DIVING ENERGETICS IN KING PENGUINS (*APTENODYTES PATAGONICUS*)

B. M. CULIK[1], K. PÜTZ[1], R. P. WILSON[1], D. ALLERS[1], J. LAGE[2], C. A. BOST[2] AND Y. LE MAHO[2]

[1]*Abteilung Meereszoologie, Institut für Meereskunde, Düsternbrooker Weg 20, D-24105 Kiel, Germany* and
[2]*Centre d'Ecologie et Physiologie Energétiques, Centre National de la Recherche Scientifique, 23 Rue Becquerel, F-67087 Strasbourg, France*

Summary

Dive duration in wild king penguins and the energetic cost of swimming in a 30 m long swim channel were determined at Ile de la Possession, Crozet Archipelago, using external data loggers and respirometry, respectively. Calibrated electronic data loggers equipped with a pressure sensor were used to determine dive durations: 95 % of dives were less than 6 min long and 66 % of dives were less than 4 min long. Dive patterns show that king penguins may intersperse long dive durations (4–6.3 min) with short ones (1.5–3 min) and make surface pauses of variable duration between them (0.5–3.5 min), or dive regularly (for up to 5 h) with long dive durations (5 min) and constant interdive surface intervals (1.5 min). The latter indicates that the aerobic dive limits (ADL) of this species could be higher and oxygen consumption lower than previously reported. Assuming that king penguins dive within their aerobic limit, different approaches to the analysis of the data obtained in the swim channel are discussed to derive the ADL. Swimming speeds observed in the channel ranged from 0.9 to 3.4 m s^{-1}. Transport costs were lowest between 1.8 and 2.2 m s^{-1}. Although at 2.2 m s^{-1} king penguins used only 10.3 W kg^{-1} over a dive + surface cycle (minimal transport costs of 4.7 J kg^{-1} m^{-1}), we speculate that tissue oxygen consumption during submergence may be as low as 0.23 ml O$_2$ kg^{-1} s^{-1} (2.1 times standard metabolic rate, SMR) or perhaps lower (which gives an ADL of 4.2 min). During surface phases, oxygen uptake would be increased to at least 1 ml O$_2$ kg^{-1} s^{-1} (9.3 times SMR). This implies that at least 70 % of all dives are aerobic. Potential physiological mechanisms allowing king penguins to partition O$_2$ consumption between submergence and surface periods remain, however, unclear.

Key words: swimming speed, dive duration, time–depth recorders, external instrumentation, flipper bands, respirometry, aerobic dive limit, Antarctica, king penguin, *Aptenodytes patagonicus*.

Introduction

Maximum dive duration and maximum dive depth in penguins are positively related to body mass (Pütz, 1994; Wilson, 1995). King penguins (*Aptenodytes patagonicus*) and their congeners, emperor penguins (*Aptenodytes forsteri*), are the largest of all diving birds and thus have exceptional diving abilities. When foraging for myctophids during the breeding season, king penguins travel as far as 500 km during a 7 day round trip (Adams, 1987; Jouventin *et al.* 1994) and reach depths greater than 300 m during dives lasting up to 8 min (Kooyman *et al.* 1992*a*; Pütz, 1994). These performances suggest that penguins of the genus *Aptenodytes* have low transport costs, great breath-holding capacities and extended aerobic dive limits (ADL) compared with other penguin species. Kooyman *et al.* (1992*a*) recently concluded that 'king penguins seem to swim too fast and dive for too long, and too often, to be in agreement with our physiological models of diving'. In the present paper, we attempt to shed new light on this enigma.

Culik and Wilson (1991*a*) presented a method whereby energy requirements of sub-surface-swimming air-breathing animals could be measured under semi-natural conditions. They used a 21 m long swim channel with respiration chambers at each end to measure the oxygen uptake of Adélie penguins (*Pygoscelis adeliae*) after a dive. Penguins in the channel could swim freely and also reached speeds at which they swam in the wild. Furthermore, Wilson *et al.* (1993) and Bannasch *et al.* (1994) developed an activity recorder to determine dive depth, dive duration and swimming speed of penguins at sea and shaped the device so that the drag increment incurred by the birds was minimal (Culik *et al.* 1994*a*).

We used a calibrated depth recorder on king penguins at sea and a 30 m long swim channel in conjunction with respirometry. The aims of this study were as follows: (1) to determine the frequency distributions of diving duration and the patterns of diving; (2) to determine the energy expenditure of resting and swimming for the birds swimming at their preferred speeds; (3) to estimate the minimum cost of transport and the optimal swimming speed from 2; (4) to test different

methods of data analysis to derive oxygen consumption during the dive from measured oxygen uptake of the birds in the respiration chamber during recovery; (5) to calculate the ADL and other variables from 4 and to compare them with measured dive durations.

Materials and methods

All experiments were carried out at Ile de la Possession, Crozet Archipelago, Indian Ocean (46° 25′ S, 51° 45′ E). Experiments on the diving behaviour of free-living king penguins were conducted between 10 January and 21 March 1993 at the breeding colony 'Grande Manchotière' located at Baie du Marin using externally attached time and depth recorders. Swimming energetics were investigated between 12 February and 4 March 1994 at the same site using a swim channel and respirometry.

Diving behaviour

For experiments involving activity recorders, we chose king penguins still brooding their egg or birds whose chicks were not older than 5 weeks. From within the fenced-in harbour enclosure, which is situated in the centre of the colony, we marked several birds with Methylene Blue on the chest using a 3 m pole with a syringe (without needle) attached. In order to avoid unnecessary stress to the breeding birds in the colony (see Culik and Wilson, 1991b; Le Maho et al. 1992, 1993), the marked penguins were captured outside the colony on their way to the sea after a change-over between partners had occurred. Mean mass of the birds (N=50) used in this part of the study was 10.9±0.1 kg (S.E.M.).

Dive recorders

Dive recorders consisted of a 12-channel data-logging unit with 64 K memory (DKLog 100 series, Driesen + Kern, Bad Bramstedt, Germany) equipped with a pressure sensor enabling us to determine time under water (maximum dimensions 150 mm×57 mm×37 mm, mass 200 g). Data from other sensors contributing to the size of the device, such as speed, direction, light and temperature sensors, are published elsewhere (Pütz, 1994). The unit and the sensors were powered by a 6 V lithium battery and could be connected to an IBM-compatible personal computer via an external interface for programming and data transfer. The components were embedded in epoxy resin (Epoxy-Glosscoat, Voss-Chemie, Uetersen, Germany). The shape of the devices corresponded to that described by Bannasch et al. (1994).

Each unit was attached to the dorsal feathers of the birds using Tesa tape (Beiersdorf, Hamburg, Germany) according to the method described by Wilson and Wilson (1989). The units were attached in a caudal position to minimize hydrodynamic drag (see Culik et al. 1994a; incremental power input in the much smaller Adélie penguin swimming with these units was only 5.6%). Data analysis was performed using specially designed software (Jensen Software Systems, Kehl, Germany).

Experiments in the swim channel

The swim channel consisted of a 30 m long plywood construction 1.5 m wide and 1.2 m deep (approximately 54 m³), pre-built in segments (Beck und Thiel, Kiel, Germany). The channel was sealed with one transparent polyethylene sheet (35 m×4.5 m, thickness 0.5 mm, Ewert, Munich, Germany) and filled with sea water from the nearby beach (130 m) using a motor pump equipped with a filter (2 mm mesh). Mean water temperature during the experiments was 9.1±0.1 °C (S.E.M., N=29) in the channel, and that of sea water at the beach was 6.5 °C. The channel was covered approximately 10 cm below the water surface with transparent polyvinylchloride (PVC) sheets (1.5 m×3 m, 5 mm thick, Richter, Kiel, Germany) to prevent the birds from surfacing and breathing at localities other than in the respiration chambers. The PVC sheets were made more conspicuous for the birds by placing wire fencing on top, although behavioural observations were still possible from above. Water in the channel had to be replaced every 4 days because of rising water temperatures and contamination with excreta and algae.

The activity of the birds was monitored from an observation seat with a table, 4.5 m above the ground, which was attached to the channel. The behaviour and position of birds in the channel were recorded in real time using a Husky Hunter II field computer (Husky, Coventry, England) and specially designed software. In brief, each key on the computer was associated with a particular behaviour or position of the bird. Each time one of the keys was pressed, time (in hours, minutes, seconds and tenths of a second) as well as the identity of key were stored. A behaviour ended when a new behaviour was recorded, while positional information was associated with the exact time at which it was recorded. The data obtained were saved in individual files for each experiment and later analysed using specially designed software to obtain (a) the duration of the various activities, (b) the swimming speed, (c) the distance swum and (d) the dive duration for each individual diving event.

