are also accessible *via* examination of heart rate (e.g. Butler, 1993). In our treatment of the effects of antennae on the behaviour of marine animals we have limited ourselves solely

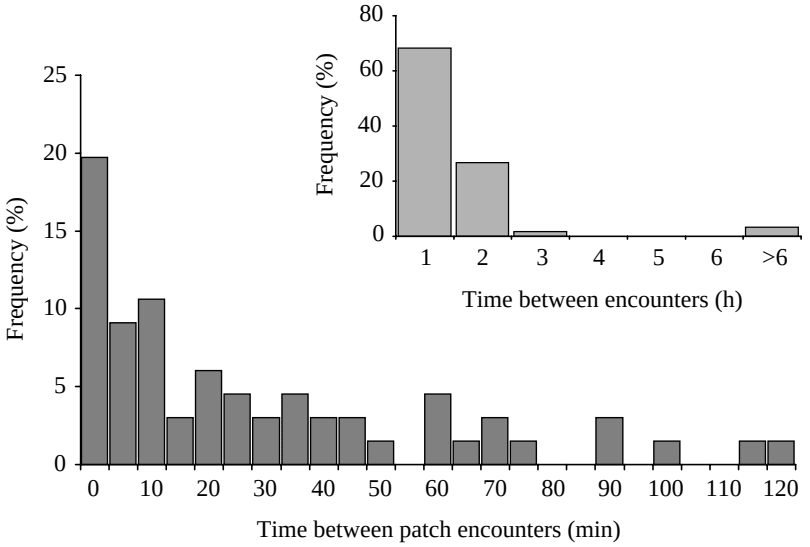

Fig. 7. Frequency distribution (*N*=60) of the time between prey patches for four Magellanic penguins foraging from Punta Norte, Argentina. The inset shows all data for periods up to, and including, 6 h, to highlight the bimodality of the data, whereas the main graph shows only those data for up to and including 120 min, to show more detail. Note that these data do not include periods where birds presumably rested overnight.

to consideration of the energetic consequences of potentially increased drag. This ignores a number of important features that we could not quantify, but which should be mentioned. Firstly, penguins at the surface may be subject to spray drag. Secondly, Magellanic penguins undergo considerable changes in both angular and absolute acceleration during foraging (see e.g. Wilson et al., 2002; Simeone and Wilson, 2003), whereas we only treat the energetically more mild constant-velocity scenario. Finally, it is likely that birds equipped with antennae incur extra energy costs from induced drag associated with trying to maintain trim because the position of the antenna would produce a torque that would pitch the anterior part of the penguin upward. All these features will tend to make the case of penguins swimming with attached antennae more detrimental than we describe below.

In our treatise of the changing energetics of penguin swimming resulting from increased drag associated with attached antennae, we can allude to potential limitations of maximum swim speed, but we cannot relate this to prey capture success. After making a few assumptions about the way penguins forage we can, however, speculate as to whether birds carrying external antennae can balance energy expenditure with energy gain during normal foraging. This process is based on coupling various necessary elements on penguin energetics and foraging together: derivation of the antenna-dependent drag, as experienced by the bird using the data from the swim canal tests, use of published data on energy expenditure of penguins as a function of speed (and therefore drag), and finally data on foraging parameters (dive durations and swim speeds coupled with prey ingestion rates) of free-living penguins.

Derivation of antenna-dependent drag

A penguin swimming with a rigid antenna on its back perpendicular to water flow experiences an additional drag (in N) from the antenna. This drag results in a torque that acts on the antenna at the lever arm *r*. At the fulcrum, at the base of the antenna, there is a balance of forces and moments. The acting force operates against the swim direction, braking the penguin and necessitating greater energy expenditure to maintain speed. In our tank tests the resulting torque, *M*, was translated *via* the fulcrum to the second moment arm, leading to the sensor, so that the cork bung exerted a force on the pressure transducer. During movement, an effective water speed profile is produced in the boundary layer close to the surface of the device. According to Bohl (1991), the layer thickness of the turbulent boundary layer *d* is greater than the laminar boundary layer, so that we assume a turbulent boundary layer and use:

$$d \approx 0.37\sqrt[5]{[(\nu_{H_2O} s^4)/\nu\infty]}\,, \qquad (2)$$

where ν_{H_2O} is the kinematic viscosity of fresh water at 20°C, *s* is the distance from the beginning of the body to the point where the maximum boundary layer is established and $\nu\infty$ is the speed of current flow. Thus, at a speed of $\nu\infty$=1 m s^{-1} and *s*=420 mm (the distance between the beak tip and the antenna), there is a boundary layer that is maximally 1.17 cm thick. This is about 5.8% of the length of a 200 mm long antenna. In addition, the velocity profile in a turbulent boundary layer is progressive with increasing distance from the surface, so that a value of 80–90% that of $\nu\infty$ is already reached at *d*/2 (Bohl, 1991). Thus, the unknown effective current speed in the boundary layer is only a small fraction of the total torque and will not be further discussed here.

