HYDRODYNAMIC ASPECTS OF DESIGN AND ATTACHMENT OF A BACK-MOUNTED DEVICE IN PENGUINS

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Summary

Wind tunnel and water tank experiments were carried out on a penguin model in order to optimise the shape and attachment of a back-mounted datalogger. Device-induced turbulence was minimised when the unit was placed in the most caudal position. Drag was further reduced by shaping the device to match the body contour. The hydrodynamic resistance of the package could be reduced by 65 % compared with an earlier unit. These results are discussed together with results from new studies on kinematics and energetics of underwater swimming of live instrumented penguins.

Introduction

It is virtually impossible to follow most marine homeotherms at sea. Consequently, many recording and transmitting devices have been developed to facilitate the study of the marine ecology of these animals (e.g. Castellini *et al.* 1992; Kooyman *et al.* 1992*a,b*; Martin and Smith, 1992). Such devices are, for the most part, attached to the external surface of the animal and are consequently liable to disturb patterns of water flow over the animal's body during swimming. Despite this, rather little has been published on their possible effects on the animal's behaviour or energetics.

Penguins have proved to be particularly tractable for studies involving externally attached packages (e.g. Kooyman *et al.* 1992*a*; Chappel *et al.* 1993). Some researchers have even attempted to determine the extent to which externally attached packages might alter penguin behaviour or energetics (for reviews, see Wilson *et al.* 1986; Wilson and Culik, 1992). However, such studies were rather crude because the mechanics and hydrodynamics of penguin locomotion were poorly understood. Some progress in hydrodynamic research has been made by Clark and Bemis (1979), Nachtigall and Bilo (1980) and Hui (1983). Using the deceleration method, Nachtigall and Bilo (1980) have determined a frontal drag coefficient (C_D) of 0.07 in gentoo penguins (*Pygoscelis papua*).

For the penguin body without wings these authors assumed a C_D of 0.05. Extremely low drag coefficients ($0.03<C_D<0.04$) have recently been measured by Bannasch (1994) for penguin models without wings. These measurements as well as flow visualisation experiments (Oehme and Bannasch, 1989; Bannasch, 1994) showed that the penguin body is highly streamlined. Consequently, any item attached to the penguin is likely to disturb the flow pattern around the body and thus to cause a substantial impediment to the bird. However, consideration of penguin swimming kinematics, body geometry and drag should enable us to design devices that, when attached to swimming birds, will lead to minimal additional energy expenditure and, therefore, cause minimal changes to their behaviour.

A pioneering study on the reduction of drag caused by devices mounted on the back of flying birds was carried out by Obrecht *et al.* (1988). We have used penguin models in wind tunnel and water flume experiments in an attempt to optimise the shape of a new logger to be attached externally to pygoscelid penguins (Wilson *et al.* 1993). We studied the form of the device and the attachment position on the bird.

Materials and methods

Casts of the wingless body of a gentoo (*Pygoscelis papua*) and a somewhat smaller chinstrap penguin (*P. antarctica*), made from fibreglass-reinforced plastic (Bannasch and Fiebig, 1992), were available from earlier experiments (Oehme and Bannasch, 1989). A previous study showed that the hydrodynamic drag characteristics of both models were similar, when compared at similar Reynolds numbers (Bannasch, 1994).

The initial (non-optimised) datalogger, including electronics, batteries and sensors, measured $120\,\text{mm}\times57\,\text{mm}\times33\,\text{mm}$ (maximum dimensions) when incorporated into an approximately streamlined package. To prevent fin or rudder effects we used a flat construction. We decided to use tape to attach the package (see Wilson and Wilson, 1989) to living birds in order to eliminate long-term and harness effects such as those described by Kenward (1987). The aim of this study was to optimise the device. In the respective experiments, we could vary the position of the package on the bird and the shape of the housing. The main electronic unit (dimensions $90\,\text{mm}\times55\,\text{mm}\times10\,\text{mm}$) was invariable in size and shape, but we could vary the arrangement of the other components relative to this unit. For testing, replicas of all components were made from plastic.

Point of attachment

Flow disturbance becomes most pronounced at lower Reynolds numbers, so a wind tunnel, in combination with the smoke-wire technique for flow visualisation [Herrman-Föttinger-Institut (HFI), Technische Universität Berlin, see Leder and Geropp, 1988], was considered to be appropriate for the determination of the best position for device attachment. In the wind tunnel, a thin wire (diameter 0.3 mm) was mounted vertically approximately 1.5 m in front of the penguin. The wire was dampened with oil (Odina 17) and then heated to 200 °C by a 4 A electrical current. The oil formed small droplets before vaporising and producing a thin layer of parallel smoke lines in the air-stream.