When in the channel, king penguins could only breathe in two respiration chambers (transparent PVC, volume depending on water level, approximately 90 l) partially immersed at both ends of the channel and thus sealed from the outside air. Each chamber was fitted inside with a 50 cm×1 cm tube with 2 mm holes drilled every 20 mm as an air inlet, allowing outside air to be drawn into the chamber and ensuring rapid mixing with chamber air. Gas mixing in the chamber was additionally achieved by using a 12 V ventilator (Trumavent TEB, Truma, Putzbrunn, Germany) with directable air inlets and outlets and mixing the air volume in each chamber within 2 s. Air from the chambers was cleared at a rate of 50 l min^{-1} using two seawater-resistant pumps (MC4, Vacuubrand, Wertheim, Germany) and fed directly to the laboratory via gas-impermeable tubing (9.5 mm diameter, Tygon, Norton, USA). In the laboratory, gas flow from each chamber was measured using one of two mass flow meters (MAS 3015, Kobold, Hofheim, Germany) and a subsample was dried (Drierite, Aldrich Chemicals) and passed into one

of two paramagnetic oxygen analysers (OXYGOR) and subsequently one infrared carbon dioxide analyser (UNOR, both Maihak, Hamburg, Germany). During the experiments, gas concentrations in the respiration chambers remained between 20 and 21 % (O_2) and 0 and 1 % (CO_2). Absorption of CO_2 by sea water during the experiment was assumed to be negligible and estimated to amount to a maximum of 0.015 % min^{-1} (from $6.28{\times}10^{-3}$ $mol\,CO_2\,m^{-2}\,year^{-1}\,Pa^{-1}$); A. Körtzinger, personal communication; Liss and Merlivat, 1986). Data from the three analysers and the two flow meters were sampled every 2s by an IBM-compatible 386SX (Chicony, Hamburg, Germany) computer fitted with an analog–digital conversion card and using purpose-made software.

The whole system was calibrated and checked daily. Mean measurement error of the entire system (range −3 to +6 %, N=13) was determined by recovery tests using known volumes of nitrogen (99.995 % pure, Messer Griesheim, Kiel, Germany) pumped into the respiration chambers through a standard gas meter. Response time until a decline in oxygen level could be detected by the analysers after N_2 injection (range 25–32 s) was mainly due to the Drierite columns and tubing within the laboratory. The difference in response times between the two chambers (due to different distances from the laboratory) was 7 s and hysteresis (hysteresis = response time$_{end}$ minus response time$_{start}$ plus duration of N_2 injection) of the system after termination of N_2 injection was 3 s.

Prior to an experiment, a king penguin returning from the sea was captured at the nearby beach, weighed and placed into one of the two respiration chambers. As a consequence, birds may have experienced stress when first immersed into the channel, resulting in higher oxygen consumption rates. However, these wild birds were in good condition, had perfect plumage and were not kept in an enclosure, advantages which may have somewhat counterbalanced increased respiration rates due to the stress of capture. The feeding status of the birds could not be assessed (but judging from bird shape, all birds had full stomachs; see respiratory quotient determination below). Two people were required to ensure that the bird found the respiration chamber after its first dive. If this was not the case, the transparent PVC sheets covering the channel were slid open and the bird rescued from above. However, all penguins except one found a respiration chamber within 1–2 min after the beginning of the experiment and subsequently explored the channel to find an exit, thereby beginning to swim up and down, from one chamber to the other. Apart from these restrictions, the penguins used in these experiments were unrestrained and swam of their own free will and at their preferred speeds. A total of 11 birds were used (mean body mass 11.5±0.4 kg, s.e.m.) in experiments lasting between 120 and 240 min. Experiment duration was dependent on the performance of the penguins in the channel, duration being shortest with very cooperative or very restful birds. In general, birds had adopted a regular swimming pattern within 60–120 min of the beginning of the experiment.

Oxygen consumption

Oxygen consumption of penguins in the respiration chambers was calculated for every 2 s interval using the formula of Woakes and Butler (1983) as modified by Culik *et al.* (1990) and summed for values above a threshold of $1\,ml\,s^{-1}$. This ensured that 'noise' in the apparatus was not recorded while birds were not in the chambers. Activity and respirometry data were individually matched for each interdive interval. Before further analysis, the complete data set was filtered to include only periods during which the birds swam for a minimum of 30 m before surfacing (mean distance swum 44.7±1.6 m, s.e.m., N=243) or rested at the surface for a minimum of 10 min (N=22). Thus, prior to surfacing in a respiration chamber, the birds had been absent from that chamber for a minimum of 15 s. This delay was sufficient to
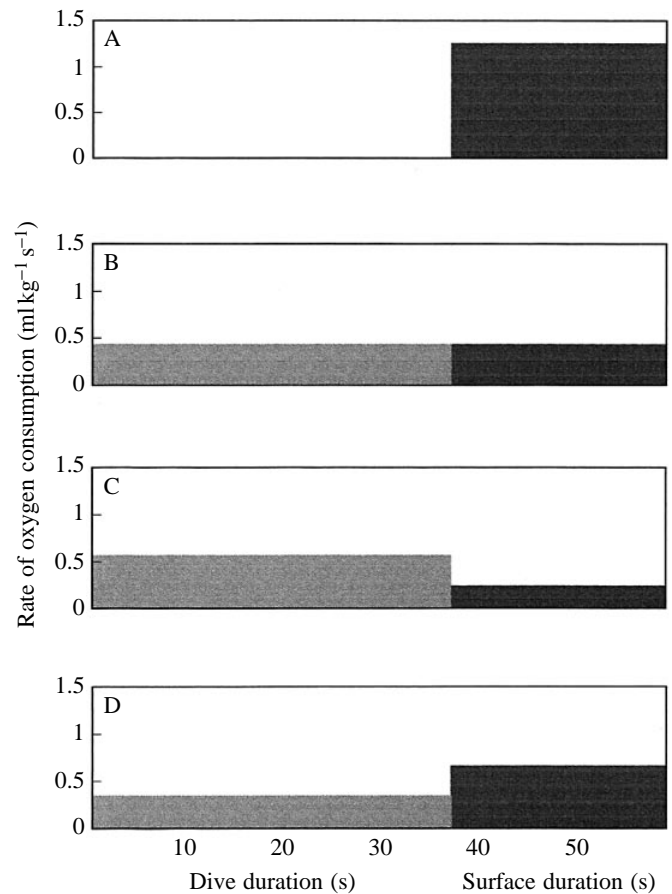

Fig. 1. (A) Rate of oxygen consumption ($\dot{V}_{O_2}$) of king penguins as measured by gas analysis during the recovery phase after a dive. (B) If the amount of oxygen consumed during recovery is divided by the total dive+surface time, we assume that O_2 consumption is constant irrespective of whether the animal is submerged or not. (C) In order to calculate $\dot{V}_{O_2}$ required for swimming, we subtracted $\dot{V}_{O_2}$ required for resting at the surface from the value shown in A. In this case, the swimming animal apparently has a higher oxygen consumption rate than during recovery at the surface. (D) Two-way regression analysis of oxygen consumption as measured in A *versus* duration of dive and surface times yields a higher oxygen consumption during recovery than during swimming. See text for further details.

separate individual dive+surfacing events. All dives followed by shivering or unrest (i.e. unquantifiable activity) were deleted from the analysis.

We assumed that oxygen consumption in the chambers during surface time (Fig. 1A) reflected oxygen consumption while swimming (and breath-holding) just prior to surfacing plus oxygen consumption during the current recovery period. Total V_{O_2} consumed during the surface interval after each dive (mean value of $1.24\,\mathrm{ml\,kg^{-1}\,s^{-1}}$ in the data presented here) was analysed in three different ways.

(i) The total amount of oxygen consumed (ml) during the recovery period ($V_{O_2\text{total}}$) was divided by the time (in s) of breath-holding (t_{dive}) plus the time of recovery (t_{surface}) (Fig. 1B) according to Castellini *et al.* (1992):

$$\dot{V}_{O_2\text{total}} = V_{O_2\text{total}}/(t_{\text{surface}} + t_{\text{dive}}). \qquad (1)$$

For example, for a 36 s dive and a subsequent 19 s recovery period, the oxygen used during the 19 s at the surface was divided by the total dive+surface time of 55 s to arrive at an oxygen consumption rate for the *entire event* (mean of $0.43\,\mathrm{ml\,kg^{-1}\,s^{-1}}$).