If we assume that the drag acts equally over the full length of the antenna, then *M* can be deduced from the integral of the force, F_d, over the length of the antenna, *L*:

$$M = \int F_d.dr\,, \qquad (3)$$

which, after taking into account antenna angle α, can be resolved to be:

$$M = F_d \times L \times \sin\alpha/2\,, \text{ so that } F_d = 2M / (L \times \sin\alpha)\,. \qquad (4)$$

The torque, *M*, over the whole of the antenna length is effectively the same as a specific torque applied at the point at half the antenna length, this being the force with which the penguin must deal. Our laboratory calibrations of the transducer used in the tank allowed us to derive the force acting on the antenna with the torque (Equation 1) so that Equations 1 and 4 can be combined in:

$$F_d = (p + 316.25) / (L \times \sin\alpha \times 134902.28)\,, \qquad (5)$$

This process can be carried out for results from various antennae of differing lengths and diameters made to move up the channel on the model penguin at different speeds (Fig. 8A).

The power output *P*o (W) necessary to transport the antenna is:

$$Po = E / t\,, \qquad (6)$$

where *E* is the energy (J) and *t* is the time (s). Using the standard formula for work done:

$$W = Fs\,, \qquad (7)$$

where F=F_d and is the drag (in N) and *s* is the distance (m):

$$Po = F_d s / t = F_d v\,, \qquad (8)$$

where *v* is the speed (m s^{-1}). Thus, a penguin swimming with an external antenna must provide an additional power given by Equation 8 (Fig. 8B). This describes the power output needed by the penguin to counteract the effects of an antenna. Two further steps are necessary to be able to assess the actual effect that an external antenna might have on penguin swimming energetics: (i) determination of the power input by an unequipped penguin as a function of speed so as to relate this to drag and (ii) summing the drag effects of the penguin body plus antennae as a function of speed before inputting these values into the relationship derived in (i), so as to access overall power input for a penguin swimming with an external antenna.

Costs of swimming for equipped and unequipped penguins

Although there are virtually no data available on the

energetics of Magellanic penguins, there is information on the highly similar (see Williams, 1995) congeneric Humboldt *Spheniscus humboldti* and African penguins *Spheniscus demersus*. In fact, it is notable that there are no radical differences in energy expenditure as a function of activity in any of the medium-sized penguins (see e.g. Pinshow et al., 1977; Culik et al., 1996). We therefore assume that we could estimate energy consumption of Magellanic penguins quite closely.

The mass-specific power requirements for a swimming penguin are reported to be approximated by a third degree polynomial function (Culik et al., 1996) according to:

$$P_{\text{swim}} = av^3 + bv^2 + cv + k\,, \tag{9}$$

where, for Humboldt penguins, a=2.954, b=–6.354, c=5.818 and k=5.9, and v is the speed. Note that parameter k gives the mass-specific resting metabolic rate (Luna-Jorquera and Culik, 2000).

The equation for calculating the drag on a penguin gliding underwater is:

$$F_{\text{d}} = 0.5v^2\rho C_{\text{d}}A_{\text{q}}\,, \tag{10}$$

where ρ is the density of water (kg m^{-3}), v is the speed (m s^{-1}), C_{d} is the drag coefficient (0.0368 for penguins; Culik et al., 1994a) and A_{q} is the cross-sectional area of the penguin at the point of its greatest girth (0.02083 m^2; Oehme and Bannasch, 1989). This equation allows us to calculate the drag experienced by a Magellanic penguin as a function of speed and, since the relationship between energy expenditure and swim speed is known for Humboldt penguins (Luna-Jorquera and Culik, 2000; see above), the relationship between energy expenditure per unit time (power input) and drag can also be determined (Fig. 9). Using this relationship the combined drag of the penguin (from Equation 9) plus antenna (Equation 5) for any particular speed can determined, as well as the effect that this will have on penguin energy expenditure at various swimming speeds (Fig. 10A).

Of particular note is that derived values for drag for the antennae differ from that predicted using Equation 10, where the antenna is treated as an elongated cylinder (C_{d}=1,2). This presumably stems from the complexities of water flow over the penguin's body which, among other things, cause the water flowing proximate to the body to be moving faster than that moving an infinite distance away. In addition, as pointed out by Obrecht et al. (1988), simple addition of the two different drags, as derived from Equation 10 (of antenna and penguin), is erroneous since the overall drag is greater than the sum of its parts.

