PRECISE MONITORING OF PORPOISING BEHAVIOUR OF ADÉLIE PENGUINS DETERMINED USING ACCELERATION DATA LOGGERS

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Summary

A new method using acceleration data loggers enabled us to measure the porpoising behaviour of Adélie penguins (*Pygoscelis adeliae*), defined as a continuous rapid swimming with rhythmic serial leaps. Previous hydrodynamic models suggested that leaping would be energetically cheaper when an animal swims continuously at depths of less than three maximum body diameters below the water surface. In the present study, free-ranging Adélie penguins leapt at a mean speed of $2.8\,\mathrm{m\,s^{-1}}$ above the predicted threshold speed (0.18–$1.88\,\mathrm{m\,s^{-1}}$). Wild penguins reduced drag by swimming deeper ($0.91\,\mathrm{m}$) and did not swim continuously within the high-drag layer while submerged. This indicates that previous calculations may be incomplete. Moreover, leaps represented an average of only $3.8\,\%$ of the total distance travelled during the porpoising cycle, which would make energy savings marginal. Among the six penguins used in our study, two did not porpoise and three porpoised for less than $7\,\mathrm{min}$, also indicating that this behaviour was not important during travel to and from foraging sites, as has been previously suggested. Birds mainly porpoised at the start and end of a trip. One explanation of porpoising might be an escape behaviour from predators.

Key words: porpoising, locomotion, Adélie penguin, *Pygoscelis adeliae*, acceleration data logger, monitoring.

Introduction

During swimming in the wild, animals such as dolphins and porpoises can leap briefly out of the water to breathe without reducing their speed. This is termed 'porpoising' behaviour and has also often been observed from the shore for penguins (Murray Levik, 1914; Ainley, 1972; Stonehouse, 1972; Trivelpiece et al., 1986; Chappell et al., 1993).

Various hydrodynamic models have suggested that this behaviour functions to conserve energy (Au and Weihs, 1980; Blake, 1983; Blake and Smith, 1988). Most aquatic animals are highly streamlined, with drag coefficients as low as 0.03 (e.g. penguins; Bannasch, 1995). When a streamlined body with a fineness ratio (body length/maximum body diameter) of 5.6 is towed within three times its diameter from the water surface, the drag coefficient can increase by up to five times (Hertel, 1969). A comparison between the energy required for swimming continuously at this depth below the surface and the energy expended during a leap suggested that leaping above a threshold speed (0.18–$1.88\,\mathrm{m\,s^{-1}}$ in the case of Adélie-sized penguins; Blake and Smith, 1988) should be more efficient than swimming continuously within the high-drag layer (Au and Weihs, 1980; Blake, 1983; Blake and Smith, 1988).

However, to date, these predictions have not been verified by measurements in wild free-ranging penguins, because the measurements have been difficult to make. Trivelpiece et al. (1986) used signal characteristics from radio transmitters to distinguish five types of foraging behaviour of gentoo (*Pygoscelis papua*) and chinstrap (*Pygoscelis antarctica*) penguins, including porpoising. However, because their units received the signal only when the bird was at the surface, when the antenna was not submerged, it was impossible to separate porpoising from swimming with brief pauses at the surface for short breaths but no leaping.

Here, we report on a new device and method to measure accurately the swimming behaviour of seabirds or mammals. Using this device on free-ranging Adélie penguins for the first time, depth and acceleration data were obtained to provide information about the porpoising behaviour of penguins during a foraging trip. Using these data, the role of porpoising behaviour is discussed.

Materials and methods

This study was conducted at a colony of approximately 1800 breeding pairs of Adélie penguins (*Pygoscelis adeliae*) in

Dumont D'Urville, Terre Adélie (66.7°S, 140.0°E), during austral summer 1996/1997.