(ii) The total amount of oxygen consumed during the recovery period ($V_{O_2\text{total}}$) was used to calculate oxygen consumption rate during *underwater swimming* ($\dot{V}_{O_2\text{swim}}$). We assumed that if O_2 consumption in the chamber during the surface period was higher than that measured for birds continuously resting in water, the difference was due to the previous exercise (i.e. paying for the oxygen debt at the surface) or a consequence of it (i.e. an increased recovery metabolic rate to minimize surface time). Consequently (Fig. 1C), we subtracted the amount of oxygen which would have been consumed at the surface had the animal been resting from $V_{O_2\text{total}}$ and divided the remainder by the dive time, i.e. 36 s in the above example (which yields $0.56\,\mathrm{ml\,kg^{-1}\,s^{-1}}$) according to the formula:

$$\dot{V}_{O_2\text{swim}} = (V_{O_2\text{total}} - \dot{V}_{O_2\text{rest}} \times t_{\text{surface}})/t_{\text{swim}}, \qquad (2)$$

where $\dot{V}_{O_2\text{rest}}$ is the rate of oxygen consumption while resting in sea water at the same temperature ($0.235\,\mathrm{ml\,kg^{-1}\,s^{-1}}$) and t_{surface} is the duration of the recovery period (s), i.e. 19 s in the above example (see Culik *et al.* 1994a,b).

(iii) In a two-way regression analysis including all measurements of total amount of oxygen consumed *versus* t_{dive} and t_{surface}, we determined (Fig. 1D) parameters a and b of the equation:

$$\dot{V}_{O_2\text{total}} = at_{\text{dive}} + bt_{\text{surface}}. \qquad (3)$$

With a dive duration of 36 s and a recovery period of 19 s, we obtained $0.34\,\mathrm{ml\,kg^{-1}\,s^{-1}}$ for O_2 consumption under water and $0.65\,\mathrm{ml\,kg^{-1}\,s^{-1}}$ for O_2 consumption at the surface (Fig. 1D).

Oxygen consumption was subsequently analysed with respect to swimming speed and averaged for $0.1\,\mathrm{m\,s^{-1}}$ speed classes (see Culik and Wilson, 1991a; Culik *et al.* 1994a,b, for further details). All statistical analyses were computed using SYSTAT. Values are given as means ± S.E.M.

Results
Diving behaviour

Dive duration of king penguins at sea was obtained from 14 birds fitted with data loggers recording at intervals between 20 and 32 s. A total of 10 930 measurements of dive duration including travelling (shallow) as well as feeding (deep) dives were obtained (see Pütz and Bost, 1994). Dive durations were not normally distributed (Fig. 2), apparently being strongly skewed to the left with a mode at 1.5 min (but for a detailed description of the influence of sampling interval on dive duration frequency distribution see Boyd, 1993; Wilson *et al.* 1995). The cumulative curve (Fig. 2) was obtained by adding the frequencies of dive durations from 0 to 8 min. 33 % of all dives exceeded a duration of 4 min, while only 10 % of all dives were longer than 5.3 min.

Typical diving behaviour of king penguins could be classified into two broad categories. (1) (Fig. 3A) long (4–6.3 min) and deep (>180 m, see Pütz, 1994) dives interspersed with short (1.3–2.7 min) and shallow (<40 m, see Pütz, 1994) dives (mean dive durations of 3.25±0.26 min, N=50). Here, mean surface durations were approximately 1.7±0.3 min (range 0–3.3 min, N=50), although some surface durations were less than the duration (20 s) of the recording interval (marked by asterisks in Fig. 3A). (2) (Fig. 3B) consistently long (mean of 5.03±0.07 min, N=46) and deep (>180 m, see Pütz, 1994) dives with no intervening short dives (Fig. 3B) and with surface durations averaging only 1.45±0.06 min (N=46). Both types of dive profiles were observed in all king penguins during every foraging trip.
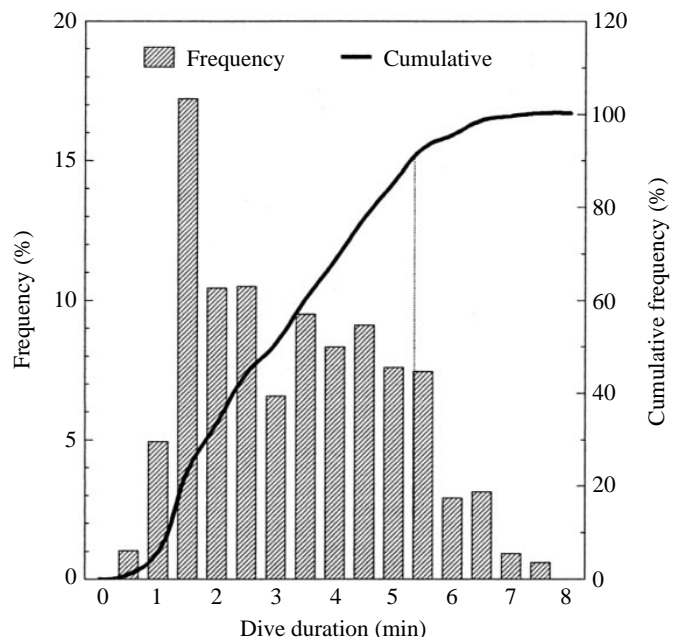

Fig. 2. Frequency distribution of dive durations of king penguins at sea including deep and shallow dives (left-hand *y*-axis). The curve (right-hand *y*-axis) shows the cumulative frequency and gives 66 % of the dives shorter than 4 min and 90 % of the dives shorter than 5.3 min (vertical dotted line). Recording interval was 20–32 s.
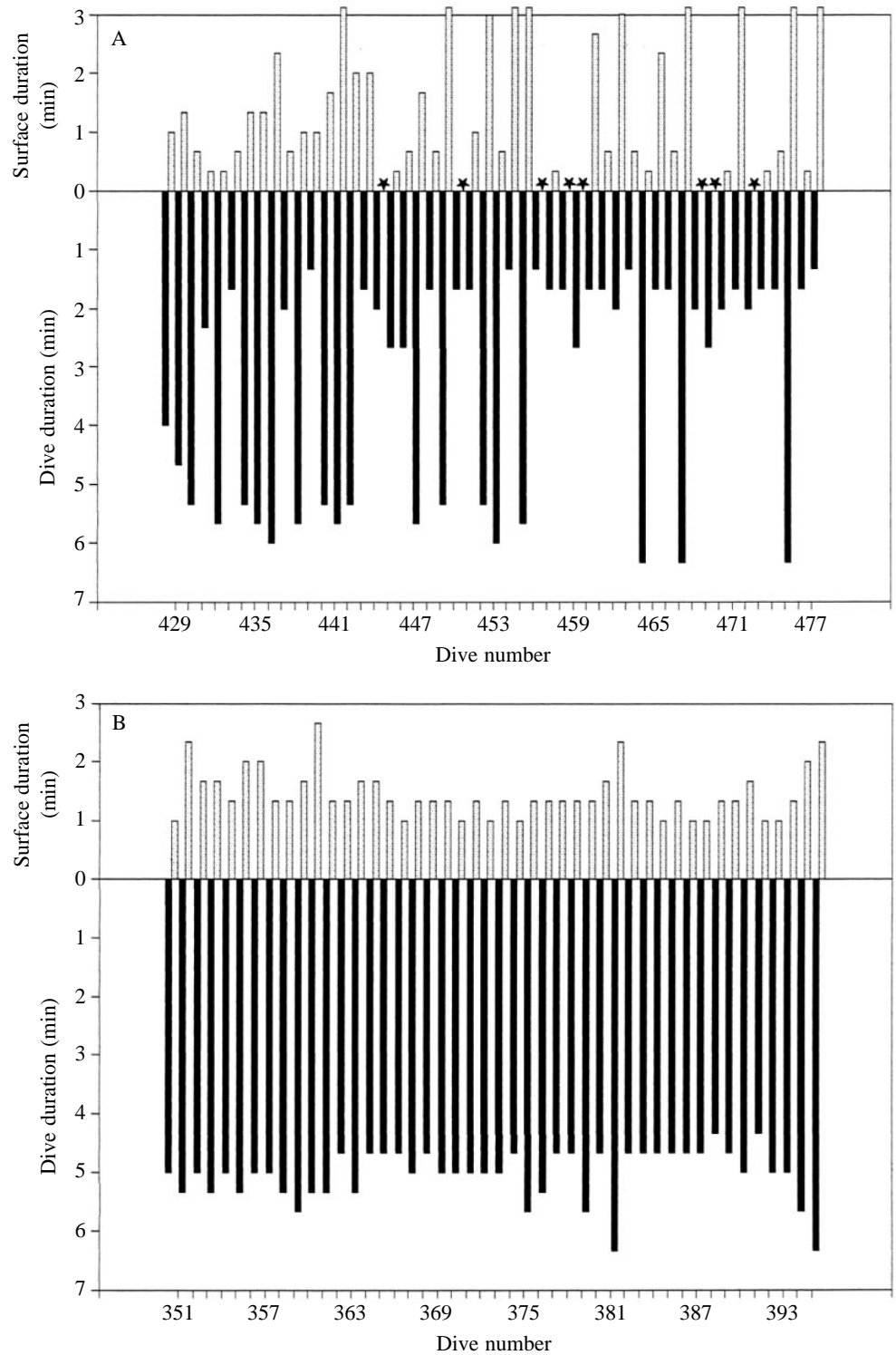
Fig. 3. (A) Dives of variable duration in a king penguin followed by variable surface times. The bird was diving on 5 February 1993 between 05:53 h and 09:47 h. Mean dive duration is 3.25±0.3 min (S.E.M., range 1.3–6.3 min, *N*=50) and mean recovery time is 1.7±0.3 min (range 0–3.3 min). Surface intervals shorter than the sampling rate (20 s) are denoted by stars. (B) Dive pattern of a king penguin (same bird as in A) on 4 February 1993 between 13:58 h and 18:54 h, showing nearly constant dive times followed by almost constant surface times. Mean dive duration is 5.03±0.07 min (range 4.3–6.3 min, *N*=46) and surface time is 1.45±0.06 min (range 1–2.6 min).

