

Diving behaviour and energetics in breeding little penguins (*Eudyptula minor*)

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(With 7 figures in the text)

We present data on the diving behaviour and the energetics of breeding little penguins in Tasmania, Australia. Using an 18 m long still water canal in conjunction with respirometry, we determined the energy requirements while diving. Using electronic devices measuring dive depth or swimming speed, we investigated the foraging behaviour at sea. Cost of Transport was calculated to be minimal at the speed the birds prefer at sea (1.8 m/s) and averaged 11.1 J/kg/m (power requirements at that speed: 20.0 W/kg). Metabolic rate of little penguins resting in water was found to be 8.5 W/kg. The externally-attached devices had no significant influence on the energy expenditure.

Foraging trips can be divided into four distinct phases with different diving behaviours. A mean of 500 dives was executed per foraging trip lasting about 18 hours with 60% of this time being spent swimming. The total distance travelled averaged 73 km per day, although foraging range was about 12 km. Mean swimming speed of little penguins at sea was 1.8 m/s, maximum swimming speed was 3.3 m/s. More than 50% of all dives had maxima not exceeding 2 m. Maximum depth reached was 27 m. Mean dive duration was 21 s. There were inter-sex differences in diving behaviour as well as changes in foraging behaviour over the breeding period. Aerobic dive limits (ADL) in the wild were estimated between 42 and 50 s. From the swim canal experiments we derived an ADL of 44 s. Total oxygen stores were calculated to be 45 ml O₂/kg. Only 2% of all dives exceeded the ADL. FMRs at sea were calculated to be between 1280 and 1500 kJ/kg/d according to chick size. The yearly food requirements of a breeding little penguin amount to 114 kg.

Introduction

The behaviour and locomotion of penguins at sea and the energetic costs involved are fundamental aspects of their ecology. However, until recently, relatively little was known about the energetic demands of penguins and other sub-surface swimmers because the determination of these demands has proved difficult to measure. The doubly-labelled water and heart rate techniques (e.g. Butler & Woakes, 1984; Gales & Green, 1990) have problems with unknown experimental conditions. Swim flumes and canals (e.g. Baudinette & Gill, 1985) put the birds under unnatural conditions, but do offer better control of experimental variables. In a swim canal the birds can select their own swimming speed while all activities, swimming speed and gaseous exchange can be closely monitored. Since Culik & Wilson (1991) first determined the energy requirements of swimming Adélie penguins (*Pygoscelis adeliae*) in Antarctica using a swim canal, several other penguin species have been studied in this manner (e.g. Culik, Wilson & Bannasch, 1994a; Kooyman & Ponganis, 1994). Energy demands

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for diving were found to be much lower than expected, principally due to the remarkably low drag of these birds (Bannasch, Wilson & Culik, 1994).

The foraging ecology of penguins has been examined in numerous studies (e.g. for the emperor penguin, *Aptenodytes forsteri* (Ancel *et al.*, 1992), king penguin, *Aptenodytes patagonicus* (Kooyman *et al.*, 1992; Pütz 1994), African penguin, *Spheniscus demersus* (Wilson, 1985; Wilson & Wilson, 1995), Adélie penguin, *Pygoscelis adeliae*, or gentoo penguin, *Pygoscelis papua*, (Wilson *et al.*, 1991a,b; Culik, 1994; Wilson, 1995). However, such research has been essentially limited to the larger species, in part due to their size-linked ability to carry attached systems for measuring behaviour. With a mean body mass of only 1.2 kg (this study), the little penguin is difficult to equip with systems to study at sea behaviour.

With the exception of a study on maximum dive depths by Montague (1985), the first attempt to elucidate the behaviour of little penguins at sea was made by Gales, Williams & Ritz (1990), who equipped two birds with data-loggers which recorded swimming speed and dive depth. However, the units amounted to about 10% of the penguin's cross-sectional area (Gales *et al.*, 1990) and were thus likely to have hindered the birds' foraging ability (Wilson & Culik, 1992). In addition, Weavers (1992) used radio-telemetry to determine the foraging areas of little penguins breeding at Phillip Island, Victoria, Australia. Recently, however, enhanced understanding of penguin hydrodynamics (Bannasch *et al.*, 1994), as well as advances in solid state electronics, have enabled us to construct devices which can be attached to penguins without significantly increasing energy expenditure during swimming and diving above that of non-equipped conspecifics (Culik, Wilson & Bannasch, 1994b; Wilson, 1995).

In this paper, we present data on the swimming and diving behaviour of free-living little penguins equipped with such devices, as well as data on the energetic costs of locomotion derived from swim canal experiments. The data are of particular interest because the little penguin is by far the smallest penguin species, a feature that makes it allometrically interesting with respect to other penguin species. The small body size and the large surface area to volume ratio of little penguins should have consequences for the energetic costs of diving, for foraging strategies and for the energetics of little penguin breeding colonies. In addition, data on the energetics of little penguins, in combination with behavioural data, should allow conclusions on their food demands and foraging ranges. This may help to clarify an observed population decline in the last years (Dann, 1992) and to elucidate their behavioural ecology at sea.

Materials and methods

Swim canal experiments

Little penguins *Eudyptula minor* from Marion Bay (42°50'S, 147°55'E) on the Tasmanian east coast were studied in a swim canal in August/September 1993 (Animal permit No. 05/94, Department of Parks, Wildlife and Heritage, Hobart, Tasmania). Twelve birds (mean body weight: 1.2 kg (S.D. = 0.09)) were caught and held in captivity at the Department of Anatomy & Physiology/University of Tasmania for about 2 weeks in a covered outdoor enclosure which was provided with a nesting box and swimming trough. The penguins quickly adapted to being hand fed on a diet of black-back salmon (*Arripis trutta*) with a calcium supplement.

The swim canal was constructed of corrugated iron and was 18 m long, 0.45 m wide and 0.52 m deep and was filled with freshwater (mean water temperature: 10 °C (S.D. = 1.44)). It was covered 12 cm beneath the water's surface with transparent plastic sheeting, resulting in an under-water tunnel which prevented the birds from surfacing over most of the length of the canal. The penguins were only allowed to breathe in one respiration chamber (Vol. = 12 l) placed at one end of the canal. The chamber was equipped with a mixing fan and was open

to outside air. Air was drawn through it by a pump at a mean flow rate of 23 l/min, measured by a mass flow meter (TYLAN model FM-380). A subsample of the air was dried and passed on to the oxygen-analyser (Applied Electrochemistry Inc., Sunnyvale, California, model S-3A). Data from the oxygen-analyser and the mass flow meter were sampled every 0.5 s using a Mac-Lab (Analog Digital Instruments Pty Ltd, Castle Hill, NSW) and an Apple Macintosh-Computer Classic II. The whole system was calibrated following Fedak, Rome & Seeherman (1981) using known volumes of nitrogen. Mean measurement error was < 1%.

Twice daily the penguins were put into the swim canal for experiments lasting 30 min. Prior to the beginning of the experiments, the penguins were trained to swim up and down the canal using 2 respiration chambers, one at each end. For measurements, one of the chambers was closed. The penguins were continuously observed from the middle of the canal while swimming speed and activity were recorded using a specially-designed computer program and a laptop computer.