The behaviour of penguins was studied using a multi-channel data logger that recorded depth data and the magnitude of acceleration every second (NIPR-400D2G: 42.7 g, 19 mm diameter, 90 mm length; Little Leonardo, Tokyo, Japan). Depth resolution was 1.56 m. The logger used two piezo-resistive accelerometers (model 3031, IC sensors) with filtering of the analog sensor signal in the band pass between 0.53 and 64 Hz. The measuring ranges of the device were 0–11.8 m s^{-2} (parallel to the main axis of the logger) and −11.8 to 11.8 m s^{-2} (parallel to the vertical axis of the logger). The acceleration is recorded as an integrated value during the sampling interval. The D2G logger was attached to the back of penguins to record vertical acceleration in the direction of the main axis of the penguin and horizontal acceleration along the axis crossing the penguin's body from back to breast.

Swimming speed and depth were monitored using a speed/depth/temperature (PDT) logger (UWE-200PDT: 59.2 g, 20 mm diameter, 120 mm length, sampling interval 1 s; Little Leonardo, Tokyo, Japan). The depth range was 0–200 m (resolution 0.05 m) and the temperature range was −22 to 50 °C. The PDT logger was calibrated using depth and speed data collected from the animals (Fletcher et al., 1996; Crocker et al., 1997): the rate of change in depth, or vertical speed, was calculated every 1 s and plotted against the total number of propeller rotations over the same 1 s, expressed in revolutions per second (RPS). Assuming that the lowest RPS value for a given swimming speed represents vertical diving, then the lowest swimming speed for each vertical speed is equal to the rate of change in depth. A regression line through the lowest RPS value for each vertical speed is the calibration line for swimming speed. The stall speed of the recorder was determined experimentally to be 0.3 m s^{-1}. Speeds below this value were considered indistinguishable from zero. The linearity in the relationship between RPS and flow speed was tested in a pool. An electric fishing reel was used to tow the loggers at several speeds. The relationship was linear from 1.0 to 2.5 m s^{-1}, and the coefficient of determination for each logger was greater than 0.98.

Twelve free-ranging adult Adélie penguins were equipped with D2G loggers ('single-set loggers'), and four birds were equipped with both D2G and PDT loggers ('double-set loggers') during the breeding period. Penguins were captured on their nests. They had a mean mass of 4.4±0.28 kg (mean ± s.d., N=12). The data loggers were fixed using cyanoacrylate glue (Loctite) onto their back in a medium caudal position to reduce drag (Bannasch et al., 1994; Culik et al., 1994). The data logger units represent only 1.6 % of the penguin's cross-sectional area so have little effect on the swimming speed (Wilson et al., 1986; Culik and Wilson, 1991). Penguins were caught following their return from foraging, and the loggers were retrieved. Each penguin was released within 30 min of capture. Six of the single-set loggers worked properly and delivered reliable data for one foraging trip (birds A, B, C, D, E and F). None of the double-set loggers recorded the complete foraging trip. The data from single-set loggers were used in the analysis of the distribution of porpoising and of the variables that are not related to the swimming depth because the depth resolution was insufficient for the purpose, whereas the data from double-set loggers were used to analyze variables such as swimming depth, speed and distance travelled between leaps derived from these birds.

Additional experiments were performed at the Port of Nagoya Public Aquarium, Japan. The pool used was 21 m long and 2.1 m deep, with width ranging from 0.25 m to 4 m. It was filled with salt water at 7 °C. The behaviour of two Adélie penguins equipped with a D2G data logger was recorded by a video camera (30 frames s^{-1}) to determine the acceleration profile of porpoising and to evaluate the effect of the logger on the swimming behaviour of the penguins.

The porpoising cycle was defined as one leap followed by a swimming phase. A porpoising period was defined as several porpoising cycles with no inter-leap phase longer than 1 min and a swimming depth shallower than 5 m.