Surface times in penguins can be variable (Fig. 3A), and the birds could be paying off an oxygen debt incurred during a long dive by increasing their surface duration several dives later (Kooyman *et al.* 1992*a*). In order to account for this possibility, we determined the minimum number of consecutive dives which would yield a constant ratio of surface duration to dive duration and found it empirically to be eight dives. We only

used data derived from time–depth recorders operating with a recording interval of 20 or 24 s and eliminated all dives which were followed by surface durations longer than 10 min to avoid long resting periods. From the resulting data (*N*=4123), we computed the running mean of dive and corresponding surface durations for series of eight consecutive dives (modified from Horning, 1992, who used the running sum) and determined the
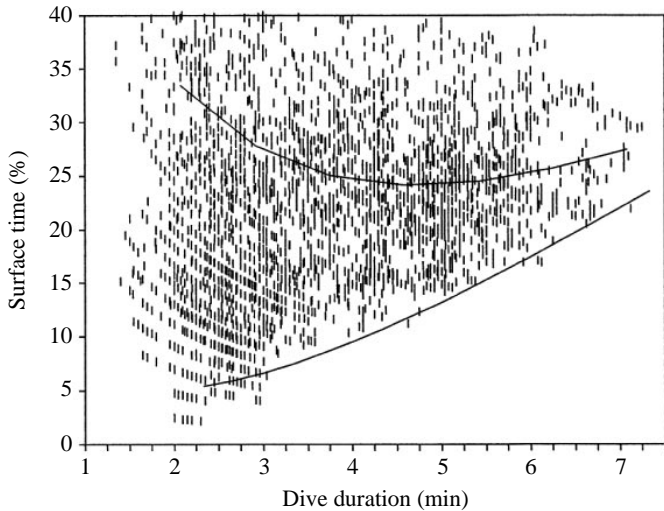
Fig. 4. Surface time (%) for each dive+surface cycle as a function of dive time (min) in king penguins diving at sea for dive durations greater than 1 min. (N=4123). The upper and lower curves show median and minimum surface times, respectively.

relationship between these. Minimum surface duration (min) was related to dive duration (min) by:

$$\text{Minimum } t_{\text{surface}} = 6.23 \times 10^{-2} + (5.58 \times 10^{-3}) t_{\text{dive}}^3. \quad (4)$$

Median surface duration followed the relationship:

$$\text{Median } t_{\text{surface}} = 1.005 + (4.716 \times 10^{-3}) t_{\text{dive}}^3. \quad (5)$$

While running means of less than eight dives showed a different relationship, those including more than eight dives did not. Fig. 4 shows percentage surface time (for each dive+surface cycle) of king penguins diving at sea calculated from equations 4 and 5 and was obtained using:

$$\text{percentage surface time} = 100 t_{\text{surface}}/(t_{\text{dive}} + t_{\text{surface}}). \quad (6)$$

Energetics

Swimming speeds of 11 birds in the channel (Fig. 5) ranged from 0.9 to $3.4\pm0.03\,\text{m s}^{-1}$ (median $1.5\,\text{m s}^{-1}$, mean $1.54\,\text{m s}^{-1}$, N=243). During experiments in the swim channel, eight king penguins were also observed to rest in one of the respiration chambers for mean periods of $11.4\pm0.9\,\text{min}$ (N=22). The respiratory quotient (RQ) of these birds was 0.74 ± 0.03, which is close to that of post-absorptive animals (0.71; Gessaman and Nagy, 1988). Presumably, food absorption from the stomach was halted to provide food for the chicks (see Pütz, 1994; G. Peters, unpublished data). Consequently, we used a conversion factor of $19.8\,\text{J ml}^{-1}\text{O}_2$ (Schmidt-Nielsen, 1983) in all our experiments. While resting in water at $9.1\,^{\circ}\text{C}$, energy expenditure of king penguins (N=8) averaged $4.65\pm0.17\,\text{W kg}^{-1}$, which corresponds to 2.1 times the predicted SMR (Aschoff and Pohl; 1970: $\dot{V}_{\text{O}_2}=0.013M^{0.729}$, where $\dot{V}_{\text{O}_2}$ is in l min^{-1} and body mass, M, is 11.5 kg).

Mean power requirements (W kg^{-1}) for the entire dive+surface cycle (see equation 1) were analysed with respect
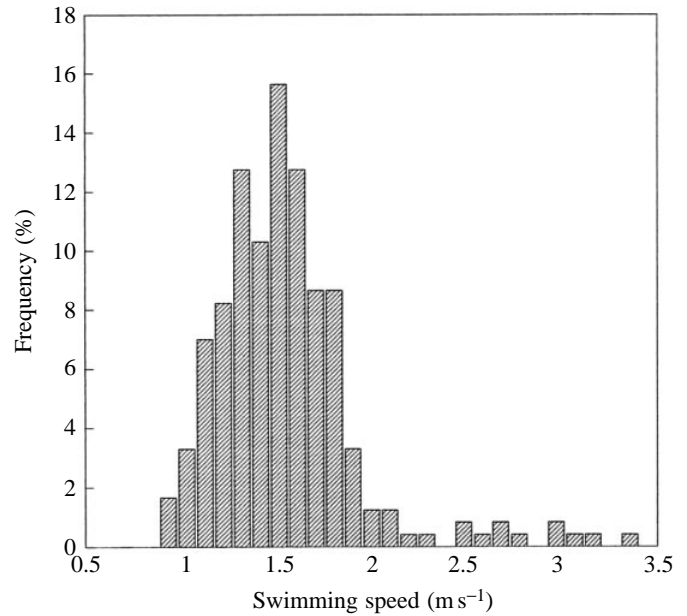

Fig. 5. Distribution of swimming speeds of king penguins in the swim channel (mean $1.54\pm0.03\,\text{m s}^{-1}$, s.e.m., N=243; median $1.52\,\text{m s}^{-1}$) calculated from positional observations made visually and recorded on a hand-held computer.

