

The Emperor's Domain: Adaptations & Energetic Requirements for Life on the Ice

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The Antarctic environment is renowned for being among the most extreme on earth, presenting a range of challenges to any organism living there. One of the most successful species to do so is the Emperor penguin (*Aptenodytes forsteri*). Emperor penguins owe this capability to the evolution of a variety of anatomical, physiological and behavioural adaptations. This review sets out to explore the relationship between some of these adaptations, as well as the energetic requirements for living and breeding on the ice.

Evolution

Emperor penguins live at an average latitude of 66.7°S where temperatures drop to around -60°C and wind gusts reach 180 kilometres per hour (Croxall and Davis 1999). However, the emperor penguin or its ancestors did not always live in such an environment. Penguins evolved in the Cretaceous (between 140-65 million years ago), when the earth was generally warmer than it is at present (Baker *et al.* 2006). *Aptenodytes* is thought to be the basal penguin lineage from which other extant genera diverged, and as temperatures decreased most of these genera were either already further north or migrated north and adapted to the conditions there. However, *Aptenodytes* and *Pygoscelis* remained in Antarctica and adapted through the process of natural selection to the climate as it changed (Baker *et al.* 2006).

Energetic requirements

Emperor penguins are the only bird species to live entirely on the ice and doing so means travelling distances of 200km during breeding, going without food for up to 125 days and replacing their plumage in its entirety once a year. There is selection for those traits that make the individual possessing them more likely to survive and reproduce in its environment. Adaptive traits, such as those that economise the use of energy, increase the chance of that individual's genes being passed to the next generation and so confer a fitness advantage (Freeman and Herron 2001). While traits conducive to living in a polar environment should not be interpreted as having been initially selected for that reason, it is likely that its adaptive value has at least in part ensured its persistence (Fordyce and Jones 1990). For the Emperor penguin, traits that economise the use of energy stores are likely to aid survival and reproduction and so confer a fitness advantage.

Survival

Body size

Emperor penguins are the largest of the 17 extant penguin species (Kooyman 2002), standing at 1-1.3m tall and weighing about 36kg (Marchant and Higgins 1990), but fossil evidence suggests some of the earlier penguin species were much larger (Simpson 1975). Being a larger allows greater storage of energy reserves, which in turn makes extended fasting periods more feasible. Simpson (1976) describes the tendency for birds living in colder environments to be heavier. Greater size is thought to aid survival in particularly cold conditions, since the ratio of volume to surface area is greater, promoting heat retention. However, it is important not to assume that emperors are large or heavy for insulation purposes alone. While the insulation advantages associated with being large might have contributed to selection of the trait, it should not be assumed that large size is an exclusive product of the cold environment. A range of other factors, are likely to have favoured its selection, particularly in light of the fossil evidence (Fordyce and Jones 1990).

Emperor penguins also have reduced appendages, even in comparison to its closest living relative, the King penguin, which is a much lighter bird (Müller-Schwarze 1984). Having smaller appendages reduces heat loss thereby retaining core body temperature (Kay 1998). Similarly, temperatures in these appendages can also be significantly lower than the core body temperature, (which averages at about 37.5°C). Ponganis *et al.* (2003) found that Emperor penguins employ regional heterothermy while diving; wing and foot veins temperatures reduced to almost 0°C, averaging at 7.6 and 20.2°C respectively.

Insulation

Emperor penguins rely heavily on their plumage for insulation in the air (Dewasmes *et al.* 1980) and it is likely to play an important insulation role in water too. However, Ponganis *et al.* (2003) found sub-feather

temperatures dropped between 10-20°C during diving, suggesting that insulation provided by even fully grown plumage is less efficient in water than air. A thick layer of blubber also plays a role in insulation. It is metabolically inactive, so blood it can be diverted away from the surface of the penguin, increasing the insulation the blubber provides (Randall *et al.* 1998). The combined insulation provided by plumage and blubber, along with the employment of counter-current heat exchange allows an emperor penguin to withstand -10°C temperatures before needing to use energy stores to maintain core body temperature (Groscolas 1990).

Reproduction

In addition to the challenges individuals face in merely surviving in this environment, they must also invest in reproduction to ensure the long term viability of the species. A single egg is produced in winter, incubated on the feet and under the abdominal fold of the male penguin. This traditional role reversal is unique among penguins (Groscolas and Robin 2001), and is likely to be due to inability of the female to continue fasting after having invested energy into egg production. While the initial egg mass, at 450 grams, is greater than that of any other extant penguin, it is the smallest relative to the body weight of an adult Emperor (2.3%) (Williams 1995). This is consistent with the general trend for larger penguins to produce eggs that represents a smaller proportion of adult body weight. Assuming that larger birds tend to live at higher latitudes, this might indicate that these environments impose greater demands on energy economy and the smaller relative egg sizes are a reflection of the trade-off between conservation of energy in the female and initial investment in reproduction.