For calculating the O_2 -consumption, a modification of the formula given by Woakes & Butler (1983) was used, which incorporates chamber volume and allows accurate measurement of fast changes in O_2 -concentrations irrespective of the lag time of the system:

$$VO_2 = (c_2 - c_1) \times V + [(c_1 + c_2 - 2 \times cb)/2] \times (t_2 - t_1) \times Q \quad (1)$$

where:

VO_2 = O_2 -consumption between t_1 and t_2 [l] (STPD)

c_1, c_2 = fractional concentration O_2 at time t_1, t_2 [sec] leaving the chamber

cb = fractional concentration O_2 entering the chamber (0.2095)

Q = flow-rate through the chamber [l/s]

V = chamber volume [l]

Following Withers (1977), we corrected for the respiratory quotient (RQ) of the penguins (RQ = 0.75 for little penguins (Stahel & Nicol, 1982)). Correction of equation (1) for RQ yields:

$$VO_2(c_2 - c_1) \times V + \frac{(c_1 + c_2 - 2 \times cb) \times (t_2 - t_1) \times V_E}{(2 \times (1 - (1 - RQ) \times cb))} \quad (2)$$

where:

VO_2 = O_2 -consumption between t_1 and t_2 [l] (STPD)

V_E = flow-rate measured behind the respiration chamber [l/s] (STPD)

RQ = respiratory quotient (0.75 (Stahel & Nicol, 1982))

Using this formula it was possible to determine the total amount of oxygen consumed during the recovery period after each dive ($VO_{2(TOTAL)}$). This O_2 -consumption was used to calculate the rate of oxygen consumption during underwater swimming ($VO_{2(SWIM)}$). We assumed that O_2 -consumption in the chamber was identical to resting values at the surface (see **Results**) and calculated the rate of oxygen consumption for underwater swimming following Culik & Wilson (1991):

$$VO_{2(SWIM)} = (VO_{2(TOTAL)} - VO_{2(REST)} \times t_{SURFACE})/t_{SWIM} \quad (3)$$

where:

$VO_{2(TOTAL)}$ = total O_2 -consumption between time of surfacing (t_1) and leaving the chamber (t_2) [l]

$VO_{2(REST)}$ = O_2 -consumption rate for resting at the water surface [l/s]

$t_{surface}$ = time at the surface [s]

t_{swim} = time swimming [s]

Oxygen consumption for each dive was analysed with respect to mean swimming speed for the same dive and averaged for 0.1 m/s speed classes ranging from 0.6 to 1.4 m/s. Conversion into W/kg was made assuming a conversion factor of 19.7 kJ/l of oxygen (Stahel & Nicol, 1982) following:

$$P = \frac{VO_{2(SWIM)} \times c.f.}{t \times m} \quad (4)$$

where P = Power [W/kg]

c.f. = conversion factor [kJ/l O₂]

t = dive time [s]

m = body mass [kg]

Transport costs (COT, the cost of transporting 1 kg of mass over 1 m [J/kg/m]) were obtained using the function:

$$COT = P/v \quad (5)$$

where v = swimming speed [m/s].

The penguins in the canal had to accelerate and decelerate once every 18 m, something which they would presumably not do in nature. In order to compensate for this, the physical energy required for acceleration and deceleration in the canal was subtracted from the power calculated in the swim canal as follows (Culik *et al.*, 1994a, modified following R. Bannasch (pers. comm.: deceleration needs only half the energy of acceleration)):

$$P_s = P - \frac{3v^2}{2 \times e_M \times e_F \times t} \quad (6)$$

where:

e_M = 0.25 = muscle efficiency (Schmidt-Nielsen, 1990)

e_F = 0.4 = flipper efficiency (Oehme & Bannasch, 1989)

P = Power [W/kg] required for swimming in the swim canal at speed v

P_s = corrected Power requirements [W/kg], t = dive time [s]

To determine the effect of the externally-attached speed and depth recorders on the energy requirements of the penguins, the birds were equipped with speed and depth recorders (see below) in about one-third of the experiments.

Field experiments

Field experiments were carried out at Marion Bay (42°50'S, 147°55'E), Tasmania from November to December 1993 (Animal permit No. 05/94, Department of Parks, Wildlife and Heritage, Hobart, Tasmania). The birds for the experiments were selected from pairs engaged in exchanging incubation and brooding duties. Eight birds were equipped with depth gauges and 12 birds with speed meters (12.5 × 1.5 × max. 1.5 cm, 35 g weight, about 2% of the penguin's cross-sectional area). Both units were derived from the Pillbox Logger (DK-Log PB-2.5, Driesen + Kern GmbH, Bad Bramstedt, Germany) and measured data with 8 bit resolution up to a maximum of 128 kbytes at 8 second intervals. Both units were powered by four 3V CR1220 Lithium batteries set to provide 6V. The depth gauges recorded depth via a pressure transducer up to a maximum value of 7 Bar. They were calibrated in a pressure tank ($r^2 = 0.99$, $n = 11$, S.E. = 0.10) and found to be good for depths greater than 0.5 m. Swimming speeds were measured by using a paddle wheel. Speed sensors were calibrated (device 1: $r^2 = 0.76$, $n = 74$, S.E. = 0.16; device 2: $r^2 = 0.70$, $n = 108$, S.E. = 0.24) in the swim canal (see above) on both living little penguins and on a penguin model by equipping the birds with the speed recorders and examining the response of the devices to various swimming speeds. The distance swum per day was derived from speed data.

All devices were streamlined according to suggestions by Bannasch *et al.* (1994) and were attached in a 5-minute procedure with tape (Tesa 4651, Beiersdorf AG Hamburg, Wilson & Wilson, 1989) to the lower back of the birds in order to minimize hydrodynamic drag. After 1 day at sea the devices were removed, the weight and the sex of the birds were determined, as well as chick age. Bird sex was determined by measuring beak length and height (Gales, 1989). Chicks were aged according to a key given in Stahel & Gales (1987).

To analyse the dive data with respect to dive depth, dive duration, bottom duration, vertical speed and inter-dive duration, the computer program ANDIVE 4 was used (Jensen Software Systems, Kehl/Germany).

Results

Swim canal experiments

Penguins placed in the canal learned within two experiments, each of 30 minutes duration, where they could surface to breathe and subsequently swam constantly up and down the canal. Mean speed in the canal was 1.0 m/s (S.D. = 0.11, $n = 258$, range 0.6 to 1.4 m/s). The birds had to turn round in the canal once each dive to return to the respiration chamber. Of all dives, 60% were made along two lengths of the canal (36 m); in all other dives, the birds turned round before reaching the end of the canal (mean dive distance: 32.8 m (S.D. = 5.99, $n = 258$)). Neither slightly different water temperatures (mean: 10°C (S.D. = 1.44)), nor individual differences between the tested penguins, had a significant influence on the Cost of Transport while diving (nested ANOVAS, $P > 0.14$ and $P > 0.223$, respectively). A total of 433 dives from eight different penguins were analysed: 258 without data-logger attached, 175 with data-logger attached.

Power requirements of little penguins while resting in water were found to be 8.5 W/kg (S.D. = 1.83, $n = 9$). Data were obtained from four different penguins resting for up to 30 minutes in the respiration chamber. Mean water temperature during these experiments was 10°C (S.D. = 1.77, $n = 9$).

