Onshore energetics in penguins: Theory, estimation and ecological implications

Lewis G. Halsey [a,*], Craig R. White [a], Andreas Fahlman [b], Yves Handrich [c], Patrick J. Butler [a]

[a] Centre for Ornithology, School of Biosciences, University of Birmingham, Edgbaston B15 2TT UK
[b] Department of Zoology, University of British Columbia, 6270 University Blvd. Vancouver, BC, Canada V6T 1Z4
[c] Institut Pluridisciplinaire Hubert Curien (IPHC), UMR 7178 CNRS-ULP, Département Ecologie, Physiologie et Ethologie (DEPE),
23 rue Becquerel, F-67087 Strasbourg Cedex 02, France

Abstract

Penguins are known to have high pedestrian locomotory costs in comparison to other cursorial birds, but the ecological consequences of this difference have received limited attention. Here we present a method for the accurate estimation of onshore energetics based on measurements of body mass, simple morphometrics and distance moved. The method is shown to be similarly accurate to other field-based estimates of energy expenditure, but has the advantage of logistical simplicity. King penguins spend 30–50% of their time ashore and may walk distances of several kilometres to and from their breeding colonies. However, in such cases the total energetic cost of pedestrian locomotion is estimated to be only 1.0% of the energy expended whilst ashore. Thus, despite a high instantaneous cost, pedestrian locomotion is a small and possibly negligible component of total energy turnover in king penguins.
© 2007 Elsevier Inc. All rights reserved.

1. Introduction

King penguins (*Aptenodytes patagonicus*) spend a large proportion of their breeding cycle ashore (about 30% in successfully breeding birds and 50% in unsuccessful breeders (Descamps et al., 2002)). While ashore, they undergo prolonged fasts where changes in body mass can be substantial (around 25% for a 29 day fast during courting and first incubation shift by the male (Gauthier-Clerc et al., 2001)). These changes have a large effect on metabolic rate because they reflect changes in nutritional status (Fahlman et al., 2006). While ashore, king penguins spend the majority of their time resting (Challet et al., 1994; Dewasmes et al., 2001). Fahlman et al. (2006) showed that body mass and morphometric measures of king penguins accurately estimate resting $\dot{V}_{O_2}$ ($\dot{V}_{O_2}$ rest), presumably because these metrics correlate well with the nutritional condition and structural size of the bird. Thus, once several easily measured

morphometric characteristics from an adult individual have been obtained (which do not change with body mass), an estimate of $\dot{V}_{O_2}$ rest of a king penguin at any stage of a fast can be derived by simply weighing the bird.

Another energetic cost for king penguins ashore is incurred through pedestrian locomotion. Having returned to shore after a foraging trip at sea, king penguins walk to and within their colony. Several studies have described the particularly high costs of pedestrian locomotion in penguins compared to that of other species of cursorial birds (Pinshow et al., 1976, 1977; Dewasmes et al., 1980; Baudinette and Gill, 1985). While many studies have recognised the potential importance of this high cost to the energy budgets of penguins (e.g. Gales and Green, 1990; Miyazaki and Waas, 2003; Walker et al., 2004), only two attempts have been made to quantify walking costs in an ecological context. The earlier of these two studies concluded that emperor penguins (*Aptenodytes forsteri*) walking 200 km (from the sea to the rookery and back) require up to 15% of the energy reserves of a breeding male initially weighing 35 kg (Pinshow et al., 1976). This equates to around 4% of the total energy expended over a breeding season (assuming a total

* Corresponding author. Tel.: +44 121 414 3822; fax: +44 121 414 5925.
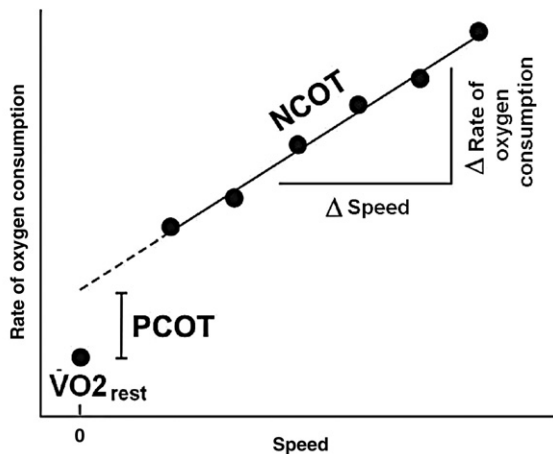E-mail address: l.g.halsey@bham.ac.uk (L.G. Halsey).