to swimming speed (Fig. 6). The black line represents a cubic fit of the data (N=223) using the equation:

$$P_{\text{total}} = xv^3 + yv^2 + zv + P_{\text{rest}}, \quad (7)$$

where P_{total} is the mean power required for the whole cycle (W kg^{-1}), v is swimming speed (m s^{-1}) and P_{rest} is the power required (W kg^{-1}) during rest in water. The cubic polynomial used to describe P_{total} was first introduced by Culik et al. (1994b), who also discussed the reasons for choosing this fit. The parameters for the equation are given in Table 1. Table 1
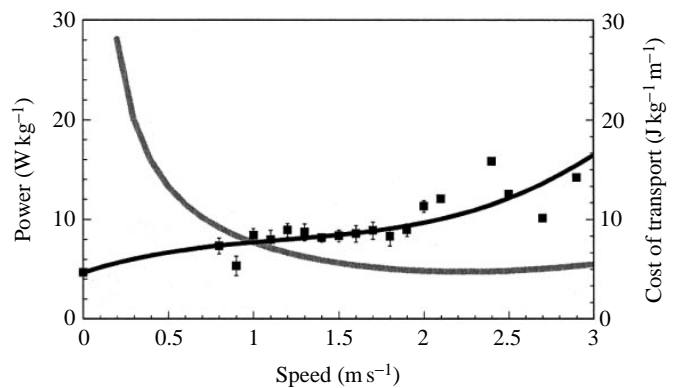

Fig. 6. Power input $(P_{\text{total}}, \text{W kg}^{-1})$ of king penguins swimming in the swim channel versus swimming speed (values are means ± s.e.m.). The black line shows P_{total} (see Table 1) and the grey line gives the cost of transport $(\text{J kg}^{-1}\text{m}^{-1})$ in king penguins with respect to speed (cost of transport = P/v, where v is swimming speed in m s^{-1}). Transport costs were lowest at $2.2\,\text{m s}^{-1}$. For details see text.

Table 1. *Parameters used to calculate power input ($W\,kg^{-1}$)
of king penguins while swimming in the channel*

	P_{total}	P_{swim}	P_{dive}
x	0.98	2.15	1.01
y	−3.46	−6.89	−2.38
z	5.50	9.44	2.88
P_{rest}	4.65	4.65	4.65
r^2	0.87	0.77	0.65

Power input ($W\,kg^{-1}$) was calculated according to three different approaches (see Materials and methods) and is best described by $P=xv^3+yv^2+zv+P_{rest}$.

$N=23$.

P_{total}, power required over entire dive+surface cycle; P_{swim}, power required during swimming; P_{dive}, power required during breath-holding; P_{rest}, power required during resting.

also presents the parameters for the calculation of P_{swim} (equation 2) and P_{dive} (equation 3).

From the parameters shown in Table 1, we calculate that at a speed of $1.5\,m\,s^{-1}$ (mean speed in the swim channel) a king penguin used on average $8.4\,W\,kg^{-1}$ over the entire dive+surface cycle (P_{total}). Assuming that all oxygen consumption above resting levels is due to previous exercise, swimming *per se* requires $10.6\,W\,kg^{-1}$ (P_{swim}). With a two-way regression analysis of dive and surface time on power (equation 3), oxygen consumed during the underwater phase of the cycle (P_{dive}) corresponds to only $7.7\,W\,kg^{-1}$, a substantial amount of the oxygen requirements of swimming being repaid during the subsequent recovery period ($11.7\,W\,kg^{-1}$). Cost of transport ($J\,kg^{-1}\,m^{-1}$) is power ($J\,kg^{-1}\,s^{-1}$) divided by speed ($m\,s^{-1}$; Pinshow *et al.* 1977). From P_{total} we derived minimum transport costs of $4.7\,J\,kg^{-1}\,m^{-1}$ at $2.2\,m\,s^{-1}$ amounting to $10.3\,W\,kg^{-1}$ (grey line, Fig. 6).

In foraging wild birds, percentage surface time [percentage surface time = $t_{surface} \times 100/(t_{surface} + t_{dive})$] varies with dive duration (Fig. 4). We therefore selected data subsets from the experiments in the swim channel according to different percentage surface times . For this, we calculated the ratio $k = t_{dive}/t_{surface}$ and only included those data in the subset for which k was larger than a predetermined value. For example, a data subset with $k>1$ only includes data where $t_{dive}>t_{surface}$ and has a mean percentage surface time of 29 % (Table 2). For $k>0$ (all data), percentage surface time averaged 41.4 % of the surface+dive cycle. Mean dive duration in the channel (t_{dive}) remained almost constant in all the data subsets with a minimum of 28.5 s and a maximum of 35.5 s, whereas surface duration ($t_{surface}$) decreased with decreasing percentage surface time. With the data subsets thus obtained, we recalculated (Table 2) the parameters a (rate of O_2 consumption under water in $ml\,kg^{-1}\,s^{-1}$) and b (rate of O_2 uptake at the surface in $ml\,kg^{-1}\,s^{-1}$) in equation 3. We assume that oxygen uptake at the surface includes all metabolic activities required to replenish the oxygen reserves, as well as the oxygen reserves themselves.

Table 2. *Regression coefficients for the equation
$V_{O_2}=at_{dive}+bt_{surface}$ using different data subsets from the
swim channel experiments*

Surface time (%)	a ($ml\,kg^{-1}\,s^{-1}$)	b ($ml\,kg^{-1}\,s^{-1}$)	r^2	N	t_{dive} (s)	$t_{surface}$ (s)
41.4	0.39	0.59	0.90	243	34.0	24.0
34.3	0.34	0.66	0.90	223	35.5	18.5
29.0	0.34	0.68	0.91	197	35.0	14.3
24.1	0.23	1.02	0.92	166	35.0	11.1
20.2	0.21	1.09	0.90	141	32.0	8.1
17.8	0.18	1.23	0.87	124	31.0	6.7
16.4	0.16	1.39	0.85	109	30.0	5.9
15.0	0.15	1.44	0.83	97	30.0	5.3
14.5	0.11	1.71	0.83	88	30.0	5.1
13.6	0.20	1.06	0.89	77	29.2	4.6
12.3	0.24	0.70	0.86	60	28.5	4.0

Percentage surface time=$100\times t_{surface}/(t_{dive}+t_{surface})$; N=sample size.

Fig. 7 shows the values obtained for a and b with respect to percentage surface time. The rate of oxygen uptake at the surface reaches a maximum ($1.7\,ml\,kg^{-1}\,s^{-1}$) and oxygen consumption during the dive reaches a minimum ($0.11\,ml\,kg^{-1}\,s^{-1}$) when percentage surface time averages 14.5 % ($k>4$). At surface times lower or higher than 14.5 %, O_2 uptake at the surface is lower, while O_2 consumption during the dive is higher.
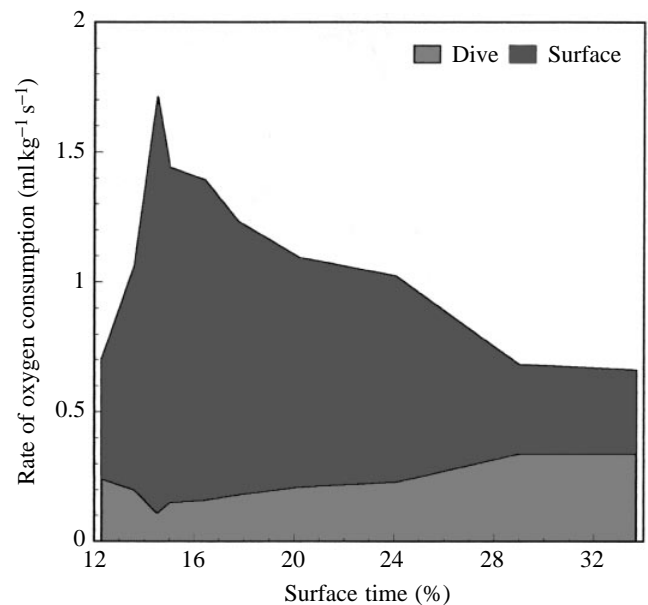

Fig. 7. Rate of oxygen consumption during a dive and a subsequent surface period *versus* percentage surface time. The curves show the parameters a (oxygen consumption during the dive) and b (oxygen uptake at the surface) in the equation $\dot{V}_{O_2} = at_{dive} + bt_{surface}$. Minimum O_2 consumption during a dive and maximum O_2 uptake during the recovery period are observed at a surface time of 14.5 %. For details see Table 2 and text.

