Heat production studies on normal and oil-covered jackass penguins (*Spheniscus demersus*) in air and water

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Heat production and the importance of intact feathers for insulation were studied in jackass penguins *Spheniscus demersus* at various temperatures (5 – 25°C) by comparing their oxygen consumption in air and water with that of birds whose feather insulation was impaired when they were accidentally covered in partially weathered crude oil. Special attention was given to employing an experimental procedure that could relate oxygen consumption to level of activity. The mean ± *SD* metabolic rate recorded for normal inactive birds (188 ± 24 kJ kg^{-1} day^{-1}) was the same in air and water but only 80% of the mass specific rates predicted for non-passerine birds. Wetting a bird increased the inactive rate in air 1,33 times while slow swimming in water above 10°C caused a 1,76-fold increase. At low air temperatures (5°C) postural changes and feather fluffing were associated with a very low rate of 122 ± 29 kJ kg^{-1} day^{-1}, which we interpret as behavioural control of penguins over energy expenditure. Jackass penguins in sea water at 10°C and above were within their thermal neutral range thus indicating that the water phase of their life cycle is not energetically more expensive than the terrestrial phase. Activity level of the birds was an important influence on oxygen consumption; we suggest it is the main reason for the variations in metabolic rates within closely related species reported in the literature.

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Suurstofopnames by verskeie temperature (5 – 25°C) is gebruik om die hitteproduksie van pikkewyne *Spheniscus demersus* asook die belangrikheid van normale vere vir insulasie in lug en water te bepaal deur hierdie waardes te vergelyk met dié van voëls wat toevallig met gedeeltelik verweerde olie besoedel is. Spesiale aandag is gegee aan 'n eksperimentele tegniek wat suurstofopnames en aktiwiteitspeile kan korreleer. Die gemiddelde ± *SA* metaboliese peile vir normale onaktiewe voëls was 188 ± 24 kJ kg^{-1} dag^{-1} en was dieselfde in lug en water. Hierdie waarde is slegs 80% van die voorspelde waarde vir nie-passeriene voëls. 'n Nat pikkewyn in lug se onaktiewe tempo van hitteproduksie is 1,33 keer hoër, terwyl stadige swembewegings in water by 10°C en hoër 'n toename van 1,76 keer veroorsaak. By lae lugtemperatuur (5°C) het die voëls 'n besondere lae metabolisme van 122 ± 29 kJ kg^{-1} dag^{-1} getoon. Dit het altyd gepaard gegaan met gepofde vere en 'n sittende posisie en dit word geinterpreteer as 'n vorm van gedragsbeheer oor hitteproduksie. Pikkewyne in seewater by 10°C en hoër was nog binne hul termoneutrale sone wat 'n aanduiding is dat die waterfase van hul lewe nie energie-gewyse duurder is as die landfase nie. Die belangrikheid van aktiwiteit op die tempo van suurstofopname word beklemtoon en word aangebied as een van die hoofredes vir die variasie in hitteproduksie tussen naverwante spesies wat in die literatuur gerapporteer word.

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In a previous article (Erasmus, Randall & Randall 1981) we reported on the implications of the loss of feather insulation due to oil pollution on core body temperatures in jackass penguins (*Spheniscus demersus*). From the data we concluded that oil-covered penguins would die of hypothermia in water at 20°C, but could maintain normal body temperatures in air at the same temperature. Insulation by feathers is therefore an important protection for jackass penguins against the heat sink effect of the surrounding water. No data could be found to quantify the energy requirement of a bird with impaired insulation. An opportunity arose when several penguins were accidentally polluted at sea with partially evaporated crude oil. In this paper we compare the heat production (oxygen consumption) of normal penguins in air and water with that of those whose feather insulation was apparently impaired by oil. We draw attention to the importance of intact feathers when the birds emerge wet from the water, as well as the effect of activity level on rates of heat loss.

Material and Methods

The penguins used all came from St Croix Island, (33° 48'S/25° 37'E) the main breeding island for this species on the south-east coast of southern Africa. Five normal birds were used. The oiled birds were collected on the landing stages at the island. Where possible, recently oiled birds were used to minimize starvation and emaciation effects on oxygen consumption. More than 15 oiled birds were used in the experiments, but only the results from four that survived to give readings at all four experimental temperatures are reported on. The degree of oiling could be classified as medium, based on the grams of oil residue that could be dissolved in ether from birds with various degrees of oiling. A medium oiled bird carried between 4 and 7 g of ether extract.