A key element in determining travelling efficiency is the cost of transport, this being given by the power input divided by the speed. Determination of the cost of transport for penguins with and without external antennae shows that the increase in drag caused by the antenna results in an overall increase in cost of transport, particularly at speeds in excess of 1 m s^{-1}, but also that the speed at which the minimum cost of transport occurs is shifted to lower values in birds carrying antennae, with the effect being most pronounced for antennae that produce most drag (Fig. 10B).

Behavioural consequences of transporting an antenna for Magellanic penguins

The most parsimonious reaction to the fact that Magellanic penguins must ostensibly expend more energy to swim at normal speeds with externally attached antennae would be to say that the birds must simply work correspondingly harder to compensate. There are, however, reasons to believe that a small, inappropriately designed body such as an antenna might result in an exacerbation of deleterious effects so that ultimately the foraging efficiency of penguins could be seriously compromised. This can be alluded to by a simple mathematical model.

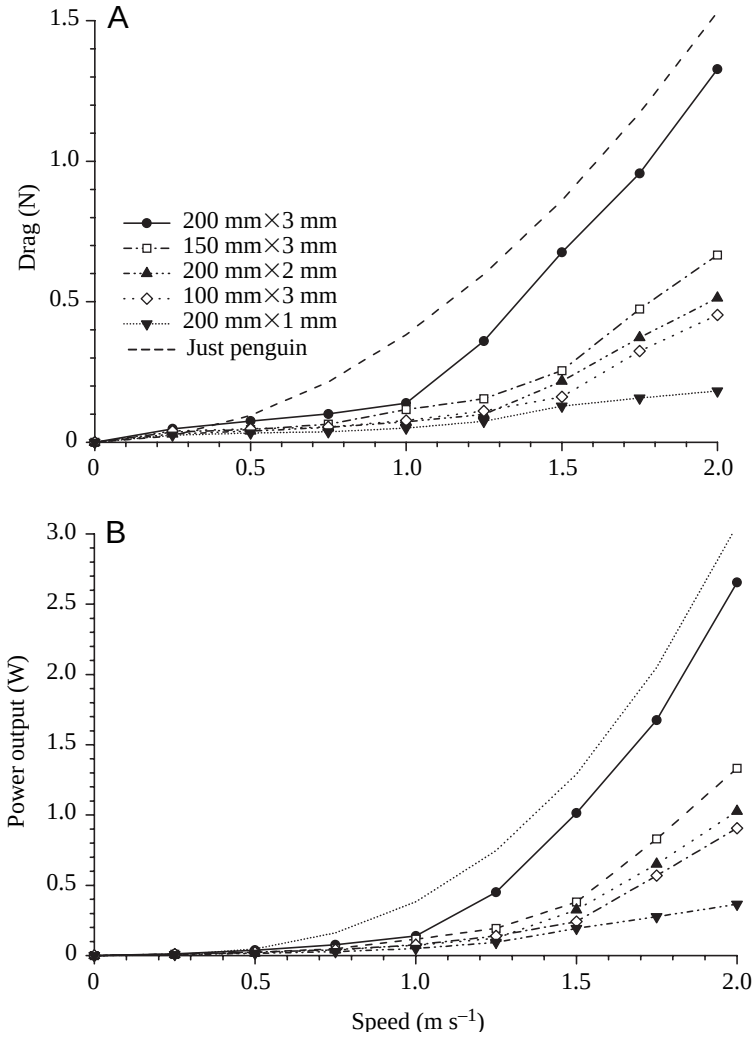

Fig. 8. (A) Drag (for calculations, see text) induced by antennae of various dimensions on a model penguin as a function of swim speed. (B) Power output needed to drive antennae of different dimensions attached to the body of a penguin through water at various speeds.