In the present configuration, flow visualisation was limited to relatively low wind

speeds (v_{max}=5.6 m s^{-1}). This wind speed may have been too low to prevent flow separation at the surface of a small body. An increase of wind speed causes a downstream shift of flow detachment (Oehme and Bannasch, 1989, and unpublished data). As the geometry of the flow around a body depends on the Reynolds number, a delay of flow detachment can be achieved either by increasing the flow velocity or by increasing the size of the body. We therefore used the larger penguin model (gentoo) in this series of experiments.

On the basis of earlier experience and a consideration of the functional anatomy of penguins (Bannasch, 1986, 1987) as well as various ethological aspects (Wilson and Culik, 1992), it was decided to attach the device to the back of the penguin. In penguins, the point of attachment is not restricted to the bird's centre of gravity, which is an important consideration in flying birds (Kenward, 1987). A fairly large area in line with the backbone, beginning at the level of the shoulder joints and ending in front of the first free vertebra of the tail, was available as a potential attachment site. A wind velocity of 5.6 m s^{-1} was found to be sufficient to prevent any flow separation in that area of the penguin model. The velocity distribution in different zones of the boundary layer around the penguin was measured using small hot-wire sensors (HFI) steered in three dimensions by electronic remote control. They were connected to a PSI constant-temperature anemometer (Prosser, UK).

The size and shape of our logger were largely determined by the main electronic unit. We started the optimisation tests with a replica of that unit. The device was placed in the most anterior position (directly behind the penguin model's 'neck') and then moved backwards in subsequent tests. Smoke-wire experiments were carried out for each point of attachment. Several sequences were videotaped from the side and then analysed frame by frame in order to distinguish clearly between device-induced effects and those possibly caused either by turbulence in the tunnel or by a temporarily inhomogeneous smoke pattern.

Shape optimisation

In a second series of experiments, the shape of the package fixed in the final position was optimised to minimise flow disturbance. This was carried out under visual control using the smoke-wire system and video camera described above. The contours of the main unit appearing to cause turbulence were gradually smoothed by adding plasticine. Then, maintaining the shape, most of the plasticine was replaced by replicas of the other components of the logger.

Finally, the optimised device (logger$_f$, suffix f for final shape) and attachment position were examined by making drag measurements in a water tank (3.3×10^6 l) capable of circulating water at 60 000 l s^{-1} [Versuchsanstalt für Wasserbau und Schiffbau (VWS), Berlin]. In the test section of the tank (5 m wide), water depth was adjusted to 1.5 m by elevation of the floor. The penguin model was fixed to a 1 m long steel bar (diameter 15 mm) placed in the long axis of the body. The end of the bar was mounted on a vertical rod encapsulated by a low-drag profile, and the rod was connected to a balance for drag measurement. The model was submerged in the middle of the test section to a depth of 75 cm. Further details are given in Bannasch (1994).

In the water tank experiments, we could cover the whole range of Reynolds numbers likely to be reached by swimming penguins in nature. We were interested in determining the most adverse effect (maximum drag increase) induced by our device, so we decided to use the smaller chinstrap model for this experiment, for which the increase in drag caused by instrumentation was expected to be highest.

Measurements of logger$_f$ were compared with those for a device (logger$_i$) shaped following the suggestions of Obrecht *et al.* (1988) for telemetric devices in flying birds. Because stream velocity varied slightly between series of measurements, comparisons were made by using a square function approximation. We then used the procedure described by Obrecht *et al.* (1988) to determine, for each of the two devices, the stream-velocity-dependent incremental drag ΔD (N) by subtracting the measurements made without the device from those made with the device. This value was converted into incremental effective flat-plate area (ΔA, m^2) using:

$$\Delta A = \Delta D / q, \tag{1}$$

where q is dynamic pressure (N m^{-2}), itself given by:

$$q = \rho v^2 / 2, \tag{2}$$

where ρ is water density (kg m^{-3}) and v is stream velocity (m s^{-1}).

Dividing the incremental flat-plate area by the actual frontal area of the device (A_d), we obtained the drag coefficient (C_D) for the device using:

$$C_D = \Delta A / A d. \tag{3}$$

Preliminary data from live penguins

In Antarctica, before deployment in the field, the device was tested on live Adelie penguins swimming in a water canal. Swimming speed and energetics were measured and compared with those of birds without a logger (for details see Culik *et al.* 1994). The care and experimental use of animals were approved by, and within, institutional guidelines.