The horizontal distance travelled by swimming between individual leaps was calculated as:

$$H = \sum_{t=t_1}^{t_2} \sqrt{[TS(t)]^2 - [D(t) - D(t-1)]^2}, \qquad (1)$$

where H is the horizontal distance travelled, T is the sampling interval (s), $S(t)$ is the swimming speed (m s^{-1}), $D(t)$ is the diving depth (m), t is time (s) and t_1 and t_2 represent the start and finish time of the swimming phase of each porpoising cycle, respectively.

Results

The porpoising behaviour observed in Adélie penguins in the aquarium often occurred among many birds simultaneously. These recordings were used to determine the porpoising profile recorded by the D2G and PDT loggers (Fig. 1): vertical acceleration remained relatively constant at approximately 0.5 m s^{-2} during subsurface swimming between leaps. Vertical acceleration increased to approximately 3 m s^{-2} during a jump phase, which includes jumping from and re-entering the water.

In wild birds, foraging trip duration averaged 16.8±6.8 h (mean ± s.d., range 8.3–25.7 h, N=6 birds). During the jump phase in the wild, vertical acceleration increased to approximately 1 m s^{-2}, twice the value during subsurface swimming (Fig. 2). Porpoising speed was constant at approximately 3 m s^{-1} except during the jump phase, when speed decreased because the propeller of the logger does not rotate in air.

We used this specific acceleration pattern, the sharp peak and the constant shape of vertical acceleration as the criteria to distinguish this porpoising behaviour from other behaviour patterns.

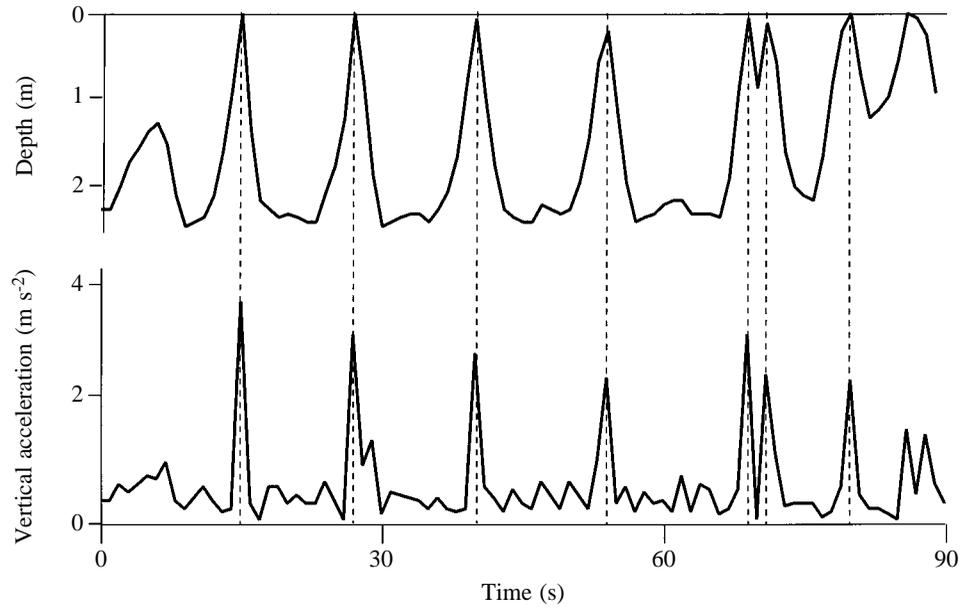Among the six birds, two exhibited no porpoising during the