Fig. 1. Relationship between rate of oxygen consumption ($\dot{V}_{O_2}$) and speed in king penguins walking on a treadmill. Net cost of transport (NCOT) is calculated as the slope of the relationship relating $\dot{V}_{O_2}$ to speed for speeds greater than zero. Postural cost of transport (PCOT) is calculated by subtracting resting $\dot{V}_{O_2}$ ($\dot{V}_{O_2}$ rest) from the extrapolated y-intercept of relationship describing NCOT.

distance walked of 400 km over 9.5 months; based on data from Pinshow et al. (1976) and Nagy et al. (2001). In contrast, the latter of these two studies concluded that royal penguins (*Eudyptes schlegeli*), which walked a total distance of 63 km during 22 trips to and from the colony during the breeding season, would expend only 0.006% of the total energy expenditure over the breeding season on pedestrian locomotion (Hull and Wilson, 1996).

However, in the Hull and Wilson (1996) study, walking costs were not measured but rather were estimated from data for other species. In the study of Pinshow et al. (1976), measurements of pedestrian costs for emperor penguins were measured directly, although only at a single body mass. Therefore they may not represent changes in costs of pedestrian locomotion arising from the large body mass losses incurred during an extended fast in this species (Williams, 1995). Wilson and Scolaro (1999) cast doubt on such estimations of walking costs in penguins and no validation of the predictive accuracy of these estimates has been undertaken. Thus, it is not clear if the apparent difference between emperor and royal penguins in terms of the proportion of overall energy expenditure used for walking is genuine, or arises from methodological differences. Accurate, validated estimates of pedestrian costs in the field for additional species of penguin are required in order to determine if the high instantaneous costs of locomotion in penguins result in important ecological costs.

An accurate estimate of pedestrian locomotion in king penguins is possible by partitioning the oxygen cost of this activity and estimating each of these elements separately. In most species that use pedestrian locomotion, $\dot{V}_{O_2}$ is a linear function of speed, where values of speed do not include 0 (e.g. Schmidt-Nielsen, 1972; Taylor et al., 1982). Thus, the slope of the regression is a speed-independent quantity (the net cost of transport, NCOT; mL O_2 m^{-1}) that is the amount of oxygen, above that represented by the y-intercept, required by an animal to move a unit distance. The extrapolated y-intercept of this line back to speed=0 is often higher than $\dot{V}_{O_2}$ rest (Taylor et al.,

1970). The total cost of pedestrian locomotion (the gross cost of pedestrian transport; GCOT; mL O_2 m^{-1}) can therefore be calculated as the sum of three costs: (1) $\dot{V}_{O_2}$ rest multiplied by the time spent walking, (2) the cost associated with the elevated y-intercept calculated by multiplying the difference between resting $\dot{V}_{O_2}$ and the y-intercept by time, and (3) the cost of moving the body mass of the animal, calculated by multiplying NCOT by distance (Fig. 1).

Visual inspection of data published in Fahlman et al. (2004) suggests that the linear regressions of $\dot{V}_{O_2}$ against speed for king penguins in different nutritional states all have a similar gradient. In the present study, we show that this relationship is statistically similar across years as well. Thus it can be concluded that NCOT is independent of body mass and speed in king penguins and is constant within and between birds. The elevated y-intercept of the regression of $\dot{V}_{O_2}$ against speed was originally labelled a 'postural' effect (Schmidt-Nielsen, 1972), implying that it represents the energetic cost of maintaining the body in a locomotory posture. In the current study, we show that this 'postural' cost of transport (PCOT) can be estimated in king penguins across multiple birds from their body mass. Given that $\dot{V}_{O_2}$ rest can be estimated accurately in king penguins from body mass and morphometrics (Fahlman et al., 2006), it is possible to derive an estimate of GCOT in this species from these same measurements.