Results

Point of attachment

Substantial turbulence was generated by the incomplete but non-optimised package in the two most anterior positions (Fig. 1). The general conclusion that a device causes least turbulence when placed most caudally was also supported by measurements of the velocity distribution in the boundary layer on the back of the penguin (Fig. 2). As predicted by theory, in the frontal part of the body (open squares in Fig. 2), the boundary layer was thin, with a steep velocity gradient and a pronounced zone of hypervelocity caused by displacement. This hypervelocity means that any item placed at this point

Fig. 1. Smoke visualisation of flow disturbances caused by a non-optimised device (main unit of our logger, dimensions 90 mm×55 mm×10 mm) attached to three positions on a model of a gentoo penguin.
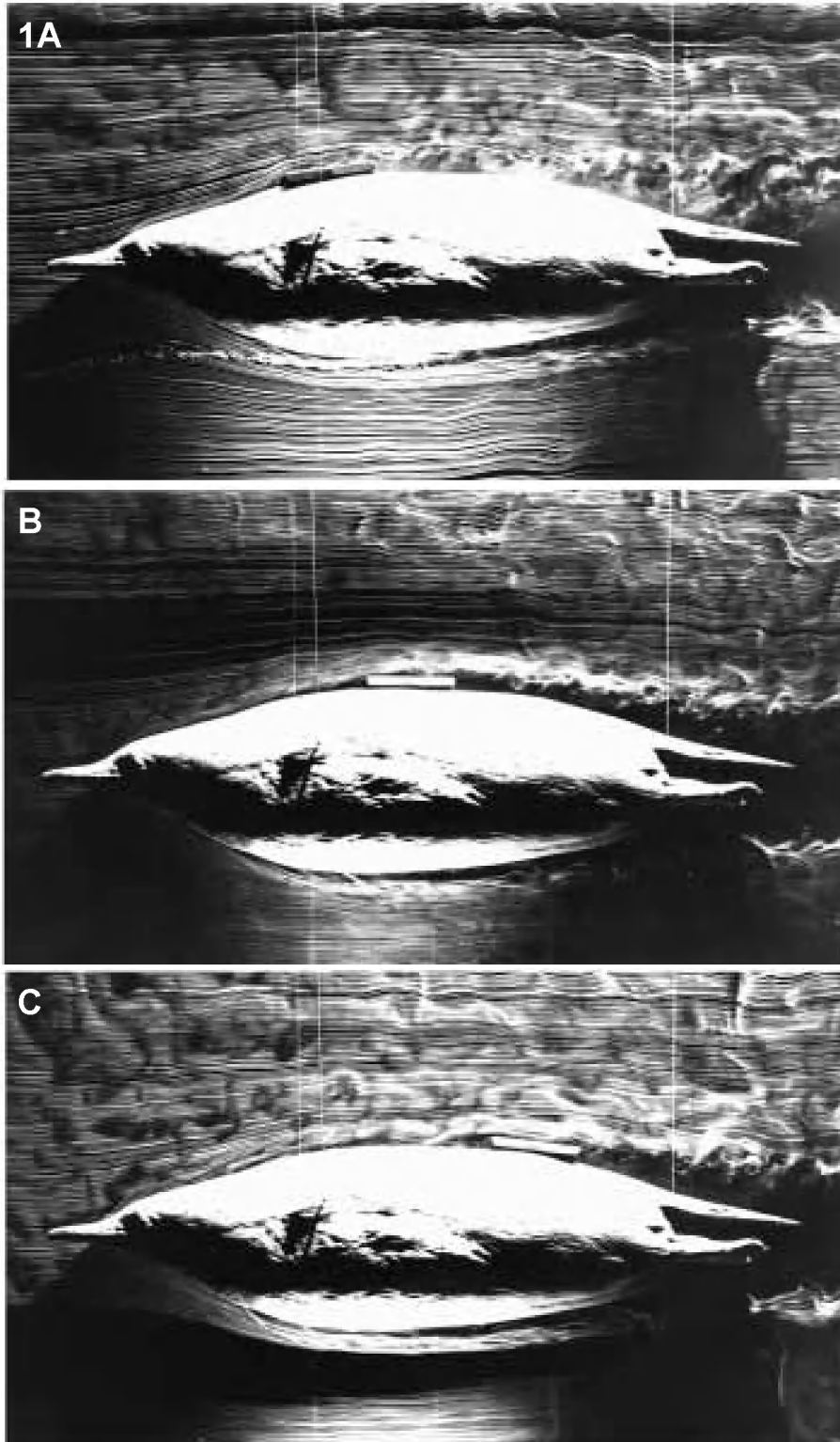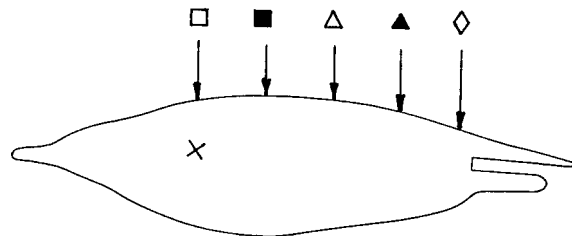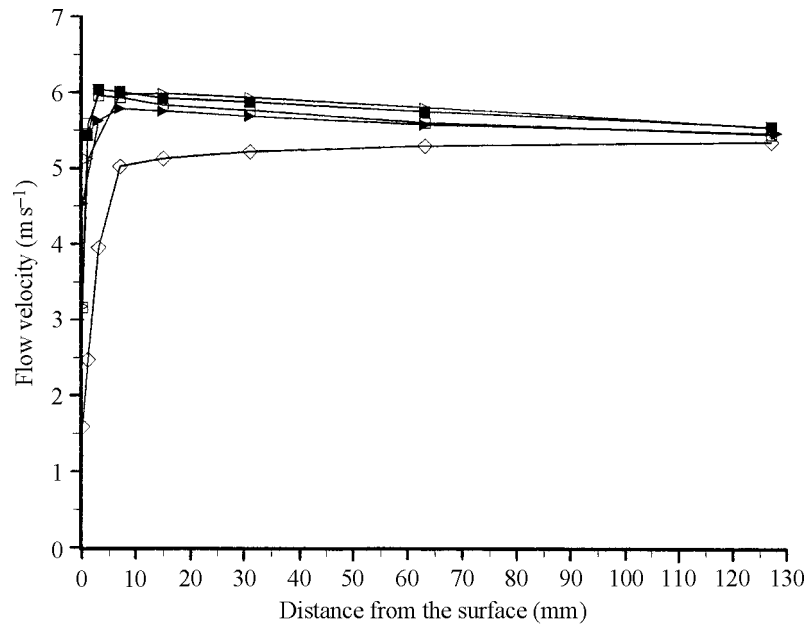
Fig. 1