Power requirements while diving ranged from 13.1 W/kg at 0.7 m/s up to 19.5 W/kg at 1.4 m/s. Cost of Transport averaged between 24.8 J/kg/m (0.6 m/s) and 11.8 J/kg/m (1.3 m/s). The results were corrected with respect to acceleration and deceleration in the canal following equation (6). The corrected power requirements P_s are an approximation for the power required for sustained swimming at sea (Culik *et al.*, 1994a). Corrected power requirements ranged from 12.9 W/kg at 0.7 m/s to 18.5 W/kg at 1.4 m/s, Cost of Transport from 11.1 J/kg/m at 1.3 m/s up to 24.5 J/kg/m at 0.6 m/s. In the examined speed range, Cost of Transport decreased with increasing swimming speed while power requirements for diving slightly increased. Cost of Transport and power requirements for mean speeds of little penguins in the wild (1.8 m/s) could not be determined since little penguins did not reach such high speeds in the canal.

Field experiments

Swimming speeds were determined in 12 birds (mean mass 1.2 kg, 6 males + 6 females) for 12 foraging trips. Mean speed was 1.8 m/s (S.D. = 1.0, $n = 67980$) (Fig. 1). About 60% of the time spent swimming at sea was spent under water, so that the overall travelling speed of little penguins at sea equipped with speed recorders averaged 1.1 m/s (Table I). Maximum measured speed was 3.3 m/s.

Little penguins equipped with speed loggers spent a mean time of 18 hours per day at sea. First swimming activity occurred at 04:00 h before sunrise (sunrise *c.* 05:30 h), with last swimming activity being recorded after sunset (sunset *c.* 20:15 h) at 22:00 h. Mean distance travelled per foraging trip was 73.4 km (range: 44.4 to 97.8 km, $n = 12$).

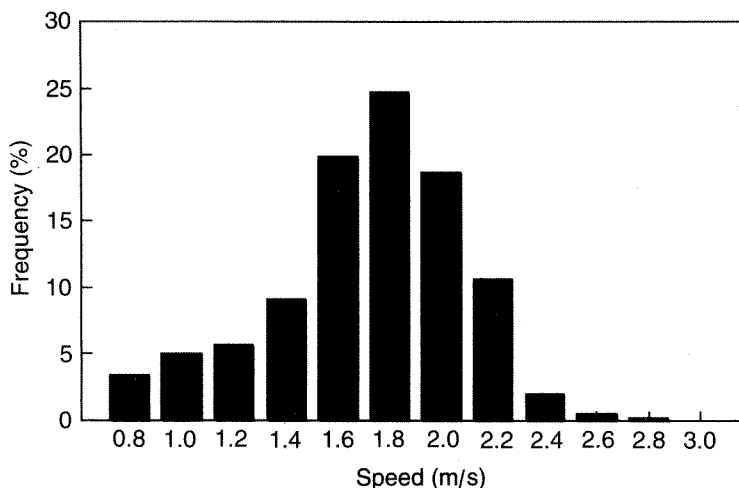


FIG. 1. Frequency histogram of the swimming speeds of little penguins at sea ($n = 67980$, from 12 birds).

Diving activity was determined in eight birds (mean mass 1.2 kg, 5 males, 3 females) for a total of 12 foraging trips during which 6025 dives were recorded. The penguins swam mainly in the upper water layers (Fig. 2) with about 500 dives per foraging trip. Maximum depth reached was 27 m (mean max. per trip = 22 m, $n = 12$), mean dive depth was 3.4 m (S.D. = 3.94, $n = 6025$). Mean dive duration was 21 s (S.D. = 8.4, $n = 6025$) and maximum was 88 s. At a mean speed of 1.8 m/s the distance travelled during a mean dive would be 38 m (Table I).

Sexual dimorphism is not very marked in little penguins. The mean mass of the investigated males (1.21 kg, S.D. = 0.06, $n = 11$) was only marginally higher than that of the females (1.13 kg, S.D. = 0.08, $n = 9$). However, we found significant differences between males and females with respect to swimming speeds (t -test, $t = 9.06$, $P < 0.001$, sample size: 6 males, 6 females), dive depths

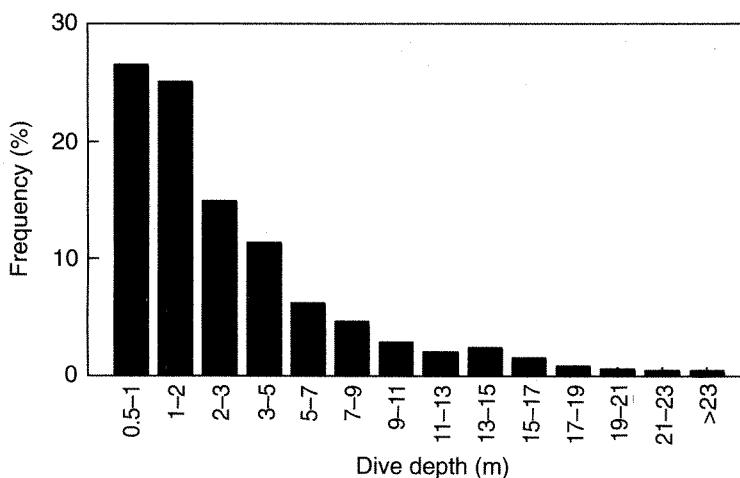


FIG. 2. Frequency histogram of dive depths of little penguins at sea ($n = 6025$, from 12 birds).

TABLE I
Dive parameters of little penguins at sea

	Mean	S.D. or range	<i>n</i>
Underwater speed [m/s]	1.8	1.04	67980
Max. speed [m/s]	3.3		67980
Daily time at sea [hh:mm]	18:00	16:40 to 19:50	12
Distance swum per day [km]	73.4	44.4 to 97.8	12
Overall travelling speed [m/s]	1.1	0.24	12
Activity at sea [%]	60	41.5 to 78.1	12
Start time [hh:mm]	04:00	03:10 to 05:00	12
Return time [hh:mm]	22:00	21:10 to 23:40	12
Dives per foraging trip (<i>n</i>)	500	160 to 900	12
Dive depth [m]	3.4	3.9	6025
Max. dive depth [m]	27.4		6025
Dive duration [s]	21.3	8.42	6025
Max. dive time [s]	88		6025

and dive durations (*t*-tests, $t = 4.36$, $P < 0.001$ and $t = 7.43$, $P < 0.001$, respectively, sample size: 3 females, 5 males). In addition, distance travelled per day and activity at sea were slightly higher in males. However, the results have to be interpreted carefully as differences are only based on a small number of penguins and bill measurements can cause some errors in sexing.

By dividing the foraging trips into one-hour intervals and analysing them with respect to the time of day, a number of time-dependent changes in the foraging behaviour of the penguins were apparent. The foraging behaviour during a typical foraging trip followed a characteristic pattern and could be divided into four different phases (Fig. 3 and Table II). The first hour of the foraging trip (phase 1), from leaving the beach at about 04:00 h up to about 05:00 h, was characterized by only a few shallow dives which never exceeded 1 m depth. At this time, mean swimming speed (1.5 m/s) and activity (40% of the time spent underwater) were low. Between about 05:00 and 10:00 h (phase 2) birds dived often, maintaining high mean speeds and intense activity, with 70% of the time being spent under water. However, the dives were shallow. Between 10:00 and about 18:00 h (phase 3), the dives were deeper, the number of dives exceeding 5 m being significantly higher than during phase 2 (*t*-test, $t = 7.54$, $P < 0.001$) and phase 4 (*t*-test, $t = 8.26$, $P < 0.001$). Periods of intense activity were interrupted by extended surface pauses. Finally, between about 18:00 h and the return to the beach at 22:00 h (phase 4), diving activity decreased and followed a pattern similar to that at the beginning of the foraging trip during phase 1, with deep dives being rare.

