Review

Energy saving processes in huddling emperor penguins: from experiments to theory

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Summary

This paper investigates the energy savings of male emperor penguins *Aptenodytes forsteri* linked to their huddling behaviour, the key factor that allows them to assume their incubating task while undergoing a long fast. Drawing on new studies by our team, this review examines the energetic benefits accrued from huddling and estimates the respective contributions of wind protection, exposure to mild ambient temperatures, reduction in cold-exposed body surfaces and body temperature adjustments in these energy savings. The metabolic rate of 'loosely grouped' birds (restrained in small groups of 5–10 individuals, which are unable to huddle effectively) is reduced by 39% compared to metabolic rate of 'isolated' birds, with 32% of these energetic benefits due to wind protection. In addition, metabolic rate of 'free-ranging' emperors, i.e. able to move freely and to huddle, is on average 21% lower than that of 'loosely grouped' birds. Exposure to mild ambient temperatures within the groups and reduction in cold-exposed body surfaces while huddling, though overestimated, would represent a 38% metabolic reduction. About two thirds of metabolic lowering is attributable to the reduction in cold-exposed body surfaces and one third to the mild microclimate created within the groups. Moreover, body temperature adjustments contribute to these energetic benefits: maintaining body temperatures 1°C lower would represent a 7–17% reduction in energy expenditure. These processes, linked together, explain how huddling emperors save energy and maintain a constant body temperature, which ensures a successful incubation in the midst of the austral winter.

Key words: huddling, emperor penguin, energetic benefit, wind protection, microclimate, body temperature.

Introduction

The emperor penguin *Aptenodytes forsteri* is the only bird to breed in the middle of the Antarctic winter (Prévost, 1961). Males and females fast for 45 days during the pairing period, and males fast another 70 days to assume the incubation task (Prévost, 1961; Isenmann, 1971), during which their body temperature has to be constant and high in order to maintain their egg at 35°C (Prévost, 1961; Prévost and Sapin-Jaloustre, 1964; Boyd and Sladen, 1971; Le Maho et al., 1976; Pinshow et al., 1976; Groscolas, 1986; Gilbert et al., 2007). Although they are adapted to minimize heat loss (Le Maho, 1977), energetically costly heat production mechanisms must be activated because ambient temperatures are always below their lower critical temperature [T_{Lcrit}: –10°C (Le Maho et al., 1976; Pinshow et al., 1976)]. Breeding success then relies on the males' ability to make economic use of their body fuels. Pioneering studies suggested that huddling is the key factor for emperor penguins to protect themselves against cold and lower their energy expenditure in order to survive their 4-month breeding fast during the Antarctic winter (Cendron, 1952; Stonehouse, 1953; Prévost, 1961). Similarly, many studies on small mammals support the view that huddling efficiently decreases metabolic heat production and maintenance cost by 10–40% (Pearson, 1960; Gorecki, 1968; Gebczynski, 1969; Gebczynska, 1970; Fedyk, 1971; Tertil, 1972; Glaser and Lustick, 1975; Stanier, 1975; Alberts, 1978; Martin et al., 1980; Andrews and Belknap, 1986; Yahav and Buffenstein, 1991; Perret, 1998).

According to heat transfer physics, for any animal heat losses equivalent to metabolic rate in a thermal steady state are dependent on the gradients between the external temperature and its body temperature. These gradients, moreover, depend on the cold-exposed body surface area and the thermal conductance of the animals (Scholander et al., 1950). Small animals closely packed together reduce their body surface area exposed to the cold, contributing to energy savings (Contreras, 1984; Canals et al., 1997). Small mammals possess a high surface:volume ratio, leading to important heat losses compared with their metabolic heat production, and the reduction in cold-exposed body surface area is estimated to account, on average, for 58–94% of the huddling energy savings of small rodents, depending on the number of individuals involved and on the density of the group (Canals et al., 1997). A second process involved in energy savings is the increase in temperature surrounding the grouped animals, which decreases heat losses by reducing the gradients between external and body temperatures. A 5°C increase in ambient temperature caused by huddling short-tailed field voles *Microtus agrestis* accounted for 55% of the energetic benefits during huddling (Hayes et al., 1992). A third mechanism explaining energy savings relies on adjustments in body temperatures of huddling animals (Vickery and Millar, 1984): huddling mammals and birds maintain a higher and more constant body temperature than isolated ones, suggesting that huddling is used as a warming mechanism (Stanier, 1975; Howell, 1976; Alberts, 1978; Andrews et al., 1987; Yahav and Buffenstein, 1991; Boix-Hinzen and Lovegrove, 1998; McKechnie and Lovegrove, 2001; Bautista et al., 2003; Cutrera et al., 2003). However, other biological models lower their body temperature during huddling bouts, presumably allowing them to maximize

their energy savings through a reduction of their metabolic heat production. For example, great snow geese goslings *Chen caerulescens atlantica* lower their body temperature during huddling by 0.8°C (Fortin et al., 2000). Similarly, mouse lemurs *Microcebus murinus* nesting in pairs increase the duration of their hypothermic bouts compared with males nesting alone (Séguy and Perret, 2005).

With respect to the emperor penguin, no study has yet evaluated the respective parts of processes such as the reduction in cold-exposed body surface area and the increase in temperature surrounding the grouped animals and body temperature adjustments, in their energy savings during huddling. Emperor penguins face thermal trade-offs that are different from small mammals. Breeding male emperor penguins weigh on average 30 kg and are 1.2 m tall (Prévost, 1961), and thus possess a relatively low surface:volume ratio. Furthermore, they are highly insulated and adapted to reduce any heat loss (Le Maho, 1977). Hence, reduction in their cold-exposed body surfaces may make a lesser contribution to the energy savings permitted by huddling, compared with small animals. Variations in body temperature of emperor penguins should also be limited by the inertia inherent to their significant body mass. The warmth created inside huddles was actually considered by pioneer authors to be the only mechanism explaining energy savings observed in huddling emperor penguins (Prévost, 1961; Jouventin, 1971; Jarman, 1973; Le Maho, 1977), and the reduction in cold-exposed body surface area during huddling and any consequent body temperature adjustment was neglected. However, it was hypothesized that huddling penguins may save energy through a lowering of their body temperature (Ancel et al., 1997). In support of that, pioneering studies reported that the rectal temperature of huddling free-ranging birds was 1°C lower than in captive birds held in small groups and 2°C lower than in captive birds held in isolation, even though they all experienced similar climatic conditions within the general colony area (Prévost, 1961; Prévost and Sapin-Jaloustre, 1964; Mougin, 1966).

Recent studies by our group provide new insights into this complex social behaviour and its related physiological mechanisms (Gilbert et al., 2006; Gilbert et al., 2007), permitting an exploration of the respective contributions of these processes to huddling energetics. Throughout their breeding cycle, males huddle, i.e. are packed together, on average 38% of their time (Gilbert et al., 2006), and experience ambient temperatures within their thermoneutral zone thanks to grouping [from –10°C to +20°C (Le Maho et al., 1976; Pinshow et al., 1976)]. In parallel, their body temperature is adjusted during the breeding cycle: it decreases by 1.7°C over the pairing period, and is maintained during incubation. Overall, the body temperature of free-ranging birds during their breeding cycle averages 36.7°C (Gilbert et al., 2007). Furthermore, birds engaged in particularly tight huddles do not show any sign of hyperthermia. We have suggested, based on the heat transfer physics, that birds saving energy over their winter fast enter a metabolic depression during huddling, the extent of which depends on the reduction of their body surface area exposed to the cold (Gilbert et al., 2007).

