

## SWIMMING ENERGETICS AND PERFORMANCE OF INSTRUMENTED ADÉLIE PENGUINS (*PYGOSCELIS ADELIAE*)

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### Summary

The effects of implanted and of externally attached instruments (1.8% of body cross-sectional area) were studied on Adélie penguins (*Pygoscelis adeliae*) using a 21 m long canal in conjunction with respirometry at Esperanza Bay, Antarctica. Penguins in both groups covered the same mean distance (173 m in 5 min) as controls. Implanted birds preferred to swim at slower speeds ( $1.3\text{--}1.7\text{ m s}^{-1}$ ) than did the controls ( $1.9\text{--}2.1\text{ m s}^{-1}$ ), whereas penguins with external instruments had a bimodal speed distribution with maxima at  $1.7\text{--}1.9$  and  $2.3\text{--}2.5\text{ m s}^{-1}$ . Power input during swimming averaged 20% less in implanted penguins ( $12.7\text{ W kg}^{-1}$ ) and 42% more in penguins fitted with external instruments ( $22.5\text{ W kg}^{-1}$ ) compared with controls ( $15.8\text{ W kg}^{-1}$ ). Similarly, cost of transport was 23% lower in implanted penguins ( $7.0\text{ J kg}^{-1}\text{ m}^{-1}$ ) and 25% higher in externally instrumented birds ( $11.3\text{ J kg}^{-1}\text{ m}^{-1}$ ) compared with controls ( $9.0\text{ J kg}^{-1}\text{ m}^{-1}$ ). Possible reasons for the effects caused by the devices are discussed and the advantages and disadvantages of implanted and externally fitted devices are compared.

### Introduction

External attachment or implantation of remote-sensing devices to free-living birds enables researchers to determine ecological and physiological variables that are not otherwise measurable. Unfortunately, the use of such instruments may alter the behaviour and performance of the study animal, and this should be quantified before extrapolating any data to unimpeded animals in the wild.

Birds may attempt to remove externally attached instruments (Perry, 1981; Wilson and Wilson, 1989a) or preen the area of the wound more frequently after implantation (Butler and Woakes, 1979; Skirnisson and Feddersen, 1984). Although it is usually reported that implanted animals behave and perform normally after a few days of recovery (Butler and Woakes, 1979; Folk and Folk, 1980; Skirnisson and Feddersen, 1984; Culik *et al.* 1990a,b) this has never been tested in detail and in the long term.

Externally attached devices have repeatedly been found to impair study animals even after lengthy acclimation. For example, the frequency and duration of

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foraging trips were significantly changed in guillemots (*Uria aalge*) and razorbills (*Alca torda*, Wanless *et al.* 1988), Adélie penguins (*Pygoscelis adeliae*, Wilson *et al.* 1989) and canvassbacks (*Aythya valisseria*, Perry, 1981). More detailed studies have revealed that externally attached instruments affect bird body drag (Obrecht *et al.* 1988), which explains decreased flight speed and increased metabolic rate in device-equipped homing pigeons (*Columba livia*, Gessaman and Nagy, 1988) and decreased swimming speed and diving depths in penguins (Wilson *et al.* 1986; Wilson, 1989).

After external instrumentation of African penguins (*Spheniscus demersus*), Nagy *et al.* (1984) found no increase in metabolic rate, whereas Gales *et al.* (1990) report a 20% decrease in energy expenditure in device-fitted Little penguins (*Eudyptula minor*), which they attributed to reduced activity at sea. Metabolic rates in both these studies were measured with doubly labelled water, integrating over large time intervals (days) and yielding relatively few data points.

We used respirometry in conjunction with a 21 m still water canal to measure in detail the energy expenditure of Adélie penguins while swimming under water. We continuously monitored the behaviour of the birds and compared penguins implanted with heart-rate/body-temperature transmitters and penguins with externally attached remote-sensing devices with control birds. Variables recorded were duration of the observed activities, distance swum, swimming speed, power input ( $P_i$ ) and cost of transport (COT). Some of the data presented here (control group) have been submitted for publication elsewhere (Culik and Wilson, 1991).

### Materials and methods

Adélie penguins living at Esperanza Bay (56°59'W, 63°24'S), Antarctic Peninsula, were studied during December 1989 and January, 1990. Five birds were caught from the beach (controls, mean mass  $4.2 \pm 0.3$  kg, s.d.) for single experiments lasting 90–120 min. Another five penguins caught at the same locality (mean mass  $3.9 \pm 0.4$  kg) were equipped immediately after capture with an externally attached remote-sensing device (Fig. 1, see Wilson and Wilson, 1988) attached to the feathers of the lower back with tape (Wilson and Wilson, 1989b). Handling time was about 10 min per bird. The device was purpose-built to be slim and streamlined, measuring 25 mm (wide)  $\times$  100 mm (long)  $\times$  20 mm (height above penguin back is only 17 mm). The maximum frontal cross-sectional body area of an Adélie penguin is between 31 400 mm<sup>2</sup> (Wilson *et al.* 1989) and 20 000 mm<sup>2</sup> (Oehme and Bannasch, 1989), so this device corresponds to 1.4–2.1% of the birds' cross-sectional area. With a mass of 35 g (in air) the device constitutes 0.9% of bird body mass.

