Metabolic rates of swimming Humboldt penguins

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ABSTRACT: As one of the elements for a model on the food requirements of Humboldt penguins *Spheniscus humboldti* we determined, via gas respirometry, metabolic rates while swimming and resting in water. During rest in water at 19°C Humboldt penguins (mean body mass 3.6 kg) required 5.95 W kg^{-1}. This corresponds to a thermal conductance in water of 0.2975 W (kg °C)$^{-1}$ (at T_a 19°C and assuming a T_b of 39°C). When swimming in a 20 m long channel, metabolism rose from 8 W kg^{-1} at a speed of 0.6 ms^{-1} to 23.1 W kg^{-1} at 2.2 m s^{-1}. Transport costs (the cost to move 1 kg of body mass over a distance of 1 m) reached a minimum at 1.4 ms^{-1} with 8.1 J (kg m)$^{-1}$, which corresponds to 0.89 J (Nm)$^{-1}$. We corrected for acceleration and deceleration in the channel to determine transport costs of free-ranging Humboldt penguins travelling at sea, which were calculated as 7 J (kg m)$^{-1}$ (0.71 J [Nm]$^{-1}$), at 1.7 m s^{-1}. Birds feeding chicks need to balance the costs of either (1) returning to the breeding island for the night and travelling back to the feeding grounds in the morning or (2) incurring increased thermoregulatory costs associated with resting at sea overnight. Simple calculations show that at water temperatures of 19°C we expect Humboldt penguins to show a tendency to remain at sea overnight if foraging areas are >4 km from their island. In colder waters (12°C), this distance increases to >9 km. Using previously published data on at-sea activity of Humboldt penguins, we found that foraging costs during chick rearing amount to 340 g anchovies d^{-1}. Finally, we present a general model to convert Humboldt penguin activity data at sea to food requirements.

KEY WORDS: Oxygen consumption · Resting metabolic rate · Swimming energetics · Swimming speed · Cost of transport · Aerobic dive limit · Food requirements · Modelling

INTRODUCTION

Humboldt penguins *Spheniscus humboldti* are distributed between 5 and 42° S along the Pacific coast of South America and have recently been classified as vulnerable, the population remaining at low levels (ca 13 000 birds) since the early 1980s (Ellis et al. 1998). The factors preventing a recovery to higher population densities are presumably a shortage of prey due to over-fishing by commercial anchovy *Engraulis ringens* and sardine *Sardinops sagas* fisheries, unfavourable oceanic conditions such as repeated small-scale ENSO (El Niño Southern Oscillation) in the early 1990s and a major ENSO event in 1997-98, marine pollution, and other deleterious anthropogenic influences (Culik et

al. 1998). These factors are also acting on Humboldt penguins at Pan de Azúcar National Park (26° S, 70° W), one of the most important breeding colonies for this species in northern Chile, with a population of 1750 individuals in 1995 (Ellis et al. 1998).

Although the Humboldt penguin was, until recently, thought to be a sedentary species, recent evidence has shown that the birds are capable of migrating considerable distances to avoid unfavourable climatic conditions or in search of prey during an ENSO event (Culik & Luna-Jorquera 1997a, Culik et al. 2000). Even in normal reproductive years, Humboldt penguins from Pan de Azúcar Island search routinely within a radius of 35 km around their breeding island to find food for themselves and their chicks (Culik & Luna-Jorquera 1997b, Culik et al. 1998).

The exact nutritional requirements of Humboldt penguins, i.e. the amount of energy and food required

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per day, are to date unknown. This, however, is a crucial factor in conservation efforts, since it enables the calculation of the food requirements of entire colonies and thus a comparison with other fish consumers and commercial fisheries. Because penguins are highly adapted to life in the marine environment and spend a large proportion of their time at sea, one important parameter for the calculation of daily nutritional needs is the amount of energy expended whilst at sea.

Here we present the results of a study conducted to determine the metabolic rate of Humboldt penguins (1) resting in water and (2) swimming in a 20 m long channel at various, voluntarily chosen speeds. We used our results to (1) calculate the typical energy requirements of Humboldt penguins during swimming (travelling and foraging), (2) estimate their aerobic dive limit, (3) compare these results with data from other penguin species and (4) estimate food requirements of foraging Humboldt penguins during the reproductive season.

MATERIALS AND METHODS

Birds. Three adult non-breeding Humboldt penguins were captured on December 19, 1994, at Pan de Azúcar National Park under supervision and by license of Corporación Nacional Forestal (CONAF, IIIa Región, Copiapó, Chile). Birds were caught by hand in their burrows after administration of 0.25 ml ketamine hydrochloride (Ketavet, Parke-Davis GmbH, Berlin, Germany) to tranquillise them (Luna-Jorquera et al. 1996). The birds were held in covered individual 70 × 60 × 70 cm cages and rapidly transported at night by car to Antofagasta (ca 400 km) in order to avoid overheating and excessive stress. Approximately 6 h after capture, the birds were transferred to an outdoor pen located 200 m from the coast in the coastal desert at the Instituto de Investigaciones Oceanológicas, Universidad de Antofagasta, Chile.

