

Changes in body mass, body temperature and plasma fuel levels during the natural breeding fast in male and female emperor penguins *Aptenodytes forsteri*

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Summary. 1. Changes in body temperature (T_b), body mass, plasma glucose, free fatty acid (FFA) and β -hydroxybutyrate levels were investigated in free-living male and female emperor penguins throughout the 115- and 45-day, respectively, natural breeding fast on the sea-ice. Moreover, changes during a prolongation of this fast that mimicked the supplementary energy expense for walking back to the open sea, were also studied in captive emperors.

2. A decrease of the daily weight loss (DWL), T_b and plasma fuel levels during the days following the arrival in the breeding area (Table 1) probably reflected recovery from the strenuous exercise emperors had to perform walking towards the colony.

3. Plasma FFA levels were slightly and markedly increased during oesophageal 'curd' secretion in males, and egg-yolk formation in females, respectively. Marked hyperthermia and hyperglycemia was observed during egg laying in females.

4. Long-term natural fasting was characterized by homeothermia (37.1 °C), maintenance of high plasma glucose (12.8 mmol/l) and moderate plasma FFA (0.7 mmol/l) levels, and progressive modest ketosis (1.5 mmol/l) (Figs. 1 and 2), which probably reflect continuous availability and preferential utilization of fat stores.

5. During prolongation of the fast, marked increases in DWL and decreases in plasma FFA and β -hydroxybutyrate were indicative of a metabolic shift from fat towards protein utilization after fat depletion. The decrease in plasma lipid fuels might serve to trigger the spontaneous interruption of the natural fast.

Introduction

Reproduction in the emperor penguin (*Aptenodytes forsteri*) is unique in that it is associated with prolonged periods without feeding under drastic climatic conditions. Indeed, this non-flying polar sea-bird breeds on the sea-ice during the antarctic winter (mean air temperature around -20 °C, frequent blizzards with wind speeds of 100 to 200 km/h), in a few favourable zones which may be several hundred kilometers distant from the open sea where it feeds. As a consequence of the distance from the feeding grounds, and because breeding activity competes with feeding, male and female emperors fast for as long as 4 months and 45 days, respectively, during the reproductive period. In males, this period of fasting includes courtship (45 days), whole incubation (65 days), and lastly, feeding of the newly-hatched chick by means of an oesophageal 'curd' secretion (10 days). The end of the fasting sojourn in the colony usually corresponds with the return of the female to which the chick is left (Prévost 1961). In females, the 'breeding fast' comprises only the courtship period, since they leave their only egg to their mate as soon as it is laid and then go back to the sea for feeding. To this fasting period in the colony one must add the time spent by penguins travelling between the open sea and the breeding grounds at the onset of the reproductive period, and then back to the sea after egg laying (females) or chick exchange with the female (males). Several days are required for each trip. Besides this prolonged period of starvation, male and female emperors also fast for shorter durations when rearing the chicks (trips on the sea-ice and sojourns in the colony to regurgitate sea-food).

Survival during this period of complete starvation depends to a large extent on the availability of metabolic fuels for energy metabolism, especially for maintenance of body temperature and for breeding activity, egg laying and production of oesophageal 'curd' secretion, and implies various metabolic adaptations. Previous studies have shown the primary role of fat stores in energy supply in fasting emperors (Groscolas and Clément 1976; Groscolas 1982a) and have described the changes in plasma free amino acid (Groscolas et al. 1975) and lipid (Groscolas 1982b) levels throughout reproduction. Some other aspects of the emperor penguin's strategy to live and breed in the cold have been reviewed by Le Maho (1977). To further assess the adaptations in energy and intermediary metabolism during the prolonged breeding fast, and to better understand the emperor's reproductive physiology, changes in body temperature, weight loss, and in plasma fuel levels (glucose, FFA, β -hydroxybutyrate) were investigated in free-living emperor penguins. Logistic facilities allowed investigations in birds fasting in the colony, but not during their trips between the colony and the sea. This would have been of a considerable interest because previous observations in males and females leaving for the sea at the end of their prolonged sojourn in the colony have shown that fat stores were very reduced (Groscolas 1982a). In view of the high energy cost of walking in emperors (Dewasmes et al. 1980), fat stores might be completely depleted during the travel back to the sea and marked metabolic changes might consequently occur. In order to test this hypothesis, and to get insight into the limitations of fasting capacity in relation to energy reserves, the above parameters were also measured in confined, starving birds, thereby protracting the natural breeding fast, and thus mimicking the supplementary energy expense for walking back to the sea.