Telemetric heart rate transmitters (50 mm  $\times$  20 mm  $\times$  8 mm, 20 g, see Woakes and Butler, 1975) were implanted in two adult Adélie penguins (4.1 kg and 4.7 kg) incubating eggs in a nearby colony on December 12 and 13. The eggs of the birds were sheltered for the duration of the operation (approx. 30 min). Halothane and local xylocaine were used for anaesthesia and transmitters were implanted into the

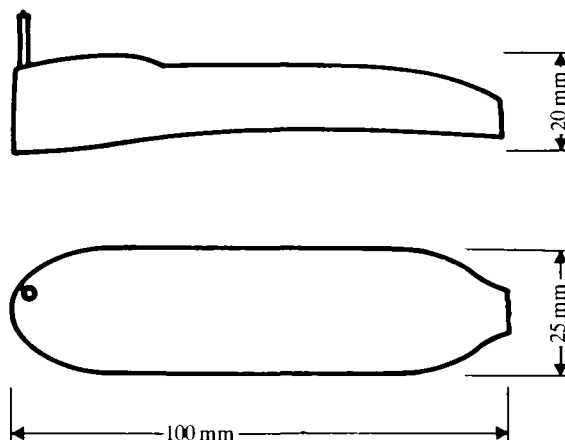


Fig. 1. Size and shape of externally attached instrument. (A) Lateral view; (B) dorsal view. The device was contoured underneath to fit snugly onto the penguin's back (maximum height above the back was 17 mm).

body cavity between the stomach and the abdominal wall; both electrodes were slid under the sternum and placed adjacent to the heart. During suture of the abdominal wall and skin, halothane anaesthesia was reduced from 2% to 0% and both penguins recovered consciousness within 5 min. After injection of the antibiotic Binotal and 1 h of recovery in the laboratory, the birds and their eggs were replaced on the nest. The penguins immediately resumed incubation. However, the effects of the anaesthesia on balance appeared to last for several hours after the operation and, for the first shift after partner changeover, the operated penguins were not observed to go foraging. Both birds preferred to rest on a nearby snowfield. Normal behaviour of the birds, including foraging at sea, was resumed 2–4 days after the operation. Experiments were conducted on these birds starting on January 7 after complete healing of the external suture. The masses of the birds were then 4.35 and 4.5 kg, respectively. We do not present data gained from the transmitters in the present study. After termination of the experiments, the transmitters were removed from the penguins in a second operation from which the animals also recovered well.

The penguins were introduced into one of the respiration chambers of a plywood tank, 21 m long, 0.9 m wide and 0.7 m deep. The tank was sealed with a light blue polyethylene sheet commonly used for swimming pools (25 m × 3 m) and supported every 1.5 m by U-shaped steel frames. A wedge-shaped respiration chamber (base area 0.5 m × 0.8 m, maximum height 0.7 m, volume 100 l) made of transparent polyvinyl chloride (PVC) was placed at each end of the tank. The tank was sealed 0.1 m below the water surface by transparent PVC sheets (0.9 m × 3 m) which covered the entire surface between the two chambers. Black netting (mesh size 2 cm) was laid over the top of the PVC sheets to make these more conspicuous

to the birds swimming below. The tank was scrubbed and filled with fresh sea water every 6 days. Mean water temperature was 2–6°C.

Both respiration chambers were equipped with a 12 V mixing fan and were open to outside air *via* a 20 cm tube. Air was sucked into each chamber by a pump next to it at a mean flow rate of 750 l h<sup>-1</sup>, and pumped to the laboratory through a flowmeter (Kobold, Kelkheim, FRG) and a volumetric gasometer. The flow rates from each chamber were constant and frequently checked during each experiment. A subsample (60 l h<sup>-1</sup>) of the combined air flow (1500 l h<sup>-1</sup>) was passed through a Drierite column (CaSO<sub>4</sub>, Aldrich chemicals) to remove water vapour, and then to a UNOR 6N infrared gas analyser and an OXYGOR 6N paramagnetic oxygen analyser (Maihak, Hamburg). Both analysers were calibrated daily for the 1 % scale using known gas mixtures from a Wösthoff pump (Wösthoff, Bochum, FRG) and ambient air, assuming 20.95 % O<sub>2</sub> and 0.03 % CO<sub>2</sub>. Every day, the whole system was checked visually for leaks, and flow rates did not change over time. Data from both analysers were recorded at 10 s intervals on a computer. Contribution to or absorption of O<sub>2</sub> and CO<sub>2</sub> by the water in the tank to the air in the chambers was considered to be negligible. Within the respiration chamber, humidity was assumed to be 100 % and air temperature, measured in the middle of each experiment, averaged +12°C. Atmospheric pressure and relative humidity of ambient air were recorded at 10 min intervals using a mini-meteorological station (Grant, Cambridge, UK). All air-flow recordings were corrected to STPD conditions. Respiration rates were computed for each 10 s interval as described in Woakes and Butler (1983), using equation 1 in Culik *et al.* (1990b) incorporating chamber volume, which allows accurate measurement of fast changes in CO<sub>2</sub> and O<sub>2</sub> concentrations, irrespective of the lag time of the system, and integrated over 5 min. The mean respiratory quotient (RQ) of the birds was 0.67 ± 0.007 (s.e.), so all oxygen recordings were converted to kilojoules using a factor of 20.1 kJ l<sup>-1</sup> O<sub>2</sub> (Schmidt-Nielsen, 1983).

The activity of the birds was continuously observed from a ladder placed over the middle of the tank, the observer's eye being 4.5 m above ground level. The birds were recorded as being in chamber A or chamber B, where they were classified as resting, active ('unrest'), preening, swimming or jumping out of the water. The swimming behaviour and position of birds swimming between chambers A and B were monitored continuously, and a special note was made every time the penguin passed a supporting frame (3 m intervals), which provided marks on the surface and on the bottom of the tank to minimize parallax error. All observations as well as real time were recorded orally onto magnetic tape (Sony Walkman Professional, quartz-locked speed) and later transcribed in the laboratory using a handheld computer (Husky Hunter, Coventry, UK). The data were analysed using specially designed software to yield the duration of the five classes of activity and, from position/time information (3 m intervals), distance swum and speed. The data were integrated over 5 min intervals (*N* refers to the number of 5 min observations), and mean speed computed for that interval was matched with the equivalent dataset from the respirometry recordings, taking into account a

mean lag time of 140 s. Integration of the data over 5 min intervals became necessary because, during diving, bird metabolic rate was highest, although this was only apparent when the bird surfaced to breathe at unpredictable intervals. The combined data were then analysed (analysis of variance, ANOVA, and 95 % least significant difference test, LSDT) using a commercially available statistics package (Statgraphics, STSC, Rockville, USA). Standard error (S.E.) is presented where appropriate.