Discussion

Swimming speeds

Speed measurements in king penguins seem to be problematic in that they appear much more variable than those of other penguin species. For example, Kooyman *et al.* (1992*a*) measured the speed of swimming king penguins according to the method of Wilson and Bain (1984) and through direct observation of birds swimming towards shore. From this, they derived mean speeds of 2.1 and 2.2 m s^{-1}, respectively. Adams (1987) reported even higher mean swimming speeds of 2.4 m s^{-1}, also using the method of Wilson and Bain (1984). Mean swimming speeds measured *via* direct observation in the swim channel, however, agree with the results obtained by Kooyman *et al.* (1992*a*) and Pütz (1994) on free-living birds using calibrated microprocessor-controlled speed recorders and reporting values between 1.3 and 1.5 m s^{-1}.

Chinstrap (*Pygoscelis antarctica*), Adélie (*P. adeliae*) and gentoo penguins (*P. papua*) swam on average 35, 32 and 21 %, respectively, slower in a swim channel (21 m long) than in the wild (Culik *et al.* 1994*b*). These authors also showed that, at sea, penguins preferred those speeds at which their cost of transport was minimal. From this and the results presented here (Fig. 6), we would expect king penguins at sea to swim at speeds of approximately 1.8–2.2 m s^{-1}.

Diving behaviour

Frequency analysis of king penguin dive durations shows that 95 % of all dives were shorter than 6 min (Fig. 2). This analysis includes shallow dives to depths between 0 and 50 m as well as deep dives between 50 and 320 m and is therefore not directly comparable with the data of Kooyman *et al.* (1992*a*). However, their estimate that 25 % of feeding dives exceed 3.5 min coincides with our estimate that 33 % of dives are longer than 4 min.

The hypothesis of Kooyman *et al.* (1992*a*) that king penguins probably accumulate lactic acid during long dives and restore metabolic acidosis to a normal state by increasing surface times or surfacing frequency is only in part supported by our own data. Kooyman *et al.* (1992*a*) developed this hypothesis after examining dive data from king penguins similar to those illustrated in our Fig. 3A. From this evidence, they concluded that during long periods of short and shallow dives and frequent surface intervals 'the birds should have no problem recovering before the next long and deep dive' and that 'it seems certain that during deep dives these birds are relying much on anaerobic metabolism' (Kooyman *et al.* 1992*a*). However, we found that king penguins may have dive durations averaging 5 min interspersed with surface times of 1.45 min and that this behaviour may continue for 5 h (Fig. 3B). Thus, there are not always short dives between long ones, nor are there always extended surface times after a series of dives as suggested by Kooyman *et al.* (1992*a*). Since a surface time of 1.45 min is theoretically inadequate for the metabolism of lactate after exceeding the ADL (Kooyman and Kooyman, 1995), we conclude that birds exhibiting this behaviour should be diving within their ADL or should metabolise lactate as a fuel during subsequent dives (Kooyman, 1989).

According to Kramer (1988), surface and dive durations should be related disproportionately. The reason for this is that while oxygen stores are recharged over the course of several breaths during recovery at the surface, the partial pressure differentials (air/blood or blood/organ) decline and the rate of oxygen gain is reduced for each subsequent breath because of lower diffusion rates. This generates a curve of diminishing returns. This means that the large oxygen stores required for longer dives are acquired over a longer time and at a lower average rate than the amount of oxygen required for short dives. Consequently, the ratio of surface duration to dive duration should increase with increasing dive duration. In order to examine this hypothesis, we determined percentage surface time from dive and surface durations recorded in free-living king penguins (equation 6, Fig. 4) and found an optimum of 24 % surface time at dive durations of 4.3–5.3 min (30 % surface time for dives lasting 8 min, 34 % surface time for dives lasting 2 min). Thus, it would appear that king penguins optimizing for dive duration should preferentially dive for 5 min followed by recovery times of 1.6 min. This coincides well with the data shown in Fig. 3B. Using the curve of minimum rather than median surface time against dive duration (Fig. 4), *minimum* recovery time after dives of 4.3–5.3 min amounts to 10.6–14.6 % of the total dive+surface cycle (46 s for a 5 min dive).

Energy requirements and ADL

Resting metabolic rate of king penguins in water (4.65 W kg^{-1}; 9.1 °C) fits in the range determined by Kooyman *et al.* (1992*a*), who measured values between 2.7 and 5.2 W kg^{-1} in somewhat heavier birds (*N*=4, mass range 11.8–19.5 kg) than ours (mean mass 11.5 kg) at a water temperature of 5 °C. Resting in sea water thus amounts to 1.4 times RMR (resting metaboic rate) on land [Kooyman *et al.* (1992*a*) measured resting rates ashore and obtained 3.3 W kg^{-1}] or 2.1 times the predicted SMR (Aschoff and Pohl, 1970).

Available oxygen stores of king penguins are estimated to be 58 ml kg^{-1} (Kooyman, 1989), which is very similar to the stores available to other species such as the Adélie penguin (Culik *et al.* 1994*b*). Only phocids have larger oxygen stores, of the order of 60 ml kg^{-1} (Kooyman, 1989). Assuming the best possible case, i.e. that king penguins only use as much oxygen under water as during rest on the water surface (0.23 ml O$_2$ kg^{-1} s^{-1}), the ADL of the birds would be 4.2 min. While this figure is in agreement with the value reported by Kooyman and Davis (1987), it is almost twice as high as the value of 2.3 min calculated by Butler and Jones (1982). However, king penguins dive repeatedly for 5 min (Fig. 3B) to depths in excess of 180 m (Pütz, 1994). In other words, normal dive durations exceed the ADL calculated from the RMR. What are the metabolic adjustments allowing king penguins to dive for such long durations?

Culik *et al.* (1994*b*) used a swim channel to determine the energy requirements of pygoscelid penguins during underwater swimming. Their data analysis corresponds to that described in equation 2 above (Fig. 1C) and yields P_{swim}. From this, they determined the ADL of pygoscelid penguins and found the resulting values to be too low to be able to explain the diving behaviour of these birds in the wild. In chinstrap, Adélie and gentoo penguins, 37, 54 and 62 %, respectively, of natural dives exceeded the calculated ADL.

Castellini *et al.* (1992), in contrast, calculated P_{total} (Fig. 1B) from data on diving Weddell seals. They considered the recovery and the dive phase as one event, which could not be separated energetically. Correspondingly, P_{total} is lower at a given speed than P_{swim}. The low increment rate in power input observed at speeds below 2 m s^{-1} (Fig. 6) may be explained by the fact that the birds require a certain amount of energy while resting in water ($v=0 \text{ m s}^{-1}$) for thermoregulation. As they start swimming, the heat required for thermoregulation becomes increasingly a byproduct of activity, while overall energy expenditure does not increase. Assuming that king penguins in nature swim at speeds at which transport costs are lowest, $P_{total}=10.3 \text{ W kg}^{-1}$ at 2.2 m s^{-1} (or $0.52 \text{ ml O}_2 \text{ kg}^{-1} \text{ s}^{-1}$), which compares well with the results of Kooyman *et al.* (1992*a*), who extrapolated their data to give a value of 9.6 W kg^{-1} at 2 m s^{-1} (bird mass 16.2 kg). However, ADL calculated from this is only 1.9 min.

Culik *et al.* (1994*b*) suggested that the discrepancy between observed dive times and calculated ADL was due to the experimental method employed, i.e. the swim channel. They suggested that penguins would not normally 'stop and go' every 21 m (the length of their channel) and thus not incur the high energetic costs required for acceleration and deceleration in the channel. After correction of their P_{swim} for this effect, calculated ADL in chinstrap and Adélie penguins (130 and 110 s, respectively) included 96 and 86 %, respectively, of all dive durations observed in the wild. In gentoo penguins, however, 45 % of dives still exceeded this corrected ADL (93 s). Applying the same method to king penguins and correcting P_{swim} (see Table 1) for the behaviour forced on the birds by a 30 m long swim channel by subtracting the power required for acceleration $P_a=v^3/mfS$ (where v is swimming speed in m s^{-1}, m is muscle efficiency, 0.25 according to Schmidt-Nielsen, 1983, f is flipper efficiency, 0.4 according to Oehme and Bannasch, 1989, and S is the length of the channel in m; see Culik *et al.* 1994*b* for details), we obtain $P_{corrected}=9.9 \text{ W kg}^{-1}$ ($0.5 \text{ ml O}_2 \text{ kg}^{-1} \text{ s}^{-1}$) at 1.8 m s^{-1} (where transport costs calculated from $P_{corrected}$ are minimal). The resulting ADL of 2.1 min is still too low and only accounts for 33 % of all observed dives. This suggests that additional factors must be responsible for the inexplicably long dive durations observed in king penguins.