In the present study, a prediction equation using body mass and morphometrics was derived from cost of transport data measured in king penguins using a treadmill and respirometer system. A second group of birds were then used to validate the equation. We show that once the body mass and structural size of a king penguin are known, GCOT can be accurately estimated in the field by an observer with only a stopwatch and distance measuring wheel (or some other reliable method for estimating the distance travelled by the penguin). GCOT can also be estimated from data on distances walked by king penguins if walking speed is known or can be estimated. We then demonstrate the utility of these
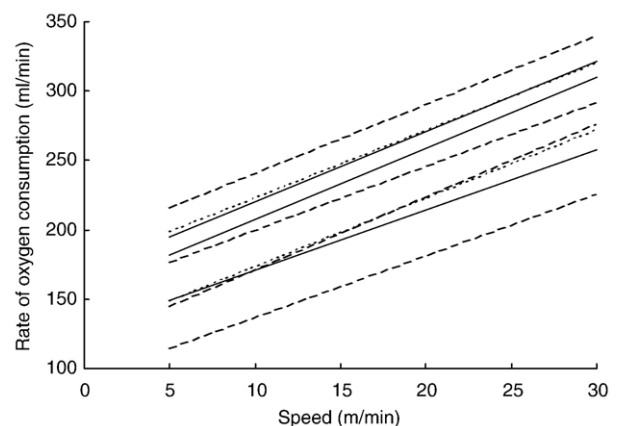

Fig. 2. $\dot{V}_{O_2}$ against speed for king penguins walking on a treadmill in various nutritional conditions in three field seasons, $N=22$. The slope of each line represents the net cost of transport (NCOT) for that nutritional condition and year. The long dashed lines represent various nutritional conditions for birds in the 2002–2003 field season, the full lines represent nutritional conditions in the 2003–2004 field season and the stippled lines represent the 2004–2005 season.
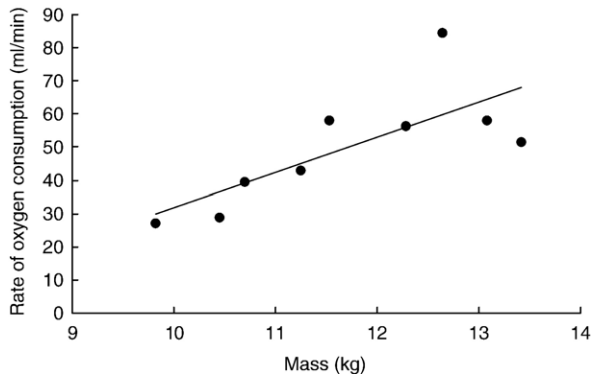
Fig. 3. Mean postural cost against mean mass for king penguins in various nutritional conditions in three field seasons, $N=22$. The line is described by $y=10.65x-74.80$. R^2 of the regression line is 0.56, $P=0.02$.

estimations for studying king penguin ecology. The estimations are applied to an investigation of whether the high costs of pedestrian transport means that those birds living in colonies inland from the coast experience high energy costs travelling to and from the sea.

2. Materials and methods

Ethical approval for all procedures used in the present study was granted by the ethics committee of the French Polar Research Institute (IPEV) and of the Ministère de l'Environnement. The experiments were carried out on Possession Island (Crozet Archipelago 46°25′ S, 51°45′ E) during three field seasons over the Austral summers 2002–2003, 2003–2004, and 2004–2005. Some of the data used in the present study from the first two field seasons have been published previously (Fahlman et al., 2004, 2006). Data were analysed from a total of 22 male king penguins. All animals were caught in the colony at La Baie du Marin, soon after returning from a foraging trip, at which point they were in the early phases of courtship. They were all assumed to have empty stomachs at this point (Gauthier-Clerc et al., 2000) and thus to be post-absorptive. Periodically during the 3 years encompassing the study, the weather conditions at the colony were recorded (Vantage Pro Weather Station, Davis Instruments, California, U.S.).

The birds undertook treadmill experiments at various stages during a fasting period on shore after their last foraging trip at sea, and hence at various body masses. Each stage during each field season is denoted as a separate nutritional condition. $\dot{V}_{O_2}$ rest, along with $\dot{V}_{O_2}$ at various treadmill speeds, was measured within a respirometer at a thermoneutral temperature (range: 5–16 °C). The length of the beak (L_{beak}, mm), flipper ($L_{flipper}$, mm) and foot (L_{foot}, mm) were measured to obtain morphometrics of each bird (see Fahlman et al., 2006 for details). These measurements are known to be highly repeatable both within and between experimenters (Fahlman et al., 2006).