To calculate the regression best describing the complete dataset from each group, we regressed the duration of each behaviour and the mass of the bird against oxygen consumption ( $\dot{V}_{O_2}$ , ml 5 min<sup>-1</sup>), and considered only those behavioural variables that were significant. The general formula derived from the dataset was:

$$\dot{V}_{O_2\text{total}} = K + at_s + bt_j + cM, \quad (1)$$

where  $a$ ,  $b$  and  $c$  are individual slopes,  $K$  is the intercept,  $t_s$  is time spent swimming (s),  $t_j$  is time spent jumping (s) and  $M$  is mass (kg). Other activities besides swimming and jumping were infrequent and did not yield significant regression parameters.

Calculations of power input and cost of transport at the observed speed were performed after eliminating all observations from the datasets where swimming time or speed were zero (Schmidt-Nielsen, 1972). The remaining data were then corrected using equation 1, to remove energy expenditure due to rest and jumping from total oxygen consumption over 5 min. The formula used for correction was:

$$\dot{V}_{O_2\text{swim}} = \dot{V}_{O_2\text{total}} - bt_j - [(300 - t_s)(cM + K)/300]. \quad (2)$$

Power input (W kg<sup>-1</sup>) was calculated as:

$$P_1 = \dot{V}_{O_2\text{swim}} \times 20.1 / (t_s M) \quad (3)$$

and cost of transport (J kg<sup>-1</sup> m<sup>-1</sup>) as:

$$\text{COT} = P_1 / v, \quad (4)$$

where  $v$  is speed (m s<sup>-1</sup>).

## Results

### *Duration of activities*

Analysis of the complete dataset showed that the time budgets of the three penguin groups were similar. Resting was the most important activity (145 ± 6.5 s, S.E.,  $N=167$ ) followed by swimming (123 ± 6.8 s,  $N=167$ ), whereas preening (2.2 ± 0.9 s,  $N=167$ ) was observed very rarely. There was no significant difference between groups for these activities (ANOVA,  $P>0.05$ ).

Jumping (Fig. 2) was more prevalent in the control group (18.5 ± 3.5 s,  $N=64$ ) than in the implanted birds (5.6 ± 3.1 s,  $N=41$ ), whereas device-fitted birds were not significantly different from controls (15.8 ± 2.7 s,  $N=62$ , ANOVA,  $F=3.9$ ,

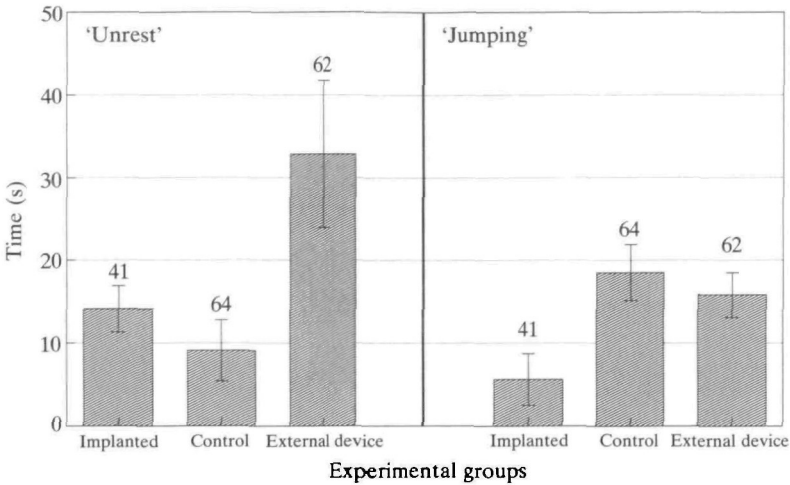


Fig. 2. Mean duration (s) of 'unrest' behaviour and jumping recorded in Adélie penguins with and without instrumentation per 5-min observation interval ( $\pm$ s.e.,  $N$ ).

$P=0.022$ , LSDT). Unquantifiable activities, grouped as 'unrest', were observed mostly in device-fitted birds ( $32.8 \pm 8.9$  s,  $N=62$ ) and less often in the implanted ( $14.1 \pm 3.7$  s,  $N=41$ ) and the control groups ( $9.1 \pm 2.8$  s,  $N=64$ ). This difference is significant (ANOVA,  $F=4.4$ ,  $P=0.013$ , LSDT).

The distance swum per 5 min interval was similar in all three groups (ANOVA,  $N=167$ ,  $F=0.9$ ,  $P=0.37$ ) with a mean of  $173 \pm 12.5$  m.

#### *Speed distribution*

Using a subset of the data (see Materials and methods) we determined that the speed at which the three groups of Adélie penguins chose to swim in the tank varied significantly (ANOVA,  $N=132$ ,  $F=5.7$ ,  $P=0.041$ ). Penguins implanted with transmitters (mean speed  $1.8 \pm 0.07$  m s<sup>-1</sup>,  $N=37$ ) swam at the same speed as the control group ( $1.8 \pm 0.05$  m s<sup>-1</sup>,  $N=43$ ). Penguins wearing externally attached devices, however, swam significantly faster, with a mean speed of  $2.05 \pm 0.05$  m s<sup>-1</sup> ( $N=53$ , LSDT).