During the 4-month fast associated with pairing and egg incubation, male emperor penguins rely completely on their body reserves to fuel energy metabolism. Energy balance during this time can thus be estimated from body mass losses, taking into account the measured and estimated composition of the mass loss (Groscolas, 1988). Based on this, some studies (Prévost, 1961; Prévost and Sapin-Jaloustre, 1964; Ancel et al., 1997) estimated the overall energetic benefits of huddling in emperor penguins, comparing body mass losses or estimated metabolic rates of: (1) 'isolated' birds, fenced in at the colony; (2) 'loosely grouped' birds, restrained in small groups of 5–10 birds fenced in at the colony but unable to huddle effectively; and (3) 'free-ranging' birds, moving freely within the colony and able to huddle (Fig. 1). In all studies, isolated and/or loosely grouped birds faced climatic conditions identical to those of free-ranging birds. Since birds were able to group themselves when loosely grouped and maintain social interactions visually and acoustically when isolated, the effect of stress due to captivity was probably far less than the thermal effects. Isolated birds were unable to shelter themselves from the wind, in contrast to grouped birds that might reduce the effect of wind-chill by grouping themselves loosely (Jarman, 1973). The energy savings of loosely grouped birds, when compared with isolated ones, could then be attributed to the fact that grouped birds were able to reduce wind-chill effects (Fig. 1). In contrast to free-ranging birds, loosely grouped birds were unable to huddle effectively and reduce their exposed body surface area by any significant extent. The energy savings observed in free-ranging birds, when compared with loosely grouped birds, can be attributed to (1) warming of the temperature around the birds, (2) reduction in their cold-exposed body surface area while huddling (Fig. 1), and (3) body temperature adjustments of free-ranging birds, maintaining lower body temperatures (Fig. 1), should form part of their huddling energy savings. The two first mechanisms should be additive, while the body temperature adjustments should contribute towards these two processes.

Our first aim was to review previous studies investigating the energetic benefits associated with huddling in emperor penguins, by
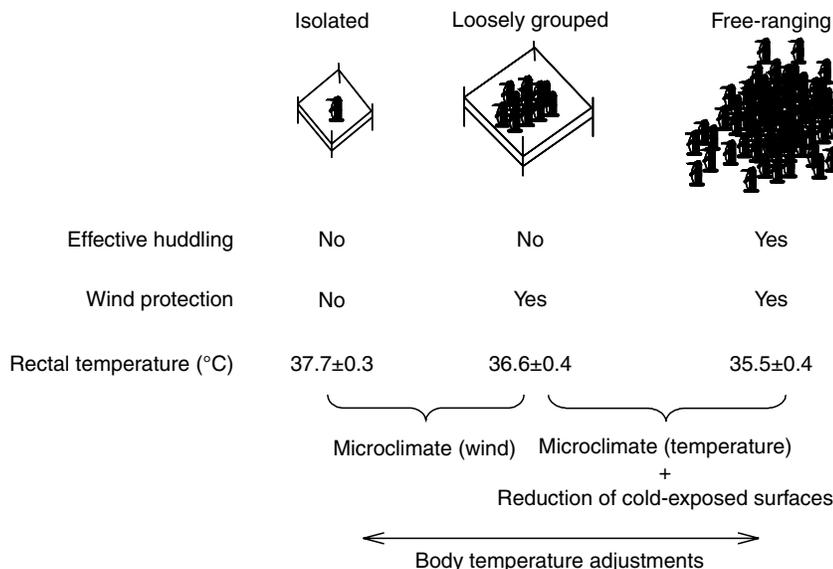

Fig. 1. Thermoregulatory status of the three bird categories investigated (isolated, loosely grouped, free-ranging), and associated processes of energetic benefits. Values are mean rectal temperatures ± s.d. (see Prévost, 1961; Prévost and Sapin-Jaloustre, 1964; Mougin, 1966).

comparing body mass losses and derived metabolic rates of free-ranging, loosely grouped and isolated birds. Estimation of huddling benefits has already been attempted, but results obtained recently enabled us to go further in examining the energy saving mechanisms. We then estimated the respective contributions to the energetic benefit from wind protection, warming of ambient temperatures when birds are not packed, reduced cold-exposed body surface area when birds are packed while huddling, and adjustments of the birds' deep body temperature. In conclusion, these estimations are discussed.

A review of energy savings comparing isolated, loosely grouped and free-ranging birds

Previous studies investigated daily body mass losses concomitantly in enclosed birds, isolated and loosely grouped birds, and in unrestrained free-ranging birds (Prévost, 1961; Prévost and Sapin-Jaloustre, 1964; Ancel et al., 1997) (Fig. 2). To minimize the impact of stress, body masses of captive birds were measured after habituation to their enclosure. On average, free-ranging and loosely grouped penguins lost 132 ± 8 and 178 ± 23 g day^{-1}, respectively (mean ± s.d.), which represents a 26% reduction in daily body mass loss. Daily body mass loss in loosely grouped birds was on average 40% lower than in isolated birds (299 ± 8 g day^{-1}). The overall difference between isolated and free-ranging birds was 56% (Fig. 2).

Two indirect methods estimated field metabolic rates (FMR) of emperor penguins. First, an estimate of metabolic rate was obtained from body mass loss and the related energy equivalent derived from the chemical composition of carcasses (Groscolas, 1988). Given that emperor penguins in the above studies were in phase II of their fast [from day 10 to day 100 (Robin et al., 1988)] and that the composition of the lost body mass was found to be steady under this condition (61.7% lipids, 5.9% proteins and 32.4% water), the energetic equivalent of 1 g body mass would be 25.5 kJ (Groscolas, 1988). Hence, according to this estimation, metabolic rate of free-ranging huddling penguins would be reduced by 26%, compared to loosely grouped birds (132 g day$^{-1}\equiv39.0$ W and 178 g day$^{-1}\equiv52.5$ W, respectively). Second, an isotopic dilution method was used to measure the daily changes in composition (Ancel et al., 1997). Ancel et al. found that body mass loss was 20% lower in free-ranging birds than in loosely grouped birds (137 and 171 g day^{-1}, respectively). The estimated metabolic rate of free-ranging birds (1.5 W kg^{-1}) was 16% lower than that of loosely grouped birds (1.8 W kg^{-1}). Based on these two methods, the metabolic rate of free-ranging birds was calculated to be on average 21% lower than in loosely grouped birds (42.8 ± 5.3 and 51.9 ± 2.1 W, respectively; mean ± s.d.; Fig. 2). Using the estimate from Groscolas (Groscolas, 1988), loosely grouped birds had an average metabolic rate 39% lower than that of isolated birds (88.2 W; Fig. 2). Hence, the average reduction in metabolic rate of free-ranging penguins, compared with isolated birds, was 51%.