2.1. Measuring $\dot{V}_{O_2}$ on the treadmill

At the start of each respirometry experiment, the bird was placed in the respirometer chamber and allowed to rest for a minimum of 1 h to obtain a stable value of $\dot{V}_{O_2}$ that was taken to represent $\dot{V}_{O_2}$ rest. The bird was then walked at 5 different treadmill speeds (0.3, 0.7, 1.0, 1.5 and 1.8 km h^{-1}) in a randomised order, with at least 20 min rest between each speed. The bird was walked at each speed until a steady state of $\dot{V}_{O_2}$ was obtained for a minimum of 3 min, which usually took between 12 and 20 min. Rates of oxygen consumption and carbon dioxide production were calculated using standard equations (Withers, 1977) as described in Froget et al. (2001). Details of this protocol are provided in Froget et al. (2001) and Fahlman et al. (2004).

2.2. Statistical analysis

Part of the 2002–2003 and 2003–2004 field season data have previously been used to derive a prediction equation of $\dot{V}_{O_2}$ rest (Fahlman et al., 2006). The same data sets were used in the present study to derive a constant value for NCOT and the prediction equation for PCOT. Estimates of $\dot{V}_{O_2}$ rest, PCOT and NCOT were then obtained from the body mass and morphometrics data of the birds from the 2004–2005 field season, for two nutritional conditions; fed (mean body mass: 13 ± 0.3 kg) and fasted (mean body mass: 10.6 ± 0.1 kg; mean number of days fasted $=18\pm1$). In each of these conditions, the three estimates were also combined to produce an estimate of GCOT. These were then compared to respirometry measurements for the same birds.

NCOT in mL O$_2$ m^{-1} was determined from data on $\dot{V}_{O_2}$ against speed. For each nutritional condition and bird, the same number of data points for $\dot{V}_{O_2}$ against speed was obtained, (not including 0 i.e. $\dot{V}_{O_2}$ rest; $N=5$). A least sums of squares best fit regression was conducted on the resulting data for each individual in each nutritional condition. The slope of the line in each

Table 1
Mean estimates of the gross cost of transport (GCOT)±SE over 25 m for fasted and fed king penguins

Walking speed (km/h)	Fasted condition			Fed condition		
	Mean estimated V_{O_2} over 25 m (mL)	Mean measured V_{O_2} over 25 m (mL)	Error of the mean estimate (%)	Mean estimated V_{O_2} over 25 m (mL)	Mean measured V_{O_2} over 25 m (mL)	Error of the mean estimate (%)
0.3	750.7±18.1	711.9±55.4	5.4	1023.6±26.7	998.5±17.3	2.5
0.7	391.1±7.7	377.0±26.4	3.7	507.9±11.4	481.9±21.1	5.4
1.0	310.6±5.4	311.9±23.7	−0.4	392.5±8.0	399.2±16.8	−1.7
1.5	247.7±3.6	251.0±30.6	−1.3	302.3±5.3	286.4±12.2	5.6
1.8	226.4±3.0	214.7±4.8	5.4	271.7±4.4	270.3±11.0	0.5

Data are for 7 birds from the 2004–2005 field season.

case represents NCOT. To test for homogeneity of regression slopes between nutritional conditions and years, the following ANOVA model was tested: $\dot{V}_{O_2}$ = Speed + Mass + Speed * Mass + Condition(Season) + Condition * Speed(Season) + Season + Season * Speed + Individual(Season)[random].

PCOT was calculated by extrapolating the slope representing NCOT back to the y axis, and then subtracting $\dot{V}_{O_2}$ rest from the estimated y-intercept (Fig. 1). To test for a relationship between PCOT and body mass, the following ANCOVA model was run: $\dot{V}_{O_2}$ = Speed + Mass + $\dot{V}_{O_2}$ rest + Individual[random]. Because the extrapolated y-intercept is sensitive to the slope of NCOT, PCOT was estimated from the slope of NCOT averaged across all the birds in each nutritional condition. Thus a single value of PCOT was calculated from the respirometry data for each nutritional condition and these were then regressed against mean body mass for each nutritional condition to derive the prediction equation.