Recorded speeds were grouped into speed classes ( $0.2$  m s<sup>-1</sup> intervals) from  $0.7$  to  $>2.6$  m s<sup>-1</sup>. The number of observations in each of these classes, i.e. the speed distribution, was different in the three groups (Fig. 3). In the control birds, the preferred speed was  $1.9$ – $2.1$  m s<sup>-1</sup> (28 observations or 67%), whereas implanted birds preferred the speed range  $1.3$ – $1.7$  m s<sup>-1</sup> (25 observations or 67%) and device-fitted birds appeared to have a bimodal preference, with a peak at  $1.7$ – $1.9$  m s<sup>-1</sup> (20 observations or 38%) and another at  $2.3$ – $2.5$  m s<sup>-1</sup> (21 observations or 40%).

#### *Energy consumption in the tank*

For wild Adélie penguins (control group) we found that oxygen consumption

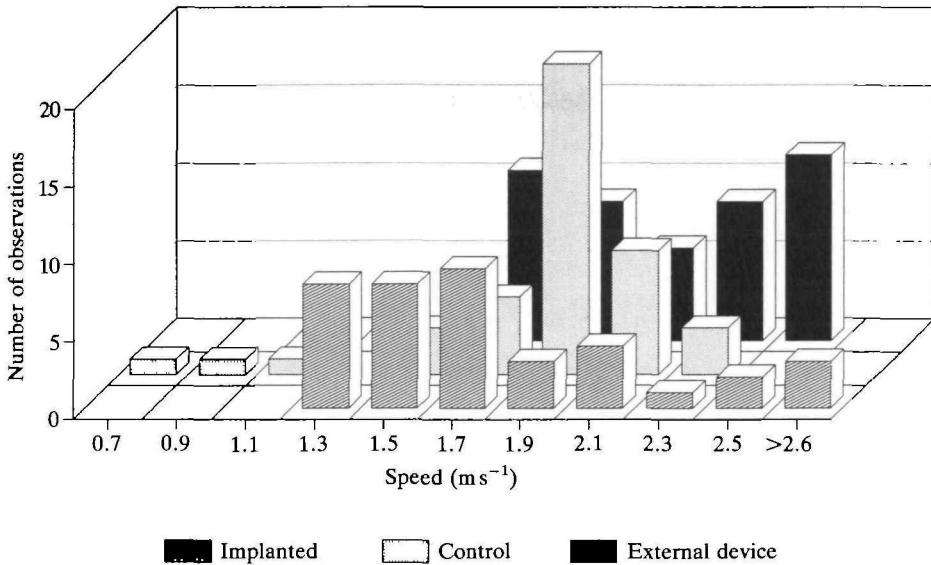


Fig. 3. Speed distribution in Adélie penguins with and without instrumentation observed in the swim canal. Columns show number of observations in each speed range.

over a 5 min interval was best described by:  $\dot{V}_{O_2} = 1240 + 1.21t_s + 1.14t_j - 148M$  ( $r^2 = 0.71$ ,  $N = 64$ ,  $F = 53$ ,  $P < 0.0001$ ). In the implanted penguins, the variable best describing the dataset was:  $\dot{V}_{O_2} = -6829 + 1778M$  ( $r^2 = 0.80$ ,  $N = 41$ ,  $F = 164$ ,  $P < 0.0001$ ); the duration of the individual activities was similar in most 5 min intervals, and thus did not correlate significantly with  $\dot{V}_{O_2}$ . From Adélie penguins fitted with externally attached instruments we calculated:  $\dot{V}_{O_2} = 517.6 + 2.56t_s$  ( $r^2 = 0.77$ ,  $N = 62$ ,  $F = 202$ ,  $P < 0.0001$ ); mass had no effect on oxygen consumption as the mass range was very narrow in this group.

In some instances, the penguins were resting in one of the respiration chambers for more than 90% of the 5 min period. Energy expenditure then averaged  $8.4 \pm 0.4 \text{ W kg}^{-1}$  ( $N = 11$ ) in the control group, with a range of  $6.5\text{--}12.1 \text{ W kg}^{-1}$ , as opposed to  $5.05 \pm 0.07 \text{ W kg}^{-1}$  ( $N = 3$ ) in penguins implanted with transmitters and  $10.4 \pm 0.95 \text{ W kg}^{-1}$  ( $N = 4$ ) in those fitted with externally attached devices. The differences are statistically significant (ANOVA,  $F = 10.8$ ,  $P = 0.012$ ) and do not correlate with the mass of the birds in these three groups.

Power input ( $\text{W kg}^{-1}$ ) and cost of transport were calculated for speed intervals ranging from  $0.7$  to  $>2.6 \text{ ms}^{-1}$ . Mean  $P_i$  for the entire speed range (Fig. 4) was least in implanted penguins ( $12.7 \pm 0.9 \text{ W kg}^{-1}$ ,  $N = 37$ ), followed by the control group ( $15.8 \pm 0.8 \text{ W kg}^{-1}$ ,  $N = 42$ ), while the highest  $P_i$  was measured in birds carrying externally attached devices ( $22.5 \pm 0.8 \text{ W kg}^{-1}$ ,  $N = 53$ ). These values are all significantly different from each other (ANOVA,  $F = 40.5$ ,  $P < 0.0001$ , LSDT). One Adélie penguin lost its externally attached device 30 min after the beginning of the experiment (Fig. 4, inset).  $P_i$  averaged  $28.8 \pm 2.0 \text{ W kg}^{-1}$  ( $N = 5$ ) while the