There were also changes in the foraging behaviour as a function of chick age. The overall distance travelled per foraging trip, an indication of foraging effort, increased as the breeding season progressed (Fig. 4) and chick age increased ($r^2 = 0.78$, $n = 12$). Both mean swimming speed (*t*-test, $t = 3.47$, $P < 0.001$) and the mean distance travelled per foraging trip (*t*-test, $t = 2.36$, $P < 0.05$) were significantly higher in the second half of the breeding period than in the first.

Instrument and experimental effects

In the past, different studies have shown that externally attached devices can have important adverse effects on penguins at sea (e.g. Sadleir & Lay, 1990; Wilson & Culik, 1992). In the data presented here, the attached instruments caused a significant increase in energy consumption in only one speed range

TABLE II

Activity at sea, swimming speed of little penguins and number of dives exceeding five metres in different phases of the foraging trip

	Activity (% of time at sea)	Mean speed [m/s] (mean/S.D.)	No. of dives > 5 m, per hour (mean/range)
Phase 1 (04:00–05:00 h)	40	1.5 (0.98)	0
Phase 2 (05:00–10:00 h)	70	1.82 (1.07)	2.4 (0–5)
Phase 3 (10:00–18:00 h)	65	1.80 (1.02)	10.2 (7–12)
Phase 4 (18:00–22:00 h)	46	1.74 (1.10)	1.8 (0–3)

during underwater swimming (at speeds of 0.9 m/s, *t*-test, $P < 0.001$). In all other speed classes, instrument effect was not significant (*t*-tests, $P > 0.05$), probably as a consequence of the streamlined shape of the devices (the units amounted to only about 2% of the penguin's cross-sectional area), which is found to be most important for minimizing instrument effect (Bannasch *et al.*, 1994). However, adverse effects of the devices on the foraging behaviour and the energy expenditure of little penguins cannot be ruled out. In swim canal experiments, mean speeds were not significantly influenced by data-logger-attachment (*t*-test, $P > 0.05$). At higher speeds observed in the wild the influence of the attached devices is likely to increase.

The swim canal method both ensures controlled experimental conditions and allows voluntary swimming in the birds. However, the narrow canal used in these experiments, coupled with the necessity for the birds to accelerate repeatedly and decelerate, will have affected the behaviour and the energetic demands of the penguins. In addition, we do not know what effects, if any, might have occurred as a result of our penguins having been tested in freshwater. Forcing birds to swim in freshwater when they are normally exclusively marine will have an effect on their buoyancy and thus perhaps on the manner in which they swim. Furthermore, the corrugated surface used for the swim canal might have acted to dampen turbulence.

These circumstances may have caused the little penguins to swim at only 1.0 m/s in the canal which differs significantly (*t*-test, $t = 8.72$, $P < 0.001$, 44% slower) from the mean speed at sea of 1.8 m/s. Similarly, chinstrap (*Pygoscelis antarctica*), Adélie (*P. adeliae*) and gentoo penguins (*P. papua*) observed in a swim canal (21 m long) swam 35, 32 and 21% slower than in the wild (Culik *et al.*, 1994a).

Energy requirements while resting in water

Our value for the resting metabolic rate of little penguins at 8.5 W/kg is consistent with the results of Stahel & Nicol (1982) who found that heat production of little penguins resting at the water surface is related to water temperature by $H \text{ [W/kg]} = 10.3 - 0.16 T_w$ at temperatures above 10 °C. This formula yields a metabolic rate of 8.7 W/kg at 10 °C and corresponds to 2.6 times BMR (Stahel & Nicol, 1987).

Energy requirements while diving

The different speed ranges of little penguins in the canal (0.6 to 1.4 m/s) and in the field (0.8 to 3.3 m/s) have to be taken into consideration when transferring swim canal results to conditions in the wild. Culik *et al.* (1994a) showed that power requirements of Adélie, chinstrap and gentoo penguins while diving increase with increasing swimming speed. However, transport costs are minimal at the

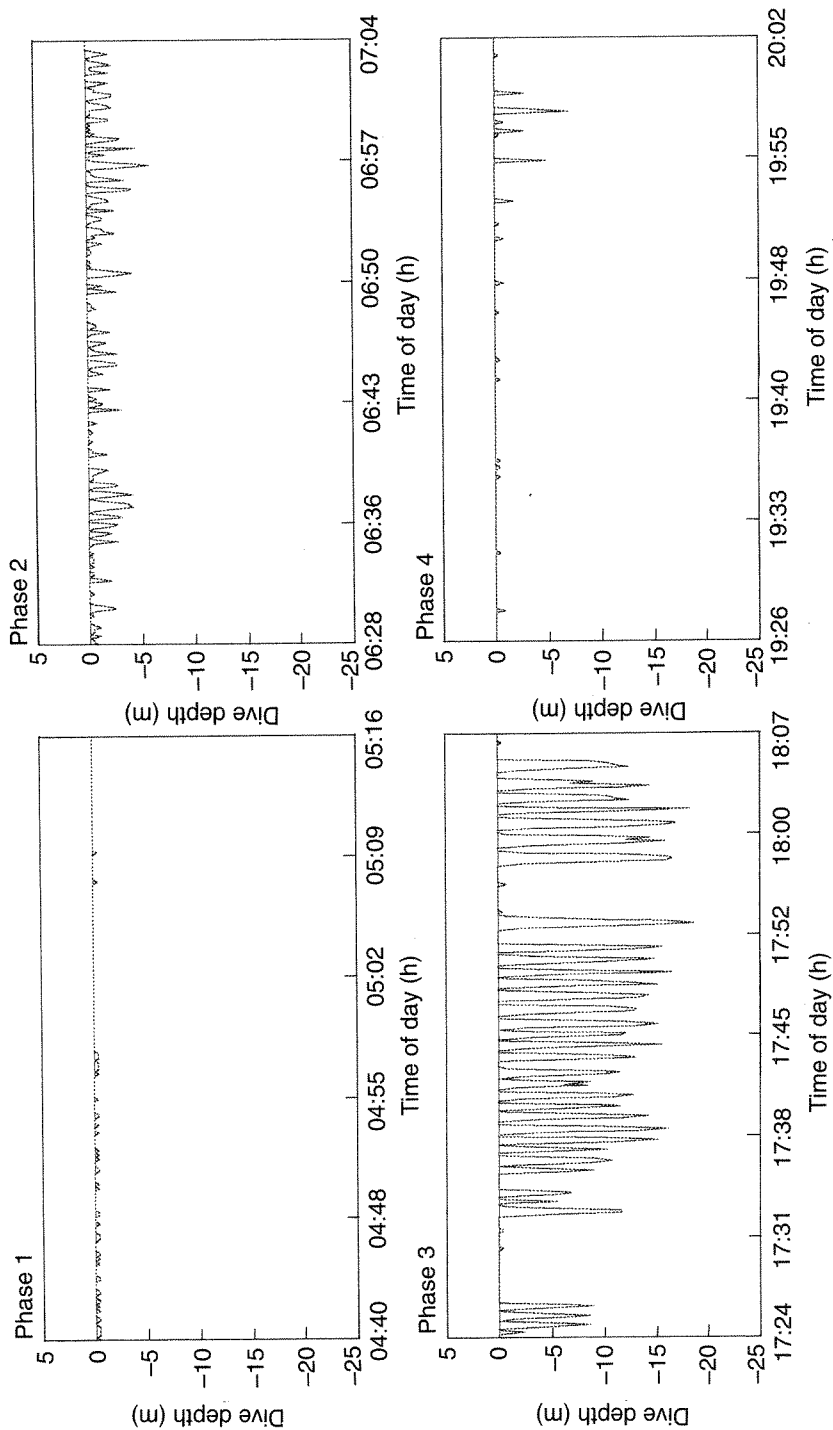


FIG. 3. An example illustrating the typical diving behaviour of little penguins in different phases of the foraging trip (phase 1—phase 2; phase 3—phase 4, see text).