In the pen, the penguins were fed daily ad libitum at 18:00 to 19:00 h local time with anchovies or sardines, a multi-vitamin and calcium supplement being administered with the fish. The birds were individually recognizable and had free access to a 1 m deep pool, filled with seawater, which was changed daily. The birds were examined occasionally by a veterinarian and were considered in good health. Experiments in the swim channel were initiated after an acclimation time of 22 d and were conducted in the mornings between 09:00 and 11:00 h and afternoons between 16:00 and 18:00 h. During experiments, mean body mass of the birds was 3.6 kg, with a range of 2.7 to 4.5 kg. All birds were released at the capture site after termination of the experiments in February 1995.

Swim channel. To determine the energy requirements of Humboldt penguins swimming underwater, we constructed and operated a swim channel described by Culik & Wilson (1991, see their schematic of the experimental setup), and modified by Culik et al. (1996) and Allers & Culik (1997). In brief, the swim channel consisted of a 20 m long U-shaped metal sheet (zinc-plated) construction 0.88 to 0.92 m wide and 0.77 m deep, pre-built in interlocking, 1.25 m long segments. This construction was immersed into a 20 × 5 m pool filled with seawater and located at the Instituto de Investigaciones Oceanológicas. Because the depth of the pool varied from 1 to 1.5 m, the channel was suspended at the top of the pool and equilibrated to avoid any inclination. The channel was covered ca 5 cm below the water surface with transparent polyvinyl-chloride (PVC) sheets (5 mm thick), bolted to the metal to prevent the penguins from surfacing and breathing at localities other than in the respiration chambers. Water in the pool had to be replaced every 2 d because of contamination with excreta and algae. To prevent rapid rising of water temperature due to solar irradiation, the pool was covered with black netting (mesh width 3 cm) installed 1 m above the pool.

Respirometry. During experiments, penguins could only breathe in respiration chambers partially immersed at both ends of the channel and thus sealed from outside air. Respiration chambers (A and B) were made of transparent PVC with an air volume of approx. 52 l. Each chamber received outside air via a 37 × 1 cm tube (perforated at 15 mm intervals with 3 mm holes). Gas mixing in the chamber was additionally achieved via a 12 V ventilator (Truma, Putzbrunn, Germany) with directable air inlets and outlets, yielding a turnover rate of 30 l s^{-1}. Air from the chambers was cleared (negative pressure) at a rate of 50 l min^{-1} using 2 seawater-resistant pumps (MC4, Vacuubrand, Wertheim, Germany) and fed directly to the laboratory via gas-impermeable tubing (9.5 mm diameter, Tygon, Norton, USA). A 3 l flask was installed in the outflow tube of the chambers to reduce pressure variations from the pump, collect condensation and act as a silencer.

In the laboratory, gas flow from each chamber was measured using 1 of 2 mass flow meters (MAS 3015, Kobold, Hofheim, Germany) and a subsample was dried (Drierite, Aldrich Chemicals) and passed into 1 of 2 paramagnetic oxygen analysers (OXYGOR) and subsequently into an infrared carbon dioxide analyser (UNOR, both Maihak, Hamburg, Germany). Calibration of the gas analysers was repeated daily using 99.995% pure N_2 and CO_2 gases (Messer Griesheim, Hamburg, Germany), as well as ambient air (20.95% O_2 and 0.03% CO_2). Calibration gases were diluted with ambient air with the aid of a Wösthoff pump

SA27/3 (Wösthoff, Bochum, Germany) to 19.90% O_2 and 1.03% CO_2. During the experiments, O_2 and CO_2 concentrations in the respiration chambers remained above 20% and below 1%, respectively. Calibration checks with ambient air were made before and after each experiment. Absorption of CO_2 by seawater during the experiment was assumed to be negligible (Williams 1989) and estimated to amount to a maximum of 0.015% min^{-1} (Liss & Merlivat 1986, A. Körtzinger pers. comm.). Data from the 3 analysers and the 2 flow meters were sampled every 2 s by an IBM-compatible 386SX computer (Chicony, Hamburg, Germany) fitted with an analogue-digital conversion card and using purpose-made software (resolution: 0.01% O_2 and CO_2).

Recovery rates for the whole system (including mass flow meter, analysers, A/D converter, and computational techniques) were determined by pumping known volumes of nitrogen (99.995% pure) into the respiration chambers with a standard gas meter. We obtained a recovery rate of 99.6% (n = 3), which compares well to the 99.8% (±5%, n = 43), previously determined by Allers & Culik (1997) for the same setup and equipment.