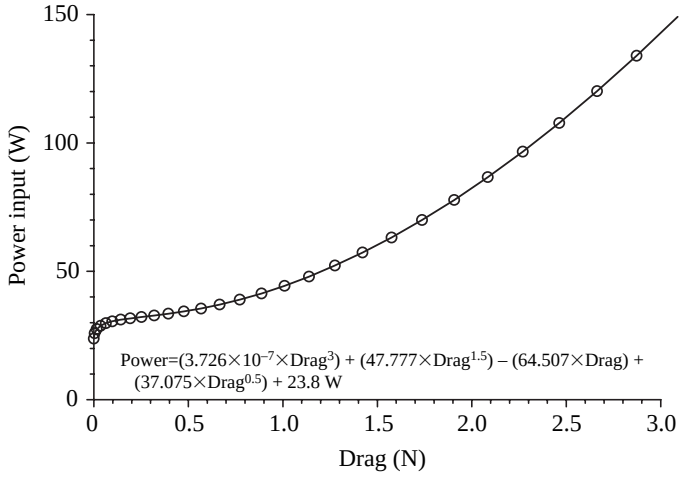

Fig. 9. Power input (energy expended per second) for a swimming Magellanic penguin as a function of drag. This was derived by using a polynomial fit for the mass-specific power requirements as a function of swim speed for Humboldt penguins given by Luna-Jorquera and Culik (2000) (Equation 9 in text) and then regressing these power-requirements against the drag experienced by the penguins swimming at the corresponding speed. The drag–speed relationship was determined from the standard formula (Equation 10 in text), which incorporates a drag coefficient of 0.03 (Bannasch, 1995) and a cross-sectional area of 0.018m^2 (see text).

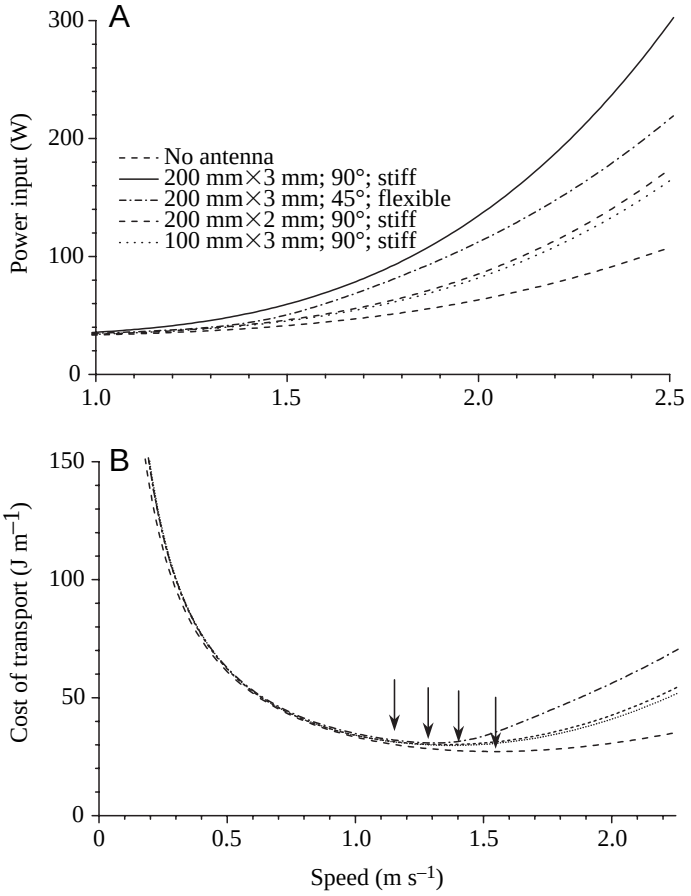

Fig. 10. (A) Relationship between energy expended per second and speed for a Magellanic penguin swimming unequipped (bottom line) and equipped with antennae (flexible or stiff) of various dimensions. (B) Relationship between the cost of transport and speed for a Magellanic penguin swimming unequipped (bottom line) and equipped with antennae (flexible or stiff) of various dimensions. The arrows show the speeds at which costs of transport are minimized for the various scenarios.

We assume that penguin foraging (for a review, see Wilson, 1995) is typified by periods during which the bird searches for prey by travelling underwater during dives interspaced with short rests on the surface. After a prey patch (normally a shoal of pelagic school fish in *Spheniscus* penguins; Wilson and Wilson, 1990) is encountered, the penguin remains underwater, ingesting more or less continuously until oxygen reserves are depleted, whereupon the bird must return to the surface. After recovery at the surface, the penguin dives again and attempts to relocate the prey patch (Wilson and Wilson, 1995). If successful, the process of ingestion is repeated. If not, the bird must begin the search for a new prey patch. The success of this strategy critically depends on prey density but can be modelled out using energy expenditure and gain over time.

The energy expended during the search phase is:

$$E_{\text{search}} = P_{\text{swim,search}}T_{\text{swim,search}} + P_{\text{rest,search}}T_{\text{rest,search}} , \quad (11)$$

where $P_{\text{swim,search}}$ are the power requirements for swimming at normal swim speeds, $T_{\text{swim,search}}$ is the time spent swimming, $P_{\text{rest,search}}$ are the power requirements during resting between dives and $T_{\text{rest,search}}$ is the time spent resting between dives during the search phase. The times spent swimming and resting can also be expressed as a percentage of the mean time spent swimming between patches.