3. Results

To investigate the accuracy of the prediction equation for $\dot{V}_{O_2}$ rest derived in Fahlman et al. (2006) for the 2004–2005 birds, the mean estimate of $\dot{V}_{O_2}$ rest was compared to the mean of the measured values of $\dot{V}_{O_2}$ rest, in both the fed and fasted conditions. Estimates of $\dot{V}_{O_2}$ rest in mL O_2 min^{-1} for each bird were determined from body mass, L_{beak}, $L_{flipper}$ and L_{foot} using Eq. (1) from Fahlman et al. 2006):

$$\log(\dot{V}_{O_2}) = 1.74 + 1.39 \cdot \log(\text{body mass}) \\ -3.98 \cdot 10^{-3} \cdot PC_1 - 6.85 \cdot 10^{-3} \cdot PC_2 \tag{1}$$

where $PC_1 = 0.49 \cdot L_{beak} + 0.59 \cdot L_{foot} + 0.64 \cdot L_{flipper}$ and $PC_2 = 0.84 \cdot L_{beak} - 0.52 \cdot L_{foot} - 0.16 \cdot L_{flipper}$.

The error of the estimate ([measured − estimated]/measured * 100) of mean $\dot{V}_{O_2}$ rest was −9.7% in the fasted condition and −0.2% in the fed condition.

The results of the ANCOVA indicated a significant main effect of speed on $\dot{V}_{O_2}$ ($P<0.001$) but the interaction terms indicated no significant effect of nutritional condition or field season ($P=0.77$ and $P=0.89$, respectively). The range of mean slopes for the nutritional conditions were 4.343–5.260 mL O_2 m^{-1}; Fig. 2. This shows that NCOT is body mass independent and furthermore, does not vary from season to season. The NCOT estimated from the ANCOVA was 4.88 ± 0.24 mL O_2 m^{-1}. ANCOVA showed that body mass was a significant predictor of $\dot{V}_{O_2}$ ($P<0.001$) and since $\dot{V}_{O_2}$ rest was also included as a covariate in the analysis, it can be concluded that body mass is significantly related to PCOT. The resultant prediction equation derived from a regression of mean PCOT against mean body mass for each nutritional condition is the following (Fig. 3):

$$\text{PCOT} = 10.63 * \text{body mass} - 72.52 \tag{2}$$

Using mean body mass, a mean value of PCOT in mL O_2 min^{-1} was estimated for the two nutritional conditions (fasted: 40.2 ± 1.4; fed: 66.3 ± 2.9).

By combining Eqs. (1) and (2) and including the coefficient for NCOT, the following equation was produced that estimates GCOT in king penguins from body mass and three morphometric measurements:

$$\text{GCOT} = \dot{V}_{O_2}\text{rest(Eq.1)} + \text{PCOT(Eq.2)} \\ + \text{NCOT(coefficient)}$$

$$\text{GCOT} = 1.74 + 1.39 \cdot \log(\text{body mass}) - 3.98 \cdot 10^{-3} \cdot PC_1 \\ -6.85 \cdot 10^{-3} \cdot PC_2 + 10.63 \cdot \text{body mass} \tag{3} \\ -72.52 + (1/\text{Speed} \cdot 4.88)$$

For each of the two nutritional conditions and at each value of speed, estimated and measured GCOT over 25 m, averaged across all birds, are reported. The percentage error of each mean estimate was calculated. These values are shown in Table 1. The mean estimate errors ranged between −5.4 and 1.3% in the fasted condition and −5.6 and 1.7% in the fed condition.

4. Discussion

The accuracy of the estimates of $\dot{V}_{O_2}$ rest across birds using Eq. (1) is comparable to those reported by Fahlman et al. (2006); 7.8%. The accuracy of predicting mean GCOT across several king penguins during treadmill walking, using body mass and morphometric measures (Eq. (3)), is comparable to that of the heart rate technique (Froget et al., 2001; Butler et al., 2004; Fahlman et al., 2004), particularly given that in the present study, a different set of birds was used to validate the prediction equation from those used to derive it.