All the birds were force fed daily at 16h00 to satiation with marine fish (Mugilidae) and a multivitamin additive. The oiled birds gained some weight on this regime (mean starting mass 2,33 ± 0,37 kg). The normal birds maintained their weight at 2,88 ± 0,52 kg. The birds were kept in a large temperature-controlled room at 20°C with a natural light regime. For oxygen consumption studies each bird was transferred to an adjacent room with temperature settings at 20, 15, 10 or 5°C for the normal birds and 25, 20, 15 or 10°C for the oiled birds. After transfer, 60 min were allowed for acclimation to a specific air temperature before oxygen consumption was measured. Only 10 min acclimation time was allowed after transferring a bird to water, because of the frantic escape behaviour of the oiled penguin when immersed for extended periods in water. This escape behaviour also prevented us from obtaining satisfactory readings resembling inactivity from the oiled penguins at 5°C.

Oxygen consumption measurements were obtained by drawing laboratory air through a face mask and silica gel at the rate of $11\ \ell\ \mathrm{min}^{-1}$ before it entered the polarographic oxygen probe (Bioscience OX140 oxygen transducer in a specially built cell coupled to an amplifier) coupled to a recorder. This flow rate was selected to give a sensitive, but rapid response so that the rate of oxygen consumption of the bird could be related to its activity pattern. The flow rate of air through the system corrected to STP and the difference in O_2 concentration between the incurrent and excurrent air were used to calculate oxygen consumption and this was converted to an average energy equivalent using $1\ \ell\ O_2 = 20$ kJ. The oxygen probe was calibrated for the specific flow rates and the expected exhaled air composition against a known mass of air from a gas cylinder (Precigas) with a known gas concentration, drawn through the entire system. The rate of oxygen consumption had to be constant for at least three and preferably five consecutive minutes at a specific activity level before it was accepted as a valid reading. At least two valid readings per behaviour pattern per treatment were used to calculate the corresponding rate of heat production. Consumption rates were first determined in air with the birds standing still. Thereafter, with the bird still connected to the oxygen analyser, the bird was transferred carefully to a seawater pool (2 m diameter) equilibrated with the respective air temperature. Readings were taken as the bird drifted passively as well as during bouts of slow swimming on the surface. At the end of the water readings, the bird was transferred carefully to a wire box and readings were taken while it was still wet, and in a standing posture. Satisfactory readings were possible only between 08h00 and 14h00, because the anticipatory activity associated with feeding time at 16h00 gave more variable and consistently higher results. Each bird was tested at only one temperature in air and water on any one day. As special care was taken to ensure minimum levels of activity the rates measured are called the Inactive Metabolic Rate (IMR).

Results

Heat production in normal birds

The effects of temperature on the oxygen consumption of birds at rest in air and water and limited activity in water are given in Table 1. Inactive metabolic rate (IMR) in air between 10 and 20°C was 185 ± 34 kJ $\mathrm{kg}^{-1}\ \mathrm{day}^{-1}$ ($x \pm SD$). The low reading of 122 ± 29 kJ $\mathrm{kg}^{-1}\ \mathrm{day}^{-1}$ obtained at 5°C for the five normal birds was accompanied by feather fluffing and a reluctance to change from a crouched posture. This behaviour was evident only in well-trained birds and we interpret it as behavioural control over insulation. Values for the birds in water (190 ± 22 kJ $\mathrm{kg}^{-1}\ \mathrm{day}^{-1}$) did not differ significantly ($p > 0{,}05$) from the values in air (excluding 5°C) and the rates of heat production in air and water at 10°C, 15°C and 20°C were therefore pooled to give a mean IMR of 188 ± 24 kJ $\mathrm{kg}^{-1}\ \mathrm{day}^{-1}$. Wet penguins in air increased their metabolism on the average 1,33 times. Slow swimming increased metabolism 1,76 times when in water above 5°C. At 5°C a marked increase (2,36 times) was noted. The large *SD* at these low water temperatures is indicative of the variation introduced by varying degrees of activity elicited by cold water.