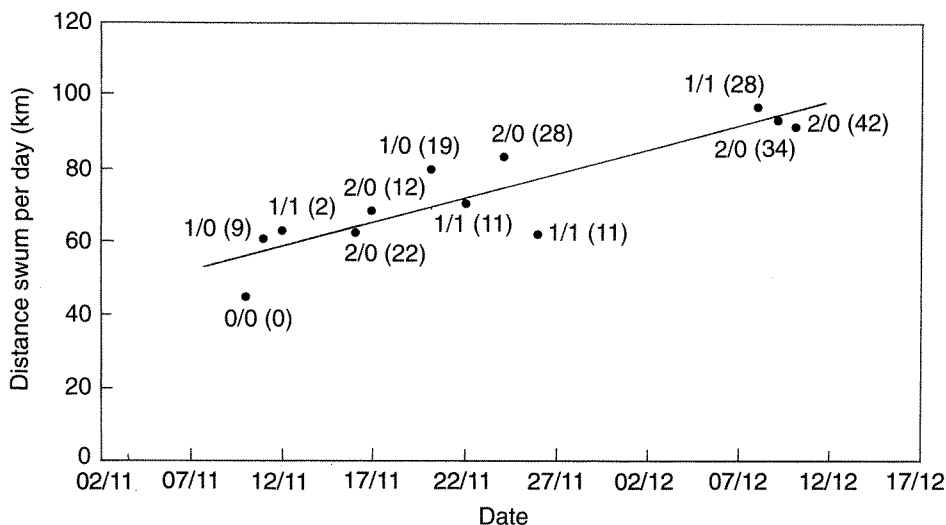


FIG. 4. Total distance travelled by little penguins per day as a function of date; the distance travelled increases as the breeding season progressed ($r^2 = 0.78$, $n = 12$); for each point the first figure indicates the no. of chicks in the nest, the second the no. of eggs, and the figure in brackets gives the sum of the chick ages.

preferred speed of the birds at sea (Nagy, Siegfried & Wilson, 1984; Hui, 1988; Culik *et al.*, 1994a). Similarly, we expect the COT of little penguins to be lowest at speeds of 1.8 m/s. In order to examine this more closely, the results obtained in the swim canal (Fig. 5) were extrapolated from 1.4 to 2.0 m/s in accordance with methods proposed by Culik *et al.* (1994a). Power requirements while swimming (in W/kg) were best matched by a cubic function of the type $P_s = a \times v^3 + b \times v^2 + c \times v + P_R$ where

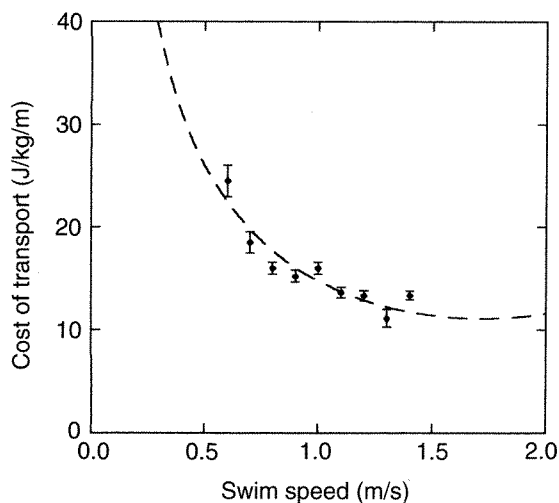


FIG. 5. Extrapolated Cost of Transport of little penguins swimming at sea ($r^2 = 0.89$, $n = 9$) and COT derived from swim canal experiments, plotted as a function of swimming speed; bars show standard error of the means

v is swimming speed [m/s] and P_R is the metabolic rate of little penguins resting in water (in W/kg). Transport Costs were obtained using the function $COT = P_s/v$. The resulting curve for COT (Fig. 5, $a = 4.22$, $b = -11.51$, $c = 13.34$, $P_R = 8.5$ W/kg) shows a minimum of 11.1 J/kg/m at a swimming speed of 1.8 m/s ($r^2 = 0.89$, $n = 9$). Power requirements of little penguins while swimming at 1.8 m/s were predicted by this equation to be 20.0 W/kg ($6.3 \times \text{BMR}$).

Aerobic dive limits

The maximum length of time that a penguin can dive depends, in part, on its aerobic dive limit (ADL), that is the time the bird can remain underwater before oxygen stores are fully utilized and anaerobic metabolism begins to take over. Anaerobic metabolism presumably requires longer post-dive rest periods at the surface than during aerobic metabolism because lactate has to be removed. However, determination of the ADL by simple inspection of the post-dive surface intervals is problematic since birds may redive for short periods soon after surfacing despite carrying an increased lactate load. Horning (1992) suggests, however, that consideration of the surface interval versus dive duration over a number of consecutive dives can help elucidate this question.

Accordingly, we used our field data to estimate the ADL of little penguins. We regressed the mean surface duration against the mean dive duration over 12 successive dives (Fig. 6). This was the minimum number of dives required to obtain a constant proportion between surface and dive duration. The 8-s-measurement interval of the recorders implies that surface and dive durations shorter than 8 s could not be resolved and that there is an 8 s error in the estimate of ADL. The calculated range for ADL is 42 to 50 s. All dives lasting longer always had an increased surface duration, probably caused by a lactate load that had to be removed. The minimal surface duration for dives lasting longer than the estimated ADL is best described by the function $\text{surface duration} = 0.7 \times \text{dive duration} - 24.28$ (Fig. 6).