The energy expended during the patch exploitation phase is:

$$E_{\text{dive,patch}} = \xi(P_{\text{swim,patch}}T_{\text{swim,patch}} + P_{\text{rest,patch}}T_{\text{rest,patch}}) , \quad (12)$$

where ξ is the number of dive cycles during which a single prey patch is exploited, $P_{\text{swim,patch}}$ and $P_{\text{rest,patch}}$ are the power requirements to swim at speeds used during patch exploitation and to rest between dives, respectively, $T_{\text{swim,patch}}$ is the time spent actively swimming while exploiting a patch and $T_{\text{rest,patch}}$ is the time spent resting between dives while exploiting a patch. Again, the times spent swimming and resting can also be expressed as a percentage of the mean time spent in one dive cycle while exploiting prey. Both $P_{\text{swim,patch}}$ and $P_{\text{swim,rest}}$ can be determined from the work of Luna-Jorquera and Culik (2000) (Equation 9). It is important to note, however, that the time available to exploit the patch during any dive ($T_{\text{swim,patch}}$) is limited by the bird's oxygen reserves (O_{tot}) and the rate at which they are used up ($\dot{V}_{O_2}$), so that:

$$T_{\text{swim,patch}} = O_{\text{tot}} / \dot{V}_{O_2} . \quad (13)$$

The rate of oxygen consumption is proportional to the power input required for swimming so that:

$$\dot{V}_{O_2} = \alpha 1 P_{\text{swim}} , \quad (14)$$

where $\alpha 1$ is a constant with units of $cm^3\ j^{-1}$. Combining Equations 9 and 12–14:

$$E_{\text{dive, patch}} = \xi[(O_{\text{tot}}/\alpha 1) + P_{\text{rest,patch}} T_{\text{rest,patch}})] \ . \quad (15)$$

Note that the power requirements for swimming at different speeds are contained within the $\alpha 1$ term (see Equations 9, 14). The energy gain during patch exploitation is:

$$E\gamma_{\text{dive patch}} = \xi(T_{\text{swim,patch}}.dE/dt) \ , \quad (16)$$

where dE/dt is the rate of energy gain during prey exploitation. Overall, the total energy used to locate and exploit one prey patch is given by:

$$E_{\text{tot}} = E_{\text{search}} + E_{\text{dive,patch}} \ . \quad (17)$$

The foraging efficiency E_{ff} (cf. Nagy and Shoemaker, 1984) is:

$$E_{ff} = E\gamma_{\text{dive,patch}} / E_{\text{tot}} \ . \quad (18)$$

Values for penguins can theoretically be applied to this general solution for birds with and without antenna, so as to examine the energetic consequences of the extra drag. In practice, however, there are a number of uncertainties in the literature values for the necessary parameters.

If we assume that Magellanic penguins conform to the equation for energy expenditure over time with respect to speed described earlier (Equation 9), then birds swimming at cruising speeds of 1.77 m s^{-1} and engaging in prey capture speeds of 2.25 m s^{-1} (for Magellanic penguins feeding on small sardines; see Wilson et al., 2002) theoretically expend 12.7 and 20.5 W kg^{-1}, respectively. This is 50.7 and 81.9 W, respectively, for a standard Magellanic penguin weighing 4 kg (see Williams, 1995). If we use literature values for total body oxygen stores from *Pygoscelis* penguins as applicable for Magellanic penguins (data summarized in Culik et al., 1994a), then birds have 59.5 ml O_2 kg^{-1} or 238 ml O_2 $bird^{-1}$. Since the consumption of 1 ml oxygen corresponds to approximately 20 J (Schmidt-Nielsen, 1990), Magellanic penguins swimming at 1.77 and 2.25 m s^{-1} would be able to dive aerobically for only 93.9 and 58.1 s, respectively. We note that the formulation that we use is most appropriate for swim speeds up to ca. 2.5 m s^{-1} but may become increasingly problematic at higher speeds. This is because Luna-Jorquera and Culik (2000) only worked with Humboldt penguins that swam at maximum speeds of 2.2 m s^{-1} in their experimental setup, resulting in increasing uncertainties at higher speeds.