Penguin behaviour. Prior to the initiation of experiments, penguins were trained 3 times (during 3 consecutive days for at least 2 h) in the pool. The first time a bird was in the channel, 2 people were required to ensure that it found the respiration chamber after its first dive. The penguins rapidly adapted to the new situation and found a respiration chamber within 1 to 2 min after the beginning of an experiment and subsequently explored the channel, presumably to find an exit, thereby swimming up and down, from one chamber to the other. In the channel the penguins were undisturbed and swam voluntarily at their preferred speeds. The typical duration of experiments was 1 h, depending on the performance of the penguins. In general, the birds were co-operative and adopted a regular swimming pattern.

The activity of the birds in the swim channel was monitored from an observation seat 3 m above the ground. The behaviour and position of the birds in the channel were recorded in real time using a Husky Hunter II field computer (Husky, Coventry, England) and specially designed software. Each key on the computer was associated with a particular type of behaviour or position of the bird. Each time one of the keys was pressed, time (0.1 s resolution) as well as the key just pressed were stored. Each type of behaviour ended when a new type of behaviour was recorded, while positional information (the swim channel was marked at 1 m intervals) 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: (1) swimming speed, (2) distance swum, (3) dive duration and (4) surface duration for each individual diving event. If a bird turned around between 2 markers, no speed was computed until the penguin swam again in a straight line.

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 either rested in one of the chambers or swam for a minimum of 18 m through the channel, including occasional turns, and then surfaced and recovered quietly. Prior to surfacing in a respiration chamber, the birds had been absent from that chamber for a minimum of 10 s, a sufficient delay to separate individual dive + surfacing events. All dives followed by shivering, unrest and preening were deleted from the analysis. We conducted a total of 216 experiments with the 3 penguins and obtained 688 individually analysed dives or dive series in the channel.

Oxygen consumption. Oxygen consumption of penguins in the respiration chambers was calculated for every 2 s interval using the formula of Woakes & Butler (1983) as modified by Culik et al. (1990), which accounts for analyser drift. Oxygen consumption was corrected for respiratory quotient (Withers 1977) and summed only if values were above a threshold of 1 ml s^{-1} for 3 consecutive measurements. This ensured that 'noise' in the apparatus was not recorded when birds were absent from the chambers.

According to Culik et al. (1996), penguin oxygen consumption in the chambers during surface time reflects oxygen consumption while swimming (and holding breath) just prior to surfacing, plus oxygen consumption during the current recovery period. The duration of recovery is defined as the time required for elevated O_2-consumption rates after a dive series to return to resting levels (here, resting in water; Castellini et al. 1992). The total amount of oxygen consumed during the recovery period after a dive series was therefore divided by the time spent holding breath plus the time of recovery to obtain the rate of O_2 consumption (ml O_2 s^{-1}) for the entire event (dive + recovery). The corresponding power input (P) should reflect the energy expenditure of birds travelling or foraging at sea.

In order to analyse energy requirements of diving penguins with respect to swimming speed, P was averaged for 0.1 m s^{-1} speed classes (e.g. power data obtained at mean swimming speeds between 0.45 and 0.54 m s^{-1} were summarised into the 0.5 m s^{-1} speed class, and so on). All data were statistically treated using SYSTAT for Windows. Data were tested for normality and homoscedasticity before applying paramet-

ric or non-parametric tests as appropriate (Zar 1984). Means are presented ± standard error (SE).

RESULTS

Resting metabolic rate

After a period of 22 d of acclimation to captivity, the penguins had habituated well to human handling, voluntarily accepted being hand-fed and did not show evidence of stress when approached. During several experiments in the swim channel, the 3 Humboldt penguins were observed to rest for more than 10 min in one of the respiration chambers, floating quietly at the surface. Mean energy expenditure for rest in water (Table 1) did not significantly differ between birds (ANOVA, $F = 0.010$; p = 0.98). Consequently, all data were pooled, yielding a mean resting oxygen consumption in water of 1.09 ± 0.07 ml O_2 s^{-1}. Respiratory quotient (RQ) was 0.78 ± 0.05, resulting in a conversion factor of 20 J ml^{-1} O_2 to convert to W kg^{-1} (Eckert 1993, Schmidt-Nielsen 1993). Metabolic rate of Humboldt penguins resting in water (RMR_{water}) therefore amounts to 5.95 W kg^{-1} (n = 20 measurements, $T_{water} = 19 \pm 1.0°C$).

Swimming metabolism

Typically, Humboldt penguins swam from one end of the channel to the other, accelerating and decelerating in the first and last 4 m, while maintaining a relatively constant speed over the middle section (12 m). Swimming speeds of the birds ranged from 0.6 to 2.2 m s^{-1} with a mean of 1.12 ± 0.01 m s^{-1} (n = 688 measurements; Table 2). Swimming speeds were significantly different between birds (ANOVA, $F = 48.228$; p < 0.001). Penguins did not always surface immediately after swimming from one end of the channel to the other, but no differences were detected between individual swimming distances (ANOVA, $F = 2.309$; p = 0.100), which averaged 19.74 ± 0.18 m (n = 688 measurements).