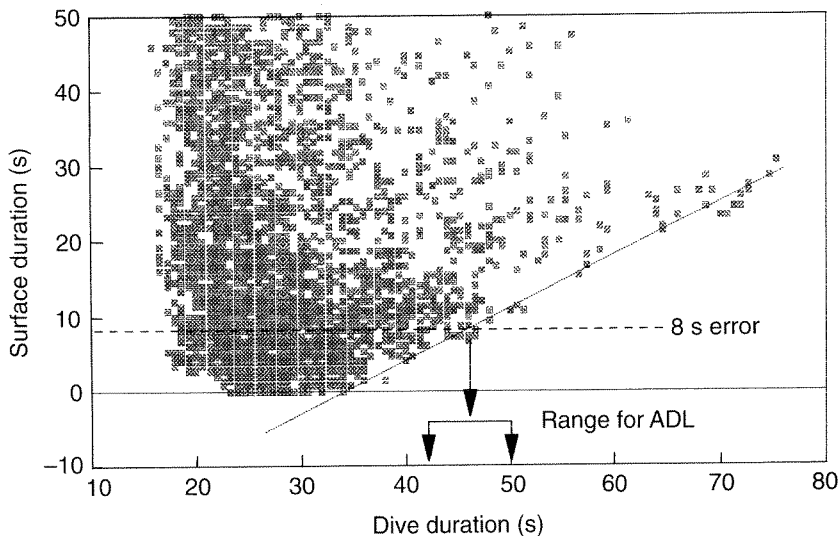


FIG. 6. Mean surface duration of 12 successive dives of little penguins against mean dive duration of the same dives; the line describes the minimal surface time; the arrows show the proposed ADL range (42–50 s); values under 8 s surface time are inappropriate due to data-logger measurement interval.

TABLE III

Total oxygen stores in little penguins amount to about 45 ml/kg prior to a dive

	Blood		Muscle	Lungs & air sacs	Source
	arterial	venous			
Proportion of body mass [%]	3.4	8.9	25 ^a		Chappell <i>et al.</i> (1993)
Amount of resp. pigment [g/l]	138 ^a	138 ^a	28		Mill & Baldwin (1983)
O ₂ -binding capacity [ml/g]	1.37	1.37	1.34		Mill & Baldwin (1983)
Saturation prior to dive [%]	95	70	100		Stephenson <i>et al.</i> (1989)
Availability during dive [%]	96	96	100		Stephenson <i>et al.</i> (1989)
O ₂ [ml/kg]	5.9	11.3	9.4	18 ^a	Total: 44.6

^a S. Nicol (unpubl. data for little penguins)

The ADL of little penguins can also be estimated using the results obtained in the swim canal experiments following $ADL = c.f. \times Oxy/P$ where c.f. is the conversion factor (19.7 kJ/l of oxygen), P the power requirements for swimming and Oxy the total amount of oxygen available to the birds while swimming. Prior to a dive, little penguins store oxygen in arterial and venous blood, muscle tissue and air sacs (Mill & Baldwin, 1983). Total oxygen stores can be estimated if parameters such as the oxygen binding capacity of blood and muscle and the saturation prior to the dive are known. For little penguins, only some of these parameters are available (Mill & Baldwin, 1983). Missing data were completed using data for Adélie penguins *Pygoscelis adeliae* (Chappell *et al.*, 1993) and tufted ducks *Aythya fuligula* (Stephenson, Turner & Butler, 1989). We calculated a total oxygen store of 45 ml/kg for little penguins (Table III). Similar calculations for *Pygoscelis* penguins yield oxygen stores between 57 and 63 ml/kg (Culik *et al.*, 1994a).

Using power requirements determined in the swim canal (20.0 W/kg), we calculated that little penguins should be able to dive aerobically for 44 s when swimming at their preferred speed of 1.8 m/s

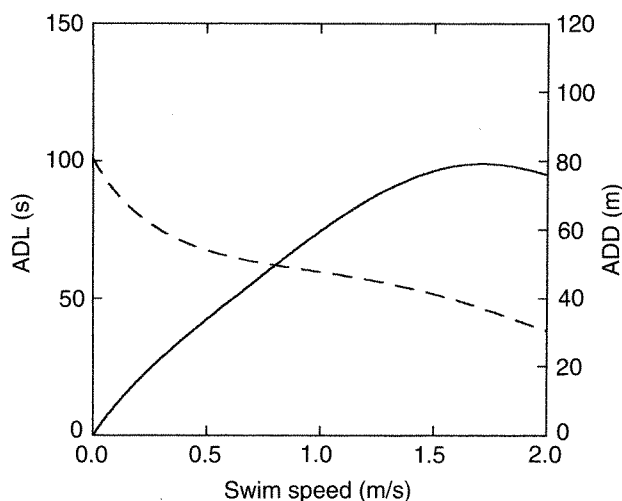


FIG. 7. Aerobic dive limit (ADL, dotted line) and Aerobic dive distance (ADD, solid line) of little penguin plotted as a function of speed; ADD is nearly maximal at preferred swimming speed at sea.

(Fig. 7). This value is consistent with the results obtained from the field data (see above). Using $ADD = ADL \times v$ where v is swimming speed, we calculated an aerobic dive distance of 79 m. The aerobic dive distance is close to its theoretical maximum at the preferred swimming speed at sea of 1.8 m/s (Fig. 7).

Our data on little penguin dive durations indicate that these birds exceed the estimated ADL in only 2% of all dives. This accords with physiological and biochemical data on the swimming muscles of little penguin. Mill & Baldwin (1983) and Baldwin (1988) showed that the muscle fibres of the pectoralis and the supracoracoideus, the muscles employed in swimming, are basically aerobic, having little anaerobic capacity. Our results support the speculation of Baldwin (1988) that little penguins may dive mainly aerobically. This is reasonable as the use of anaerobic metabolic pathways is much less efficient than aerobic metabolism (ratio 1:18). Furthermore, anaerobic metabolism necessitates longer post-dive rest periods at the surface because lactate has to be removed. The use of aerobic metabolism in most dives would allow little penguins to maximize the time spent under water.

The results derived from the swim canal experiments can be compared directly with results obtained by Culik *et al.* (1994a) who used a similar system to determine the energy requirements of Adélie penguins (*P. adeliae*), chinstrap penguins (*P. antarctica*) and gentoo penguins (*P. papua*). In addition, we compared our data with results obtained by Kooyman *et al.* (1992) who examined king penguins (*Aptenodytes patagonicus*) using the doubly-labelled water technique. Table IV summarizes the diving parameters for the different penguin species.

Little penguins have by far the highest energy requirements for diving of all penguin species studied so far. This is presumably caused by the large surface area to volume ratio of little penguins due to their small body size. Heat loss and friction are thus relatively more important than in larger penguin species. The dependency of physiological parameters on body mass in homeotherms is described extensively by e.g. Schmidt-Nielsen (1991) and Peters (1983). Accordingly, the transport costs of the five different penguin species swimming at their preferred speeds at sea were found to be $COT = 11.3 \times Mb^{-0.456}$ ($r^2 = 0.61$, $n = 5$).

Aerobic dive limits of little penguins were estimated to be 44 s at preferred swimming speed at sea. For comparison, Culik (1994) calculated aerobic dive limits of 134, 113 and 95 s for chinstrap, Adélie and gentoo penguins, respectively; Kooyman *et al.* (1992) derived 120 s for king penguins. Using data on penguin dive durations in the wild, the percentages of dives exceeding ADL were calculated as 4, 14, 44 and 40–45% for chinstrap, Adélie, gentoo and king penguins, respectively (Culik, 1994; Kooyman *et al.*, 1992).