We were unable to measure prey ingestion in relation to diving behaviour directly in our field work, since birds were either equipped with external loggers or stomach temperature loggers. Ideally, both units should be deployed together so that the mass ingested per patch exploited can be directly equated with the time spent underwater in the pursuit of prey, as measured by the depth gauges in the loggers. Generally, however, it is to be expected that the longer a bird spends in a patch feeding, the more it will ingest. In this regard, comparison of the frequency distribution of the mass of food ingested by Magellanic penguins foraging from Punta Norte, Argentina is remarkably similar to the frequency distribution of the number of dives in a feeding bout from birds from this region (cf. Fig. 5, where the number of classes has been, in each case, limited to ten to allow comparison). The implication from this is, therefore, assuming that the stomach temperature of logger-equipped birds and TDR-equipped birds were subject to the same conditions, that Magellanic penguins from the region ingest about 20 g of anchovy per successful dive. This translates to a mean of 54 g ingested per patch (assuming the average patch to be exploited over 2.7 dives – see Table 1) or ca. 82 g h^{-1} spent foraging (assuming that birds search for 36.4 min between patches and that patch exploitation takes ca. 3 min, composed of 2.7 dives of 58 s plus pauses amounting to 17% of these; see Table 1). This compares well with the value of 0.025 g of prey ingested per second at sea (or 90 g h^{-1}) noted by Wilson and Grémillet (1996) for African penguins, although it should be noted that recently acquired data suggest that in some areas Magellanic penguins may ingest much higher quantities of prey per unit time (Wilson, 2004).

For the purposes of our calculations, we assume the above conditions to be representative of those experienced by free-living Magellanic penguins and, for our presented model on the efficiency of foraging Magellanic penguins with and without antennae, we make the assumptions listed in Table 1, most of which are derived from our fieldwork or from the literature. Much fieldwork data is derived from device-equipped birds, albeit individuals without antennae. We assume that these birds behaved in the same way as non-equipped conspecifics, although it is likely that their foraging capacities were also somewhat compromised. In addition, we assume that Magellanic penguins only exploit a patch underwater aerobically (cf. Butler and Woakes, 1984), after which time they return to the surface to breathe, and that birds feed exclusively on anchovy *Engraulis anchoita* (Frere et al., 1996; Scolaro et al., 1999).

Our model indicates that if free-swimming Magellanic penguins foraging from Punta Norte, Argentina ingest 20 g of anchovy per dive when exploiting a patch, they have a foraging efficiency of 2.5. By so doing, the penguins more than compensate for the energy expended for foraging, a condition that must be fulfilled if birds are to survive in the long term. There is remarkably little information on the foraging efficiency of animals, but Nagy and Shoemaker (1984) summarize data from three major groups with values of 1.0–1.6 for sit-and-wait insectivores, 1.4–2.5 in widely foraging insectivores and 9–17 in herbivores. In seabirds a value of 1.3 has been quoted for northern gannets *Sula bassana* (Garthe et al., 1999) and ca. 3.5 for great cormorants *Phalacrocorax carbo* (Grémillet, 1997).

Our model predicts that the foraging efficiency of Magellanic penguins drops dramatically if birds are equipped with antennae with, for example, penguins carrying antennae measuring 150 mm×3 mm incurring a more than twofold reduction in foraging efficiency and birds carrying antennae measuring 200 mm×3 mm incurring an almost fivefold reduction in foraging efficiency (Table 2). This apparent

Table 1. *Parameters used to model energy and prey consumption by foraging Magellanic penguins*

Parameter	Value	Source
Mass of Magellanic penguin	4 kg	Williams (1995)
Time spent swimming during searching (%)	76%	This paper
Swim speed during searching	1.77 m s^{-1}	Wilson et al. (2002)
Power to swim during searching	50.7 W	This paper
Time resting during searching (%)	24%	This paper
Resting metabolic rate	23.6 W	Luna-Jorquera and Culik (2000)
Time swimming during patch exploitation (%)	83%	This paper
Swim speed during prey pursuit	2.25 m s^{-1}	Wilson et al. (2002)
Power used during prey pursuit	81.9 W	This paper
Time resting during searching (%)	17%	This paper
Mean time spent searching between patches	36.3 min	This paper
Mean no. of dives spent exploiting patch	2.7	This paper
Prey ingestion rates during pursuit	20 g $dive^{-1}$	This paper
Energy content of prey (anchovy) – wet mass	5.5 kJ g^{-1}	South African Fisheries Industrial Research Institute (1980), FitzPatrick et al. (1988)
Assimilation efficiency (%)	77%	Cooper (1977), Guerra (1992)
Overall energy gain from prey	4.24 kJ g^{-1}	Derived – this paper
Energy gain during pursuit	84.8 kJ $dive^{-1}$	Derived – this paper
Body oxygen stores	238 ml	Culik et al. (1994a)