Fidelity

Among penguin species, Emperors have the lowest rate of fidelity (15%) (Croxall and Davis 1999). This does not seem to have any correlation with reproductive success. The decision to locate last season's mate or find a new one is likely to depend on the relative associated costs. It would seem that for the Emperor penguin, the cost of finding a new mate is generally outweighed by the cost of locating the previous one. Williams (1995) suggests that finding a previous mate is more costly if there is no fixed nesting site at which to meet because it could cause delays in breeding. Alternatively, it could be that last season the pair did not co-ordinate their duties as well as they could have and so look for a more compatible partner (Williams 1995).

Energy reserves

Male Emperors sacrifices all food intake for up to four months to court a mate and if successful to incubate the resulting egg. This requires careful judgment of the energy reserves required in anticipation of the fasting period. Insufficient reserves would ultimately result in abandonment of the egg or young chick to re-feed. However, surplus energy stores might come at the cost of reduced manoeuvrability, thereby increasing the risk of predation while foraging.

Energy stores can be in the form of fat, protein or carbohydrates. Approximately 30% of a male emperor's body mass immediately prior to the fasting period is fat (Dewasmas *et al.* 1989). This fat is an Emperor's main source of energy and is stored in the adipose tissue. It is accumulated at a greater rate than that at which it is depleted. Stored protein is also used, but it cannot be depleted to the same extent that fat can. An emperor penguin cannot survive any more than a 50% loss of its protein stores (Gilbert *et al.* 1996). Glycogen is not used as an energy reserve in Emperor penguins (Groscolas 1990). Approximately a third of the reduction in body mass is lost in the form of water and water accounts for 61% of total body mass for breeding Emperors in July, down from 71% in December (Robertson and Newgrain 1996). This is likely to indicate dehydration during incubation.

Locomotor activity

A reduction in locomotor activity levels helps to conserve energy. Penguins have short legs (in particular, the tarso-metatarsus) and this means their centre of mass is...? Yet it has been estimated that less than 4% of total energy expenditure while fasting is spent on locomotion. When the birds *do* walk, it seems their metabolic rate decreases with decreasing body mass and temperature (Dewasmes *et al.* 1980). Thus, a penguin moves more efficiently after having fasted than prior to it. The drop in energy expended while

walking is useful for fasting penguins with little remaining energy reserves to travel from the rookery to the sea in order to forage, this distance potentially having increased to 200km during winter with sea ice formation (Dewasmes *et al.* 1980).

One study found that until that body mass loss was proportional to body mass, until that mass dropped to 23 kg, at which point loss rate increased. (Dewasmes *et al.* 1980). This was attributed to the increased locomotor activity associated with the latter stages of the fast. However, this conclusion does not necessarily follow. It is arguable that the converse is true; increases in locomotor activity levels might be in response to an increase in the rate of body mass loss. At approximately 23kg, the relative levels of lipid and protein utilisation reverses, so that protein becomes an increasingly important source of energy (Groscolas 1990). The energy concentration of protein is less than that of lipids and so this could explain the increased body mass loss at this stage in the fast. It seems that the energetic costs of walking relative to 'tobogganing' have not yet been investigated.

Huddling

As temperatures decrease during the breeding fast period, an emperor will have to increase its metabolic rate in order to sustain its core body temperature (Groscolas 1990). To offset this, Emperor penguins huddle together, reducing metabolic rate by about 40%. This behaviour is unique to the Emperor penguin (although it has also been observed in juvenile King penguins) and temperatures within the huddle regularly exceed 20°C. The accrued energy savings allow penguins to sustain itself at least a further 3 weeks before needing to re-feed, relative to those that do not engage in huddling (Ancel *et al.* 1997).

Larger huddles are more able to efficiently conserve heat and groups can be made up of several hundred birds, with up to 10 individuals per square metre (Gilbert *et al.* 2006). Huddling tends to occur at night, when temperatures are likely to be coldest (and this trend holds even after taking into account that night represents a greater proportion of time than day during winter) (Gilbert *et al.* 2006). Gilbert *et al.* found that emperor penguin huddles varied greatly in length, but most tended to last less than 2 hours. One reason for limiting the length or frequency of huddles might be to avoid becoming too warm. Ambient temperatures within the huddle have been recorded as high as 37.5°C which could cause hyperthermia in an adult or alternatively could harm an egg, which has an optimal incubation temperature of about 35°C (Gilbert *et al.* 2006). Each bird seems to receive equal benefit and this (and huddling in general) relies on the unique lack of territoriality exhibited in Emperor penguins (Kirkwood and Robertson 1997a).. This in itself also allows the conservation of energy that otherwise would be expended maintaining territorial boundaries.

Sleeping

During fasting, Emperor penguins reduce their metabolic rate, and thus their rate of body mass loss, by increasing the amount of time they spend sleeping. It was found by Dewasmes *et al.* (1989) that non-fasting emperor penguins spent equal amounts of time awake as asleep. When the birds were fasting, they tended to sleep for longer periods which were punctuated by less frequent periods of wakefulness.