When initiating a dive, king penguins anticipate dive depth and duration. This is indicated by the dive angle, which is a function of the maximum depth reached during the dive and which is maintained constant from the point at which the dive is initiated (Pütz, 1994). Besides behavioural adjustments to an anticipated dive, there are also reports that animals may make physiological adjustments. Thompson and Fedak (1993) showed that mean diving heart rates in the grey seal vary according to the anticipated duration of the dive. Heart rates ranged from 31 to 9 beats min^{-1} for dives lasting between 7 and 25 min, respectively. Irrespective of the duration of a dive, the total number of heart contractions in submerged grey seals was constant at around 220 (Thompson and Fedak, 1993). A reduction in heart rate during submergence has also been shown to occur in Adélie (Culik, 1992) and emperor (Kooyman *et al.* 1992*b*) penguins. From this evidence, it must be questioned whether oxygen consumption by penguin tissues is constant during the entire dive+surface cycle, as in the calculations of P_{total} (see Castellini *et al.* 1992), or whether metabolic rate during the period at the surface really is lower than that during underwater swimming, as assumed when calculating P_{swim} or $P_{corrected}$. Although Thompson and Fedak (1993) found that grey seals rest on the sea floor and thus reduce their metabolic rate, 'some additional reduction in metabolic demand seems to be needed to explain the ability to remain submerged for long periods'. In order to achieve long dives, Thompson and Fedak (1993) suggest that, besides anaerobiosis, seals resting quietly on the sea floor might use hypometabolism as a strategy to conserve oxygen.

If king penguin tissue O_2 consumption and metabolic rate during submerged exercise were as low as during rest (except for exercising muscles which may be cut off from the circulation), the tissues would have to be reoxygenated and metabolic rate increased once the animal was back at the surface. As a consequence, O_2 consumption of the animal would not be constant throughout the dive+surface cycle, and a significant amount of O_2 consumption would only occur at the surface. Consequently, using P_{total} or P_{swim} to estimate ADL would not be appropriate. We therefore used our data to estimate the proportion of oxygen consumed by the tissues when the birds were under water as opposed to that taken up at the surface (Table 2). We assumed that king penguins could partition their oxygen requirements between the dive and the surface phase in a manner comparable to that shown by penguin heart rates.

Before we proceeded with our analysis, we looked at the differences in behaviour between the birds in the swim channel and in the wild. In the swim channel, king penguins swam on average for 36 s followed by 19 s at the surface, i.e. surface times were on average 34 % of total cycle time (surface+dive). This is very different from the situation that we found in the wild (Fig. 4), where median surface times were only 24 % and where minimum surface times were 10–14.6 % (see Discussion above). In order to obtain a data set from the swim channel experiments which reflected the situation in the wild, we filtered the data according to different values of percentage surface times (Table 2; Fig. 7) and calculated diving oxygen consumption (*a*) and surface oxygen consumption (*b*) according to equation 3. For king penguins spending a mean of 24 % of their time at the surface, we obtained a surface oxygen consumption (*b*) of $1.02 \text{ ml O}_2 \text{ kg}^{-1} \text{ s}^{-1}$ ($N=166$, $r^2=0.92$), which corresponds to 4.3 times the resting value in

water and 9.3 times SMR as predicted from Aschoff and Pohl (1970). Kooyman and Ponganis (1994) found that the highest measured oxygen consumption in emperor penguins was 9.1 times predicted SMR during swimming exercise. Oxygen uptake rates of 9.3 times SMR therefore seem possible. For the same example, submergence O_2 consumption (a) was only $0.23\,\mathrm{ml\,O_2\,kg^{-1}\,s^{-1}}$ and corresponds to 1 times RMR or 2.1 times predicted SMR. This compares well with the results of Castellini *et al.* (1992), who reported that metabolic rates of freely diving Weddell seals were as low as RMR. Using this strategy, king penguins could dive for a duration of 4.2 min before their oxygen stores became depleted. This corresponds to 70 % of all dives recorded in the wild (Fig. 2). On the basis of the rise in lactic acid levels in Weddell seals (Kooyman *et al.* 1980), the peak lactic acid concentration during dives slightly longer than this (Fig. 3B) would be approximately 1 mmol above resting values. Recovery from such low levels of lactate accumulation could be achieved at the end of the dive bout (G. L. Kooyman, personal communication).

As shown in Fig. 7, the rate of oxygen uptake at the surface (in the swim channel) reached a maximum (15.5 times predicted SMR) at 14.5 % surface time. Although this is at the upper end of the metabolic scope of flying birds (see Kooyman and Ponganis, 1994, for a summary), it is uncertain whether penguins could elevate their O_2 uptake to such high values or decrease the metabolic rate of the non-exercising tissues to 1 times SMR while under water (G. L. Kooyman, personal communication). However, if this were the case, king penguins could swim for up to 8.8 min before reaching their ADL, and all dives observed in the wild would be aerobic. This question can only be answered if blood lactate measurements could be made during and immediately after the dive (M. A. Castellini, personal communication).

Surface times shorter than 14.5 % of the total dive+surface interval entail lower oxygen uptake rates (Fig. 7). The reason for this is unclear, but possible explanations may be (a) inertia of the experimental system, (b) incomplete physiological switching by the penguins to oxygen uptake after termination of a dive, or (c) incomplete recovery of the penguins after a dive, the oxygen deficit being balanced during the next surface period. It also remains unclear why oxygen consumption during the dive varies with changes in percentage surface times (Fig. 7). While king penguins in the wild anticipate long dives (see above) and presumably reduce their metabolic rate accordingly, we would not expect to observe this effect in the swim channel, unless this was a consequence of the chosen surface/dive rhythm, i.e. if king penguins 'worked' optimally at surface times averaging 14.5 %.

Kooyman (1989) calculated that of the $58\,\mathrm{ml\,O_2\,kg^{-1}}$ stored in king penguin tissue 33 % is found in the muscles, which make up 30 % of total body mass. Muscle O_2 stores are therefore $64\,\mathrm{ml\,kg^{-1}}$. At rest, muscle O_2 consumption in humans is $1.6\,\mathrm{ml\,kg^{-1}\,min^{-1}}$ (Weibel, 1979). If we assume that muscles remain within their ADL for most dives (dive duration less than 8.8 min), then, with $64\,\mathrm{ml\,O_2\,kg^{-1}}$ available prior to a dive, muscle O_2 consumption can rise to $7.3\,\mathrm{ml\,kg^{-1}\,min^{-1}}$ or 4.5

times human resting values. If we assume that the birds remain within their ADL in only 70 % of all dives (dives shorter than 4.2 min), muscle O_2 consumption would be $15.2\,\mathrm{ml\,kg^{-1}\,min^{-1}}$ or 9.5 times human resting values. Are muscles working at 4.5–9.5 times resting levels able to produce enough mechanical power to allow a king penguin to swim? More data on penguin hydrodynamics, muscle and wing propulsion efficiency, and the proportion of muscle utilisation and perfusion in diving penguins are necessary to answer this question.

Is it theoretically possible that an animal such as the king penguin could take up O_2 at a rate of 9.3 times SMR during the recovery phase at the surface and immediately after submergence reduce oxidative metabolic activity in most tissues to 2.1 times SMR? If heart rates of diving animals reflect oxidative metabolic activity, without necessarily being proportional to it (due to shunts), then such fast changes seem at least physiologically possible. In grey seals (Thompson and Fedak, 1993), heart rates drop from $110\,\mathrm{beats\,min^{-1}}$ at the surface to values below $20\,\mathrm{beats\,min^{-1}}$ within six beats after initiation of a dive. Similarly, emperor penguins (Kooyman *et al.* 1992*b*) reduce their heart rates from $110\,\mathrm{beats\,min^{-1}}$ at the surface to about $50\,\mathrm{beats\,min^{-1}}$ within 45 s of diving, with a further decline to $30\,\mathrm{beats\,min^{-1}}$ after 4 min.

To conclude, the rate of oxygen consumption during submergence can only be determined from swim channel experiments if the subset of the data best matching the behaviour of the birds in the wild is analysed. Although the mechanisms by which king penguins can make serial dives for so long with such short surface intervals are still unclear, a possible explanation for this could be that king penguins are able to partition oxygen utilisation by the tissues during submergence, maintaining oxygen consumption at 2.1 times SMR or perhaps lower. During surface phases, oxygen uptake would be increased to at least 9.3 times SMR. This would mean that at least 70 % of all dives (dive duration less than 4.2 min) are aerobic.

