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Long-term fasting and re-feeding in penguins

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Abstract

Spontaneous fasting during reproduction (sometimes with a full stomach) and moult is a major characteristic of the annual cycle of penguins. Long-term fasting (up to four months in male emperor penguins) is anticipated by the accumulation of fat (incubation fast) and of fat and protein (moult fast). During most of the incubation fast, birds rely almost entirely on lipids as an energy source, body proteins being spared. However, below a critical (but non-total) fat store depletion, marked behavioural, metabolic, and endocrine changes occur. Spontaneous locomotor activity increases and the egg is transitorily left unincubated for increasingly long periods, until its definitive abandon and the bird departs to re-feed at sea. These changes are thought to be activated by an endogenous re-feeding signal triggered before lethal energy depletion. An increase in body protein catabolism in the face of a reduction in lipid availability and utilisation, and an increase in circulating corticosterone vs. a decrease in plasma prolactin, are likely to be major metabolic and hormonal components of this signal. The survival and rapid restoration of energy stores in birds having departed to re-feed at a stage of near total lipid depletion demonstrates the effectiveness of the re-feeding signal. Penguins, and possibly other seabirds, are therefore appropriate animal models for understanding the long-term interactions between body energy reserves and fasting, breeding and feeding physiology and behaviour.

Introduction

Alternating long periods of feeding and fasting is the usual way of life for many wild mammals and birds. Fasting occurs because food is unavailable, e.g. during winter, or because feeding competes with other activities having priority for survival of individual or species, such as moult, migration and reproduction. Long-term fasting is common in seabirds, including Sphenisciforms (penguins) and Procellariiforms (petrels and albatrosses). These birds feed exclusively at sea, on fishes, crustaceans and squids, but must stay on land for prolonged periods when breeding, particularly during incubation (Williams, 1995, Warham, 1996). Moreover, penguins entirely replace their whole plumage each year and must spend a long-time fasting ashore because the consequent reduction in thermal insulation precludes staying in cold antarctic and subantarctic waters for feeding (Groscolas and Cherel, 1992). Depending on the species, the duration of the moult fast ranges from 2–5 weeks. During breeding, both mates alternate at incubating (except in the emperor penguin *Aptenodytes forsteri* where only the male incubates the egg) and feeding the chick(s) so that for several months they alternate periods of anorexia on land and hyperphagia at sea. As a general rule, the larger the species, the longer the fast the bird can cope with. In the smallest penguins, the little blue penguin (*Eudyptula minor*), fasting periods last 1–3 days (Williams, 1995). At the other extremity of the size range, the male emperor supports a 4-month fast while courting and then incubating on the sea-ice in the middle of the antarctic winter (Prévost, 1962). In middle-sized penguins, the duration of breeding fasts is approximately 2 weeks. In the king penguin (*Aptenodytes patagonicus*), not only do the adults fast for up to 1 month during breeding but the chicks may have to fast for up to 5 months because of winter food shortage, which temporarily stops their growth (Cherel and Le Maho, 1985).

How penguins can face long periods of total starvation while breeding and moulting, sometimes under harsh climatic conditions, has been examined in several studies over the last decades. The study of the foraging strategies of these birds is more recent and has benefited from the development of miniaturised electronic devices (Wilson, 1995). Besides improving our understanding of the adaptation to the antarctic and subantarctic environment (both terrestrial and marine), the study of fasting and feeding physiology of penguins may provide information on the long-term control of energy balance, notably on the interrelationships between energy reserves and fasting or feeding behaviour. The present paper focuses on the breeding fast of emperor and king penguins and is directed towards: (i) reviewing some of the major findings on their adaptation to long-term fasting; and (ii) answering the question of how a spontaneously fasting penguin knows that it is time to re-feed.

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Storage of energy reserves

Surviving a long period of total starvation while active, as breeding penguins do, is obviously possible only if a bird can rely on energy reserves. In penguins as in naturally fasting mammals, fat stored in adipose tissue is by far the major energy reservoir. In male emperor penguins, body fat at the beginning of the breeding fast represents approximately 30% of the body mass and 80% of body energy (Groscolas, 1982a, Groscolas, 1990). In the king penguin, the respective numbers are 18 and 60% (…

Spontaneous egg abandon

Normally, a fasting incubating penguin goes to sea for re-feeding and restoring its energy reserves when it is relieved in the incubation duties by its partner. On average, this relief occurs at body masses close to 23.5 and 10 kg in emperor (Prévost, 1962, Groscolas, 1986) and king penguins (Cherel et al., 1994b), respectively. At these body masses, 20–30% of the initial fat stores remain (Groscolas, 1990, Cherel and Groscolas, 1999) and the birds are still in the metabolic and endocrine…

Acknowledgements

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and occurs when feeding becomes of lesser importance compared to other needs, such as moulting or, precisely, reproduction (Castellini and Rea, 1992; Groscolas and Robin, 2001; McCue, 2013). By analogy to extant organisms, titanosaurians from Quebrada de Santo Domingo would have been well set to endure fasting, starting with a good fasting endurance due to their large size and the proportionally high amount of stored fat (Lindstedt and Boyce, 1985; Groscolas and Robin, 2001)....

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