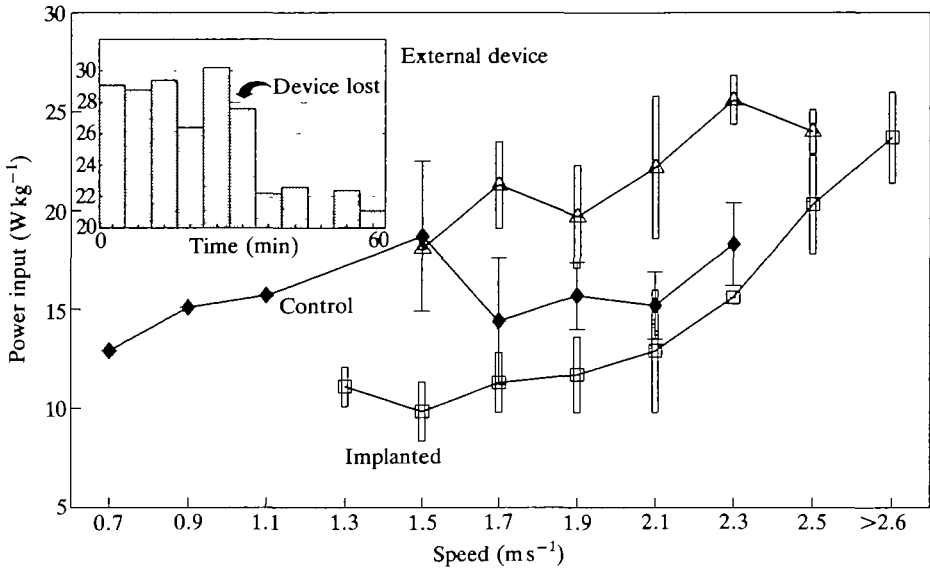


Fig. 4. Power input ( $\text{W kg}^{-1}$ ) in Adélie penguins swimming under water with and without instrumentation plotted with respect to speed ( $\text{m s}^{-1}$ ). Bars indicate standard error. Sample sizes for each speed range are given in Fig. 3. Inset: power input of an individual Adélie penguin while swimming under water before and after losing an externally attached instrument.

device was attached and decreased to  $22.1 \pm 0.5 \text{ W kg}^{-1}$  ( $N=4$ ) after the loss of the device, and this difference is significant ( $t$ -test,  $P < 0.05$ ). The speed of the bird was also reduced, from  $2.3 \pm 0.01 \text{ m s}^{-1}$  ( $N=3$ ) to  $1.9 \pm 0.06 \text{ m s}^{-1}$  ( $N=7$ ) after the loss of the device, but this difference is not significant ( $t$ -test,  $P > 0.05$ ).

Cost of transport ( $\text{J kg}^{-1} \text{ m}^{-1}$ ) followed the same trend as  $P_1$  (Fig. 5). We found a mean COT of  $7.0 \pm 0.4 \text{ J kg}^{-1} \text{ m}^{-1}$  ( $N=37$ ) in implanted penguins, compared to  $9.0 \pm 0.5 \text{ J kg}^{-1} \text{ m}^{-1}$  ( $N=42$ ) in the control group and  $11.3 \pm 0.4 \text{ J kg}^{-1} \text{ m}^{-1}$  ( $N=53$ ) in the penguins equipped with external devices. Again, the differences are significant (ANOVA,  $F=46.8$ ,  $P < 0.0001$ , LSDT).

### Discussion

Unfortunately, many reports in the literature dealing with implantation concentrate more on the electronic techniques and on the resulting data than on considering possible effects of the implantation (e.g. Duncan and Filshie, 1980; Gilbert and Grofton, 1982; Fisher *et al.* 1987). Telemetry studies, using internal transmitters, have been made in adult Emperor (*Aptenodytes forsteri*), Adélie (Boyd and Sladen, 1971) and Humboldt penguins (*Spheniscus humboldtii*, Butler and Woakes, 1984). External transmitters have been used in Gentoo (*P. papua*) and Chinstrap (*P. antarctica*) penguins (Trivelpiece *et al.* 1986). The possible effects of the instruments on the performance and behaviour of their bearers were



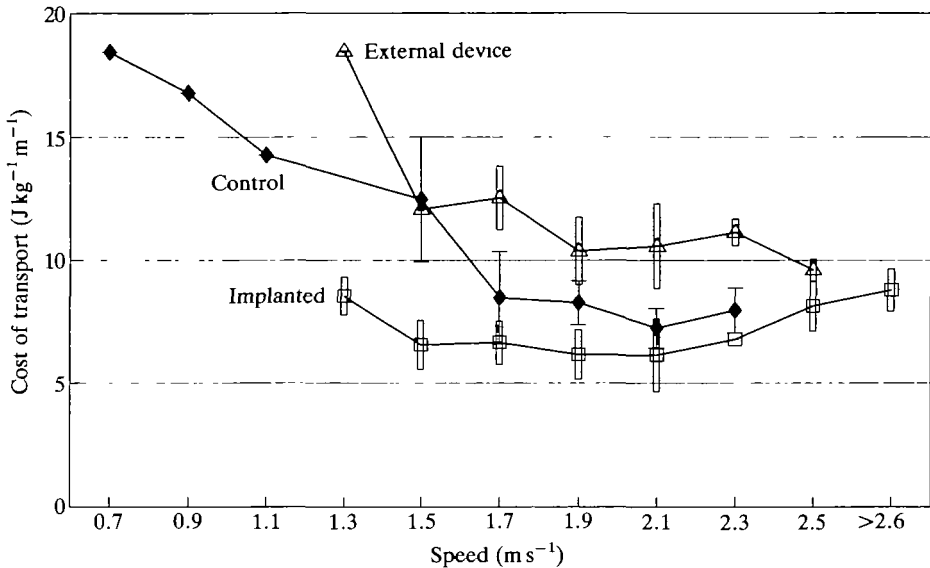


Fig. 5. Cost of transport ( $\text{J kg}^{-1} \text{m}^{-1}$ ) for Adélie penguins with and without instrumentation plotted with respect to swimming speed ( $\text{m s}^{-1}$ ). Cost of transport is power input divided by speed (Fig. 4). Bars indicate standard error. Sample sizes for each speed range are given in Fig. 3.

not noted in any of these studies. Boyd and Sladen (1971) just remark that two autopsied Adélie penguins 'had carried the implant for 1 year and re-established territories...One was incubating a single egg – significant evidence of recovery'. The two birds used in the present study both continued breeding activity. One penguin successfully raised two chicks, although the two eggs of the other never hatched. The latter penguin attended the nest until late January. However, this observation cannot be extrapolated to the performance and behaviour of the penguins at sea.