This strategy of increasing sleep duration would only be adaptive in environments with a lack of predators of which to be wary (Dewasmes *et al.* 1989). There are no land-based predators from which an adult emperor would need to remain vigilant for. This means that sleep does not come with any increased risk of predation and so has adaptive value. Equally, because fasting and foraging sites are far apart, there is no reason to stay alert for chance feeding opportunities.

Body mass loss

Energy expenditure during fasting can be estimated by the rate of body mass loss. In contrast to smaller penguin species, the Emperor's rate of loss tends to change over time (Groscolas 1990). Initially the rate of body mass loss is high, but this slows and becomes a more steady loss rate for the majority of the four month fast. However, once the fast extends beyond about 125 days without relief from the female, an increasing loss rate is observed. Here the fat stores have been almost completely depleted and the penguin relies increasingly on its remaining protein reserves for energy.

Re-feeding signal and egg abandonment

It seems that the birds have an endogenous re-feeding signal that is triggered when a bird has depleted its energy stores to a critical level below which it will begin to increase frequency and length of locomotor activity before abandoning the incubating egg altogether (Groscolas 2001). This critical point seems to be triggered before a bird has depleted its reserves to such an extent that it is unable to successfully re-feed. The signal is therefore adaptive, allowing the adult to recover and potentially make another attempt to reproduce the following year (Groscolas and Robin 2001). Without this re-feeding signal, neither the parent nor chick would survive, since the parent would not have sufficient energy reserves to fulfil its role in the continual alternation with its partner to foraging and fast in the following 6 months.

Fasting with a full stomach

Once the female has returned to the rookery, each parent takes it in turn to guard the young chick, while its partner forages. During the guarding phase, a parent will continually supply its chick with food stored in the stomach which has been prevented from being digested. Thus, the parent is fasting – despite the food content in its stomach. Each parent makes seven or eight trips to forage and about 84 kg of food is required by the chick over 5 months until it is able to feed on its own (Robertson and Newgrain 1996). While the percentage of food intake required by the growing chick increases over time, this still only amounts to a maximum of 16% of the daily food quantity ingested (Robertson and Newgrain 1996). This seems to have similar adaptive value to the re-feeding signal discussed above, where the parent will not sacrifice its own survival for that of the chick's. However, foraging becomes relatively more efficient over time; each trip tends to be quicker than the last, since the distance travelled to get to the sea decreases as temperatures increase and ice breaks up and light availability increases allow greater time to be spent foraging (Kirkwood and Robertson 1997b).

Foraging strategy

Emperor penguins have been observed to double their food intake while raising chicks relative to the amount ingested when feeding for exclusive consumption only (Kirkwood and Robertson 1997b). They tend to forage in daylight hours and as these hours increase, so too does the time they spend foraging (Kirkwood and Robertson 1997b). The main sources of food are krill, squid and silverfish and the penguins adjust their foraging strategies depending on which are more available (Kooyman 2002). Kirkwood and Robertson (1997a) suggest that deep diving is more energetically expensive but might result in a better quality food source. If this food source provides a net benefit that is greater than that received through shallower dives it is an energetically efficient strategy to do so.

Nagy *et al.* (2001) found no significant difference in energy expenditure between Emperor Penguins that dived for food or were hand fed (and so did not have to dive). This result is surprising, given that the birds swim at speeds of about 3-4 metres per second (Kooyman *et al.* 1992), faster than those recorded for other species and dive to depths of up to 500m or for up to 20 minutes. Nagy *et al.* (2001) interpreted the results to indicate that diving is not very energetically expensive. However, one could argue that a range of other variables could have confounded the results. For example, those penguins prevented from diving and handfed might have had increased stress levels, which would work to mask the energy spent in birds allowed to forage for food.

Moulting fast

On average 40% of body mass is lost during the breeding fast. Surprisingly, the yearly moulting fast which, for the comparatively short period of 5 weeks, results in an average body mass loss of 45%. This can in part be attributed to the increased thermoregulatory costs while the new feathers are growing. Prior to the loss of the old feathers, new ones begin to come through and the former are lost. However, these new feathers initially do not yet provide sufficient insulation for the birds to enter the cold water to forage, hence the need to fast. Penguins and Emperors in particular, have greater feather distribution and thickness relative to other birds. (Müller-Schwarze 1984).

Energy store comparisons

Interestingly, Emperor penguins employ different strategies in terms of the type of energy stores utilised during the breeding and moulting fasts. While fat is still the main source of energy, protein losses are about 50%, which is very high relative to the 16% loss during the breeding loss (Groscolas and Chérel 1992). One explanation for the greater use of body protein is that the constituent amino acids are used in feather production. Whether the different utilisation of energy reserves are due to the type of fast, its relative length or a combination of the two is unclear.

Conclusion

According to Jouventin (1975) “the climatic regime is [an emperor penguin’s] only enemy and Nagy *et al.* (2001) suggests that the energetic expenditure of penguins do not significantly differ to birds living in more temperate environments. However, this should not be interpreted as an indication that Antarctica’s environment is any less demanding than previously alleged. Instead, it is a reflection of the range of interrelating anatomical, physiological and behavioural adaptations possessed by penguins at high latitudes, allowing them to live there in an energetically efficient way.

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