Fig. 2. Flow velocity distribution with vertical distance from the surface measured at five points along the mid-line of the upper surface of the gentoo model at a free-stream velocity of 5.6 m s^{-1} in the wind tunnel. This air velocity corresponds to only 0.35 m s^{-1} in water (see text for interpretation).

must experience increased drag forces and, in addition, may generate turbulence that will disturb the boundary layer over a large area of the body surface behind and around it.

At the posterior end of the body, the boundary layer was thicker (open diamonds in Fig. 2) and the velocity gradient reduced. A thicker, and probably turbulent, boundary layer has the potential to smooth the flow over rough surfaces, such as the package used here.

The velocity distribution was determined at a free-stream air velocity that corresponds to only 0.35 m s^{-1} in water. At higher stream velocities, the thickness of the boundary
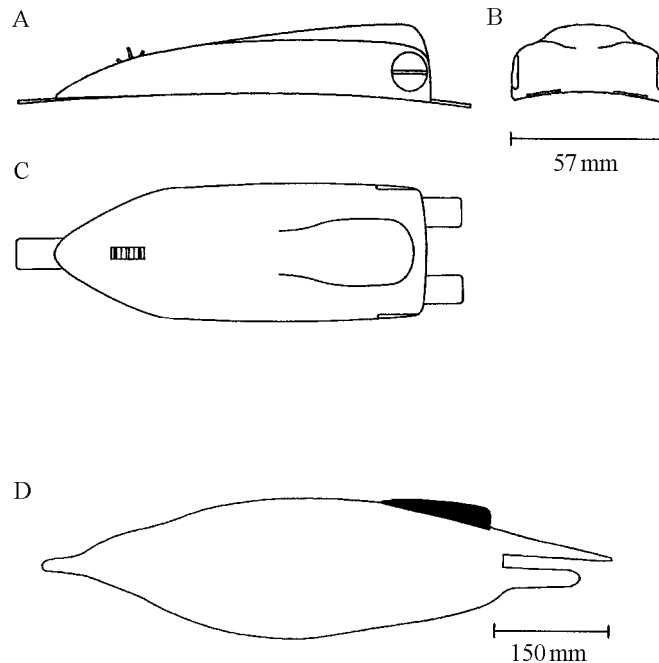
Fig. 3. Shape (A, side; B, rear; C, top view) and point of attachment of our device to a gentoo penguin body (D). In A and C, the position of the speed sensor (paddle wheel) at the front and the screw for battery and interface housing at the rear of the logger are indicated. The rectangular flat tongues in front of, and at the end of, the device were added to ease tape attachment to the feathers of live penguins.