Materials and methods

Animals. This study was carried out in Adelie Land (66°40'S, 140°01'E, Antarctica) at the French station Dumont d'Urville. Daily observations allowed the determination of the breeding stage and of the activities of the birds at the time of blood sampling. Birds were marked with paint on their backs to allow individual observation and repeated blood sampling. Marking was done chiefly on the arrival in the rookery at the beginning of breeding (early April), or at the beginning of incubation, so that the duration of fasting or incubation could be determined. Auditive signal dimorphism (Jouventin 1972), or behavioral discrimination (copulation, laying, incubation etc.) allowed sex determination. Emperor penguins are quiet birds and so they were disturbed as little as possible during blood sampling and most of the sampled birds succeeded in breeding.

At the end of the breeding fast, when leaving the colony to feed in the sea after egg laying (mid-May, females), or chick exchange with females (late July, males), a few birds were caught and kept in a fenced area in their natural climatic environment. They were experimentally starved for about 20 more days with fresh snow ad libitum, and then refed and released.

Blood sampling. Males and females were sampled throughout their whole breeding fast in the colony every 15 ± 3 days. However, the period of laying (females), and that following the arrival in the colony (onset of courtship, first chick feeding with sea-food) were studied in more detail, only few days, or even a few hours, between successive samplings. Birds were also sampled at characteristic stages of breeding such as copulation, beginning of incubation, hatching and chick feeding with oesophageal 'curd' secretion that roughly corresponded to day 30, 45, 105 and 110 of the fast in the colony. During starvation in the fence, the birds were sampled after 10, and then 20, days of confinement. From the data of Dewasmes et al. (1980) it could be roughly estimated that the energy expense, and thus the consumption of energy stores, corresponding to a 10-day fast in the fence is equivalent to that of a 100-km walk on the sea-ice. According to Pinshow et al. (1976) distances to be covered by the animals may range from 100 to 200 km.

Climatic data. Mean monthly values for air temperature and wind speed, and the total monthly sunshine were kindly supplied by the meteorological station of the Dumont d'Urville station, situated less than 1 km away from the colony.

Body weight. Body weight was measured to the nearest 50 g every day during the fast in the fence, during the first days in the colony at the onset of courtship, and at the onset of chick feeding with sea-food. In both sexes body weight was also determined at the beginning and at the end of the breeding fast in the colony.

Body temperature. Deep rectal temperature (T_b) was measured to the nearest 0.1 °C with a thin mercury thermometer inserted 8–10 cm into the rectum for at least one minute until thermal equilibrium was reached. This measurement was taken during blood sampling.

Blood sampling and analytical procedures. Immobilization and sampling technique by I.V. puncture were as reported previously (Groscolas et al. 1975; Groscolas 1978). Catching and blood sampling were always under natural climatic conditions and done as quickly as possible (less than 5 min); a few values from excited birds were discarded. In order to reduce the influence of possible circadian variations in plasma fuel levels and T_b , all blood samples were taken in the afternoon, between 1 and 5 p.m.

Blood was centrifuged at +4 °C and extracted or deproteinized immediately after sampling. Analytical procedures were exactly as reported previously (Groscolas 1978).

The data were analysed statistically by analysis of variance, or by Student's *t*-test. Significance was $P < 0.05$ in all cases.