4.1. Applicability of equations in the field

For king penguins, walking on a treadmill does not perfectly simulate walking in the wild, particularly within the colony where king penguins typically walk with a slightly adjusted body posture as they attempt to avoid territorial conspecifics. Probably the main additional factors in the field that might influence GCOT are walking on a gradient, the effects of wind and the effects of ambient temperatures outside of the thermoneutral zone. Full and Tullis (1990) provide a review of the increases in walking costs as gradient increases in a wide range of animals. They conclude that within a low range of inclines (around 0 to 5°), there is not a clear correlation between costs and gradient. This has been shown specifically in four bird species (Marabou storks, (Bamford and Maloiy, 1980); quail, (Warncke et al., 1988); black browed albatross (Kabat et al., in press). At Baie du Marin on Possession Island, around 80% of the king penguins are present in an area of the colony that represents only a negligible elevation from the front of the beach (Halsey pers. obs.). A further 10% of the birds are present in areas where the gradient to reach them from the seashore averages 2–3°. Thus at this colony at least, the vast majority of birds are walking on flat or nearly flat ground whilst ashore.

The wind velocities at many of the locations where king penguins breed are regularly very high (e.g. maximum speed recorded in November 2004 at Baie du Marin, Possession Island was 23.2 m s^{-1}, which is equivalent to a severe gale on the Beaufort scale). Strong winds are likely to affect the costs of locomotion in penguins. However, the error introduced into the estimations will be limited by the fact that the birds are as likely to be walking as often with the wind as against it and tend to reduce their frequency of walking when wind speeds are high (Halsey pers. obs.). Furthermore, at Baie du Marin at least, there are often periods of low to negligible winds, for example in November 2004 the average wind speed was around 5 m s^{-1}.

The lower critical temperature for king penguins is −5 °C (Froget et al. 2002), while ambient air temperatures at Crozet are rarely below −2 °C close to sea level (Météo France). Thermal costs to compensate for low temperatures probably therefore rarely add to the energetic demands on king penguins. Finally, while the equation cannot validly be used to estimate costs at speeds greater than 1.8 km h^{-1}, king penguins rarely if at all walk faster than this in the field.

Thus, it seems reasonable to conclude that the high degree of accuracy of Eq. (3) in estimating the cost of pedestrian walking in king penguins on a treadmill is likely to extend to the field. As such, the application of Eq. (3) represents a logistically simple way for fieldworkers to record accurate mean GCOT in king penguins. Furthermore, king penguins spend the majority of their time in the colony either resting or sleeping (Challet et al., 1994) and Eq. (1) provides an accurate estimate of $\dot{V}_{O_2}$ rest. Thus these two equations together allow simple estimates of the overall energetic costs of adult king penguins ashore, either directly from field observations or from analysis of recorded behavioural data.

4.2. Applying estimations of $\dot{V}_{O_2}$ rest and GCOT: how ecologically important is the cost of walking for king penguins?

While pedestrian locomotion is undertaken by king penguins far less frequently than resting and sleeping, the cost of walking for penguins is known to be particularly high (Pinshow et al., 1976; Dewasmes et al., 1980; Hull, 2000; Griffin and Kram, 2000). The modal range of walking speeds of king penguins is about 0.3 to 0.4 m s^{-1}, which also appears to be the most comfortable walking speed on the treadmill (Halsey pers. obs.). This is similar to, though slightly slower than, the modal speed of about 0.5 m s^{-1} observed for emperor penguins (Dewasmes et al., 1980; Pinshow et al., 1976) and indeed, animals in general (Full and Tullis, 1990). The energy cost incurred by king penguins while walking at 0.3 m s^{-1} is approximately 2 times higher than when resting.

The largest king penguin colony in the world is located on Pig Island in the Crozet Archipelago (46°25′ S, 51°45′ E). The colony is inland by approximately 1.5 km from the east side of the island and is approximately 700 m wide, from east to west (Guinet et al., 1995). Thus, penguins have to walk between 1.5 and 2.2 km inland to reach their desired position in the colony. The front of the colony is about 100 m above sea level (Guinet

et al., 1995), so the average gradient of the ground upon which the penguins walk from the shoreline to the colony is only 3.8°. Assuming that the birds walk at an average speed of 0.3 m s^{-1}, the metabolic cost to walk 2 km from the shoreline to the centre of the colony for a typical king penguin of average structural size and weighing 13 kg (i.e. it has recently finished feeding at sea) is about 31 L O$_2$. The cost to walk from the centre of the colony to the shoreline for the same king penguin having fasted to 10 kg is about 23 L O$_2$.