layer will decrease, but the general tendency illustrated here will be maintained (Hoerner, 1965; Schlichting, 1982).

Shape optimisation

To prevent unpredictable interference by flow through gaps between the trunk and the instrument (due to differences in the shape of the rounded body and the flat package), the device was shaped to the curve of the back. Then, step by step, plasticine was added mainly to the front and upper surfaces of the instrument. During this optimisation process, the device became longer and it also became thicker at its posterior end. The available extra volume around the main unit was used to incorporate the other components of the logger so that they did not alter the shape. The final device was approximately wedge-shaped. The final contours of the unit (Fig. 3A–C) extended the body line smoothly (Fig. 3D). After ensuring visually that flow over the instrument was smooth from the leading edge to the trailing edge, we attempted to reduce turbulence caused by the rear of the device.

The caudal position of the unit, however, did not allow us to streamline its rear end. To prevent flow detachment, it would have been necessary for the rear end of the device to slope towards the penguin's body surface at an angle of less than 7 ° relative to the flow
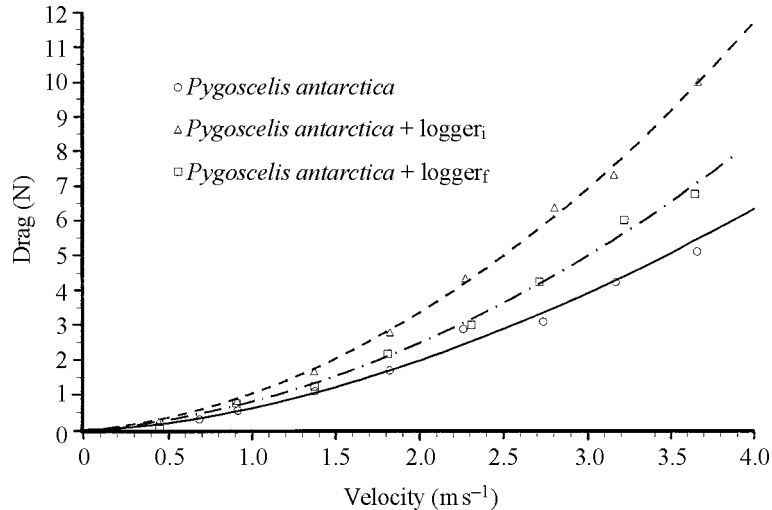
Fig. 4. Drag forces plotted against velocity for undisturbed and instrumented chinstrap penguin models. Logger$_i$, initial shape; logger$_f$, final shape.

(R. Nagel, personal communication). This would have elongated the device so that it terminated beyond the tail. Since a rounded end was considered likely to promote a rapid forward–backward shift of the point of flow detachment, possibly causing unpredictable vibration, the device was terminated with a relatively sharp edge. This ensured abrupt and controlled flow separation near the trailing edge of the model. The maximum dimensions of the device were 150 mm×57 mm×37 mm, and A_d was 2109 mm^2. When attached to a penguin, the maximum height of the device over the body contour was 29 mm (due to its concave lower side).

Drag measurements

Although the device described here (logger$_f$) and that built according to Obrecht et al. (1988) (logger$_i$) had the same frontal area and, if placed at the posterior end of the body, did not enlarge the cross-sectional area of the model penguin, logger$_i$ increased body drag by 52–71% at medium speeds ($1.5\,\mathrm{m\,s^{-1}}{<}v{<}2.5\,\mathrm{m\,s^{-1}}$) and by up to 100% at higher speeds ($v{=}4\,\mathrm{m\,s^{-1}}$). In contrast, logger$_f$ caused increases of only 15–25% and 41% respectively (Fig. 4). The drag coefficients of both devices were slightly dependent on stream velocity, increasing from 0.30 to 0.34 for logger$_i$ and from 0.09 to 0.14 for logger$_f$ at $1\,\mathrm{m\,s^{-1}}{<}v{<}4\,\mathrm{m\,s^{-1}}$. The mean values were 0.32 and 0.11, respectively, for the velocities tested. Shape optimisation therefore caused a drag reduction of approximately two-thirds.