Results

Climatic data

Except for the total monthly sunshine, there was no marked change in climatic data from April to August. Mean air temperature was -16.1 °C, with

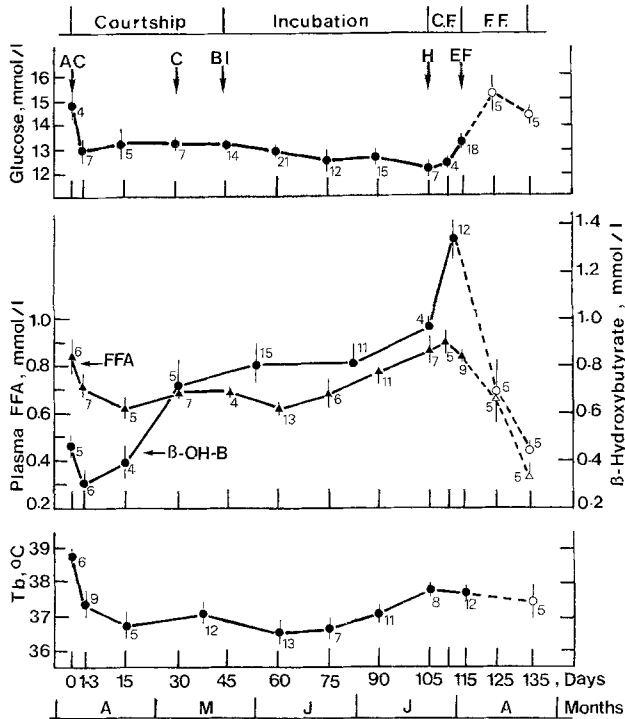


Fig. 1. Changes in body temperature (T_b) and plasma fuel levels during the natural breeding fast (filled symbols, continuous line) followed by experimental starvation (open symbols, dotted line) in male emperor penguins. Numbers besides means indicate the sample size and vertical bars show SEM. AC arrival in the colony; C copulation; BI beginning of incubation; H hatching; EF end of the fast in the colony; CF chick feeding with oesophageal secretion; FF forced fasting in a fence

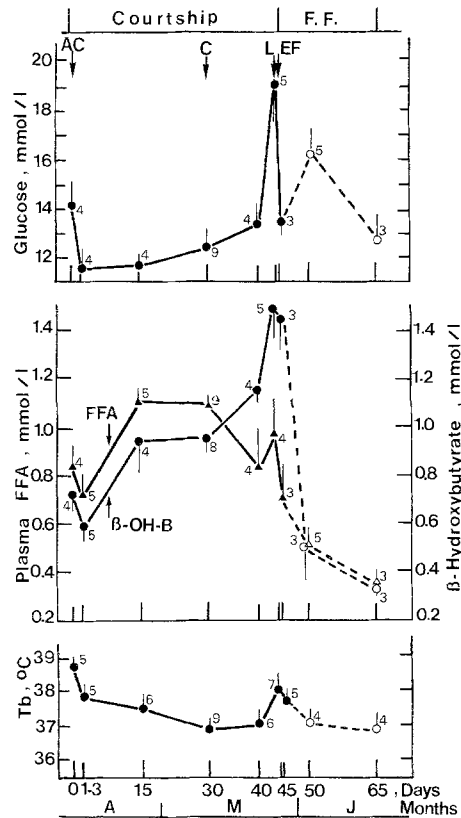


Fig. 2. Changes in body temperature (T_b) and plasma fuel levels during the natural breeding fast (filled symbols, continuous line) followed by experimental starvation (open symbols, dotted line) in female emperor penguins. Number besides means indicate the sample size and vertical bars show SEM. L laying; other abbreviations as in Fig. 1

minimum and maximum values of -33.5 and -1.8 °C, respectively. Mean monthly wind speed ranged from 5.5 (July) to 11.2 $m\ s^{-1}$ (August). The total monthly sunshine decreased from 119 h in April to 10 h in June and then increased to 100 h in August.

The first days in the colony

Simultaneous decreases in T_b , DWL and plasma fuel levels were observed in males and females during the days following arrival in the colony at the beginning of breeding (Figs. 1, 2), and at the onset of chick feeding with sea-food. Table 1 summarizes these changes, data for both sexes and beginnings of sojourn in the colony being pooled. DWL decreased significantly by 52% , T_b by 1.6 °C, plasma glucose and FFA by 10.5 and 15% , respectively, between arrival and 7–15 days later; reduction in plasma β -hydroxybutyrate was 34% after 1–3

days. The major decreases occurred during the first three days following arrival. Only changes occurring after the first week in the colony will be considered in the following results.