Increased 'unrest' and reduced jumping behaviour by implanted Adélie penguins in the swim canal, as well as a shift in speed distribution, could be attributed to discomfort caused by the implant. Folk and Folk (1980) suggest that electrode leads, such as those running from the transmitters to the heart, might have an irritating effect on the animal, and propose the use of radio-capsules with integrated electrodes to alleviate this problem. Although by visual inspection the incision appeared to have healed well at the time of the experiments, irritation from the scars in the abdominal wall, fat tissue, muscle and skin cannot be excluded. P. J. Butler and A. J. Woakes (personal communication) observed that healing was slower in captive Humboldt penguins than in other birds, which they attribute to the thick layer of fat on the abdominal wall. However, these problems may be restricted to adult penguins, as other authors noticed no change in implanted animals (Butler and Woakes, 1979; Skirnisson and Feddersen, 1984;

Korschgen *et al.* 1984) or in Adélie penguin chicks (Culik *et al.* 1990b) after surgery.

External instrumentation caused the amount of 'unrest' behaviour to increase more than threefold and led to an increase in mean speed in Adélie penguins. Speed distribution, however, was bimodal, with one peak at  $1.7\text{--}1.9\text{ m s}^{-1}$  and another at  $2.3\text{--}2.5\text{ m s}^{-1}$ . Analysis of the raw data showed that the high speeds were not only observed at the beginning of each experiment, which could have been interpreted as the effect of handling the penguins shortly before the experiment. Instead, we propose that the bimodal speed distribution can be attributed to two types of behaviour: (1) the birds swam faster than usual to get rid of the device; (2) the birds swam at normal  $P_i$  levels which, owing to the drag of the device, reduced the attainable speed to  $1.7\text{--}1.9\text{ m s}^{-1}$ .

Indeed Wilson and Wilson (1989a) observed that Adélie penguins did not habituate to externally attached devices for 14 days, and continued pecking at them. Although we did not observe pecking in the tank, fast swimming and 'unrest' behaviour might be the corresponding activities at sea. A linear decrease in swimming speed in African penguins with increased cross-sectional area of the recording device was reported by Wilson *et al.* (1986). They attributed this to drag rather than to the mass of the instruments and suggested that penguins will tend to maintain the same  $P_i$  as they would without the instruments, resulting in a reduced swimming speed. According to Wilson *et al.* (1986), a concomitant reduction in foraging range explains a reduction in food intake, which was also observed by Gales *et al.* (1990) in Little penguins. In contrast to African and Little penguins, Adélie penguins equipped with external devices spent significantly longer at sea than controls, and the duration of a foraging trip increased with increasing instrument volume (Wilson *et al.* 1989).

Two strategies seem to be adopted by externally instrumented penguins: (1) reduced speed, foraging range and food uptake (African and Little penguins); (2) increased length of foraging trips in order to compensate for device effects (Adélie penguins). This latter strategy was also observed in alcids (Wanless *et al.* 1989), where absence from the nest was longer in device-equipped birds. However, even these birds captured fewer prey than did the controls.

Energy consumption during rest in water was significantly lower in implanted birds than in controls. Although more data would be desirable to substantiate this result, it is supported by the low  $P_i$  (Fig. 4) and low COT (Fig. 5) during swimming. The mass of these penguins is comparable to that of controls, and drag was presumably not reduced after surgery. The two implanted birds, however, were observed in their colony every 4 h for 30 min during December and January. The hide for the observers was only 5 m away from their nests. Furthermore, these penguins had been caught and handled repeatedly before the experiment to assess the healing process and for preliminary experiments in the tank. It cannot be excluded, therefore, that these penguins were better acclimated to human interference and recovered faster from handling than the control birds. Although implanted birds reacted with increased heart rate whenever approached by

human (Culik *et al.* 1990a), this 'stress' might have decreased to normal levels at a faster rate than in control birds. We cannot, therefore, exclude the possibility that resting metabolic rate (RMR) in water and COT in Adélie penguins in the wild are even lower than previously reported (Culik and Wilson, 1991). In contrast, energy consumption during rest and activity in Adélie penguin chicks was not altered after implantation of transmitters (Culik *et al.* 1990b).

Adélie penguins equipped with an external device had a higher resting metabolic rate in water (4°C) than did the controls. A slight increase in RMR is to be expected in a stressed bird, and this might have been the case in the device-fitted penguins, which had been handled more than the other birds before the experiment. Culik *et al.* (1990a) showed that heart rate in Adélie penguins may rise well before the birds show any external signs of concern. Sedinger *et al.* (1990), however, report that an external device attached to black brant (*Branta bernicla nigra*) had no effect on energy expenditure in a small respiration chamber, 24 h after transmitter attachment. It is possible that the increase in RMR noted in Adélie penguins fitted with external devices might have disappeared given more time for acclimation.