Fig. 1. Vertical acceleration and depth profiles of a porpoising Adélie penguin at the Port of Nagoya Public Aquarium. Leaps are indicated by vertical dotted lines.
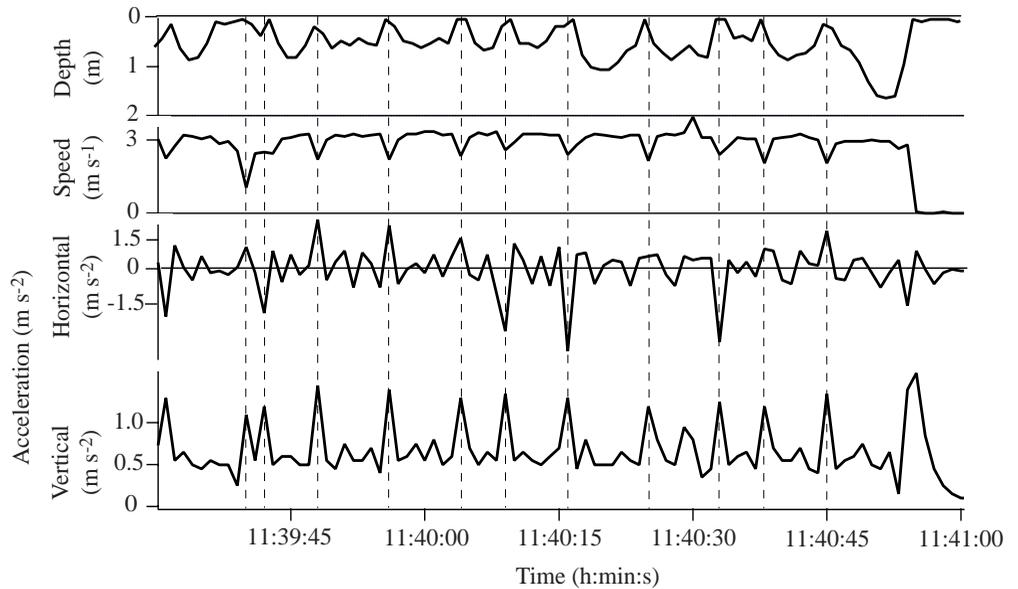

Fig. 2. Vertical and horizontal acceleration, speed and depth profiles of porpoising obtained using D2G and PDT loggers attached to a wild Adélie penguin in Dumont D'Urville. The dotted lines mark the jumps.

Table 1. *Trip duration, number of porpoising periods, total duration of porpoising periods, proportion of time allocated to porpoising during a trip and mean duration of porpoising cycles for six adult Adélie penguins measured using a D2G logger*

Bird	Trip duration (h)	Number of porpoising periods	Total duration of porpoising periods (min)	Proportion of time allocated to porpoising during trip (%)	Duration of porpoising cycles (s)	
					Mean ± s.d.	N
A	23.4	0	0	0		
B	20	4	6.5	0.54	6.7±3.7	58
C	13.1	2	2.2	0.28	5.8±2.5	23
D	8.3	1	1.2	0.24	12±3.8	6
E	25.7	0	0	0		
F	13.9	6	46	5.5	9.4±5.2	295

foraging trip (birds A and E). Thirteen porpoising periods were observed from four penguins (Table 1). The duration of porpoising periods varied within an individual from 1.0 to 11.2 min (4.3 ± 4.1 min, mean $\pm$ s.d., $N=13$). The total duration of porpoising periods ranged from 1.2 to 46 min per foraging trip, representing 0.24–5.5 % of foraging trip duration and
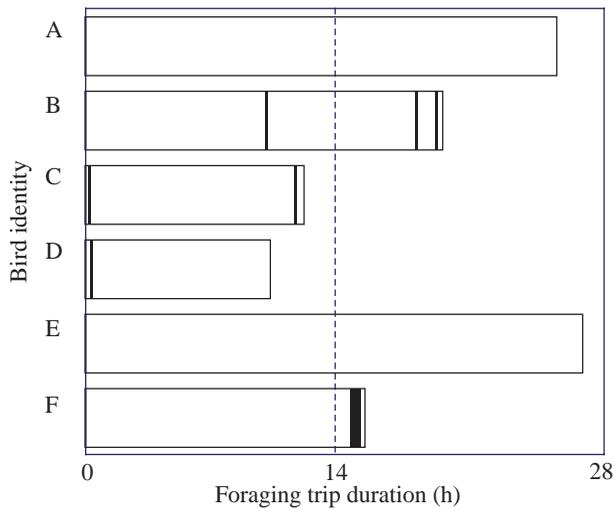
Fig. 3. Distribution of Adélie penguin porpoising behaviour in Dumont D'Urville determined using acceleration data loggers. The black bars indicate the duration and timing of the porpoising periods within the foraging trip (open bars). The black bars include several porpoising periods for birds B and F.