Breeding fast in males

Mean body weight was 38.2 ± 0.7 kg ($N=9$) and 22.75 ± 0.4 kg ($N=19$) at the beginning and at the end of the fast, respectively, i.e. there was a 40.5% total loss of body weight during the sojourn in the colony.

In free-living males, T_b , plasma glucose and FFA remained essentially unchanged throughout the breeding fast (Fig. 1); means were 37.1 ± 0.1 °C ($N=68$), 12.9 ± 0.1 ($N=103$) and 0.70 ± 0.02 mmol/l ($N=67$), respectively. However, plasma FFA and T_b were slightly higher during the final stages of the fast (hatching, chick feeding with oesophageal secretion, chick exchange, departure to

Table 1. Changes in daily weight loss (DWL), body temperature (T_b), and plasma fuel levels during the days following the arrival in the breeding colony

	Time in the colony		
	Arrival (day 0)	Days 1–3	Days 7–15
DWL (g/day)	486 ± 66 (7)	359 ± 37 (8)	232 ± 7** (6)
T_b (°C)	38.85 ± 0.10 (16)	37.75 ± 0.15*** (20)	37.25 ± 0.30*** (11)
Glucose (mmol/l)	14.28 ± 0.39 (16)	12.89 ± 0.17** (21)	12.77 ± 0.33** (22)
FFA (mmol/l)	0.87 ± 0.04 (14)	0.74 ± 0.03* (21)	0.74 ± 0.06 (9)
β -hydroxybutyrate (mmol/l)	0.73 ± 0.10 (9)	0.48 ± 0.06* (18)	–

Mean values ± SEM; numbers of values are in parentheses (values in females at day 15 of the breeding fast were discarded)

* significantly different from arrival, $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

sea) than during courtship and incubation. Compared to mid-incubation, T_b was 1.2 °C higher ($P < 0.01$) and plasma FFA 50% higher ($P < 0.001$). During the whole breeding fast, plasma FFA and T_b were directly related ($P < 0.01$). Plasma β -hydroxybutyrate rose continuously with time; it peaked at 1.35 mmol/l (chick feeding with oesophageal secretion, departure to the sea), a level 4 fold above ($P < 0.001$) the level in early courtship.

Breeding fast in females

Mean body weight was 29.5 ± 0.4 kg ($N = 7$) and 23.05 ± 0.7 kg ($N = 7$) at the beginning and at the end of the fast, respectively, i.e. a 21.8% total loss of body weight occurred during the sojourn in the colony.

Except for a transient 1.1 °C increase ($P < 0.02$) at the time of egg laying, T_b in breeding females did not change significantly (mean = 37.2 ± 0.15 °C, $N = 21$) (Fig. 2). Plasma FFA levels were initially similar to those in males but exhibited a 50% increase ($P < 0.02$) during the period of copulation, followed by a return to basal levels within the days following egg laying. At the onset of the breeding fast, plasma β -hydroxybutyrate levels in females were 2 fold those in males ($P < 0.01$). Then, it regularly increased 2.5-fold ($P < 0.001$) and reached maximum values comparable to those in males, but at a 2-fold steeper rate. Except for a sharp transient 44% increase ($P < 0.01$) at the very time of laying, plasma glucose was maintained at 12.6 ± 0.35 mmol/l ($N = 20$).

Effects of continued starvation

A group of five males and five females was confined within a fence to study the effects of prolonged starvation. At the time of confinement males and females had very similar body weights (mean = 23.0 ± 0.4 kg). A transient 2-fold increase ($P < 0.01$) in DWL was observed in very early captivity. After about 10 days in the fence, mean body weight had decreased to 19.9 ± 0.15 kg, and DWL increased in both sexes. It was 542 ± 26 g/day for a mean final body weight of 17.5 ± 0.8 kg, versus 200 ± 21 g/day in early captivity, i.e. a 2.7-fold increase ($P < 0.001$). Parallel and simultaneous 2-fold drops ($P < 0.001$) in plasma FFA (both sexes) and 3-fold (males) and 4-fold (females) decreases ($P < 0.001$) in plasma β -hydroxybutyrate developed below a body mass slightly more than 20 kg (Figs. 1, 2). In either sex plasma FFA and β -hydroxybutyrate were positively related ($P < 0.05$), and in males weighing less than 20 kg plasma FFA ($P < 0.05$) and β -hydroxybutyrate ($P < 0.001$) were positively related to body mass.