Estimating energetic benefits from wind protection: isolated *versus* loosely grouped birds

Average wind speed and ambient temperatures in June and July measured at the colony over a period of 7 years (Prévost, 1961; Guillard and Prévost, 1964; Mougin, 1966) (A.A., unpublished observations) were 4.9 ± 0.9 m s^{-1} and $-16.6\pm0.8°C$, respectively (mean ± s.d.).

Birds inside a huddling group, even if they are not packed together, shelter themselves from the wind (Jarman, 1973). Unfortunately no external temperature measurements, recorded on
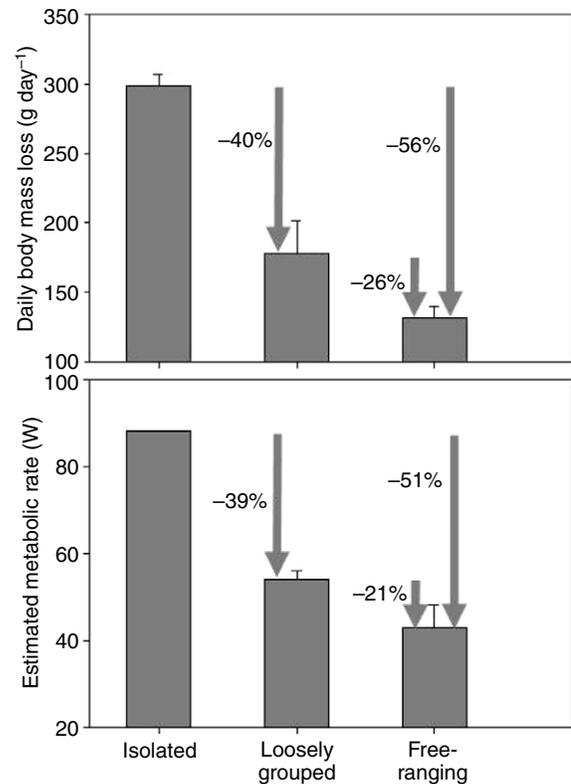

Fig. 2. Daily body mass losses and derived metabolic rates of isolated, loosely grouped and free-ranging male emperor penguins during winter (April to July). Mean daily body mass losses were calculated from published studies (Prévost, 1961; Prévost and Sapin-Jaloustre, 1964; Ancel et al., 1997). Estimated mean metabolic rates were calculated from the mean daily body mass loss applying Groscolas's method (Groscolas, 1988) and Ancel et al.'s results (Ancel et al., 1997).

loosely grouped or isolated birds' backs, are available. We can estimate the reduction in energy expenditure that a loosely grouped bird will experience through wind shelter, when compared with an isolated bird (Fig. 3). The metabolic rates of emperor penguins have been independently measured using respirometry (Le Maho et al., 1976; Pinshow et al., 1976). Both studies concluded that below an ambient temperature of $-10°C$ (lower critical temperature, T_{Lcrit}), the metabolic rate of emperor penguins increases as a function of ambient temperature. Pinshow et al. conducted measurements indoors at various low ambient temperatures but without wind (Pinshow et al., 1976). By contrast, Le Maho et al. conducted measurements outdoors, where penguins were exposed to various low ambient temperatures at low wind speeds, ranging between 0 and 5 m s^{-1} (Le Maho et al., 1976). The resulting increase in metabolic rate at temperatures below $-10°C$ from these two studies differs slightly, with a steeper slope in the study by Le Maho et al. (Le Maho et al., 1976), presumably reflecting the effect of low wind speeds on metabolic rate.

For our investigation, we decided to use the equations given by Le Maho et al. (Le Maho et al., 1976), because captive penguins kept outside and grouped loosely most likely still experience the effects of low wind speeds. Several authors (Stonehouse, 1967; Drent and Stonehouse, 1971; Le Maho et al., 1976; Taylor, 1986; Stahel et al., 1987; Dawson et al., 1999) support the view that the compact nature of penguin plumage confers a high resistance to disorganization and penetration by wind, except in strong wind

speeds (>5 m s^{-1}). Consequently, these authors argue that heat loss by convection is negligible at low wind speeds. Similarly, Chappell et al. (Chappell et al., 1989) found that metabolic rate of Adélie penguins increases at high wind speeds, especially when ambient temperatures are low. The same should be true for emperor penguins facing wind speeds averaging 4.9 m s^{-1} at mean ambient temperatures of –16.6°C. Goldstein (Goldstein, 1983) modelled the combined effects of low temperatures and wind speeds on the birds' mass-specific field metabolic rate (sFMR$_{TaV}$):

$$\text{sFMR}_{TaV} = \text{sFMR}_{Ta} + [(bV^{0.5})/M] ,$$

where sFMR$_{Ta}$=sFMR at ambient temperature (T_a) without wind, V=wind speed in m s^{-1} and M=body mass in kg, and

$$b = 0.0092 m^{0.66} \times \Delta T^{0.32} , \qquad (1)$$

where m=body mass in g, and $\Delta T = T_a - T_{Lcrit}$ of the birds in °C.

Chappell et al. (Chappell et al., 1989) measured metabolic rates in Adélie penguins at ambient temperatures of –20°C, i.e. 10°C below their lower critical temperature (T_{Lcrit}) and wind speed of 5.7 m s^{-1}, and found values that were even higher than the metabolic rate predicted by Goldstein's model (Goldstein, 1983). They attributed this difference to an increase in heat loss through poorly insulated flippers. However, the ratio between flipper surface area and whole body surface area in Adélie penguins is much greater than in emperor penguins, which are adapted to breed during the Antarctic winter (Le Maho, 1977).

We therefore applied Goldstein's model (Goldstein, 1983) to the emperor penguins exposed to average wind speeds of 4.9 m s^{-1}. Hence,

$$\text{sFMR}_I = \text{sFMR}_{LG} + [(bV^{0.5})/M] , \qquad (2)$$

with sFMR$_I$ for sFMR$_{isolated}$, and sFMR$_{LG}$ for sFMR$_{loosely\ grouped}$, V=4.9 m s^{-1}, b=0.0092$m^{0.66} \times \Delta T^{0.32}$ (m=30 000 g for a standard incubating male emperor penguin and ΔT=6.6°C, with T_a=–16.6°C and T_{Lcrit}=–10°C).

sFMR$_{LG}$ can be derived from the established equation (Le Maho et al., 1976) for penguins exposed to low winds and T_a from –30°C to –10°C:

$$\text{sFMR}_{LG} = 1.08 - 0.08 T_a . \qquad (3)$$

Therefore, at T_a of –16.6°C, with no or low winds,

$$\text{sFMR}_{LG} = 2.41 \text{ W kg}^{-1} , \qquad (4)$$

and

$$\text{sFMR}_I = 2.41 + [(0.0092 \times 30000^{0.66} \times 6.6^{0.32} \times 4.9^{0.5}) / 30] = 3.53 \text{ W kg}^{-1} . \qquad (5)$$

Following these equations, a 30 kg bird isolated at the colony would have a metabolic rate as high as 106 W, and a loosely grouped bird, sheltered from the wind by its surrounding conspecifics, would have a metabolic rate of 72 W: this represents a reduction in metabolic rate of 32%.