TABLE IV

Diving parameters for different penguin species while swimming underwater at their preferred speeds at sea (data for little penguins: this study, for chinstrap, Adélie and gentoo Penguins: Culik *et al.* 1994a, for king penguins: Kooyman *et al.*, 1992)

	Little	Chinstrap	Adélie	Gentoo	King
Body weight [kg]	1.2	3.8	4	5.5	13
Swimming speed [m/s]	1.8	2.4	2.2	1.8	2.1
Power [W/kg]	20.0	8.5	10.5	13.3	9.6
COT [J/kg/m]	11.1	3.6	4.8	7.4	4.6
Oxygen stores [ml/kg]	45	57	59	63	—
Aerobic dive limit ADL [s]	44	134	113	95	120
Dives exceeding ADL [%]	2	4	14	44	40–45
Aerobic dive distance [m]	79	322	248	171	252

TABLE V
Comparison of swimming speeds recorded for little penguins

Speed [m/s]			Distance or duration of measurement	Method	Source
mean	max.	<i>n</i>			
—	1.6	1	c. 100 m	timed from boat	Barton (1979)
—	1.7	3	c. 10 m	timed in tank	Clark & Bemis (1979)
—	1.8	6	19 m	timed from shore	Dann & Cullen (1989)
2.4	3.2	2	entire foraging trip	data-logger	Gales <i>et al.</i> (1990)
1.8	3.3	12	entire foraging trip	data-logger	This study
—	3.2	1	c. 5 m	timed in tank	Cannell (1994)

Swimming speed and dive depth at sea

There are only a few other estimates of swimming speeds in little penguins, and these are summarized in Table V. The average speed of 1.8 m/s for underwater swimming found in this study is considerably faster than most previous records. Barton (1979), Clark & Bemis (1979) and Dann & Cullen (1989) measured speeds between 1.6 and 1.8 m/s which, owing to measurement conditions, were interpreted as underwater-sprints. Our results indicate, however, that such swim speeds are likely typical for little penguins.

The only other measurement of normal little penguin underwater swimming speed was made by Gales *et al.* (1990) using a logger (see earlier) which measured speed with a paddle wheel. Their mean value for swimming speed departs radically from all other measurements being higher by some 40%. In view of the difficulty in measuring water flow over swimming marine endotherms by using paddle wheels (Bannasch *et al.*, 1994; Pütz, 1994), we would tentatively suggest that the values of Gales *et al.* (1990) are over-estimates resulting from inappropriate calibration since their devices were not calibrated on living birds.

Our estimated maximum speed of 3.3 m/s is consistent with the results of Cannell (1994) who recorded a maximum speed of 3.2 m/s for little penguins chasing fish in captivity.

Overall, swimming speeds of little penguins are substantially lower than those of the larger penguin species, there being a tendency for larger species to swim faster, both in terms of cruising and maximum speeds (Wilson, 1995). In terms of body lengths per second, however, little penguins compare favourably with other species, travelling normally at c. 4.5 body lengths per second, while values for other species range between 2.4 and 3.1 body lengths per second for gentoo and chinstrap penguins, respectively (speed data derived from the summary in Wilson (1995), body length data from Harrison (1983)).

The reduced swimming speeds of little penguins compared to other species means that, for a given dive duration, they cover less distance underwater, and are potentially less able to dive as deeply. Indeed, our recorded dive depths for little penguins (mean max. per trip = 22 m, range 17–27 m, *n* = 12), which accorded well with those from other studies (Montague (1985) — mean max. per trip = 30 m, range 9–69 m, *n* = 32; Gales *et al.* (1990) — mean max. = 27.5 m, range 5–50 m, *n* = 2), are considerably less than those of other penguin species (for summary see Wilson, 1995). For example, medium size penguins (c. 4 kg) routinely exceed dive depths of 80 m (Wilson, 1995) and king and emperor penguins may dive in excess of 300 (Kooyman *et al.*, 1992; Pütz, 1994) and 400 m (Ancel *et al.*, 1992), respectively. The reduced dive depths of little penguins are not a sole consequence of reduced swimming speed, but are also presumably dependent on dive duration since birds need time

to reach greater depths. There is a clear relationship between maximum dive duration and body size in penguins (Wilson, 1995) so that, of all penguin species, little penguins dive for the shortest periods. Our mean dive durations of 21 s were consistent with results recorded by Lalas (1983) at 24 s and Gales *et al.* (1990) at 21 s.

Discussion

Diving and foraging behaviour

Foraging behaviour of little penguins follows a pattern consistent with the behaviour of other penguin species at sea (Wilson, 1995) where a typical foraging trip follows a so-called 'looping course' (Wilson, 1995) and can be divided into four distinct phases (Fig. 3, Table II). Little penguins leave the beach before sunrise in the morning, probably to avoid enemies on land. Since these birds are optical hunters and seem to depend on visual orientation (Howland & Sivak, 1984; Stahel & Gales, 1987), it seems reasonable for them to wait near the beach for daylight before starting to forage. The behaviour we describe as phase 1 accords well with this. Similar behaviour has been observed in African penguins (Heath, 1985) and Gales *et al.* (1990) also found slow mean speeds and shallow diving during the first 1.5 hours of a little penguin's foraging trip.

During phase 2, birds swim underwater extensively, but only really move horizontally. Similar behaviour is known from other penguin species and is interpreted specifically as travelling behaviour (Wilson, 1995). At this stage of the foraging trip the penguins seem to travel relatively large distances on their way to, or in search of, prey accumulations (see for comparison see Klomp & Wooller, 1988; Gales, 1989; Cullen, Montague & Hull, 1992). While shallow dives are assumed to be typical 'travelling dives', the few interspersed deeper dives may mainly serve to prospect for prey (Wilson, 1995). Weavers (1992) used radio-telemetry to follow little penguins from Phillip Island, Victoria, on their foraging trips. He found that the route taken by penguins between the time of leaving the burrow at about dawn and 10:30 h is fairly directional. Weavers (1992) too interpreted this as travelling and prey searching behaviour.

The intense diving activity coupled with extensive vertical movement during phase 3 is hypothesized as representing primarily foraging and feeding activity. Dives of this kind are documented from other penguins as well and are considered to be 'feeding dives' (Wilson, 1995). Prey density is probably greater in these regions. Precise details on the vertical distribution of the fish (71% of diet by mass), squid (20%) and crustaceans (9%) on which little penguins from Marion Bay, Tasmania feed (Gales, 1989), are lacking. However, it is known that all prey types occur in shallow water (Gales *et al.*, 1990).

Our observations of phase 3 behaviour are well supported by results of Gales *et al.* (1990) who found similar intensive foraging behaviour with rapid bouts of deep diving. Weavers (1992) noticed that, between 10:30 and 17:00 h, the penguins often moved in a relatively confined area of only about 1 km², probably fishing where they had found schools of prey.

Phase 4 behaviour seems to consist essentially of travelling as the penguins make their way back to the colony. By radio-tagging, Weavers (1992) observed that the birds travelled very nearly in a straight line as they returned to the colony, suggesting precise navigation. As shown by our data, this behaviour begins at about 18:00 h and ends when birds reach the beach at 22:00 h. Probably again to avoid enemies on land, little penguins at Marion Bay never returned to the beach before dusk.

Foraging range

The results of this study show that little penguins travel a mean distance of about 73 km per day during the breeding season. The vertical component of this distance can be ignored owing to the shallow dives of the birds. In order to determine the actual foraging range of little penguins from the colony at Marion Bay, we used results obtained by Weavers (1992) in a radio-telemetry study. He found that little penguins tend to swim back to their colony in a more or less straight line in the evening (see above). The mean distance travelled during the return trip to the colony amounted to 12.3 km in our birds. This is the best approximation we can give for the actual foraging range of little penguins breeding at Marion Bay.