Mean power requirements (P_{dive} in W kg^{-1}) for the entire dive + surface cycle were analysed with respect to speed. Data of the 3 penguins were modelled using a third-degree polynomial (Culik et al. 1996):

$$P_{dive} = av^3 + bv^2 + cv + RMR_{water} \qquad (1)$$

where v is swimming speed (m s^{-1}). The corresponding parameters (a, b, c) were computed for each bird individually and are given in Table 3. We found that power input did not significantly differ between penguins swimming at the same speed (ANOVA, $F = 1.17$; p = 0.323). Data were therefore pooled and power input modelled to obtain a general equation for Humboldt penguins (Table 3). The corresponding curve fit is shown in Fig. 1. When swimming, the mean P of all 3 Humboldt penguins averaged 9.05 ± 0.11 W kg^{-1} (n = 688 measurements; Table 2). However, power requirements varied significantly between speed classes (ANOVA, $F = 32.85$; p < 0.001), ranging from 8.0 ± 0.47 W kg^{-1} at 0.6 m s^{-1} to 23.1 ± 2.65 W kg^{-1} at 2.2 m s^{-1}.

The polynomial equation used above also allows modelling of cost of transport (COT in J [kg m]$^{-1}$), which is obtained by dividing power (W kg^{-1} or J s^{-1} kg^{-1}) by speed (m s^{-1}):

$$COT = (av^3 + bv^2 + cv + RMR_{water})/v \qquad (2)$$

COT is the amount of energy required to transport 1 kg of body mass over a distance of 1 m (Schmidt-Nielsen 1993). Videler & Nolet (1990) suggested expressing

Table 1. *Spheniscus humboldti*. Mean and standard error (SE) of oxygen consumption of 3 Humboldt penguins at rest in the swim channel. Grand mean and respective SE were obtained by data pooling (ANOVA, p > 0.05)

Penguin	ml O_2 s^{-1}	Body mass (kg)	N
A	1.17 (0.105)	3.4 (0.380)	7
B	1.31 (0.104)	4.1 (0.125)	6
C	0.89 (0.093)	3.4 (0.110)	7
Grand mean	1.090 (0.070)	3.6 (0.126)	20

Table 2. *Spheniscus humboldti*. Mean swimming speed and distance swam of the 3 Humboldt penguins used in the swim channel experiments. SE is standard error

Penguin	Swimming speed (m s^{-1})	SE	Distance swam (m)	SE	Dives (n)	Power (W kg^{-1})	SE
A	1.11	0.020	19.9	0.29	289	9.26	0.195
B	0.99	0.014	20.1	0.36	173	8.38	0.170
C	1.25	0.014	19.2	0.30	226	9.29	0.211
Mean	1.12	0.011	19.7	0.18		9.05	0.116

Table 3. Parameters used to calculate power input (W kg^{-1}) of 3 Humboldt penguins while swimming in a channel. Power input (P) was calculated according to Culik et al. (1996) and is best described by $P = av^3 + bv^2 + cv + RMR_{water}$, where v is swimming speed (m s^{-1}) and RMR_{water} is resting metabolic rate. Power input is the power required over the entire 'dive + surface' cycle. Differences between birds were not significant (p = 0.323)

Penguin	a	b	c	RMR_{water}	r^2
A	3.150	−5.990	5.150	6.88	0.93
B	3.612	−6.210	5.790	6.39	0.93
C	3.451	−6.371	5.643	5.24	0.90
All birds	3.541	−6.382	5.841	5.95	0.94

COT as a dimensionless variable (J [N m]$^{-1}$), which is obtained by dividing COT (in J [kg m]$^{-1}$) by earth acceleration (9.81 m s^{-1}). Here we prefer to use J (kg m)$^{-1}$ to simplify comparisons with the literature. COT in Humboldt penguins averaged 9.01 ± 0.09 J (kg m)$^{-1}$ (n = 688) and ranged from 13.41 ± 0.06 J (kg m)$^{-1}$ at 0.6 m s^{-1} (n = 7) to a minimum of 8.10 ± 0.03 J (kg m)$^{-1}$ at 1.4 m s^{-1} (n = 22). COT (Fig. 1) were significantly different (ANOVA, F = 1336.65; p < 0.001) between speed classes, being maximal at speed classes <0.9 and >2.0 m s^{-1} (Tukey test, p < 0.05).
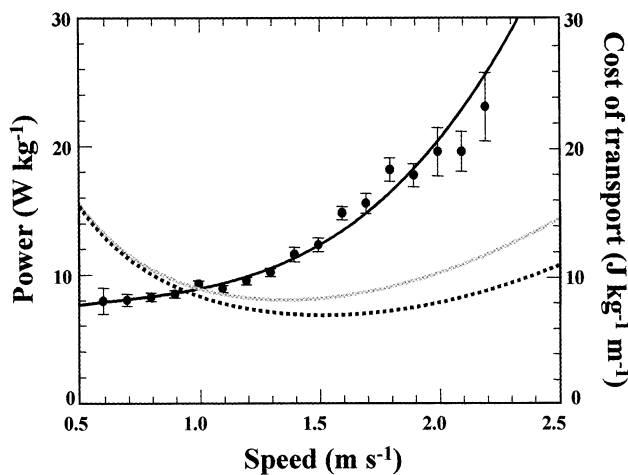