In both sexes confinement induced a transient 15% increase ($P < 0.01$) in plasma glucose, but glycemia, and T_b , were not depressed below normal values at the end of experimental starvation.

Discussion

Breeding activity

Among the factors that in breeding emperors could potentially affect T_b and plasma fuels are changes in the rate of energy expenditure, especially related

to rate of physical activity, and metabolic processes associated with egg formation and oesophageal 'curd' secretion. The sojourns in the colony are preceded by a long travel on the sea-ice and, since emperors are not morphologically adapted to walking, as reflected by a high cost of transport (Pinshow et al. 1976; Dewasmes et al. 1980), this represents a strenuous physical exercise. In man and mammals, increases in metabolic rate, T_b , plasma FFA and β -hydroxybutyrate have been reported during or shortly after exercise (Johnson et al. 1969; Carlson et al. 1971; Hagenfeldt 1979), and in the pigeon prolonged exercise leads to increased plasma FFA (John and George 1973). As shown for plasma FFA in the rat (Oscai 1979), resting values are progressively restored during the hours or the days following the end of the exercise. Thus, in emperors, the decrease in DWL, T_b and plasma fuels observed during the days following the arrival in the colony (Table 1) may be related to the recovery from the previous physical effort. On the other hand, since penguins had already been fasting for several days when they arrived in the colony, food deprivation appears unlikely to have contributed to these metabolic changes.

In males, T_b was significantly higher during the final stage of the fast than during mid-incubation (Fig. 1). In the middle of incubation males are very inactive and spend most of the time huddled together, and are therefore protected against cold. This results in a reduction of the rate of energy production, as reflected by a 40% decrease in DWL (Prévost 1961; Mougin 1966), which could explain the concurrent 1–2 °C decrease in T_b measured by these authors. By contrast, activity is increased during the period when chicks are fed with the oesophageal secretion and exchanged with the females (displays, songs). Huddling is no longer possible because pairs must be isolated from each other for recognition, which might account for the present higher T_b .

The increase in plasma FFA that in males was observed slightly before, and then during chick feeding with the oesophageal secretion, correlates with increases in plasma total lipids and triglycerides, and might be explained by an increase in lipogenesis under the stimulating effect of prolactin. This hormone is known to stimulate crop-sac secretion in the pigeon (see Groscolas 1982b). In the pigeon, March et al. (1978) also found higher plasma FFA levels during periods of crop gland activity.

In female emperors, oviposition induced a significant increase in T_b and plasma glucose (Fig. 2) which could be related to the laying effort. Intense

stances and contractions of the whole body were actually observed before egg voiding. There is some evidence in the domestic fowl that body temperature is directly related to activity and may increase during the egg-laying period (Freeman 1971). On the other hand, the high plasma FFA in pre-laying female emperors was probably related to egg-yolk synthesis rather than to changes in energy expenditure. A marked increase in plasma FFA and lipids during egg-yolk deposition is a well-known observation in birds and depends on oestrogens (Heald and Badman 1963; Hazelwood 1972). Parallel increases in plasma FFA (this study), lipids (Groscolas 1982b) and oestrogens (Groscolas et al., in press) in pre-laying female emperors agree with these previous findings and indicate that fasting does not impair the normal process of egg-yolk formation in emperors.