Heat production in oiled birds

Oil-polluted birds produced heat (IMR) at a mean rate of 230 ± 8 kJ $\mathrm{kg}^{-1}\ \mathrm{day}^{-1}$ in air, which is 24% more than normal birds and is statistically significantly higher ($p < 0{,}05$). Air temperatures had little effect on the rate. Immersion in water at 25°C increased the mean heat production of oiled birds by 1,82 times with a further increase down to 15°C where the production peaked at 2,67 times the IMR of normal birds. The slight decrease in heat production below 15°C is not statistically different ($p > 0{,}05$). The wet oiled birds had IMR's in air comparable to those in water. Oiled birds swimming slowly showed a further increase in metabolic rate at all temperatures, reaching a maximum level of 754 ± 184 kJ $\mathrm{kg}^{-1}\ \mathrm{day}^{-1}$. This is equivalent to 4 times higher than normal resting birds in air at the same temperature.

Discussion

Normal birds in air

The mean IMR in the thermal neutral zone for jackass penguins in air and water was 188 ± 24 kJ $\mathrm{kg}^{-1}\ \mathrm{day}^{-1}$ which is lower than the basal metabolic rate (BMR) of 212 kJ $\mathrm{kg}^{-1}\ \mathrm{day}^{-1}$ reported by Drent & Stonehouse (1971) for the closely related *S. humboldti*. Our values are also lower (approximately 80%) than the predicted metabolic rate for birds of their mass (Lasiewski & Dawson 1967; Kendeigh 1970), and are also consistently lower than the mass specific metabolic rates for

Table 1 The mean ± *SD* metabolic rates kJ $\mathrm{kg}^{-1}\ \mathrm{day}^{-1}$ of normal and oiled penguins as affected by various temperatures in air and water

Condition	*n*	Temp. (°C)	No activity			Active
			Air (dry)	Water	Air (wet)	Swimming
Normal	5	20	166 ± 44	183 ± 54	196 ± 39	316 ± 117
	5	15	221 ± 40	222 ± 21	303 ± 60	291 ± 36
	5	10	168 ± 31	171 ± 43	248 ± 53	268 ± 2
	5	5	122 ± 29	185 ± 68	247 ± 93	444 ± 197
$\bar{x} \pm SD$			185 ± 31[a]	190 ± 22	248 ± 44	330 ± 79
Oiled	4	25	222 ± 25	337 ± 45	321 ± 47	579 ± 66
	4	20	239 ± 76	411 ± 214	441 ± 173	–
	4	15	226 ± 48	502 ± 91	532 ± 209	754 ± 184
	3	10	233 ± 51	474 ± 60	494 ± 88	563 ± 87
$\bar{x} \pm SD$			230 ± 8	431 ± 73	447 ± 92	632 ± 106

[a] Excluding the readings at 5°C (see text)

11 species of penguins summarized by Brown (1984).

We would like to offer two explanations of the apparent discrepancy between our data and those reported in the literature. Firstly, the usual methods of determining oxygen consumption rate involve a penguin in a chamber in the dark, on the assumption that the darkness will reduce activity to a minimum (e.g. Ricklefs & Matthew 1983). In extensive preliminary determinations using such a system we found that the birds exhibited large variations in oxygen consumption rates which could be ascribed to differences in activity. The darkness and the slow response time (2 min) of chambers used, precluded the possibility of correlating consumption rate with activity levels. Many of the reported values obtained with dark chambers or closed systems therefore may not reflect true basal or standard rates. It is worth recalling that Deighton & Hutchinson (1940) emphasized the significance of activity on metabolic rates. They reported that the metabolism of fowls in the standing position was 40 – 45% above that in the sitting position, and that even neck movements (stretching so that the feathers can separate) increase metabolism by 20%. The increase in metabolism in birds is larger than the increase in metabolism (10 – 15%) experienced by cattle and sheep when changing from lying to standing (Blaxter 1962). Special care to minimize or standardize activity level is therefore of utmost importance in comparative work with birds, especially wild birds. With the face mask, training and the fast response time of the system used in the present experiment, it was possible to identify only those oxygen consumption rates for which the birds were truly inactive. Brown (1984) also queried the validity of BMR values reported in the literature, and remarked on the fact that measurements of metabolic rate on zoo penguins are the lowest reported and all are lower than predicted BMR. We suggest that low activity levels exhibited by trained birds could explain the lower than predicted values obtained in our experiment. This observation implies that there is no need to postulate some extrinsic factor to account for elevated rates of metabolism in non-incubating penguins, as suggested by Brown (1984), because the lower activity levels associated with incubation should be more than adequate to explain the lower metabolic rates of his incubating birds.