Fig. 1. *Spheniscus humboldti.* Power input (W kg^{-1}) in Humboldt penguins swimming at different speeds. Parameters of the equation describing the curve fit are given in Table 3. Bars show standard error of the means. Cost of transport (COT) of penguins in the channel (J [kg m]$^{-1}$, grey line) were fitted using COT = $(3.541v^3 − 6.382v^2 + 5.841v + 5.95)/v$ (n = 688, r^2 = 0.93). The dotted line is COT$_{cor}$ corrected for acceleration and deceleration in the swim channel (see more details in the text). The equation describing this curve fit is COT$_{cor}$ = $(2.954v^3 − 6.354v^2 + 5.818v + 5.95)/v$ (n = 688, r^2 = 0.92)

DISCUSSION

Resting metabolic rate in water

RMR$_{water}$ of Humboldt penguins in the channel (5.95 W kg^{-1} or 1.09 ml O$_2$ s^{-1}; water temperature [T_{water}] = 19°C) compares well to the value reported by Butler & Woakes (1984), who determined 0.993 ml O$_2$ s^{-1} for the same species at a water temperature of 18°C. Assuming a BMR (basal metabolic rate) for Humboldt penguins of 2.83 W kg^{-1} (Drent & Stonehouse 1971), RMR$_{water}$ corresponds to ca 2.1 × BMR. However, when compared to RMR$_{air}$ of 3.8 W kg^{-1} (measured during the active phase in normally fed Humboldt penguins within their thermoneutral zone; Luna-Jorquera 1997), RMR$_{water}$ is only 1.6 × RMR$_{air}$. This is quite low, as Bethge et al. (1997) reported that in little penguins *Eudyptula minor* RMR$_{water}$ at 10°C is 2.6 × RMR$_{air}$. Similarly, Culik & Wilson (1991) reported that mean RMR$_{water}$ of Adélie penguins (4°C) amounts to 2.2 × RMR$_{air}$. Rather than being species specific, however, these differences can probably be attributed to the effects of temperature and thermal insulation (Stahel & Nicol 1982). Mean water temperature around Pan de Azúcar Island, measured by free-ranging Humboldt penguins equipped with data-loggers (Luna-Jorquera & Culik 1999), was 14.6°C, but at the surface, water temperature ranged between 12 and 18°C, to which the effect of direct solar irradiation has to be added. Consequently, we propose that the value for RMR$_{water}$ reported here is applicable to the field situation in surface waters around Pan de Azúcar Island (26° 09′ S), during warm days.

Energy requirements during swimming

Culik et al. (1996) described 3 different methods for the calculation of O$_2$-consumption rates from experiments conducted in a channel. Because our objective in the present study was to obtain data on swimming energetics applicable to Humboldt penguins in the wild, we will discuss only the energy consumption during the entire surface + dive cycle.

The swim channel method both ensures controlled experimental conditions and allows voluntary diving by the penguins. However, artificial conditions during the experiments and the necessity for the birds to accelerate and decelerate repeatedly alter their behaviour and increase their energetic demands. For these reasons Culik et al. (1994a) suggested that swim-channel data be corrected for this effect (see below). However, swimming speed in the channel cannot be corrected. The penguins in the channel swam at an average speed of only 1.1 m s^{-1}, which is 35% slower than the mean of 1.7 m s^{-1} observed in travelling Hum-

boldt penguins at sea (Luna-Jorquera & Culik 1999). However, slow speeds were also observed by Culik et al. (1994a) and Bethge et al. (1997), in pygoscelid and little penguins during similar experiments. According to these authors, gentoo penguins *Pygoscelis papua*, Adélie penguins *Pygoscelis adeliae* and chinstrap penguins *P. antarctica* observed in a 21 m long swim channel swam 21, 32 and 35% slower than measured in the wild, respectively, whereas little penguins swam 80% slower.