Starvation

Discarding the changes that may be ascribed to breeding activity, maintenance of homeothermia, glycemia and moderate plasma FFA on one hand, progressive modest ketosis on the other hand, characterize prolonged natural starvation in free-living emperor penguins. This is indicative of energy and metabolic homeostasis and is probably related to the availability throughout the whole breeding fast in the colony, of large fat stores, with fatty acid oxidation supplying 93% of energy and allowing to spare protein (Groscolas and Clément 1976; Groscolas 1982a). Under similar circumstances of long-term fasting and fat store availability, maintenance of moderate plasma FFA has been reported in birds (Le Maho et al. 1981) and mammals (Goodman et al. 1980), which might be explained by simultaneous and balanced high rates of fatty acid mobilization and oxidation. Increased ketogenesis, through increased fatty acid oxidation, is well-known in starving birds and mammals (Hazelwood 1972); generally, high plasma levels of ketone bodies were attained. For example, 6-, 10- and 40-fold increases in plasma β -hydroxybutyrate were reported after a few days of starvation in the pigeon (Bailey and Horne 1972), the chicken (Brady et al. 1978), and the goose (Le Maho et al. 1981), with a 20-mmol/l peak level in the latter species. Since high plasma levels of FFA are a prerequisite for enhanced ketogenesis (Grey et al. 1975), the restricted rise in the FFA levels, together with a nonketogenic directed FFA metabolism in the liver and/or a high efficiency in ketone body utilization by peripheral tissues, could limit the development of excessive ketonemia in penguins. The

unusually high plasma β -hydroxybutyrate level in fed emperors (0.4 mmol/l, Groscolas and Rodriguez 1981) also suggests peculiarities in ketone body metabolism in penguins.

Maintenance of a high plasma glucose level – a characteristic of birds – during the breeding fast in the colony and also during the supplementary 3-week starvation in the fence is in agreement with our previous results in moulting and force-fasted post-moulting emperors (Groscolas 1978). Resistance to fasting hypoglycemia has been demonstrated in various bird species (Hazelwood 1972; Migliorini et al. 1973; Le Maho et al. 1981) but, to our knowledge, never for as long as 135 days as presently in male emperors. The mechanism by which normoglycemia is maintained remains unknown. A 40% reduction in glucose turnover, but not an enhancement of recycling (Groscolas and Rodriguez 1981), together with autoregulated utilization and interconversion with lactate (Groscolas and Rodriguez 1982) could partly contribute to glucose economy and maintenance of glycemia. Because glycogen stores are very limited and their utilization reduced (Groscolas 1982a), no significant amount of glucose can arise from glycogenolysis. By contrast, glycerol and amino acids arising from the hydrolysis of stored triglycerides and from the breakdown of tissue proteins, respectively, are potential sources of carbon atoms for glucose production. *In vivo* gluconeogenesis from alanine has been recently demonstrated in fasted emperors (Frain et al., unpublished data). If a daily breakdown of 80 g triglycerides, and of 15 g proteins is assumed (Groscolas 1982a), according to Krebs (1964) up to 17 g of glucose could be formed by these pathways per day in emperors fasting in the colony. Maintenance of glycemia indicates that these quantities meet the demand of glucose-dependent tissues. Based on a mean metabolic rate of 40 W in free-living breeding emperors (Groscolas 1982a), the corresponding maximum contribution of glucose oxidation to the overall energy production would be around 8%.

The increase in DWL and the concurrent decreases in plasma FFA and β -hydroxybutyrate that were observed below a body mass close to 20 kg in penguins subjected to prolonged starvation, were probably the consequence of exhaustion of fat stores. Indeed, previous studies have shown that at a body mass close to 20 kg, fat stores were depleted, and that at a body mass close to 23 kg penguins began using their protein stores to survive (Groscolas and Clément 1976; Groscolas 1982a). As a consequence of increasing protein catabolism DWL would increase; because fatty acids can no longer be supplied by adipose tissue, plasma levels