The metabolic rates derived from the above equations are much higher than the mean estimated metabolic rates calculated from previous studies by, respectively, 17% for isolated birds and 28% for loosely grouped birds (Groscolas, 1988; Ancel et al., 1997) (Fig. 2). However, the mean reduction in metabolic rate and body mass loss of birds loosely grouped compared with isolated ones was 39% and 40%, respectively. This is close to the 32% reduction estimated using Goldstein's model (Goldstein, 1983). This estimate is based on equations that were established from metabolic measurements of penguins isolated in the laboratory. The higher metabolic rate estimated using Goldstein's model (Goldstein, 1983) could possibly be due to the stress caused by the manipulations. The calculations, derived from respirometry measurements, would then underestimate the metabolic rate reduction of loosely grouped penguins compared with isolated birds by 7%. This could be explained by the fact that we estimated only the thermal effects, whereas reduction in daily body mass loss (Prévost, 1961; Prévost and Sapin-Jaloustre, 1964) encompasses all thermal and additional stress or physiological effects. In conclusion, emperor penguins able to stay in a group, even when loosely structured, gain an average thermal and, hence, energetic benefit of 32%, simply by sheltering themselves from the wind-chill.

Estimating energetic benefits from the warming of ambient temperatures and the reduction in cold-exposed body surfaces: loosely grouped *versus* free-ranging birds

The next step was to determine how much of the 26% reduction in body mass loss or the 21% reduction in metabolic rate, observed in free-ranging *vs* loosely grouped birds, is due to the temperature microclimate created inside a free-ranging group and to the reduction in the birds' cold-exposed body surfaces (Fig. 3).

Our rationale assumes, firstly, that the effect of warming ambient temperatures relies on the increased time that birds spend within their thermoneutral zone, i.e. when energy expenditure is the lowest. Throughout the 2005 pairing and incubation periods, five male emperor penguins were equipped with a data logger recording light intensity and temperature (Mk9, Wildlife Computers, Redmond, WA, USA) glued to their back feathers. From temperature recordings, we could determine the time spent by birds at temperatures above –10°C. We could also measure the time they spend huddling tightly, i.e.

MR reduction		39%		21%			
	Isolated	Loosely grouped		Free-ranging			
				Loose grouping	Loose huddling	Tight huddling	
Wind speed	4.9 m s^{-1}	~0		~0	0		
Ambient temperature	–16.6°C	–16.6°C		<–10°C	>–10°C		
% of time	100%	100%		10%	41%	49% packed	

Microclimate (wind)

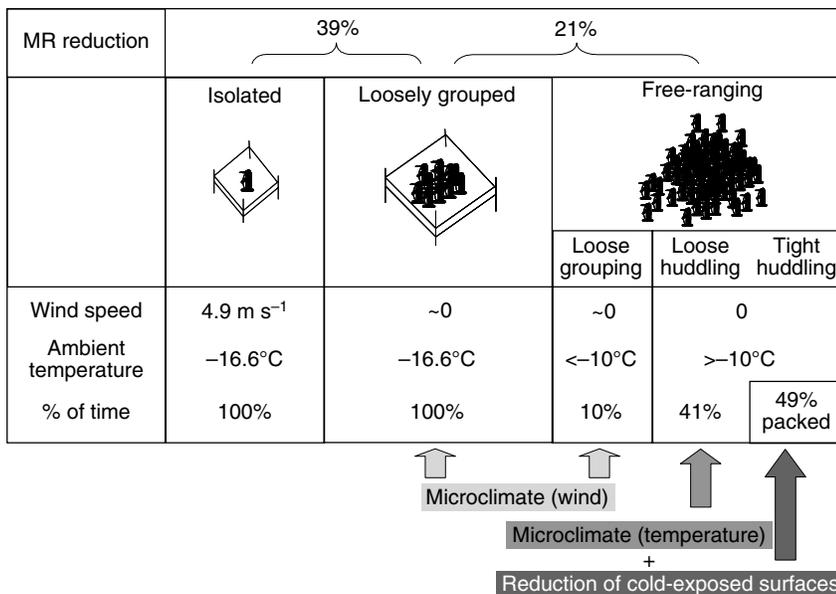Microclimate (temperature) + Reduction of cold-exposed surfaces

Fig. 3. Summary of microclimatic conditions experienced by isolated, loosely grouped and free-ranging birds, and associated benefits.

are packed together, as the light intensity recorded by the device drops rapidly to 0 when the birds' back is covered by another individual (for details, see Gilbert et al., 2006). Temperature recordings show that males spent on average only 10±5% of their time exposed to external temperatures lower than –10°C (i.e. free-ranging, loose grouping; mean ± s.d.; Fig. 3). Furthermore, they spent on average 49±5% of their time huddling, being packed (i.e. free-ranging, tight huddling; mean ± s.d.; Fig. 3). Then, the remaining 41% of their time was spent without being packed at ambient temperatures above –10°C, i.e. within their thermoneutral zone, corresponding to a minimum metabolic rate (i.e. free-ranging, loose huddling; Fig. 3).

Secondly, we can assume that when birds are huddling, their metabolic rate is lowered proportionally to the reduction in their cold-exposed body surfaces. This hypothesis is based on the observation that during bouts of tight huddling with ambient temperatures above 20°C, free-ranging emperor penguins not only show no sign of hyperthermia, but also maintain a constant body temperature, or even lower it by 0.5°C during pairing (Gilbert et al., 2007). For tightly huddling birds in close contact with neighbouring birds, thermal gradients, driving lateral heat loss from the core to lateral surfaces, nearly vanish. The surface areas exposed to the cold are restricted to the feet, the upper part of the back, the neck and the head (Fig. 4). Following heat transfer physics, tightly huddling penguins must reduce their metabolic rate by the same extent as the reduction in their cold-exposed body surface areas in order to maintain or slightly lower their core temperature. If they could not lower their metabolic rate, the cold-exposed areas might represent thermal windows for extra heat dissipation. However, this would contradict the fact that snow accumulates on their heads and upper backs during blizzards (Fig. 4), and that penguins must save energy during their incubating task. We thus suggested that they enter metabolic depression, associated with deep sleep, while huddling tightly (Gilbert et al., 2007). Although a clear experimental demonstration of this remains to be done, we do not see any other possible explanation because all living organisms are subject to the thermodynamic laws.

We were able to estimate reduction in the cold-exposed body surface of huddling emperor penguins using a dead emperor penguin, collected on the Pointe Géologie colony (Antarctica, Terre Adélie). We covered its whole body, from head to feet, by a single sheet of tissue that was adjusted to its body shape. The reduction in cold-exposed body surfaces was estimated from photographs of huddling emperor penguins (Fig. 4), and the part that would still be exposed to cold was drawn on the sheet. We estimated the mass of a given surface of tissue, and the parts corresponding to the whole and to the reduced body surfaces were weighed. The body surface of an isolated penguin would be about 6272 cm^2, which is close to the reported value of 6400 cm^2 (Le Maho et al., 1976), and to a calculated value of 6700 cm^2 from Walsberg and King's equation (Walsberg and King, 1978). The body surface still exposed to cold during huddling was estimated to be 1649 cm^2. The reduction in cold-exposed body surfaces of huddling emperor penguins would thus be about 74%.