The only data published on transport costs of Humboldt penguins during underwater swimming stem from Hui (1988). He determined a minimum COT of 13.4 J (kg m)$^{-1}$ for swimming speeds ranging from 0.5 to 1.26 m s^{-1}, a value which is 47% higher than ours for the same speed range. This discrepancy can be attributed to the methodology employed by Hui (1988) — a test cage pushed through the water by a boat — and the stress imposed on the birds because of the involuntary nature of the exercise. Nagy et al. (1984), using doubly labelled water and a speed meter attached to free-ranging African penguins *Spheniscus demersus*, and RMR-values derived from allometric equations, determined a mean COT of 15.5 J (kg m)$^{-1}$ at speeds of 2.0 m s^{-1}, or 55% higher than our measurement at the same speed. Besides additional COT imposed on the device-equipped birds by the frictional drag of the speed meters (cf. Culik et al. 1994b), the use of an allometric equation as opposed to actually measured values of RMR$_{water}$ may have led to the high estimate of swimming metabolism by Nagy et al. (1984).

During our experiments, Humboldt penguins swimming in the channel had to accelerate and decelerate once every 20 m, which they are unlikely to do in the wild (except while foraging), thereby incurring higher energetic costs (Culik et al. 1994a). In order to compensate for more than one initial acceleration, and to

estimate the energetic costs incurred by Humboldt penguins during travelling, the physical energy necessary for subsequent acceleration and deceleration (Pa, W kg^{-1}) prior to surfacing was subtracted from P_{dive}. $Pa = v^3 (mfS)^{-1}$, where v is swimming speed in m s^{-1}, m is muscle efficiency ($m = 0.25$ according to Schmidt-Nielsen 1993), f is flipper efficiency ($f = 0.4$ according to Oehme & Bannasch 1989), and S is the distance swam. The corrected data set was curve-fitted with a third-degree polynomial function to estimate corrected power input (P_{cor}):

$$P_{cor} = 2.954v^3 - 6.354v^2 + 5.818v + RMR_{water}\ (r^2 = 0.92)$$
(3)

where v is swimming speed (m s^{-1}). Using P_{cor}, we found that minimum corrected transport costs (COT$_{cor}$) are 6.81 ± 0.03 (n = 26) J (kg m)$^{-1}$ at a swimming speed of 1.5 m s^{-1}. This is 19% lower than minimum COT obtained from penguins swimming in the channel.

Minimum COT$_{cor}$ of Humboldt penguins (at 1.5 m s^{-1}) were between those of Adélie penguins (4.9 J [kg m]$^{-1}$ at 2.2 m s^{-1}) and gentoo penguins (7.6 J [kg m]$^{-1}$ at 1.8 m s^{-1}) (Culik et al. 1994a) (Table 4). In the much smaller little penguin, Bethge et al. (1997) found minimum COT of 11.1 J (kg m)$^{-1}$ at 1.8 m s^{-1}. Although minimum COT in the channel occured at 1.5 m s^{-1}, we measured that Humboldt penguins in the wild prefer to travel at 1.7 m s^{-1} (Luna-Jorquera & Culik 1999). Mean COT$_{cor}$ in travelling (1.7 m s^{-1}) Humboldt penguins is 7.0 ± 0.05 J (kg m)$^{-1}$, or only 3% higher than the minimum at 1.5 m s^{-1}. Because in the field Humboldt penguins sometimes travel much faster, reaching speeds >4.0 m s^{-1} (Luna-Jorquera & Culik 1999), we suggest that Eq. (3) be employed to calculate the corresponding energetic requirements at sea, if the birds' actual travelling speeds are known.

Table 4. Minimum power input (P_{cor}) and cost of transport (COT) calculated by assuming only one acceleration and subsequent sustained swimming speeds (Culik et al. 1994a), and aerobic dive limits (ADL) of penguins calculated from energy requirements during swimming. Sources: (1) Bethge et al. (1997), (2) Culik et al. (1994a), (3) Nagy et al. (1984), (4) Hui (1988), (5) Butler & Woakes (1984), and (6) this study

Species	Body mass (kg)	P_{cor} (W kg^{-1})	COT (J [kg m]$^{-1}$)	Speed (m s^{-1})	ADL (s)	Source
Eudyptula minor	1.2	20.0	11.1	1.8	44	1
Pygoscelis antarctica	3.8	8.9	3.7	2.4	130	2
P. adeliae	4.0	10.8	4.9	2.2	110	2
P. papua	5.5	13.7	7.6	1.8	93	2
Spheniscus demersus	3.2	31.0	15.5	2.0	38	3
S. humboldti	3.8	8.1–14.9	13.4	0.5–1.26	–	4
S. humboldti	4.6	–	–	–	136	5
S. humboldti	3.6	10.2	6.8	1.5	116	6

Aerobic dive limits

Prior to a dive, penguins store oxygen in arterial and venous blood, muscle tissue and air sacs (Kooyman 1989) and oxygen stores can be calculated from the oxygen-binding capacity of blood and muscle and oxygen saturation prior to a dive (Culik et al. 1994a). Because no data were available for Humboldt penguins, we assume here that their O_2 stores are comparable to those of other species. In pygoscelid penguins (mean of 4.4 ± 0.5 kg; range = 3.8 to 5.5 kg), total oxygen stores amount to 57 ml kg^{-1} in chinstrap penguins, 58.6 ml kg^{-1} in Adélie penguins and 63 ml kg^{-1} in gentoo penguins, with a mean of 59.5 ± 1.8 ml kg^{-1} (derived from data published by Culik et al. 1994a).