of FFA and β -hydroxybutyrate must decrease. In breeding fasting emperors penned at the onset of reproduction, and thus well adapted to captivity, Le Maho et al. (1976) have determined that the body mass corresponding to the beginning of the increase in DWL (“critical body mass”) was actually around 23 kg. That the “critical body mass” was estimated at 20 kg in the present study results from a biased calculation. The critical body mass is defined by the intercept of the steady (“basal”) and increasing parts of the curve relating DWL to body mass. In the present study, the basal level of DWL was increased about 2 fold by early captivity (stress, agitation), which has caused the intercept to shift to a lower body mass. Mean body mass of penguins leaving the colony for feeding at sea was around 23 kg (Prévost 1961; this study), equivalent to the critical body mass, and the corresponding mass of fat stores is around 2 kg (Dewasmes et al. 1980). Based on the walking metabolic rate and speed on one hand (Dewasmes et al. 1980), and on changes in body mass and energy content on the other hand (Groscolas 1982a), the body mass of emperors reaching the feeding grounds after a 100-km walk (a reasonable estimate) would be around 21 kg. We conclude that most emperors can begin to refeed just before depleting their fat stores and before drastically shifting from lipid to protein utilization as main energy source, thus avoiding severe metabolic alterations. By contrast, similar estimates in the leanest penguins (20.3–20.5 kg when leaving the colony, Prévost 1961; Groscolas 1982a) gives a final body mass close to 18 kg, thus well below the critical value. Successful refeeding by hand, of fenced penguins with body masses as low as 18 kg, suggests that this critical metabolic state is reversible (Groscolas 1982a). However, since in the wild, penguins must expend much energy to forage in cold water, and since in some years the extent of the sea-ice might reach 200 km (Pinshow et al. 1976), the suggestion appears reasonable that the leanest emperor penguins might die from the efforts of reproduction.

In conclusion, the present results are consistent with the finding that in fasting mammals depletion of fat stores leads to a marked reduction of the fast-induced increase in plasma FFA and β -hydroxybutyrate, combined with an enhanced nitrogen excretion (e.g. Goodman et al. 1980). In the breeding fasting emperor penguin, it seems that the levels of circulating lipid fuels and sparing of proteins are connected and that, more notably, the diminution in these fuels might serve as a signal for the switch from fat towards protein utilization. Moreover, since the leanest male emperors leave

the colony at the time when fat stores are exhausted, and probably after their having abandoned eggs or chicks, the decrease in plasma FFA and/or β -hydroxybutyrate might possibly serve as a metabolic signal that would contribute to trigger the spontaneous departure to the sea for refeeding. Simultaneous determinations of the final temporal changes in plasma lipid fuels, of plasma metabolites arising from protein breakdown (e.g. uric acid) and of spontaneous activity might therefore help to define possible interrelationships between fat and protein metabolism on the one hand, and behaviour on the other hand, in long-term fasting emperor penguins.