Secondly *S. demersus* is endemic to southern Africa with its relatively high water (10 – 25°) and air (8 – 35°C) temperatures (Randall, Randall, Batchelor & Ross 1981), when compared to the ambient conditions experienced by penguins in the higher latitudes (Stonehouse 1975). An analysis of the adaptation of avian metabolic rates to various climatic conditions by Weathers (1979) showed that birds living in those higher latitudes had a higher metabolic rate than that of species in tropical latitudes. One therefore might expect *S. demersus* to have a lower metabolic rate than other penguin species.

Our data support the conclusions of Dawson & Fanning (1981) and Stahel & Nicol (1982) that penguins, as aquatic birds, do not show the increased metabolism aquatic mammals have, when compared to their terrestrial counterparts (Irving 1973).

It is of ecological significance that the birds could decrease their energy expenditure to 65% of the normal value when exposed to air at 5°C. This decrease was achieved by pilo-erection of the feathers and an absence of movement presumably increasing insulation to such an extent that body temperatures could be maintained despite a decreased metabolism. Le Maho (1983) commented on the significance of similar behaviour for the conservation of energy by the emperor penguin (*Aptenodytes forsteri*) during winter fasts, but did not quantify it. We suggest that the ability to decrease metabolism behaviourally when confronted with low air temperatures is an adaptation to cope with extended periods of adverse weather and concomitant starvation on land. Stahel & Nicol (1982) did not observe a similar pattern in the smaller little penguin (*Eudyptula minor*) and they reported a lower critical temperature of 10°C. We noted that the oxygen consumption rate of a bird at 5°C in air with unfluffed feathers and standing erect was comparable to the mean value (185 kJ kg^{-1} day^{-1}) for the higher temperatures.

Normal birds in water

In water, metabolic rates were comparable to rates in air. Unfortunately there are only three reports in the literature on heat production by penguins in water despite the fact that the water phase dominates their life cycle. Kooyman, Gentry, Bergman & Hammel (1976) reported metabolic rates of 1 157 kJ kg$^{-0,73}$ day^{-1} for the Adélie penguin (*Pygoscelis adeliae*) and Stahel & Nicol (1982) recalculated the results from Barre (1980) on the king penguin (*Aptenodytes patagonica*) and reported 1 312 kJ kg$^{-0,73}$ day^{-1}. Stahel & Nicol (1982) recorded 751 kJ kg$^{-0,73}$ day^{-1} for the little penguin in water at the same temperature as the other two species (10°C). In comparison the jackass penguin consumed oxygen at the rate of 253 kJ kg$^{-0,73}$ day^{-1} in water at 10°C. The relatively high rates of the Adélie and king penguins may be due to the fact that these birds were restrained and forcibly immersed. Stahel & Nicol (1982) did not use restrained birds in their work on the little penguin, but even so, we recorded considerably lower values than they did, perhaps because our experimental set-up allowed periods of true inactivity (floating) to be distinguished from periods where movement occurred. While floating passively the jackass penguins showed a thermal neutral range down to 5°C (the lowest temperature tested). Stahel & Nicol (1982) also found that the lower critical temperature was the same in air and water but they reported a critical temperature of 10°C for their smaller birds. It would thus appear that the real lower critical temperature of the jackass penguin in air and water is less than 5°C. This figure is comparable to the 2°C in air reported for the closely related Peruvian penguin *Spheniscus humboldi* (Drent & Stonehouse 1971).