Increased COT in externally instrumented penguins results from added parasite power due to the increased drag incurred by the device. Other influences of the device on the bird presumably reduced their locomotory efficiency even more. Impairment of movements reduces mechanical propulsion efficiency of the wings (Culik and Wilson, 1991). Furthermore, we observed that devices were often not exactly on the midline of the penguins (although we spent a lot of effort trying to achieve this), which made the device act as a rudder, and device-fitted penguins had to correct their course more often than control birds. The aspect of the power curves obtained from instrumented and control penguins (Fig. 4) coincides well with the theoretically derived findings of Pennycuik and Fuller (1987) and Obrecht *et al.* (1988). The power curve of Obrecht *et al.* (1988) calculated for birds fitted with external instruments is shifted upwards with respect to the control group, as it is in Fig. 4 for penguins. Obrecht *et al.* (1988) stress the fact that 'the drag of a stream-lined body with a secondary smaller body attached to it is generally larger than the sum of the drag measured on each of the two bodies separately'. This underlines the necessity of testing device effects and of calibrating devices on the animal. Pennycuik *et al.* (1988) found in their specimens of frozen bird bodies that the feathers fluffed out in the wind canal, owing to a lack of control by pteromotor muscles, which led to significantly higher drag estimates than for birds with smooth feathers. This was also observed in frozen penguin bodies towed through the water (R. Bannasch, personal communication) and shows the importance of measuring power input directly on the *living* animal.

Such attempts have been made in the past using doubly labelled water. However, this method provides relatively few data points over several days, and thus does not allow the construction of a power curve for the entire speed range of the animal. Owing to a change in the behaviour of the penguins, Nagy *et al.* (1984),

Wilson *et al.* (1986) and Gales *et al.* (1990) were unable to detect an increase in metabolic rate in birds wearing external devices ranging from 1.4 to 11.8 % of cross-sectional body area.

The first data presented on the increase of metabolic rate in birds wearing devices came from studies on homing pigeons (Gessaman and Nagy, 1988). The birds covered a fixed distance, and it was found that devices of 2.5–5.0 % of body mass (and approximately 7 % of cross-sectional area) led to 85–100 % more energy expenditure. Gessaman and Nagy (1988) attributed this to the drag caused by the device rather than to the mass of the transmitters. In marine mammals, Gentry and Kooyman (1986) found a 19 % increase in the metabolic rate of Northern fur seals equipped with an externally attached instrument, due to a measured drag increase of up to 70 %.

Our results coincide well with those of Gessaman and Nagy (1988) and Gentry and Kooyman (1986) and show that the effect of external devices on body drag, and therefore on energy expenditure in the field, is considerable. Flying or swimming is the normal mode of locomotion and is generally the most energetically taxing activity engaged in by most birds. Therefore, energetic studies conducted in small respiration chambers neglecting these types of locomotion (e.g. Sedinger *et al.* 1990) do not yield comprehensive information on device-induced effects in free-ranging animals.

In summary, our experiments with implanted and externally attached instruments on Adélie penguins showed that both had a measurable effect on the performance and energy consumption of the bearer. Implantation, however, seemed to be superior to external attachment, since presumably body drag, and therefore energy consumption, did not increase. Using internal sensors in conjunction with implanted instruments, physiological data and physical variables such as location (e.g. Korschgen *et al.* 1984), compass heading (Wilson and Wilson, 1988) or diving depth (e.g. Wilson, 1989) can be obtained. Changes in behaviour of implanted birds might be reduced if internal electrodes, which are possible sources of irritation, can be avoided, concentrating all sensors on the body of the transmitter (e.g. Folk and Folk, 1980). Furthermore, all effects caused by the implant should diminish with the progression of healing, thus 'normalising' the bearer with time. Implantation therefore seems the best solution for recording and/or transmitting variables from an animal, especially in long-term studies.

External attachment of an instrument offers the advantage of rapid removal and no further consequence to the bearer after termination of the experiment. It is often the only possible way to record information from the outside environment (e.g. speed, light, water/air etc.). The investigator can re-use the instrument quickly after data recovery or battery replacement. However, even relatively small instruments (<2 % of body cross-sectional area) significantly increase energy expenditure during swimming or flying and decrease the performance of the animal measurably. Miniaturization of externally attached instruments to less than 1 % of body cross-sectional area, streamlining, reduction of instrument length (rudder effects), as well as refinement of attachment techniques, are the most

essential improvements required if one wishes to obtain meaningful results from unrestrained animals.