However, the same 13 kg penguin that rests continuously for 24 h will consume about 163 L O$_2$, whilst at 10 kg that penguin will consume about 113 L O$_2$. Assuming that king penguins are resting while in the colony, then over a 20 day fast they will consume approximately 2750 L O$_2$ (assuming a mean mass of 11.5 kg). Thus birds that breed at Pig Island and walk 2 km to and from the shoreline will incur approximately only a 1.0% increase in O$_2$ consumption during a 20 day sojourn ashore compared to birds that walk a negligible distance from the sea to their location in a colony. This latter scenario is mostly the case at La Baie du Marin, Possession Island (the colony being present around a river mouth). Therefore, despite the high instantaneous costs of pedestrian transport in king penguins, and the fact that some king penguins reside in colonies inland from the coast, or that they sometimes come ashore many kilometres from their coastal colony (e.g. the king penguin colony at Ratmanoff beach, Kerguelen Archipelago; Handrich pers. obs.), nevertheless the energetic costs entailed by travelling to and from such colonies are small. As such, walking in king penguins may not be subject to selection pressures (Angelier et al., 2006).

Acknowledgements

References

Angelier, F., Barbraud, C., Lorméé, H., Prud'homme, F., Chastel, O., 2006. Kidnapping of chicks in emperor penguins: a hormonal by-product. J. Exp. Biol. 209, 1413–1420.

Bamford, O.S., Maloiy, G.M.O., 1980. Energy metabolism and heart rate during treadmill exercise in the Marabou stork. J. Appl. Physiol.: Respir., Environ. Exercise Physiol. 49, 491–496.

Baudinette, R.V., Gill, P., 1985. The energetics of 'flying' and 'paddling' in water: locomotion in penguins and ducks. J. Comp. Physiol. 155, 373–380.

Butler, P.J., Green, J.A., Boyd, I.L., Speakman, J.R., 2004. Measuring metabolic rate in the field: the pros and cons of the doubly labelled water and heart rate methods. Funct. Ecol. 18, 168–183.

Challet, E., Bost, C.-A., Handrich, Y., Gendner, J.-P., Le Maho, Y., 1994. Behavioural time budget of breeding king penguins (*Aptenodytes patagonicus*). J. Zoology (London) 233, 669–681.

Descamps, S., Gauthier-Clerc, M., Gendner, J.-P., Le Maho, Y., 2002. The annual breeding cycle of unbanded king penguins *Aptenodytes patagonicus* on Possession Island (Crozet). Avian Sci. 2, 1–12.

Dewasmes, G., Le Maho, Y., Cornet, A., Groscolas, R., 1980. Resting metabolic rate and cost of locomotion in long-term fasting emperor penguins. J. Appl. Physiol.: Respir., Environ. Exercise Physiol. 49, 888–896.

Dewasmes, G., Côté, S.D., Le Maho, Y., Groscolas, R., Robin, J.P., Vardon, G., Libert, J.P., 2001. Effects of weather on activity and sleep in brooding king penguins (*Aptenodytes patagonicus*). Polar Biol. 24, 508–511.

Fahlman, A., Handrich, Y., Woakes, A.J., Bost, C.-A., Holder, R.L., Duchamp, C., Butler, P.J., 2004. Effect of fasting on the VO2–fH relationship in king penguins, *Aptenodytes patagonicus*. Am. J. Physiol. 287, R870–R877.

Fahlman, A., Halsey, L.G., Butler, P.J., Jones, D.R., Schmidt, A., Durand, S., Froget, G., Bost, C.A., Woakes, A.J., Duchamp, C., Handrich, Y., 2006. Accounting for body condition improves allometric estimates of resting metabolic rates in fasting king penguin, *Aptenodytes patagonicus*. Polar Biol. 29, 609–614.

Froget, G., Butler, P.J., Handrich, Y., Woakes, A.J., 2001. Heart rate as an indicator of oxygen consumption: influence of body condition in the king penguin. J. Exp. Biol. 204, 2133–2144.