This result is supported by the observations of Gales *et al.* (1990) who derived a maximum foraging range of 13 km for a single little penguin in Bass Street. Weavers (1992) determined a mean foraging range of 7.9 km (range 2.4 to 17.8 km) by radio-tagging little penguins breeding at Phillip Island/Victoria/Australia. Of the recorded penguin-time, 95% was within a radius of 15 km of the burrow and 9 km of the coast.

Changes in foraging behaviour over the breeding period

Increases in the distance travelled (Fig. 4), total time spent foraging, and activity at sea as the breeding season progressed (Table VI) are likely to be linked to increasing food requirements of the chicks (Gales & Green, 1990). However, changing food availability could be another reason for the observed changes in foraging behaviour and cannot be ruled out.

Increases in the distance swum per foraging trip with increasing brood food requirements have also been noted in African penguins (Wilson & Wilson, 1995). African penguins feed on pelagic school fish (Wilson & Wilson, 1995), in much the same way as little penguins do (Wilson, 1995), encountering schools of fish on a number of occasions per foraging trip and ingesting limited amounts of fish per prey encounter (Wilson, 1985; Wilson & Wilson, 1995). Increases in the time spent travelling presumably leads to increases in the distance travelled and hence the number of prey encountered, which ultimately increases the amount of prey ingested per foraging trip. We suppose that a similar mechanism may also operate in the little penguin.

FMR at sea and overall energy budget

The FMR at sea of little penguins presumably consists essentially of the energetic costs for underwater swimming and those for resting at the water surface. It is unlikely that penguins paddle on the surface over longer distances since it is energetically much less efficient than swimming under water (Baudinette & Gill, 1985; Trivelpiece *et al.*, 1986).

These assumptions, together with metabolic rates of little penguins and the field data obtained in this study, allow calculation of the FMR at sea. We multiplied surface time with the metabolic rate for resting at the water surface (8.5 W/kg) and added this to the time under water multiplied with the metabolic rate for underwater swimming (20.0 W/kg) at 1.8 m/s. Since the activity at sea changes over the breeding season (see above), we calculated the FMR at sea for three different stages of chick development and found it to average between 1280 and 1500 kJ/kg/d (Table VI).

Other authors have determined the FMR at sea of little penguins by using the doubly-labelled water technique (Costa, Dann & Disher, 1986; Gales & Green, 1990). The FMR at sea of non-breeding little penguins determined by Costa *et al.* (1986) (1124 kJ/kg/d) fits well to the results obtained in this study.

TABLE VI

Foraging parameters and FMR at sea of little penguins at different stages of chick-rearing. Activity at sea is the percentage time the birds spent underwater

Stage of chick-rearing	<i>n</i>	Time at sea [hh:mm]	Activity at sea [%]	Costs per foraging trip[kJ/kg]	FMR at sea [kJ/kg/d]	FMR/BMR
early	5	17:30	54	930	1280	4.6
mid	4	18:10	64	1040	1370	4.9
late	3	18:50	77	1180	1500	5.4

However, Gales & Green (1990) found much higher values both for non-breeding and for breeding little penguins.

To approximate the maximum energy requirements of little penguins during the breeding season, we combined our results with data on the energy expenditure of little penguins on land (661 kJ/kg/d, Gales & Green, 1990) and the energy requirements of the chicks at the end of the breeding season (867 kJ/kg/d (Gales & Green, 1990), a mean of 1.7 chicks with a mean weight of 826 g yield energy requirements of 1220 kJ/d). The calculation (see Table VII) yields maximum energetic costs of 3600 kJ for a 1.2 kg little penguin and chicks in the final stages of chick-rearing. These costs include the costs for one-day foraging, the costs for the following day on land and the costs for one day's chick-rearing. The whole amount of 3600 kJ has to be covered by the adult in one foraging trip which necessitates a foraging efficiency of 2.6 (total energy requirements divided by the energetic costs of the foraging trip; cf. Nagy *et al.*, 1984). For comparison, the energetic cost incurred in one foraging trip by non-breeders was found to be 1030 kJ for a 1.2 kg little penguin (Costa *et al.*, 1986) (Table VII).

Assuming a metabolizable energy of 3.9 kJ/g fresh mass of food (Gales & Green, 1990), an adult little penguin would have to catch 920 g food in one foraging trip in the late chick-rearing period (Table VII). For the whole colony at Marion Bay of about 350 breeding pairs, the maximum food requirements in the breeding season would amount to 320 kg of food per day. Following Costa *et al.* (1986), during the non-breeding season the same colony would need about 200 kg of food each day. If the chick-rearing period is 57 days (Gales & Green, 1990), a total of 80 tons of food is needed each year for the whole colony at Marion Bay. A breeding little penguin raising 0.85 chicks/y (1.7 chicks/pair) would consume 114 kg food each year. Gales & Green (1990) determined yearly food requirements of 137 kg for one breeding little penguin.

Conclusions and implications for management

The small size of the little penguins, and consequently high energy requirements for swimming underwater compared to other penguins, limits their diving ability. The field data show that the dives of little penguins are short and shallow. Little penguins are thus very restricted in the depths that they can exploit. We assume that the birds compensate this shortcoming by high activity at sea and a high number of dives. The results of this study indicate that little penguins are highly adapted to this lifestyle by an essentially aerobic metabolism. As shown above, the use of aerobic metabolism reduces the total surface time and maximizes foraging efficiency.

Little penguins are highly dependent on good food resources in coastal waters near their nesting sites (e.g. Gales *et al.*, 1990; Weavers, 1992). Because most foraging activity takes place in an area of about 250 km² around the colony (radius 12 km), it is important to protect this zone, as a minimum area, from disruptions of the marine environment (e.g. by oil or chemical spills, dredging). Over-fishing or other

TABLE VII

*Energy and food requirements of an adult little penguin (1.2 kg) during the final stages of chick-rearing and out of the breeding season (^aGales & Green, 1990, ^bCosta *et al.*, 1986, ^c: derived from Cullen *et al.*, 1992)*

	Late chick-rearing	Non-breeding
Energetic costs of one day with foraging trip [kJ]	1590	1030 ^b
Energetic costs of one day on land [kJ]	790 ^a	
Energetic costs of one day's chick-rearing [kJ]	1220 ^a	
Total energy requirements to be covered during one foraging trip [kJ]	3600	1030
Duration of foraging trip [hh:mm]	18:50	14:30 ^b
Energetic costs for foraging trip [kJ]	1410	815 ^b
Necessary foraging efficiency	2.6	1.3 ^b
Metabolizable energy of food [kJ/g fresh mass]	3.9 ^a	3.9 ^a
Necessary food mass [g]	920	260
Mean weight of prey [g]	5 ^c	5 ^c
Number of prey items necessary	184	52

possible interference with the food supply of, or the foraging by, little penguins has to be avoided. Out of the breeding season, little penguins are known to perform foraging trips lasting longer than one day. Even trips where birds range up to 710 km have been reported (Weavers, 1992). However, little penguins appear to travel typically within 20 km of the coast (Weavers, 1992). To ensure the future of little penguins around the coasts of southern Australia and New Zealand, it would therefore be reasonable to establish a 20 km protection zone along the coasts which connects the existing nesting sites and allows resettlement and the foundation of new colonies.

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