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References

- Bailey E, Horne JA (1972) Formation and utilization of acetoacetate and D-3-hydroxybutyrate by various tissues of the adult pigeon (*Columba livia*). *Comp Biochem Physiol* 42B:659-667
- Brady LJ, Romsos DR, Brady PS, Bergen WG, Leveille GA (1978) The effect of fasting on body composition, glucose turnover, enzymes and metabolites in the chicken. *J Nutrition* 108:648-657
- Carlson LA, Ekelund LG, Fröberg SO (1971) Concentration of triglycerides, phospholipids and glycogen in skeletal muscle and of free fatty acids and β -hydroxybutyric acid in blood in man in response to exercise. *Eur J Clin Invest* 1:248-254
- Dewasmes G, Le Maho Y, Cornet A, Groscolas R (1980) Resting metabolic rate and cost of locomotion in long term fasting emperor penguins. *J Appl Physiol: Resp Environ Exer Physiol* 49:888-896
- Freeman BM (1971) Body temperature and thermoregulation. In: Bell DJ, Freeman BM (eds) *Physiology and biochemistry of the domestic fowl*, vol 2. Academic Press, London, pp 1115-1151
- Goodman MN, Reed Larsen P, Kaplan MM, Aoki TT, Young VR, Ruderman NB (1980) Starvation in the rat. II. Effect of age and obesity on protein sparing and fuel metabolism. *Am J Physiol* 239 (Endocrinol Metab 2): E 277-E 286
- Grey NJ, Karl I, Kipnis DM (1975) Physiologic mechanism in the development of ketosis in man. *Diabetes* 24:10-16
- Groscolas R (1978) Study of molt fasting followed by an experimental forced fasting in the emperor penguin *Aptenodytes forsteri*: relationship between feather growth, body weight loss, body temperature and plasma fuel levels. *Comp Biochem Physiol* 61A:287-295
- Groscolas R (1982a) Modifications métaboliques et hormonales en relation avec le jeûne prolongé, la reproduction et la mue chez le Manchot empereur (*Aptenodytes forsteri*). Thèse d'Etat, Université de Dijon
- Groscolas R (1982b) Changes in plasma lipids during breeding, molting, and starvation in male and female emperor penguins (*Aptenodytes forsteri*). *Physiol Zool* 55:45-55
- Groscolas R, Clement C (1976) Utilisation des réserves énergétiques au cours du jeûne de la reproduction chez le Manchot empereur, *Aptenodytes forsteri*. *CR Acad Sci Paris* 282D:293-300
- Groscolas R, Rodriguez A (1981) Glucose metabolism in fed and fasted emperor penguins (*Aptenodytes forsteri*). *Comp Biochem Physiol* 70A:191-198
- Groscolas R, Rodriguez A (1982) Glucose and lactate kinetics and interrelations in an antarctic bird (emperor penguin). *Am J Physiol* 242 (Regul Integr Comp Physiol): R 458-R 464
- Groscolas R, Charpentier C, Lemonnier F (1975) Variation de la concentration des acides aminés libres du plasma au cours du cycle reproducteur chez le Manchot empereur, *Aptenodytes forsteri*. *Comp Biochem Physiol* 51B:57-67
- Groscolas R, Jallageas M, Goldsmith A, Assenmacher I (in press) The endocrine control of reproduction and molt in male and female emperor (*Aptenodytes forsteri*) and adélie (*Pygoscelis adeliae*) penguins. I. Annual changes in plasma levels of gonadal steroids and LH. *Gen Comp Endocrinol* 61
- Hagenfeldt L (1979) Metabolism of free fatty acids and ketone bodies during exercise in normal and diabetic man. *Diabetes* 28:66-70
- Hazelwood RL (1972) The intermediary metabolism of birds. In: Farner DS, King JR (eds) *Avian biology*, vol 2. Academic Press, New York, pp 471-526
- Heald PJ, Badman HG (1963) Lipid metabolism and the laying hen. I. Plasma free fatty acids and the onset of laying in the domestic fowl. *Biochim Biophys Acta* 70:381-388
- John TM, George JC (1973) Effect of prolonged exercise on levels of plasma glucose, free fatty acids and corticosterone and muscle free fatty acids in the pigeon. *Arch Internat Physiol Biochim* 81:421-425
- Johnson RH, Walton JL, Krebs HA, Williamson DH (1969) Metabolic fuels during and after severe exercise in athletes and non-athletes. *Lancet* II:452-455
- Jouventin P (1972) Un nouveau système de reconnaissance acoustique chez les oiseaux. *Behaviour* 43:176-186
- Krebs HA (1964) The metabolic fate of amino acids. In: Munro HN, Allison JB (eds) *Mammalian protein metabolism*, vol 1. Academic Press, New York, pp 125-176
- Le Maho Y (1977) The emperor penguin: a strategy to live and breed in the cold. *Am Scientist* 65:680-693
- Le Maho Y, Delclitte P, Chatonnet J (1976) Thermoregulation in fasting emperor penguins under natural conditions. *Am J Physiol* 231:913-922
- Le Maho Y, Vu Van Kha H, Koubi H, Dewasmes G, Girard J, Ferré P, Cagnard M (1981) Body composition, energy expenditure, and plasma metabolites in long-term fasting geese. *Am J Physiol* 241 (Endocrinol Metab): E 342-E 354
- March GL, McKeown BA, John TM, George JC (1978) Diurnal variation in circulating levels of free fatty acids and growth hormone during crop gland activity in the pigeon (*Columba livia*). *Comp Biochem Physiol* 59B:143-145
- Migliorini RH, Linder C, Moura JL, Veiga JAS (1973) Gluconeogenesis in a carnivorous bird (black vulture). *Am J Physiol* 225:1389-1392
- Mougin JL (1966) Observation écologiques à la colonie de Manchots empereurs de Pointe Géologie (Terre Adélie) en 1964. *L'Oiseau et la RFO* 36:166-226
- Oscari LB (1979) Effect of acute exercise on tissue free fatty acids in untrained rats. *Can J Physiol Pharmacol* 57:485-489
- Pinshow B, Fedak MA, Battles DR, 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*. Hermann, Paris