Preliminary data from live penguins

Before deployment in the field, the effects of the device on swimming kinematics and energetics of pygoscelid penguins were studied in a water canal in Antarctica. In Adelie penguins, although logger$_f$ was 10.5 % of bird cross-sectional area, swimming speed was

reduced by only 8.3 % (mean $1.57 \, \mathrm{m \, s^{-1}}$ *versus* $1.70 \, \mathrm{m \, s^{-1}}$, $N=185$ and 118, respectively, t-test, $P=0.018$). Mean metabolic power input (P_i) required for swimming at speeds was not higher (t-test, $P=0.37$) for instrumented penguins ($P_i=66.3 \, \mathrm{W}$, $N=157$) than for those without a device ($P_i=62.8 \, \mathrm{W}$, $N=109$). The power increment averaged only 5.6 % while swimming with the logger (for more complete data see Culik *et al.* 1994). P_i multiplied by muscle efficiency and thrust power efficiency of the wings yields the mechanical power output of the swimming bird. Mechanical power divided by speed gives the drag force experienced by the body. Note that wing-generated drag is included in thrust power efficiency (see Bannasch, 1994). Assuming that the muscle efficiency and wing efficiency were not altered by the extra loading in Adelie penguins carrying a device, then total body drag was increased by 14.3 %. Considering that our chinstrap model was slightly smaller than the Adelie penguins tested in the swim canal, this estimation agreed surprisingly well with the measurements obtained in the water tank at comparable flow velocities. Although our device was five times more voluminous than one of our older units (logger$_i$ was removed from our research programme), optimization of shape and attachment reduced its effect on swimming energetics by 87%.

We also observed some changes in the swimming kinematics of instrumented penguins. At lower swimming speeds, some penguins lifted their tail slightly, probably to compensate for the turbulence generated by the package. Instrumented penguins must increase their thrust production to balance the surplus drag forces of the device. The birds cannot enlarge their wing area, but they can increase their wing span by decreasing the sweepback angle and they can increase either the frequency or the amplitude of the wing beat (appropriate angles of attack have to be adjusted) (Clark and Bemis, 1979) or both. Our kinematic pictures (video and high-speed films) showed large variations in all these variables in consecutive wing-beat cycles of the same bird, as well as between individuals. Generally, the amplitude and the wing span were more variable than the wing-beat frequency. Thus, because of the lower average speed, the stride length became shorter. These considerations suggest that, in penguins carrying a device, not only body drag but also the thrust power efficiency of the wings may be affected. Therefore, the agreement between the device-induced drag increment measured in a rigid chinstrap model and that calculated for live Adelie penguins may be rather fortuitous. The cost of transport, which is an important consideration in energetics of swimming animals, is calculated as metabolic power input divided by speed. Therefore, assuming that the error introduced by the assumption of (nearly) constant muscle and wing efficiencies for instrumented birds is moderate, the incremental cost of transport (%) would numerically equal the device-induced drag increment (%). Using this assumption, drag measurements can be used directly to estimate possible energetic and ecological effects of an external device on swimming animals.

Discussion

Point of attachment

When positioning back-mounted devices, a number of constraints other than hydrodynamic effects must be considered. A caudal position, determined here to be

favourable in penguins, may not be applicable to flying animals because it will change their centre of gravity (Kenward, 1987). In flying birds, devices should be placed between the shoulder blades to be optimally balanced (see Obrecht *et al.* 1988). In aquatic animals, device mass is considered to be less important (see Wilson *et al.* 1991), but attachment to the caudal part of the body may impede the generation of thrust by animals that use their tail for propulsion (e.g. fish, dolphins and seals). McGovern and McCarthy (1992) attached acoustic transmitters mid-way along the body of eels, which may partially avoid such problems. Caudal attachment may not be suitable for devices that can only transmit information when they are out of the water. In seals, transmitters are often fixed to the head for this reason (e.g. Hammond *et al.* 1992). In penguins, transmitters have been attached in front of the mid-point of the back (e.g. Ancel *et al.* 1992) or just behind the point of maximum girth (Kooyman *et al.* 1992a).