The metabolic rate of the jackass penguins increased 1,7 times from 190 ± 22 kJ kg^{-1} day^{-1} when floating passively to 330 ± 79 kJ kg^{-1} day^{-1} when swimming calmly in water at temperatures from 10 to 20°C. At 5°C, however, the metabolic rate of birds swimming calmly increased 2,3 times to 444 ± 197 kJ kg^{-1} day^{-1}. This increase is due partially to increased energy expenditure associated with movement through water, the loss of the small thermal boundary layer during movement (Erskine & Spotila 1977) as well as the increased blood supply to the poorly insulated flippers and resulting heat loss. We noticed this increase in blood supply to the flippers when swimming by virtue of ease of drawing blood from the veins of the flippers of a bird just returned from swimming in the sea. Control of blood flow to the extremities of penguins therefore can be expected to become more critical at higher latitudes.

A jackass penguin actively swimming in water at temperatures below 10°C is outside its thermal neutral zone whereas by floating passively it extends this zone to below 5°C. As the sea frequented by these birds usually has a temperature above 10°C, the jackass penguin is usually within its thermal neutral zone in the sea. Furthermore, even passive drifting in the open sea will keep the metabolic rate above the IMR measured in the laboratory. The metabolic rate of 291 kJ kg^{-1} day^{-1} we measured when the penguins were swimming quietly in water at 10 – 20°C therefore may be closer to the actual resting metabolism of these penguins in the sea and may be the preferred value to use when constructing energy activity budgets of birds at sea. The 1,55 times increase above IMR in air is similar to the 1,6 to 1,7 times BMR reported by Stahel & Nicol (1982) for the little penguin in water in a darkened metabolic chamber, so that the increased heat production they observed for the little penguin in water may have been due to slow swimming movements.

The argument above may explain why Stahel & Nicol's (1982) data indicate that the water phase of a penguin's life cycle is an energetically expensive phase, compared to air, whereas our data indicate that the jackass penguin is well adapted to air and water in temperatures from 25°C down to below 10°C. The available information does not permit us to say whether the differences between these two sets of data can be explained entirely by different activity levels in water, or whether differences in the size and insulation characteristics of the feathers of the two species are responsible. Nevertheless the relationship between weight and insulation in birds reviewed by Drent & Stonehouse (1971), suggests that expected size effects are much less than the recorded differences in response.

The metabolic rate of wet birds in air immediately after being taken out of the water increased by approximately 32% over the rates recorded when dry, or drifting in the water. This observation is surprising, because if the insulation is adequate in water it should be more than adequate in air. The increase may be necessitated by evaporative cooling from wet poorly insulated surfaces such as the flippers, feet and head and may also explain the heliothermic behaviour of penguins when they emerge from the sea (Erasmus *et al.* 1981).

Oil-covered birds

Oil-covered feathers still have some insulation capacity in air, because the mean level of heat production of oiled penguins in air increased a mere 22% above normal. The caking of oil may enable the feathers to trap some air for insulation. It is also noteworthy that the rate of heat production did not vary between the various air temperatures as much as it did in normal birds, which is consistent with the observation that oil-covered birds are more lethargic than normal birds. Observations on oiled birds at lower air temperatures (10°C) showed that these birds also adopted a typical crouched posture, but could not ruffle their oil-caked feathers as the normal birds did. Oiling therefore deprived them of the behavioural mechanism which allows a decrease in heat production at low air temperatures on land.

Oil-covered birds in water increased their metabolic rates (Table 1). Peak IMR observed at 10 and 15°C was 488 kJ kg^{-1} day^{-1}, which represents an increase of 2,6 times the normal inactive rate. The birds were obviously stressed in the water and the excape behaviour evident at the lower temperatures required special care in the recording of acceptable inactivity values.

Swimming increased metabolic rates even further and although the activity level associated with slow swimming was the same for normal and oiled birds, the oiled birds had double the rates of heat production. The peak value was recorded in water at 15°C with rates more than four times the inactivity level of a normal bird.

No loss of buoyancy was observed in oiled birds; they maintained their depth of floating in water. It may be the inability to maintain homeothermy, and not the possible loss of buoyancy which drives these birds to dry land. Once on land, homeothermy is again possible at a slight metabolic expense. However, such a bird can not forage and eventually dies of dehydration and starvation.

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