The aerobic dive limit (ADL) is defined as the maximum dive duration prior to which an increase in blood lactic acid concentration occurs (Gentry & Kooyman 1986). ADL can be estimated from: ADL = kOXY/P, where k is the conversion factor (20 J ml^{-1} O_2, see 'Results'), OXY are the total oxygen stores prior to a dive and P is the energy required for swimming. Correspondingly, aerobic dive distance is ADD = vADL, where v is swimming speed. Using minimum P_{cor} determined above (at 1.5 m s^{-1}) and OXY from pygoscelid penguins, we estimate that Humboldt penguins should be able to dive aerobically for 116 s and cover a distance of 174 m within that time, if swimming in a straight line without energy-consuming manoeuvres. This value is consistent with the results obtained using dive recorders in free-ranging Humboldt penguins (Luna-Jorquera & Culik 1999), which showed that 95 % of all dives were shorter than 90 s. Only 1 % of all dives recorded in the wild exceed the aerobic dive limit calculated here. Our result also compares well with that of Butler & Woakes (1984), who calculated that Humboldt penguins diving at a rate of 5.46 W kg^{-1} would have an ADL of 136 s, a value only 17 % higher than our estimate.

In a previous study on the foraging behaviour of breeding Humboldt penguins using VHF telemetry (Culik et al. 1998), we calculated the running mean dive and surface duration (Horning 1992) of a series of dives and determined the behavioural aerobic dive limit (bADL). Surprisingly, bADL, i.e. the threshold in dive duration followed by a steep increase in surface pause times, was reached in dives lasting 50 s, or only ca 43 % of ADL determined above. This apparent discrepancy could suggest that oxygen utilisation in foraging birds is only in part governed by metabolic requirements of straight-line swimming (i.e. by P_{cor} above). Indeed, frequent acceleration and deceleration and manoeuvres required to pursue prey, as well as to investigate foraging areas, and the effects of buoyancy may lead to increased oxygen consumption and perhaps lactate production (Culik et al. 1994a) in wild Humboldt penguins. As a consequence, surface pauses required for the replenishment of oxygen reserves and to ensure metabolic turnover of lactic acid have to be extended in wild birds diving for longer than 50 s.

To remain at sea or to rest on land?

Humboldt penguins often rest at sea for extended periods. Foraging birds sometimes remain at sea overnight (Culik & Luna-Jorquera 1997b, Luna-Jorquera & Culik 1999) and in winter the penguins are capable of migrating as far as 600 km to the north of their colony, reaching the coast only at intervals of approx. 15 d (Culik & Luna-Jorquera 1997a). What are the energetic implications of this behaviour? From RMR-measurements in the channel, thermal conductance in water was calculated as 0.2975 W (kg °C)$^{-1}$ (at T_a 19°C and assuming a T_b of 39°C; Drent & Stonehouse 1971, Luna-Jorquera et al. 1997), or ca 2× the calculated thermal conductance (0.15 W [kg °C]$^{-1}$) below the thermoneutral zone in air (Luna-Jorquera 1997), reflecting the high rate of heat loss in water. From the equation of thermal conductance (C, in W [kg °C]$^{-1}$):

$$C = P/(T_b - T_a) \qquad (4)$$

where P is power input (W kg^{-1}), T_b is body temperature (°C) and T_a is ambient or seawater temperature (°C); it is possible to derive RMR_{water} at different water temperatures (Schmidt-Nielsen 1993). At the maximum temperatures recorded in surface waters around Pan de Azúcar Island, we estimate that RMR_{water} is comparable to the value determined in the channel. However, at water temperatures of 12°C, RMR_{water} should increase by 35 %.

Our field data (Culik & Luna-Jorquera 1997b, Luna-Jorquera & Culik 1999) show that during daylight, penguins swim actively with only short resting periods at the surface. By analogy to African penguins *Spheniscus demersus*, whose body temperature rises when they swim, and sinks again when they rest at the surface (Wilson & Grémillet 1996), we would expect thermoregulatory costs in active penguins to be covered by waste heat from locomotion (Hind & Gurney 1997). However, since Humboldt penguins do not actively forage at night (Luna-Jorquera & Culik 1999), which is supported by all the evidence currently available for penguins of the genus *Spheniscus* (see Wilson 1995), we would expect thermoregulatory costs to rise at that time. For birds feeding chicks, the optimal energy solution lies in balancing the costs of either (1) returning to the breeding island for the night and travelling back to the feeding grounds in the morning or (2) incurring

increased thermoregulatory costs associated with resting at sea overnight.