0.54–13.9 % of transit time. The mean duration of a porpoising cycle varied between 5.8 and 12 s (Table 1) and varied significantly among individuals ($P<0.0001$, Kruskal–Wallis test). Furthermore, for bird B, the mean duration of the porpoising cycle differed significantly among porpoising periods ($P<0.0001$, Kruskal–Wallis test), whereas it did not for birds C ($P>0.1$, Mann–Whitney U-test) and F ($P>0.4$, Kruskal–Wallis test). The distribution of porpoising within the foraging trip was examined (Fig. 3). Birds porpoised mostly towards the beginning or end of a trip.

The mean swimming speed between leaps was $2.8\pm0.46\,\mathrm{m\,s^{-1}}$ (mean ± S.D., range 0.98–$3.9\,\mathrm{m\,s^{-1}}$, $N=276$) and the mean swimming depth between leaps was $0.91\pm0.53\,\mathrm{m}$ (range 0.19–$2.6\,\mathrm{m}$, $N=276$). The mean horizontal distance between leaps within a porpoising period was $16.4\pm9.4\,\mathrm{m}$ (range 2.5–$46\,\mathrm{m}$, $N=42$). The mean speed before a leap (=take-off speed) was $2.6\pm0.49\,\mathrm{m\,s^{-1}}$ (range 0.98–$3.1\,\mathrm{m\,s^{-1}}$, $N=42$).

Discussion

Attachment of external devices to penguins can affect their swimming speed because of increased hydrodynamic drag (Wilson et al., 1986; Kooyman, 1989; Wilson and Culik, 1992; Bannasch, 1995). In the present study, instrumented penguins in the aquarium were observed to porpoise synchronously with non-instrumented animals, so porpoising variables between penguins with and without loggers could be compared using the frame-by-frame analysis of the video data. We could detect no differences in swimming speed, flipper beat frequency, distance between leaps or leap height between instrumented birds and control birds and between penguins that wore one or two recorders. The behaviour of the penguins appeared not to be affected by the addition of loggers during two days of

experiments in the aquarium. Instrumented wild penguins seemed to be able to forage successfully, as indicated by the quantity of food they brought back to their nests (mass 573±214 g, mean ± S.D., $N=3$), which was similar to the average stomach contents of uninstrumented returning foragers at Terre Adélie (mass 251±163 g, mean ± S.D., $N=105$; Ridoux and Offredo, 1989), Béchervaise Island and Edmonson Point (range 200–550 g; Clarke et al., 1998).

The porpoising speed measured in this study of wild penguins can be compared with the predicted threshold speeds above which leaping becomes energetically less costly than swimming within the high-drag subsurface layer (Au and Weihs, 1980; Blake, 1983; Blake and Smith, 1988). The mean porpoising speed of $2.8\,\mathrm{m\,s^{-1}}$ is greater than the predicted threshold range for this species (0.81–$1.88\,\mathrm{m\,s^{-1}}$; Blake and Smith, 1988), and therefore porpoising probably represents an energy saving over subsurface swimming.

An alternative way to avoid the high drag associated with swimming in the subsurface layer would be to swim at a deeper level. A fivefold decrease in drag is achieved by swimming at depth of more than three times the body diameter of the birds (Gordon, 1980). The cross-sectional area of Adélie penguins is approximately $20\,000\,\mathrm{mm^2}$ (Oehme and Bannasch, 1989); the maximum width is $0.16\,\mathrm{m}$. Penguins in the wild swam at an average depth of $0.91\,\mathrm{m}$ between leaps, which is below the high-drag layer. Therefore, they greatly reduced the potential drag by swimming below the threshold depth, as predicted by Gordon (1980). This finding suggests that the energy requirements of porpoising should be compared with those for steady swimming below the high-drag layer rather than within it, and that previous calculations indicating energy savings may be incomplete (Au and Weihs, 1980; Blake, 1983; Blake and Smith, 1988).