increasing deleterious effect of what appears a relatively trivial body attached to the penguin reflects two primary processes: (i) that the power output necessary to achieve particular swim speeds with the antennae increases dramatically with speed, and (ii) that the power input from the penguin also increases as an approximately cubed function of the drag. An obvious consequence of this is that the conditions under which the penguin must operate are particularly sensitive to speed (Fig. 11). We note that Adélie Penguins, which capture prey at speeds lower than their travelling speeds (1.7 m s^{-1} and 2.0, respectively; Wilson et al., 2002) and, in any event, have prey capture speeds markedly lower than those of Magellanic penguin, have a foraging efficiency just above one, even if equipped with an external antenna (200 mm×3 mm). Thus, even in the case of the Adélie penguin, although foraging efficiency with such an antenna is reduced compared to non-equipped birds by a factor of just over three, the chances of the birds surviving would be increased considerably (apart from prey capture speed, all other parameters taken are those from the Magellanic penguin). Since there is a general relationship between prey swim speed and prey size (Wardle, 1975; Peters, 1983) and the general division of penguin feeding habits is divided into those species that feed on fish and squid and those that feed on considerably smaller crustacea (Williams, 1995), we would predict that fish-feeding penguins equipped with external antennae will be more compromised than crustacean-feeders.

In fact, penguins may be able to compensate for the effects of externally attached devices by altering swim speed in a general sense (Wilson et al., 1986) so as to reduce metabolic rates. This can occur if species concentrate on smaller, slower-moving prey species than they might otherwise take or if travelling speeds are decreased. The consequences for the latter for foraging efficiency can be readily assessed using our model. If, for example, a penguin reduced travelling speed to 1 m s^{-1}, although the time spent travelling between patches would increase proportionately, overall foraging efficiency would rise to almost two even if prey capture speed were 1.7 m s^{-1} (Fig. 11). Thus, appropriate changes in foraging parameters might allow penguins equipped with antennae to

Table 2. *Effects of external antennae on foraging by Magellanic penguins*

	Antenna size (length × diameter)		
Effect (%) cf. Control birds	200 mm×2 mm	150 mm×3 mm	200 mm×3 mm
Increase in penguin mass	0.07	0.12	0.16
Increase in penguin cross-sectional area	0.22	0.25	0.33
Increase in drag at normal speed (1.77 m s^{-1})	30	39	81
Increase in energy expenditure at normal speed (1.77 m s^{-1})	23	31	79
Increase in drag at prey capture speed (2.25 m s^{-1})	39	49	95
Increase in energy expenditure at capture speed (2.25 m s^{-1})	48	65	147
Percentage effective foraging efficiency of equipped bird	49	41	22

Control birds = 100% for all parameters.

forage more efficiently than they would otherwise if they adopted their standard pattern and this may, in part, explain why penguins equipped with larger devices tend to travel more slowly (Wilson et al., 1986).

The process of determining the survival likelihood of Magellanic penguins can be examined conversely by setting a minimum foraging efficiency of 1.0 and determining the rate at which birds must encounter prey in order for them to be able to compensate for the increased drag imposed by external antennae. This might help us identify whether penguins could potentially be fitted with devices including antennae if they occurred at localities where prey are particularly abundant (although this premise assumes that the birds never stop foraging). Our model predicts that unequipped Magellanic penguins need to encounter a prey patch at least once every 85 min to have a foraging efficiency of exactly 1, whereas birds equipped with antennae 200 mm long and with a diameter of 3 mm would have to encounter a prey patch once every ca. 17 min. For prey densities in excess of this, penguins would be able to gain mass.

Our model is necessarily simplistic. For example, we only consider the effect of the antenna rather than the antenna plus attached device (cf. Culik et al., 1994b). In addition, we consider, for example, that the prey capture speed is that used for the whole of the dive during which prey are exploited, something that ignores the time (and energy) that birds need to descend from the water surface to the foraging depth. However, the energy for transit will also use body oxygen reserves, further limiting the time available for prey capture. Normal swim speeds of 1.77 m s^{-1} for Magellanic penguins swimming with an external antenna (200 mm×3 mm) will give an aerobic dive limit of ca. 40 s, which will allow a bird diving vertically to sample only the top 20 m of the water column. An unequipped bird swimming at this speed may dive for 94 s, reaching 80 m. Note that this treatise ignores recent buoyancy findings by Sato et al. (2002) and Wilson and Liebsch (2003), and the fact that Magellanic penguins do not descend vertically anyway (cf. Wilson and Wilson, 1995).