To estimate the energetic benefits from the mild ambient temperatures created within the loose huddling group and the reduction in the cold-exposed body surfaces while tightly huddling, we compared the field metabolic rate (FMR) of a free-ranging bird (FMR$_{FR}$) spending 41% of its time within its thermoneutral zone without being packed and 49% of its time being packed, with the FMR of a loosely grouped bird (FMR$_{LG}$), which is sheltered from the wind but spends 100% of its time at temperatures below its thermoneutral zone (TNZ).

Fig. 4. Picture of incubating birds huddling tightly during a blizzard. Note the reduction in body surface area exposed to the cold for birds inside the huddling group, and the snow on the surfaces still exposed to cold.

Mass-specific metabolic rate outside the thermoneutral zone (sFMR$_{LG}$)

According to Le Maho et al.'s equations (Le Maho et al., 1976) (see above):

$$sFMR = 1.08–0.08T_a ,$$

and at T_a of –16.6°C,

$$sFMR_{LG} = 2.41 \text{ W kg}^{-1} . \tag{6}$$

Mass-specific metabolic rate within the thermoneutral zone (sFMR$_{TNZ}$)

The mass-specific metabolic rate when birds are within their TNZ can be estimated from published respirometry measurements [1.98 W kg^{-1} (Le Maho et al., 1976) and 1.83 W kg^{-1} (Pinshow et al., 1976]. For our calculation, we used the 1.98 W kg^{-1} value (Le Maho et al., 1976). Hence,

$$sFMR_{TNZ} = 1.98 \text{ W kg}^{-1} . \tag{7}$$

Mass-specific metabolic rate when birds are huddling (i.e. packed; sFMR$_H$)

Under huddling conditions we estimated that only 26% of the body surface is still exposed to cold. Following our above assumption, metabolic rate of huddling birds would be reduced by 74%, compared to that of an isolated bird exposed to ambient temperatures below its thermoneutral zone. We chose to consider the metabolic rate of an isolated bird, exposed to wind, as the body surfaces (head, neck and upper back) still exposed to cold in huddles are submitted to wind-chill. Hence,

$$sFMR_H = 3.53×0.26 = 0.92 \text{ W kg}^{-1} . \tag{8}$$

Estimation of the energetic benefit accrued from warmer ambient temperatures and reduction of cold-exposed body surfaces

The sFMR for a free-ranging emperor penguin (sFMR$_{FR}$) that spends 10% of its time at ambient temperatures below –10°C, 41% at temperatures above –10°C (without being packed) and 49% huddling (i.e. being packed), would be as follows:

$$sFMR_{FR} = 0.10sFMR_{LG} + 0.41sFMR_{TNZ} + 0.49sFMR_H =$$
$$0.10×2.41 + 0.41×1.98 + 0.49×0.92 = 1.50 \text{ W kg}^{-1} . \tag{9}$$

Comparing this value to the sFMR of a bird spending 100% of its time exposed to an ambient temperature of –16.6°C (sFMR$_{LG}$=2.41 W kg^{-1}), illustrates that the warmer microclimate and the reduction in cold-exposed body surface averages a reduction in metabolic rate of 38%. This is much higher than the metabolic energy

savings accomplished by free-ranging birds (on average a 21% reduction in metabolic rate and 26% in body mass loss), when compared with loosely grouped birds; however, the above estimation of the metabolic rate for free-ranging birds is equivalent to Ancel et al.'s estimation of 1.5 W kg^{-1} (Ancel et al., 1997).

Estimation of the energetic benefit accrued from the reduction of cold-exposed body surfaces

In the above calculation, we considered both processes of energy savings, i.e. exposure to warmer ambient temperatures and reduction in cold-exposed body surfaces. To evaluate the energy savings due to reduction in cold-exposed body surfaces only, we compared the field metabolic rates of birds spending 90% of their time within their thermoneutral zone (sFMR$_{0.9TNZ}$), with the above calculation of sFMR$_{FR}$ (1.50 W kg^{-1}) for birds spending 41% of their time within their thermoneutral zone and 49% of their time packed in huddles:

$$\text{sFMR}_{0.9TNZ} = 0.10\text{sFMR}_{LG} + 0.90\text{sFMR}_{TNZ} = 0.10 \times 2.41 + 0.90 \times 1.98 = 2.02 \text{ W kg}^{-1}$$

and
$$\text{sFMR}_{FR} = 1.50 \text{ W kg}^{-1} . \tag{10}$$

Then, the energy savings due to the reduction in cold body surfaces would account for 26% within the 38% reduction in metabolic rate, representing about two thirds of this metabolic reduction. Assuming that energy savings due to exposure to warmer ambient temperatures and reduction in cold-exposed body surfaces are additive, exposure to a mild microclimate would then represent about one third of the overall reduction in metabolic rate. Contrary to the classic view (Prévost, 1961; Jarman, 1973), the role of ambient temperatures in energy savings would thus be of less importance than the reduction in cold-exposed body surfaces.

We must bear in mind, however, that the above estimates (sFMR$_{FR}$ and sFMR$_{LG}$) are based on metabolic rate measurements of captive birds, even if they were otherwise kept under natural conditions (Le Maho et al., 1976). These measurements thus overestimate the energy expenditure of penguins during breeding on their colony, either when isolated or loosely grouped. Ancel et al. estimated that the metabolic rate of loosely grouped birds was 1.8 W kg^{-1} (Ancel et al., 1997), which is 25% lower than our estimate of 2.41 W kg^{-1}. The overestimation of our study, based on Le Maho et al.'s calculations (Le Maho et al., 1976), might be explained by the stress caused by the manipulations, a different physiological status of the birds studied from birds in the colony, and/or the higher body temperatures of the birds studied in the laboratory [38.2°C, as determined by stomach temperature measurements (Le Maho et al., 1976)]. However, free-ranging emperor penguins maintain a metabolic rate equivalent to our estimate of 1.50 W kg^{-1} (Ancel et al., 1997). Thus, we must consider that the 38% reduction permitted by mild ambient temperatures and reduction in cold-exposed body surfaces were overestimated due to the 25% overestimation of the metabolic rate of loosely grouped birds. These calculations, applied to birds that maintained a higher body temperature, did indeed overestimate the energy savings due to the reduction in heat loss gradients. Heat loss gradients between body and external temperatures are indeed increased if body temperature is higher. Thus, lastly, we had to estimate the energy savings permitted by physiological adjustments in body temperature, which should reduce heat loss gradients and thus temporize the energetic benefits of ambient temperatures and reduced cold-exposed body surfaces in the above calculations.