Devices whose position is not restricted by the constraints of radiotelemetry (e.g. depth gauges) have been attached in many positions (Wilson *et al.* 1991; Culik and Wilson, 1992; Gales *et al.* 1990). Our results demonstrate that some of the adverse effects caused by external devices could be reduced by changing their point of attachment. Chappell *et al.* (1993) attached their time–depth recorders to 'the centre of the lower back' of Adelie penguins. Kooyman *et al.* (1992a) emphasised that they did their best to streamline their dive recorders and to place them caudal enough 'to be behind where flow separation occurs and turbulent flow begins, thus reducing drag as much as possible'.

Previous experiments with flow visualisation on penguin models (Oehme and Bannasch, 1989; Bannasch, 1994), the data presented here and recent comparative studies that used models of little (*Eudyptula minor*) and emperor (*Aptenodytes forsteri*) penguins (R. Bannasch and B. Cannell, unpublished data) indicate that all these penguin species are shaped to prevent any flow separation over the contours of their body. Drag measurements from five penguin species (R. Bannasch and B. Canell, unpublished data) support this general conclusion. Nevertheless, for the attachment of external devices, we can use the effect that the boundary layer is, or becomes, turbulent and increases rapidly in thickness when the pressure increases behind the maximum girth of the bird's body (Bannasch, 1993, 1994). In the boundary layer, the flow velocity is reduced. Consequently, if placed in that area, the device may cause less drag (possibly assisted by relaminarisation), and flow disturbances may be kept to a minimum. However, the size and design of the external units must correspond to body shape in this region as well as to the respective flow geometry.

In larger animals (e.g. king and emperor penguins), the boundary layer may become too thick to allow accurate speed measurements by caudally mounted loggers. In these cases, reversed flow may occur close to the body.

Although we were unable to quantify the effect of changing the point of attachment on the resulting drag increment, the quality of the flow pattern alone clearly indicates that the most caudal position is best for back-mounted devices in penguins and can be recommended generally for devices that do not rely on telemetric data transmission in aquatic environments, or where speed measurements are not relevant. Alternatively, devices could even be attached underneath the tail, if size permits. In this case they would be in the wake of the body and the drag increment might even be zero. However, other

problems could arise from excrement or from shocks caused by contact with the ground (e.g. when the bird jumps out of the water or passes over rocks).

Finally, if devices could be designed to be preened under the contour feathers, their drag might be negligible. Under such conditions, the point of attachment to the body would no longer be restricted by the hydrodynamic aspects considered above.

Shape optimisation

A great variety of devices have been attached to flying and swimming animals. Some were box-like, sometimes with oblique or rounded edges (satellite transmitters applied to birds, e.g. Howey, 1992; dive recorders applied to penguins, e.g. M. Whitehead, personal communication). Others were cylinders (speed meters on penguins, Wilson and Bain, 1984), some with a rounded leading edge (time–depth recorders on seals and penguins, e.g. Gentry and Kooyman, 1986).

Fluid-dynamic characteristics (drag coefficients) of simple geometric shapes can be found in the literature (e.g. Nachtigall and Bilo, 1980; Schlichting, 1982; Bohl, 1991). Drag coefficients range from 1.05 for a cube placed perpendicular to the stream to 0.04 for spindles with zero angle of attack. A cylinder with a length:thickness ratio of 4:1, if placed with its long axis in the direction of the stream, has a drag coefficient of 0.85 (Bohl, 1991). For a streamlined penguin body (without wings), which has nearly the same length:thickness ratio, the lowest value for the drag coefficient was found to be 0.03 (Bannasch, 1994). Therefore, at a fixed speed, a cylinder whose frontal area is only 3.5 % of that of a penguin's body is likely to produce a drag similar to that of the bird. Such a cylinder corresponding to a chinstrap penguin (frontal area approximately $0.02\,m^2$, c.f. Oehme and Bannasch, 1989) would have a diameter of only 3 cm.

The conclusion, however, that an external device shaped like a penguin, with a diameter at maximum girth of 3 cm, would cause a drag increment of only 3.5 % for a swimming penguin is misguided. von Mises (1945, cited in Obrecht *et al.* 1988) showed that the drag of a streamlined body with a secondary smaller body attached to it is generally *greater* than the sum of the drag measured on each of the two bodies separately. In penguins, this effect may be avoided only by extremely small devices attached underneath the tail or preened under the contour feathers. Shape optimisation should therefore be carried out with the external device in place on the animal.