Froget, G., Handrich, Y., Le Maho, Y., Rouanet, J.-L., Woakes, A.J., Butler, P.J., 2002. The heart rate/oxygen consumption relationship during cold exposure of the king penguin: a comparison with that during exercise. J. Exp. Biol. 205, 2511–2517.

Full, R.J., Tullis, A., 1990. Energetics of ascent: insects on inclines. J. Exp. Biol. 149, 307–317.

Gales, R., Green, B., 1990. The annual energetics cycle of little penguins (*Eudyptula minor*). Ecology 71, 2297–2312.

Gauthier-Clerc, M., Le Maho, Y., Clerquin, Y., Drault, S., Handrich, Y., 2000. Penguin fathers preserve food for their chicks. Nature 408, 928–929.

Gauthier-Clerc, M., Le Maho, Y., Gendner, J.-P., Durant, J., Handrich, Y., 2001. State-dependent decisions in long-term fasting king penguins, *Aptenodytes patagonicus*, during courtship and incubation. Anim. Behav. 62, 661–669.

Griffin, T.M., Kram, R., 2000. Penguin waddling is not wasteful. Nature 408, 929.

Guinet, C., Jouventin, P., Malacamp, J., 1995. Satellite remote sensing in monitoring change of seabirds: use of spot image in king penguin population increase at Ile aux Cochons, Crozet Archipelago. Polar Biol. 15, 511–515.

Hull, C.L., 2000. Comparative diving behaviour and segregation of the marine habitat by breeding Royal penguins, (*Eudyptes schlegeli*), and eastern Rockhopper penguins, (*Eudyptes chrysocome filholi*), at Macquarie Island. Can. J. Zool. 78, 333–345.

Hull, C.L., Wilson, J., 1996. Location of colonies in royal penguins *Eudyptes schlegeli*: potential costs and consequences for breeding success. EMU 96, 135–138.

Kabat, A.P., Phillips, R.A., Croxall, J.P., Butler, P.J., in press. Differences in metabolic costs of terrestrial mobility in two closely related species of albatross. J. Exp. Biol.

Miyazaki, M., Waas, J.R., 2003. Influence of parental body size on sea-to-nest distances and food provisioning in little penguin (*Eudyptula minor*). EMU 103, 239–243.

Nagy, K.A., Kooyman, G.L., Ponganis, P.J., 2001. Energetic cost of foraging in free-diving emperor penguins. Physiol. Biochem. Zool. 74, 541–547.

Pinshow, B., Fedak, M.A., Battles, D.R., Schmidt-Nielsen, K., 1976. Energy expenditure for thermoregulation and locomotion in emperor penguins. Am. J. Physiol. 231, 903–912.

Pinshow, B., Fedak, M., Schmidt-Nielsen, K., 1977. Terrestrial locomotion in penguins: it costs more to waddle. Science 195, 592–594.

Schmidt-Nielsen, K., 1972. Locomotion: energy cost of swimming, flying, and running. Science 177, 222–228.

Taylor, C.R., Schmidt-Nielsen, K., Raab, J.L., 1970. Scaling of energetic cost of running to body size in mammals. Am. J. Physiol. 219, 1104–1107.

Taylor, C.R., Heglund, N.C., Maloiy, G.M.O., 1982. Energetics and mechanics of terrestrial locomotion. J. Exp. Biol. 97, 1–21.

Walker, B.G., Dee Boersma, P., Wingfield, J., 2004. Physiological condition in Magellanic penguins: does it matter if you have to walk a long way to your nest? Condor 106, 696–701.

Warncke, G., Bandholtz, J., Schultze-Motel, P., 1988. Metabolic cost and body temperatures during grade running in quail (*Coturnix coturnix*). Comp. Biochem. Physiol. A 89, 93–96.

Williams, T.D., 1995. The Penguins (Spheniscidae). Oxford University Press, Oxford.

Wilson, R.P., Scolaro, J.A., 1999. To think or swim: does it really cost penguins more to waddle? J. Avian Biol. 30, 221–224.

Withers, P.C., 1977. Measurement of VO2, VCO2, and evaporative water loss with a flow-through mask. J. Appl. Physiol.: Respir., Environ. Exercise Physiol. 42, 120–123.