Estimating energetic benefits from body temperature adjustments

Free-ranging emperors maintain a rectal temperature of 35.5°C, i.e. 1.1°C lower than loosely grouped birds (36.6°C) and 2.2°C lower than isolated birds [37.7°C (Prévost, 1961; Prévost and Sapin-Jaloustre, 1964; Mougin, 1966) (Fig. 1)]. Lowering deep body temperature is an efficient strategy for decreasing energy expenditure in birds and mammals [e.g. for birds (Butler and Woakes, 2001; McKechnie and Lovegrove, 2002)]. Free-ranging birds have a mean core temperature that is higher [36.7±0.3°C; mean ± s.d. (Gilbert et al., 2007)] than rectal temperatures measured by previous authors (Fig. 1), except for the temperature range reported by Groscolas, who measured a mean rectal temperature of 37.1°C for incubating and huddling birds (Groscolas, 1986). Free-ranging birds maintain a body temperature that is adjusted throughout their breeding cycle: it is lowered when pairing by 1.7°C, and maintained constant during incubation (Gilbert et al., 2007). Furthermore, during the short period of egg exchange, a highly active phase for the pairs, the body temperature of male emperor penguins significantly increases by 1.2°C, to reach 37.7±0.2°C (mean ± s.d.) (Gilbert et al., 2007); this is a body temperature 1°C higher than their mean body temperature. From newly analysed data, we can also approximate an active temperature of males before their breeding cycle, i.e. of newly arrived males on the colony, and after the completion of their incubation. During winter 2005, three males were equipped with body temperature loggers (SMAD, DEPE-IPHC, Strasbourg, France). Their temperature profiles were similar to our previous results: lowered during pairing and maintained during incubation at about 36.9±0.2°C (mean ± s.d.). Moreover, their body temperature at the beginning of the pairing period was 37.9±0.4°C, and their body temperature after their incubation, i.e. after they had exchanged the chick with the female, was 37.5±0.3°C (mean ± s.d.). Hence, while the emperor penguins' mean body temperature is on average 36.7°C during their breeding cycle, their body temperature at arrival and after departure from the colony averaged 37.7±0.4°C (mean ± s.d.). Body temperature adjustments should thus play an important role in the energy savings of breeding emperor penguins.

Reported mean stomach temperatures of isolated birds measured during respirometry studies in the laboratory were 37.8°C (Pinshow et al., 1976), 38.2°C (Le Maho et al., 1976) and 39.4°C (Dewasmes et al., 1980). As expected, the measured mass-specific metabolic rate (measured at rest, within the TNZ) of emperor penguins was positively correlated with stomach temperature: 1.83 W kg^{-1} (Pinshow et al., 1976), 1.98 W kg^{-1} (Le Maho et al., 1976) and 2.32 W kg^{-1} (Dewasmes et al., 1980), accounting for body mass differences, which were small: 23.4 kg (Pinshow et al., 1976), 24.8 kg (Le Maho et al., 1976) and 25.0 kg (Dewasmes et al., 1980). Dewasmes et al. discussed the link between the decrease in metabolic rate and body temperature decline, since mean stomach temperature in their birds ranged from 38.5°C to 40.0°C (Dewasmes et al., 1980). They suggested that a core temperature decrease of 1°C might reduce metabolic rate by as much as 40%. However, if we assume an apparent Q_{10} between 2 and 3, and that ambient temperature and conductance remain equal, a core temperature decline of 1°C (from 37.7°C to 36.7°C) would represent a reduction in metabolic rate by about 7–10% (Heldmaier and Ruf, 1992; Butler and Woakes, 2001). We could also use the values from the above studies to plot mass-specific metabolic rate as a function of body temperature (Fig. 5). Using this relationship, a core temperature decline of 1°C between temperatures of 37.7°C (active body temperature) and 36.7°C (observed during the breeding cycle), would thus represent a metabolic reduction of 17% (from 1.83 to 1.51 W kg^{-1}).

We can explain why loosely grouped birds may maintain a higher heat production and a body temperature higher by 1°C than free-ranging birds (Fig. 1) (Prévost, 1961; Prévost and Sapin-Jaloustre, 1964; Mougin, 1966). Assuming that tightly huddling penguins reduce their metabolic rate to the same extent as the reduction in cold-exposed body surface area, they run no risk of cooling off or overheating. By contrast, an emperor penguin in a small group is unable to achieve tight packing densities and, therefore, to drastically reduce its cold-exposed body surface area. A decline in metabolic heat production in this case would lead to body cooling that would jeopardize a successful incubation. Support for this hypothesis emerges from Prévost's first studies (Prévost, 1961). Thyroid glands of free-ranging male emperor penguins were sampled throughout their breeding cycle, and it was found that the epithelium thickness of these glands decreased after the arrival at the colony, was minimal from April to July, and finally increased again in August, when males departed to sea. Prévost concluded that the thyroid gland, active before arrival, was likely to be inactive during the males' breeding fast (Prévost, 1961). As the thyroid is the major organ stimulating thermogenesis, this implies that active thermogenesis is somehow depressed during the breeding fast of male emperor penguins. Furthermore, T3 and T4 plasma levels were reduced during incubation (Groscolas and Leloup, 1986). Inactivity of the thyroid gland can be linked to the metabolic depression occurring during huddling, and also to downregulation of the core temperature throughout the breeding cycle. Groscolas and Leloup also showed that the depressed plasma T4 level in incubating males was associated with a low body temperature, and suggested huddling behaviour as the cause (Groscolas and Leloup, 1986). This is consistent with body temperature profiles of breeding male emperor penguins recorded in the 2005 study. The possible link between huddling behaviour, reduction in thyroid hormone activity, and a reduced metabolic rate has also been suggested in reproductively inhibited huddling prairie deer mice *Peromyscus maniculatus bardii* (Cronin and Bradley, 1988).

Conclusion

We estimated that loosely grouped emperor penguins experienced a 32% metabolic reduction, as they could shelter themselves from the wind. However, we assumed that they would be protected from wind 100% of their time, neglecting the time when birds are on the windy side. Furthermore, we assumed that their whole body would be protected, which may not be the case, as heads and necks of penguins placed in the centre of these small groups would possibly still be exposed to cold. Thus, we presumably overestimated the savings due to wind protection. Moreover, when estimating the energetic benefit of huddling for free-ranging birds, we hypothesized that penguins spent 41% of their time within their thermoneutral zone, i.e. that their whole body surface was exposed to ambient temperatures above −10°C. This is presumably incorrect, however, as the heads and necks of birds should still be exposed to lower ambient temperatures. Indeed, we used recordings of ambient temperatures inside groups from data loggers glued to the lower back feathers of the birds. We thus presumably overestimated the effect of the mild ambient temperatures in the metabolic reduction due to huddling. Detailed measurements of wind and ambient temperatures experienced by the birds should be performed. This could be done by attaching several data loggers recording temperature on the feathers of the birds, on their chest, their head, and the upper and lower parts of their back. Though it could be criticised ethically, this would permit a better estimate of the microclimate surrounding the birds. Furthermore, we estimated that when birds were packed, their metabolic rate was
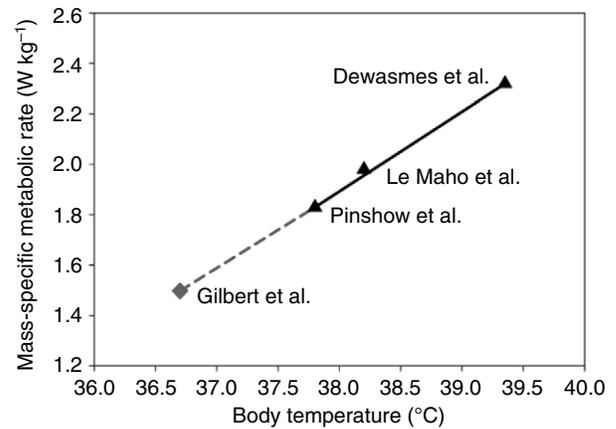