Indeed, the swimming distance between leaps indicates that the primary function of leaping is not energy conservation. Free-ranging Adélie penguins swam $16.4\,\mathrm{m}$ between leaps. The leap follows an approximately parabolic trajectory (Hui, 1987). Thus, the distance covered while the centre of gravity of the animal is out of the water, neglecting spray effects and air density, is:

$$L = U^2\sin 2a/\boldsymbol{g}\,, \qquad (2)$$

where L is the distance covered, $\boldsymbol{g}$ is the gravitational acceleration, a is the emergence angle, measured from the horizon, and U is the initial velocity. The initial velocity was approximated as the speed measured before the leap, or $2.6\,\mathrm{m\,s^{-1}}$. In a previous study, the emergence angle of captive gentoo penguins (Pygoscelis papua) was $32.2°$; this was similar to the observed angle for free-ranging Adélie penguins (Hui, 1987). Using a value of $32.2°$, the distance covered during a leap is $0.62\,\mathrm{m}$ for wild Adélie penguins, equivalent to only 3.8% of the total distance travelled during the porpoising cycle. If leaping does function primarily for energy conservation, the small fraction of the total distance travelled during leaps would provide energetic benefits for only 3.8% of the total distance travelled during porpoising. This value is

much lower than that measured for captive gentoo penguins, which leapt for 22 % of the 14 m length of a holding channel (Hui, 1987).

In addition, the total duration of porpoising periods was less than 7 min for all birds except bird F; two birds did not leap at all during the foraging trip. These observations make it doubtful that porpoising functions in terms of energy conservation for travel.

With regard to the role of porpoising, there are two suggested functions. First, it has been suggested that porpoising has a function in allowing breathing periods without reducing swimming speed (Blake and Smith, 1988). The time spent in the air T can be expressed as:

$$T = 2U\sin a/\mathbf{g}\,. \tag{3}$$

This gives a value of T of 0.28 s for free-ranging Adélie penguins, long enough for one inhalation (0.24 s; Hui, 1987). The alternative option for a penguin to ventilate would be to return to the surface without a leap, which would involve a loss of speed (Hui, 1987). Porpoising may be the better strategy for breathing without reducing swimming speed.

Second, porpoising could be a direct response to the threat of predation. Penguins usually leapt at the start and end of a foraging trip (Fig. 3), i.e. when they were near the colony. At sea, penguins face a variety of predators, including several species of seal (Penney and Lowry, 1967; Cooper, 1974; Müller-Schwarze, 1984; Williams, 1995). Leopard seals (*Hydrurga leptonyx*) and killer whales (*Orcinus orca*) congregate close to the shore where penguins nest (Wilson, 1995). Porpoising may be a way of rapidly crossing the shallow inshore water where predators hunt. This is supported by the observation that penguins swim rapidly away from ships (Kooyman, 1975) and that *Spheniscus* species do not appear to leap unless they are alarmed by a predator (Wilson, 1995).

The fact that the duration of the porpoising cycle differed among and within individuals suggests that the cause and function of porpoising probably vary among individuals and situations. For example, short porpoising cycles may represent escape behaviour. Other functions are also possible: for example, enjoyment or to allow the penguins to observe a landing place directly. The frequent porpoising observed in the aquarium may be an example of porpoising for enjoyment. Further experiments on other species in the wild using data loggers would be the best way to obtain a more complete understanding of this behaviour.

The acceleration data loggers attached here to Adélie penguins for the first time provide a useful and reliable system for measuring animal activity at sea. This new technique will allow researchers in the future to monitor and integrate a variety of activities of different animals.

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