Assuming a constant seawater temperature of 19°C, the energetic costs for Humboldt penguins resting at sea correspond to RMR_{water} (see above) or ca 77 kJ h^{-1} bird^{-1} (104 kJ h^{-1} at 12°C) or 616 kJ bird^{-1} for an 8 h night at sea (832 kJ at 12°C). During an equivalent period on land a single Humboldt penguin would expend only ca 394 kJ (3.8 W kg^{-1} [RMR on land] × 3.6 kg × 3600 s × 8 h; Luna-Jorquera 1997). The difference between these 2 values can be translated in terms of distance travelled in order to determine whether a foraging adult would energetically benefit by remaining at sea or returning to land overnight. Since swimming costs are ca 12 W kg^{-1} (P_{cor} for typical travelling swim speeds of 1.7 m s^{-1}), the 222 kJ difference would allow the penguin to swim for 222 000/(12 × 3.6) or 5138 s, during which time the penguin could travel roughly 8.7 km in a straight line. This value must be divided by 2 (to and from feeding grounds) in order to derive the approximate range. Thus, at water temperatures of 19°C, we might expect Humboldt penguins to show a tendency to remain at sea overnight if foraging areas are 4 km or more distant from the island. In colder waters (12°C), all other things being equal, birds should decide to return to land if closer than approximately 9 km to the coast. This approach is obviously simplistic, because it does not take into account parameters such as satiation, prey availability, chick-feeding frequency, or convoluted travelling routes (Culik et al. 1998), but it nevertheless highlights one energetic aspect acting on penguins foraging at sea.

Food requirements during foraging and migration

In a previous study on the foraging behaviour of Humboldt penguins we used time-depth-speed recorders (MK6, Wildlife Computers), to determine (amongst others parameters) time spent at the surface and underwater and the swimming speed of 12 penguins rearing chicks (Luna-Jorquera & Culik 1999). Mean speed for travelling and foraging dives were 1.7 and 1.9 m s^{-1}, respectively (Luna-Jorquera 1999). Porpoising was considered to be negligible. Estimating the energy required for straight-line travelling dives using P_{cor} above (Eq. 3) yields 12 W kg^{-1}, whereas using P_{dive} (Eq. 1) for foraging dives with naturally occurring stop and go activity and manoeuvres yields 18.3 W kg^{-1}.

The general equation for this model allows an approximation of field metabolic rate (FMR, J kg^{-1}) of Humboldt penguins at sea depending on T_{water} (°C) as well as on the duration of resting (t_{rest}, s) foraging (t_{forage}, s) and travelling (t_{travel}, s):

$$FMR = 5.95 \times 0.05 \times (T_b - T_a) \times t_{rest}$$
$$+ 12 \times t_{travel} + 18.3 \times t_{forage} \qquad (5)$$

where T_b is body temperature (°C), and T_a is ambient or seawater temperature (°C) for temperatures between 22 and 6°C. RMR_{water} is 5.95 W kg^{-1} (at 19°C) and can be converted to other temperatures via 0.05 × $(T_b - T_a)$.

The main prey of Humboldt penguins is the anchovy, with a mean energy content of 5.93 kJ g^{-1} wet mass (Fitzpatrick et al. 1988). Assuming an assimilation efficiency of penguins feeding on anchovy of 77 % (Guerra 1992), FMR converts to food requirements (FI, g) as:

$$FI = 0.218 \times FMR \times M \times 10^{-3} \qquad (6)$$

where M is penguim body mass (kg).

From these general equations, foraging and migratory costs can be converted to approximate fish requirements if more data on the behaviour of Humboldt penguins at sea become available.

From Luna-Jorquera & Culik (1999) we know that breeding Humboldt penguins (M = 3.6 kg) foraging around Pan de Azúcar island spend on average 0.8 ± 0.5 h d^{-1} travelling (with mean energetic costs amounting to 124 kJ) and 3.7 ± 2.0 h foraging (mean energetic cost of 877 kJ). Activities at sea therefore add up to 1000 kJ d^{-1}. Because the birds spend on average 7.2 h d^{-1} resting at the surface, this yields additional energetic demands of 555 kJ d^{-1} (at T_{water} = 19°C) and the energy used during a foraging trip amounts to a total of 1555 kJ d^{-1}.

From Eq. (6), a single breeding Humboldt penguin must therefore consume ca 340 g anchovies d^{-1} just to balance its foraging costs at sea. For the penguin population of Pan de Azúcar Island (1750 ind.), this amounts to foraging costs of ca 600 kg anchovies d^{-1}, to which other costs, such as incubation, resting on land and chick feeding, have to be added. Behavioural data recorded on Humboldt penguins during weak (Culik & Luna-Jorquera 1997b) and strong (Culik et al. 2000) El Niño events suggests, however, that these demands at times exceed food availability, leading to breeding failure and emigration of the birds.

paration. Carlos Guena and the Instituto de Investigaciones Oceanológicas, Universidad de Antofagasta, provided laboratory space, the pen in which the penguins were housed and an experimental pool, where the swim channel was installed.

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