Fig. 5. Mass specific metabolic rate (sMR, W kg^{-1}) of emperor penguins plotted as a function of body temperature (T_b,°C). The relationship was best described by the linear regression: sMR=−9.937+0.312T_b (r^2=0.9973, P=0.033). (Data from Le Maho et al., 1976; Pinshow et al., 1976; Dewasmes et al., 1980; Gilbert et al ., 2007).

reduced by the extent of reduction in their cold-exposed body surfaces. This assumption is based upon our previous results, as body temperatures of tight huddling birds were either maintained constant or slightly lowered, while at the same time we noticed that snow did not melt on their heads during blizzards, suggesting that birds do not dissipate extra heat *via* these cold-exposed surfaces (Gilbert et al., 2007). Indeed, according to the experiment we designed, we estimated that 74% of cold-exposed body surfaces would be reduced, leading to a metabolic rate as low as 0.92 W kg^{-1}. This metabolic reduction occurring in tightly packed birds should, however, be tested, possibly using infrared thermography images, which would prove that the remaining cold-exposed body surfaces are not efficient thermal windows to dissipate heat, and thus that emperor penguins inside huddles enter metabolic depression.

Moreover, estimations of metabolic reduction due to wind protection, mild ambient temperatures within groups, and reduction in cold-exposed body surfaces were performed using metabolic equations designed with captive penguins that maintained higher body temperatures than birds in the colony. We thus overestimated the metabolic rate of isolated and loosely grouped birds. Mass-specific metabolic rates for a standard penguin of 30 kg, isolated and loosely grouped, would be 2.93 W kg^{-1} and 1.73 W kg^{-1}, respectively, according to Fig. 1. However, the values found from our calculations are 3.53 W kg^{-1} for isolated penguins and 2.41 W kg^{-1} for loosely grouped penguins. This represents an overestimation of 17% and 28%. However, the estimated metabolic rate of free-ranging emperor penguins is close to Ancel et al.'s estimation (Ancel et al., 1997). This is partly due to the high percentage of time spent inside huddles, while their metabolic rate is drastically reduced. Another limit to this study is that all the processes are linked together. We estimated independently the effect of wind protection, gained from being loosely grouped. We also assumed that microclimate warming and reduction in cold-exposed body surfaces benefits should be additive in huddling benefits. However, energy savings linked to a downregulation of body temperature should interfere with these three mechanisms, reducing their contribution through reduced heat loss gradients.

This study provides new insights into the processes involved in the energy savings due to grouping and huddling in free-ranging birds in their colony. We estimated that a major part of energy savings for

loosely grouped birds is due to wind protection (32%). Furthermore, though overestimated, exposure to mild ambient temperatures and reduction of cold-exposed body surfaces would represent a 38% reduction in metabolic rate. The reduction in cold-exposed body surfaces in huddling emperor penguins would account for about two thirds of the energy savings due to huddling. This contradicts pioneering hypotheses that attributed the major energy savings to the microclimate created within the huddling groups (Prévost, 1961; Jouventin, 1971; Jarman, 1973; Le Maho, 1977). However, it corresponds to the lower range of the benefits due to reduction in cold-exposed body surfaces in small mammals, representing 58–94% of huddling energy savings (Canals et al., 1997).

Hence this review, as a first-step analysis, provides an explanation of the complex contributions of four processes towards the energetic benefits gained by huddling. This study should permit the design of an improved model of energy savings in huddling emperor penguins, these energetic benefits being the key for them to successfully assume their incubation in the midst of the Antarctic winter.

References

Alberts, J. R. (1978). Huddling by rat pups: group behavioral mechanism of temperature regulation and energy conservation. *J. Comp. Physiol. Psychol.* **92**, 231-245.

Ancel, A., Visser, H., Handrich, Y., Masman, D. and Le Maho, Y. (1997). Energy saving in huddling penguins. *Nature* **385**, 304-305.

Andrews, R. V. and Belknap, R. W. (1986). Bioenergetic benefits of huddling by deer mice (*Peromyscus maniculatus*). *Comp. Biochem. Physiol.* **85A**, 775-778.

Andrews, R. V., Phillips, D. and Makihara, D. (1987). Metabolic and thermoregulatory consequences of social behaviors between *Microtus townsendii*. *Comp. Biochem. Physiol.* **87A**, 345-348.

Bautista, A., Drummond, H., Martinez-Gomez, M. and Hudson, R. (2003). Thermal benefit of sibling presence in the newborn rabbit. *Dev. Psychobiol.* **43**, 208-215.

Boix-Hinzen, C. and Lovegrove, B. G. (1998). Circadian metabolic and thermoregulatory patterns of red-billed woodhoopoes (*Phoeniculus purpureus*): the influence of huddling. *J. Zool.* **244**, 33-41.

Boyd, J. C. and Sladen, W. J. L. (1971). Telemetry studies of the internal body temperatures of Adélie and emperor penguins at cape Crozier, Ross Island, Antarctica. *Auk* **88**, 366-380.

Butler, P. J. and Woakes, A. J. (2001). Seasonal hypothermia in a large migrating bird: saving energy for fat deposition? *J. Exp. Biol.* **204**, 1361-1367.

Canals, M., Rosenmann, M. and Bozinovic, F. (1997). Geometrical aspects of the energetic effectiveness of huddling in small mammals. *Acta Theriol.* **42**, 321-328.

Cendron, J. (1952). Une visite hivernale à une rookerie de manchots Empereurs. *La Terre et la Vie* **40**, 101-108.

Chappell, M. A., Morgan, K. R. and Souza, S. L. (1989). Convection and thermoregulation in two Antarctic seabirds. *J. Comp. Physiol. B* **159**, 313-322.

Contreras, L. C. (1984). Bioenergetics of huddling - Test of a psycho-social hypothesis. *J. Mammal.* **65**, 256-262.

Cronin, K. L. and Bradley, E. L. (1988). The relationship between food intake, body fat and reproductive inhibition in prairie deermice (*Peromyscus maniculatus bardii*). *Comp. Biochem. Physiol.* **89A**, 669-673.

Cutrera, A. P., Antinuchi, C. D. and Busch, C. (2003). Thermoregulatory development in pups of the subterranean rodent *Ctenomys talarum*. *Physiol. Behav.* **79**, 321-330.

Dawson, C., Vincent, J. F. V., Jeronimidis, G., Rice, G. and Forshaw, P. (1999). Heat transfer through penguin feathers. *J. Theor. Biol.* **199**, 291-295.

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

Drent, R. H. and Stonehouse, B. (1971). Thermoregulatory response of the Peruvian penguin, *Spheniscus humboldti. Comp. Biochem. Physiol.* **40A**, 689-710.

Fedyk, A. (1971). Social thermoregulation in *Apodemus flavicollis* (Melchior, 1834). *Acta Theriol.* **16**, 221-229.

Fortin, D., Gauthier, G. and Larochelle, J. (2000). Body temperature and resting behavior of greater snow goose goslings in the high Arctic. *Condor* **102**, 163-171.

Gebczynska, Z. (1970). Bioenergetics of a root vole population. *Acta Theriol.* **15**, 33-66.

Gebczynski, M. (1969). Social regulation of body temperature in the bank vole. *Acta Theriol.* **14**, 427-440.