References

ADAMS, N. J. (1987). Foraging range and chick feeding rates of king penguins *Aptenodytes paragonicus*, during summer at Marion Insland. *J. Zool., Lond.* **212**, 475–482.

ASCHOFF, S. AND POHL, H. (1970). Rhythmic variation in energy metabolism. *Fedn Proc. Fedn Am. Socs exp. Biol.* **29**, 1541–1552.

BANNASCH, R., WILSON, R. P. AND CULIK, B. M. (1994). Hydrodynamic aspects of design and attachment of a back-mounted device in penguins. *J. exp. Biol.* **194**, 83–97.

BOYD, I. L. (1993). Selecting sampling frequency for measuring diving behavior. *Mar. mammal. Sci.* **9**, 424–430.

BUTLER, P. J. AND JONES, D. R. (1982). The comparative physiology of diving in vertebrates. In *Advances in Comparative Physiology and Biochemistry* (ed. O. Lowenstein), pp. 179–364. New York: Academic Press.

CASTELLINI, M. A., KOOYMAN, G. A. AND PONGANIS, P. J. (1992). Metabolic rates of freely diving Weddell seals: correlations with oxygen stores, swim velocity and diving duration. *J. exp. Biol.* **165**, 181–194.

CULIK, B. M. (1992). Diving heart rates in Adélie penguins (*Pygoscelis adeliae*). *Comp. Biochem. Physiol.* A **102**, 487–490.

CULIK, B. M., BANNASCH, R. AND WILSON, R. P. (1994*a*). External devices on penguins: how important is shape? *Mar. Biol.* **118**, 353–357.

CULIK, B. AND WILSON, R. P. (1991*a*). Energetics of under water swimming in Adélie penguins (*Pygoscelis adeliae*). *J. comp. Physiol.* B **161**, 285–291.

CULIK, B. M. AND WILSON, R. P. (1991*b*). Penguins crowded out? *Nature* **351**, 340.

CULIK, B. M., WILSON, R. P. AND BANNASCH, R. (1994*b*). Under-water swimming at low energetic cost by pygoscelid penguins. *J. exp. Biol.* **197**, 65–78.

CULIK, B. M., WOAKES, A. J., ADELUNG, D., WILSON, R. P., CORIA, N. R. AND SPAIRANI, H. J. (1990). Energy requirements of Adélie penguin (*Pygoscelis adeliae*) chicks. *J. comp. Physiol.* B **160**, 61–70.

GESSAMAN, J. A. AND NAGY, K. A. (1988). Energy metabolism: errors in gas-exchange conversion factors. *Physiol. Zool.* **61**, 507–513.

HORNING, M. (1992). Die Ontogenese des Tauchverhaltens beim Galapagos-Seebären *Arctocephalus galapogensis* (Heller 1904). Dissertation an der Fakultät für Biologie der Universität Bielefeld. 101pp.

JOUVENTIN, P., CAPDEVILLE, D., CUENOT-CHAILLET, F. AND BOITEAU, C. (1994). Exploitation of pelagic resources by a non-flying seabird: satellite tracking of the king penguin throughout the breeding cycle. *Mar. Ecol. Prog. Ser.* **106**, 11–19.

KOOYMAN, G. L. (1989). *Diverse Divers. Physiology and Behavior.* Berlin, Heidelberg, New York: Springer-Verlag.

KOOYMAN, G. L., CHEREL, Y., LE MAHO, Y., CROXALL, J. P., THORSON, P. H., RIDOUX, V. AND KOOYMAN, C. A. (1992*a*). Diving behavior and energetics during foraging cycles in king penguins. *Ecol. Monogr.* **62**, 143–163.

KOOYMAN, G. L. AND DAVIS, R. W. (1987). Diving behaviour and performance, with special reference to penguins. In *Seabirds: Feeding Biology and Role in Marine Ecosystem.* (ed. J. P. Croxall), pp. 63–75. London: Cambridge University Press.

KOOYMAN, G. L. AND KOOYMAN, C. A. (1995). Diving behavior of emperor penguins nurturing chicks at Coulman Island, Antarctica. *Condor* **97**, 536–549.

KOOYMAN, G. L. AND PONGANIS, P. J. (1994). Emperor penguin oxygen consumption, heart rate and plasma lactate levels during graded swimming exercise. *J. exp. Biol.* **195**, 199–209.

KOOYMAN, G. L., PONGANIS, P. J., CASTELLINI, M. A., PONGANIS, E. P., PONGANIS, K. V., THORSON, P. H., ECKERT, S. A. AND LE MAHO, Y. (1992*b*). Heart rates and swim speeds of emperor penguins under sea ice. *J. exp. Biol.* **165**, 161–180.

KOOYMAN, G. L., WAHRENBROCK, E. A., CASTELLINI, M. A., DAVIS, R. A. AND SINNETT, E. E. (1980). Aerobic and anaerobic metabolism during diving in Weddell seals: Evidence of preferred pathways from blood chemistry and behavior. *J. comp. Physiol.* **138**, 335–346.

KRAMER, D. L. (1988). The behavioral ecology of air breathing by aquatic animals. *Can. J. Zool.* **66**, 89–94.

LE MAHO, Y., GENDNER, J.-P., CHALLET, E., BOST, C. A., GILLES, J., VERDON, C., PLUMERÉ, C., ROBIN, J.-P. AND HANDRICH, Y. (1993). Undisturbed breeding penguins as indicators of change in marine resources. *Mar. Ecol. Prog. Ser.* **95**, 1–6.

LE MAHO, Y., KARMANN, H., BRIOT, D., HANDRICH, Y., ROBIN, J.-P., MIOSKOWSKI, E., CHEREL, Y. AND FARNI, J. (1992). Stress in birds due to routine handling and a technique to avoid it. *Am. J. Physiol.* **263**, 775–781.

LISS, P. S. AND MERLIVAT, L. (1986). Air–sea gas exchange rates: Introduction and synthesis. In *The Role of Air–Sea Exchange in Geochemical Cycling* (ed. P. Buat-Ménard), pp. 113–125. Dordrecht, The Netherlands: D. Reidel Publishing Co.

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.

PINSHOW, B., FEDAK, M. A. AND SCHMIDT-NIELSEN, K. (1977). Terrestrial locomotion in penguins: it costs more to waddle. *Science* **195**, 592–594.

PÜTZ, K. (1994). Aspects of the feeding ecology of emperor penguins (*Aptenodytes forsteri*) and king penguins (*Aptenodytes patagonicus*). *Rep. pol. Res.* **136**, 139pp. (in German).

PÜTZ, K. AND BOST, C. (1994). Feeding behavior of free-ranging king penguins (*Aptenodytes patagonicus*). *Ecology* **75**, 489–497.

SCHMIDT-NIELSEN, K. (1983). *Animal Physiology.* Cambridge, UK: Cambridge University Press.

THOMPSON, D. AND FEDAK, M. A. (1993). Cardiac responses of grey seals during diving at sea. *J. exp. Biol.* **174**, 139–164.

WEIBEL, E. R. (1979). Oxygen demand and the size of respiratory structures in mammals. In *Evolution of Respiratory Processes* (ed. S. C. Wood and C. Lenfant), pp. 289–346. New York: Dekker.

WILSON, R. P. (1995). Foraging ecology. In *The Penguins* (ed. T. D. Williams), pp. 81–106. Oxford: Oxford University Press.

WILSON, R. P. AND BAIN, C. A. R. (1984). An inexpensive speed meter for penguins at sea. *J. Wildl. Mgmnt* **48**, 1360–1364.

WILSON, R. P., PÜTZ, K., BOST, C., CULIK, B., BANNASCH, R., REINS, T. AND ADELUNG, D. (1993). Diel dive depth in penguins in relation to vertical migration of prey: whose dinner by candlelight? *Mar. Ecol. Prog. Ser.* **94**, 101–104.

WILSON, R. P., PÜTZ, K., CHARRASSIN, J.-B. AND LAGE, J. (1995). Artifacts arising from sampling intervals in dive-depth studies of marine endotherms. *Polar Biol.* **15**, 575–581.

WILSON, R. P. AND WILSON, M.-P. (1989). Tape: A package attachment technique for penguins. *Wildl. Soc. Bull.* **17**, 77–79.

WOAKES, A. J. AND BUTLER, P. J. (1983). Swimming and diving in tufted ducks, *Aythya fuligula*, with particular reference to gas exchange. *J. exp. Biol.* **107**, 311–329.