Data on the frontal area of devices without consideration of fluid-dynamic shape characteristics, as commonly reported in the literature, provide limited information about the drag force that they will cause. Wilson's (1989) attempt to correlate maximum dive depth per foraging trip with device cross-sectional area for Adelie and gentoo penguins should be reconsidered in this context. The general conclusion that devices should be miniaturised cannot be overstressed, so data on the frontal area of devices are useful, if only to stimulate miniaturisation. At present, however, miniaturisation is limited by technology and, if some progress is achieved, it is often offset by the addition of new functions and/or sensors to obtain more complete data sets. In aquatic animals, where the mass of the device is considered to be less important, its shape improvement will be more substantial than some degree of miniaturisation in drag minimisation.

The importance of streamlining devices has been stressed by many authors. As far as

we know, however, the only serious experimental work to address this question was carried out by Obrecht *et al.* (1988). They found that, apart from arranging the device components into an elongated shape, which minimises the frontal area, the drag of a device can be reduced by approximately one-third by adding a rounded fairing to the front and a pointed fairing to the back. Similarly, we varied the shape of the package (main unit) by adding material to the front and rear only. The advantage of the flow-visualisation method applied here was that the material could be added gradually and the surplus volume could be used to incorporate the other components of our logger. Thus, shape optimisation was not limited to the choice between a number of end or blister fairings prepared in advance (see Obrecht *et al.* 1988), and the final construction was as compact as possible. The final shape was developed under visual control, ensuring that device-induced turbulence could be minimised.

The final design, which had contours that extended those of the body smoothly behind the maximum girth and did not alter the frontal area of the animal, seems to be the best solution for devices that are to be attached to penguins. In combination with the use of tape for attachment, this allows a large part of the frontal and lateral edges of the device to be covered by the contour feathers of the bird. This may further reduce any dynamic pressure peak at the front of the package.

Drag measurements

The drag measurements show that attachment of a device to the lower back is most efficient in conjunction with shape optimisation. Compared with $logger_i$, which was considered to be streamlined, $logger_f$ reduced the device-induced drag increment by another 65%. However, the measurements with a rigid model may overestimate the device-induced drag increment in live animals for several reasons. (1) The models we used were copies of animals arranged in an optimal posture for uninstrumented penguins. A live animal may adjust its body shape, or the posture of the head, tail and feet, in order to compensate for some of the changes in the flow conditions caused by the package. (2) In our experiments, we did not assess whether the compliant and micro-structured plumage surface, as discussed by Bannasch (1994), influenced drag reduction. It is unclear whether these mechanisms would compound or compensate for the effects of the device on live penguins. (3) In order to estimate the most adverse effect caused by an external device, we used a particularly small animal model in the experiments. In larger penguins, or using a smaller device, the drag increment would be more moderate. (4) In these experiments, we only considered the fluid resistance of the trunk under steady flow conditions. During swimming, however, the wings produce drag forces (profile drag and induced drag) that represent a substantial proportion of the total fluid resistance. In addition, there is a complex interaction between the alternating flow around the wings and the flow around the body (Oehme and Bannasch, 1989; Bannasch, 1994). There is no approach, other than studies on live birds, that can estimate device effects under such complex (non-steady) flow conditions. Generally, we had expected that the total drag increment in live animals would be less than in our experiments. This, however, was not confirmed by studies on the energetics of instrumented penguins swimming in a water canal (Culik *et al.* 1994). We do not know whether, in these tests, the various effects

mentioned above may have compensated for each other. At present, it seems that data on incremental drag caused by devices on models can be related directly to quantitative energetic and ecological effects in live instrumented animals. There is no doubt that they represent a useful and strong criterion for device optimisation.

Observations

Our observations indicate that external devices may affect penguin swimming in a rather complex way. The consideration of drag measurements obtained in experiments with models alone would be incomplete without tests on live birds.

Finally, it should be mentioned that, in the wild, penguins forage in groups. In studies on emperor penguins swimming between ice holes, Kooyman *et al.* (1992*b*) found that encumbered birds departed with the other birds but usually returned last, although still as part of the group. However, the swimming effort of the instrumented birds was greater and they compensated, not so much by lagging behind the other birds, but by occasionally skipping dives with the group. The design of low-drag devices is thus particularly important in studies on penguin species, which travel great distances, and for enabling us to measure foraging variables that approach those of unequipped individuals as closely possible. At present, apart from miniaturisation, substantial improvement to external devices can be achieved by optimisation of their shape and attachment.

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