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### References

- BOYD, J. C. AND SLADEN, W. J. (1971). Telemetry studies of the internal body temperatures of Adélie and Emperor penguins at Cape Crozier, Ross Island, Antarctica. *Auk* **88**, 366-380.
- BUTLER, P. J. AND WOAKES, A. J. (1979). Changes in heart rate and respiratory frequency during natural behaviour of ducks, with particular reference to diving. *J. exp. Biol.* **79**, 283-300.
- BUTLER, P. J. AND WOAKES, A. J. (1984). Heart rate and aerobic metabolism in Humboldt penguins *Spheniscus humboldtii* during voluntary dives. *J. exp. Biol.* **108**, 419-428.
- CULIK, B., ADELUNG, D. AND WOAKES, A. J. (1990a). The effect of disturbance on the heart rate and behaviour of Adélie penguins (*Pygoscelis adeliae*) during the breeding season. In *Antarctic Ecosystems. Ecological Change and Conservation* (ed K. R. Kerry and G. Hempel), pp. 171-182. Berlin: Springer-Verlag.
- CULIK, B. AND WILSON, R. P. (1991). Energetics of under-water swimming in Adélie penguins (*Pygoscelis adeliae*). *J. comp. Physiol.* (in press).
- CULIK, B., WOAKES, A. J., ADELUNG, D., WILSON, R. P., CORIA, N. R. AND SPAIRANI, H. J. (1990b). Energy requirements of Adélie penguin (*Pygoscelis adeliae*) chicks. *J. comp. Physiol.* **160B**, 61-70.
- DUNCAN, I. J. H. AND FILSHIE, J. H. (1980). The use of radio-telemetry devices to measure temperature and heart rate in domestic fowl. In *A Handbook on Radio-telemetry and Tracking* (ed. C. J. A. Amlaner and D. MacDonald), pp. 579-588. London: Pergamon Press.
- FISHER, R., GILBERT, F. F. AND ROBINETTE, J. D. (1987). Heart rate as an indicator of oxygen consumption in the pine marten (*Martes americana*). *Can. J. Zool.* **65**, 2085-2089.
- FOLK, G. E. AND FOLK, M. A. (1980). Physiology of large mammals by implanted radio capsules. In *A Handbook on Radio-telemetry and Tracking* (ed C. J. A. Amlaner and D. MacDonald), pp. 33-43. London: Pergamon Press.
- GALES, R., WILLIAMS, C. AND RITZ, D. (1990). Foraging behaviour of the Little penguin (*Eudyptula minor*): initial results and assessment of instrument effect. *J. Zool., Lond.* **220**, 61-85.
- GENTRY, R. L. AND KOOYMAN, G. L. (1986). Methods of dive analysis. In *Fur Seals: Maternal Strategies on Land and at Sea* (ed. R. L. Gentry and G. L. Kooyman), pp. 28-41. Princeton, USA: Princeton University Press.
- GESSAMAN, J. A. AND NAGY, K. A. (1988). Transmitter loads affect the flight speed and metabolism of homing pigeons. *Condor* **90**, 662-668.
- GILBERT, F. F. AND GROFTON, N. (1982). Heart rate values for beaver, mink and muskrat. *Comp. Biochem. Physiol.* **73A**, 249-251.
- KORSCHGEN, C. E., MAXSON, S. J. AND KUECHLE, V. B. (1984). Evaluation of implanted radio-transmitters in ducks. *J. Wildl. Mgmt* **48**, 982-987.
- NAGY, K. A., SIEGFRIED, W. R. AND WILSON, R. P. (1984). Energy utilization by free-ranging Jackass penguins *Spheniscus demersus*. *Ecology* **65**, 1648-1655.
- OBRECHT, H. H., PENNYCUICK, C. J. AND FULLER, M. R. (1988). Wind tunnel experiments to assess the drag of back-mounted radio transmitters on bird body drag. *J. exp. Biol.* **135**, 265-273.

- OEHME, H. AND BANNASCH, R. (1989). Energetics of locomotion in penguins. In *Energy Transformation in Cells and Organisms* (ed. W. Wieser and E. Gnaiger), pp. 230–240. Stuttgart, Germany: Thieme Verlag.
- PENNYCUICK, C. J. AND FULLER, M. R. (1987). Considerations of the effects of radio-transmitters on bird flight. *Biotelemetry* **9**, 327–330.
- PENNYCUICK, C. J., OBRECHT, H. H. AND FULLER, M. R. (1988). Empirical estimates of body drag of large waterfowl and raptors. *J. exp. Biol.* **135**, 253–264.
- PERRY, M. C. (1981). Abnormal behaviour of canvassbacks equipped with radio transmitters. *J. Wildl. Mgmt* **45**, 786–789.
- SCHMIDT-NIELSEN, K. (1972). Locomotion: Energy cost of swimming, flying and running. *Science* **177**, 222–228.
- SCHMIDT-NIELSEN, K. (1983). *Animal Physiology: Adaptation and Environment*, third edition. Cambridge, UK: Cambridge University Press.
- SEDINGER, J. S., WHITE, R. G. AND HAUER, W. E. (1990). Effects of carrying radio transmitters on energy expenditure of pacific black brant. *J. Wildl. Mgmt* **54**, 42–45.
- SKIRNISSON, K. AND FEDDERSEN, D. (1984). Erfahrungen mit der Implantation von Sendern bei freilebenden Steinmardern. *Z. Jagdwiss.* **30**, 228–235.
- TRIVELPIECE, W. Z., BENGTSON, J. L., TRIVELPIECE, S. G. AND VOLKMAN, N. J. (1986). Foraging behavior of Gentoo and Chinstrap penguins as determined by new radiotelemetry techniques. *Auk* **103**, 777–781.
- WANLESS, S., HARRIS, M. P. AND MORRIS, J. A. (1988). The effect of radio transmitters on the behavior of common mures and razorbills during chick rearing. *Condor* **90**, 816–823.
- WANLESS, S., HARRIS, M. P. AND MORRIS, J. A. (1989). Behavior of alcids with tail-mounted radio transmitters. *Col. Waterbirds* **12**, 158–163.
- WILSON, R. P. (1989). Diving depths of Gentoo (*Pygoscelis papua*) and Adélie (*P. adeliae*) penguins at Esperanza Bay, Antarctic peninsula. *Cormorant* **17**, 1–8.
- WILSON, R. P., CORIA, N. R., SPAIRANI, H. G., ADELUNG, D. AND CULIK, B. (1989). Human-induced behaviour in Adélie penguins (*Pygoscelis adeliae*). *Polar Biol.* **10**, 77–80.
- WILSON, R. P., GRANT, W. S. AND DUFFY, D. C. (1986). Recording devices on free-ranging marine animals: does measurement affect performance? *Ecology* **67**, 1091–1093.
- WILSON, R. P. AND WILSON, M.-P. (1988). Dead reckoning: a new technique for determining penguin movements at sea. *Meeresforsch.* **32**, 155–158.
- WILSON, R. P. AND WILSON, M.-P. (1989a). A peck activity record for birds fitted with devices. *J. Field Ornithol.* **60**, 104–108.
- WILSON, R. P. AND WILSON, M.-P. (1989b). Tape: a package attachment technique for waterbirds. *Wildl. Soc. Bull.* **17**, 77–79.
- WOAKES, A. J. AND BUTLER, P. J. (1975). An implantable transmitter for monitoring heart rate and respiratory frequency in diving ducks. *Biotelemetry* **2**, 153–160.
- WOAKES, A. J. AND BUTLER, P. J. (1983). Swimming and diving in tufted ducks *Aythya fuligula*, with particular reference to heart rate and gas exchange. *J. exp. Biol.* **107**, 311–329.