Gilbert, C., Le Maho, Y., Robertson, G., Naito, Y. and Ancel, A. (2006). Huddling behavior in emperor penguins: dynamics of huddling. *Physiol. Behav.* **88**, 479-488.

Gilbert, C., Le Maho, Y., Perret, M. and Ancel, A. (2007). Body temperature changes induced by huddling in breeding male emperor penguins. *Am. J. Physiol.* **292**, R176-R185.

Glaser, H. and Lustick, S. I. (1975). Energetics and nesting behavior of the northern white-footed mouse (*Peromyscus leucopus noveboracensis*). *Physiol. Zool.* **48**, 105-113.

Goldstein, D. L. (1983). The effect of wind on avian metabolic rates, with particular reference to Gambell's quail. *Physiol. Zool.* **56**, 485-494.

Gorecki, A. (1968). Metabolic rate and energy budget in the bank vole. *Acta Theriol.* **13**, 341-365.

Groscolas, R. (1986). Changes in body mass, body temperature and plasma fuel levels during the natural breeding fast in male and female emperor penguins *Aptenodytes forsteri. J. Comp. Physiol. B* **156**, 521-527.

Groscolas, R. (1988). The use of body mass loss to estimate metabolic rate in fasting sea birds: a critical examination based on emperor penguins (*Aptenodytes forsteri*). *Comp. Biochem. Physiol.* **90A**, 361-366.

Groscolas, R. and Leloup, J. (1986). The endocrine control of reproduction and molt in male and female emperor (*Aptenodytes forsteri*) and Adelie (*Pygoscelis adeliae*) penguins. II. Annual changes in plasma levels of thyroxine and triiodothyronine. *Gen. Comp. Endocrinol.* **63**, 264-274.

Guillard, R. and Prévost, J. (1964). Observations écologiques à la colonie de manchots empereurs de Pointe Géologie (Terre Adélie) en 1963. *L'Oiseau et la R. F. O.* **34**, 33-51.

Hayes, J. P., Speakman, J. R. and Racey, P. A. (1992). The contributions of local heating and reducing exposed surface-area to the energetic benefits of huddling by short-tailed field voles (*Microtus agrestis*). *Physiol. Zool.* **65**, 742-762.

Heldmaier, G. and Ruf, T. P. (1992). Body temperature and metabolic rate during natural hypothermia in endotherms. *J. Comp. Physiol. B* **162**, 696-706.

Howell, D. J. (1976). Weight loss and temperature regulation in clustered versus individual *Glossophaga soricina. Comp. Biochem. Physiol.* **53A**, 197-199.

Isenmann, P. (1971). Contribution à l'éthologie et à l'écologie du manchot empereur (*Aptenodytes forsteri* Gray) à la colonie de Pointe Géologie (Terre Adélie). *L'oiseau et la R. F. O.* **40**, 136-159.

Jarman, M. (1973). Experiments on the emperor penguin in various thermal environments. *Bull. Brit. Antarct. Surv.* **33-34**, 57-63.

Jouventin, P. (1971). Comportement et structure sociale chez le manchot empereur. *La Terre et la Vie* **25**, 510-586.

Le Maho, Y. (1977). The emperor penguin: a strategy to leave and breed in the cold. *Am. Sci.* **65**, 680-693.

Le Maho, Y., Delclitte, P. and Chatonnet, J. (1976). Thermoregulation in fasting emperor penguins under natural conditions. *Am. J. Physiol.* **231**, 913-922.

Martin, R. A., Fiorentini, M. and Connors, F. (1980). Social facilitation of reduced oxygen consumption in *Mus musculus* and *Meriones unguiculatus. Comp. Biochem. Physiol.* **65A**, 519-522.

McKechnie, A. E. and Lovegrove, B. G. (2001). Thermoregulation and the energetic significance of clustering behavior in the white-backed moosebird (*Colius colius*). *Physiol. Biochem. Zool.* **74**, 238-249.

McKechnie, A. E. and Lovegrove, B. G. (2002). Avian facultative hypothermic responses: a review. *Condor* **104**, 705-724.

Mougin, J.-L. (1966). Observations écologiques à la colonie de manchots empereurs de Pointe Géologie (Terre Adélie) en 1964. *L'oiseau et la R. F. O.* **36**, 167-226.

Pearson, O. P. (1960). The oxygen consumption and bio-energetics of harvest mice. *Physiol. Zool.* **33**, 152-160.

Perret, M. (1998). Energetic advantage of nest-sharing in a solitary primate, the lesser mouse lemur (*Microcebus murinus*). *J. Mammal.* **79**, 1093-1102.

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

Prévost, J. (1961). *Ecologie du Manchot Empereur, Expéditions Polaires Françaises.* Paris: Hermann Press.

Prévost, J. and Sapin-Jaloustre, J. (1964). A propos des premières mesures de topographie thermique chez les Sphéniscidés de la Terre Adélie. *L'oiseau et la R. F. O.* **34**, 52-90.

Robin, J.-P., Frain, M., Sardet, C., Groscolas, R. and Le Maho, Y. (1988). Protein and lipid utilization during long-term fasting in emperor penguins. *Am. J. Physiol.* **254**, R61-R68.

Scholander, P. F., Hock, R., Walters, V. and Irving, L. (1950). Adaptation to cold in arctic and tropical mammals and birds in relation to body temperature, insulation, and basal metabolic rate. *Biol. Bull.* **99**, 259-271.

Séguy, M. and Perret, M. (2005). Factors affecting the daily rhythm of body temperature of captive mouse lemurs (*Microcebus murinus*). *J. Comp. Physiol. B* **175**, 107-115.

Stahel, C. D., Nicol, S. C. and Walker, G. J. (1987). Heat production and thermal resistance in the little penguin *Eudyptula minor* in relation to wind speed. *Physiol. Zool.* **60**, 413-423.

Stanier, M. W. (1975). Effect of body weight, ambient temperature and huddling on oxygen consumption and body temperature on young mice. *Comp. Biochem. Physiol.* **51A**, 79-82.

Stonehouse, B. (1953). The Emperor penguin *Aptenodytes forsteri* Gray. I. Breeding behaviour and development. *Falk. Isl. Dep. Surv. Sci. Rep.* **6**, 1-33.

Stonehouse, B. (1967). The general biology and thermal balances of penguins. In *Advances in Ecological Research* (ed. J. B. Cragg), pp. 131-196. London: Academic Press.

Taylor, J. R. E. (1986). Thermal insulation of the down and feathers of pygoscelis penguin chicks and the unique properties of penguin feathers. *Auk* **103**, 160-168.

Tertil, R. (1972). The effect of behavioral thermoregulation on the daily metabolism of *Apodemus agrarius* (Pallas, 1771). *Acta Theriol.* **22**, 295-313.

Vickery, W. L. and Millar, J. S. (1984). The energetics of huddling by endotherms. *Oikos* **43**, 88-93.

Walsberg, G. E. and King, J. R. (1978). The relationship of the external surface area of birds to skin surface area and body mass. *J. Exp. Biol.* **76**, 185-189.

Yahav, S. and Buffenstein, R. (1991). Huddling behavior facilitates homeothermy in the naked mole rat *Heterocephalus glaber. Physiol. Zool.* **64**, 871-884.