This work indicates that apparently relatively trivial bodies attached to swimming and diving animals may do more than simply substantially affect their energetics, although this in itself may affect standard dive parameters such as swim speeds, dive depths and rates of change of depth. Animals may also switch foraging strategies. The implications of this are profound and in light of this we would suggest that more careful assessment of the effects of externally attached devices is needed. This could be facilitated by current advances in logging technology, which are so substantial that is it now possible to equip free-living animals with minimal recording systems so that device-dependent changes in their behaviour can be documented as the attached units are carefully expanded in size. Such an approach would allow researchers to work with free-living animals, benefiting from all the advantages that this brings with it, while at the same time gaining quantitative data on the more intractable effects of devices.

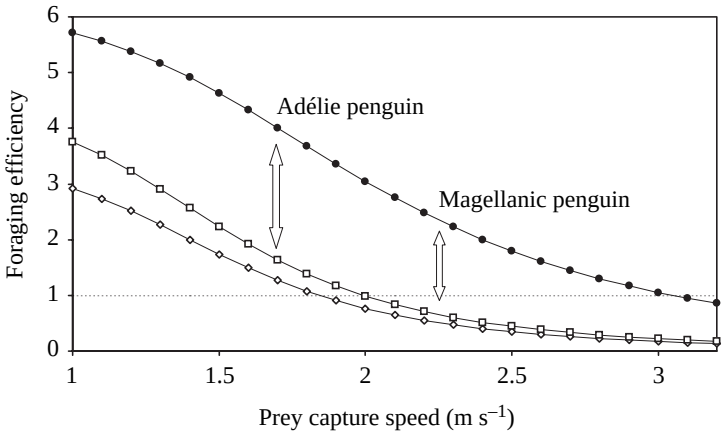

Fig. 11. Relationship between foraging efficiency (dimensionless) and prey capture speed for a Magellanic penguin foraging according to the conditions set out in the text. The upper line (closed circles) shows the efficiency for an unequipped bird while the lines delineated by squares and diamonds show the efficiency of birds transporting external antennae (200 mm×3 mm) at cruising speeds of 1 m s^{-1} and 1.77 m s^{-1}, respectively. The formula used for the antenna-derived drag was $F_d=0.913v^2–0.91v^{1.5}+0.183v^{0.5}+0.014$ and is the best-fit curve ($r^2=0.99997$, $F=10946$, $P<0.0001$) from the data corresponding to the relevant antenna (see Fig. 8A). Note that the model assumes that birds encounter a prey patch once every 36.3 min, travelling at a mean speed of 1.77 m s^{-1}, which corresponds to a patch separation of 3.86 km. Thus, swimming at 1 m s^{-1}, patches with the same spatial distribution are encountered less often (only once every 64.25 min), although the overall foraging efficiency rises. Arrows show the approximate scenarios expected for Adélie and Magellanic penguins due to their different prey capture speeds (see text).

Recommendations for antennae design

Although our treatise involves a number of assumptions, it is clear that externally attached antennae can be potentially extremely detrimental to the well-being of equipped marine animals. In order that effects be minimized we suggest the following avenues be explored:

(1) That researchers attempt to minimize both antenna length and diameter.

(2) That antennae be mounted at an angle as acute as possible to the normal direction of water flow.

(3) That antennae be as flexible as possible, or be set-up with a hinge system at their base, so that they lie flat at higher swim speeds, reducing the effective cross-sectional area of the antennae and thus the drag.

(4) That workers consider shaping the cross-section of the antennae so that they are tear-drop-shaped so as to minimize drag.

In any event, in view of the worrying consequences on penguin well-being implied by this study, we suggest that any workers using devices with external antennae on penguins set up rigorous controls to examine differences in foraging

behaviour between equipped and unequipped birds. The aim should be to demonstrate, *via* appropriate device modification etc., that equipped animals are able to perform in manner that is a broadly similar to unequipped conspecifics.

This study is dedicated to Günter Dorn on the occasion of his retirement, although this is no cause for celebration for us. The work was funded by the Deutsche Forschungsgemeinschaft and the VW Stiftung. We are grateful to many people for helping with field work, which was instrumental in enhancing our interpretation of antenna-induced effects on behaviour; Carlos Cendron, Raul Clarke, Esteban Frere, Hector Galleli, Patricia Gandini, David Grémillet, Mandy Kierspel, Sonia Laurenti, Alejandro Scolaro, Jorge Upton. We are also grateful to Ursula Siebert from the marine mammal unit and to Klaus Vanselow and Gero Bojens of applied physics section of the FTZ Büsum for excellent support with regard to swim canal usage. Finally we would like to thank Dave Gilgun and Bill Allsbrooke for putting up with us in Boston.

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