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Plasma thyroid hormone pattern in king penguin chicks: a semi-altricial bird with an extended posthatching developmental period

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Abstract

Plasma concentrations of thyroid hormones (TH) were investigated during the extended posthatching developmental period (~11 months) of a semi-altricial bird species, the king penguin (*Aptenodytes patagonicus*). The first period of growth in summer was marked by a progressive rise in plasma T_4 concentration that paralleled rapid increases in body mass and in structural and down growth. By contrast, plasma T_3 concentration had already reached adult levels in newly hatched chicks and did not change thereafter. Circulating TH of king penguin chicks thus follow an original pattern when comparing to altricial and precocial species. During the austral winter, the long period of undernutrition of king penguin chicks was characterized by a decrease in circulating TH that can be related to a seasonal stop in growth and energy saving mechanisms. Plasma TH concentrations increased again during the second growth phase in spring, and they reached their highest levels at the end of the fledging period, slightly before juveniles initiated their first foraging trip at sea. As expected, plasma T_4 levels were elevated when chicks moulted, developing a true-adult type waterproof plumage. The data also suggest that T_4 plays a major role in skeletal development and pectoral muscle maturation in anticipation of marine life. Plasma T_3 was at its highest during the period when juveniles improved resistance to cold waters by going back and forth to the sea, suggesting a role for circulating T_3 in cold acclimatization occurring at that time.

Keywords: Growth; Moult; Pectoral muscle; Skeletal development; T_3; T_4; Thermogenesis

1. Introduction

At hatch, the chicks of various species of birds differ markedly in the degree of maturation of many aspects of their behaviour, physiology, and anatomy. Variation among taxa in these developmental characteristics has led to the separation of avian species into altricial and precocial developmental types. The altricial–precocial spectrum extends from songbirds and parrots, whose chicks hatch in an almost embryo-like state, to the megapodes, whose hatchlings resemble adult birds and can fly from the first day after hatching (Starck, 1993; Starck and Ricklefs, 1998). A general hypothesis is that hormones and growth factors play fundamental roles in determining the different developmental patterns in the altricial–precocial spectrum (McNabb et al., 1998). The two main groups of hormones involved in growth in birds are growth hormone (GH) together with the associated insulin-like growth factors, and the thyroid hormones (TH), thyroxine (T_4) and triiodothyronine (T_3). Normal growth of posthatching birds requires GH, but, despite marked differences in growth rates between groups, the few data available indicate that the developmental pattern of GH is similar in both precocial and altricial species (McNabb and Olson, 1996; McNabb et al., 1998). On the other hand, there are fundamental differences with respect to plasma TH that are linked to the development of thermoregulation between these two groups. Chicks of precocial species have dramatic peaks of plasma concentrations of both T_4 and T_3 at hatching,

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which is marked by the initiation of thermoregulation. By contrast, plasma TH concentrations do not peak and are very low at hatching in altricial species. They then progressively increase to approach adult values by the time of the greatest endothermic improvements during nestling life (McNabb and Olson, 1996; McNabb et al., 1998; Olson et al., 1999).

Hormonal control of avian growth has been nearly exclusively studied in poultry species, which have the precocial pattern of development. Consequently, an issue that needs to be addressed is whether the endocrine changes observed to date are truly representative of precocial and altricial patterns or simply species-specific differences (McNabb et al., 1998). More work on wild birds, including species from several orders, are therefore needed to confirm our current views of hormonal control of developmental differences, including the poorly investigated semi-altricial and semi-precocial types. Semi-altricial neonates, including penguins (order Sphenisciformes), have open eyes and are relatively active soon after hatching when comparing to truly altricial chicks (Starck, 1993; Starck and Ricklefs, 1998). Newly hatched penguins have only a thin covering of downy feathers, they remain in the nest, and are entirely dependent on their parents for food for several weeks to months. In addition, penguin chicks are unable to regulate their own body temperature at birth and they are therefore brooded by their parents for between 2 and 6 weeks, depending on the species. Afterwards, chicks are left alone and group together during the so-called crèche period, both parents foraging at sea and returning at intervals to feed their offspring. Finally, large chicks moult, developing true-adult type waterproof feathers, before going at sea to feed by themselves for the first time (Williams, 1995). At the end of the chick-rearing period, the terrestrial chicks thus face an intensive and prolonged energetic demand during their passage from shore to marine life in cold waters (Barré and Roussel, 1986).

King penguins (*Aptenodytes patagonicus*) have a unique reproductive cycle among birds, since an entire cycle including moult lasts 14–15 months. The main striking feature is an extended chick-rearing period, which can be divided into three parts: a first period of growth in summer and early fall, a prolonged period of undernutrition in late fall and winter, and a second period of growth that precedes moult in spring. The whole chick-rearing period therefore lasts about 11 months between hatching in January and departure to sea in December (Barrat, 1976; Stonehouse, 1960). The aim of the present work was to describe TH pattern during the unusual posthatch development of king penguins. Emphasis was made on the first growth period to compare TH pattern of a semi-altricial bird with that of altricial and precocial species. Time-correlations between TH and both moult and the departure to sea of king penguin chicks in spring were also investigated, because TH are required for moult (Groscolas and Cherel, 1992; Kuenzel, 2003) and they are involved in the control of thermogenic processes in birds (McNabb and Olson, 1996; Silva, 1995).

Finally, since food limitation is associated with decreasing plasma TH concentrations in avian species (Le Ninan et al., 1988; Sharp and Klandorf, 1985), we investigated time-correlations between chicks' body condition and circulating TH concentrations, focusing on the winter fast and on the period preceding departure to sea in spring. Nutritional status of the chicks was assessed through the determination of plasma β-hydroxybutyrate (a ketone body) and uric acid (the main nitrogen excretory product in birds), which are good indices of lipid and protein utilization, respectively. Plasma β-hydroxybutyrate is low and uric acid high in fed king penguins (Cherel and Le Maho, 1988; Le Ninan et al., 1988). Conversely, plasma β-hydroxybutyrate is high and uric acid low in fasting birds, which preferentially use their lipid reserves while sparing their endogenous body proteins (Cherel and Le Maho, 1985; Cherel et al., 1988c).

2. Materials and methods

Fieldwork was carried out on the Île de la Possession, Crozet Archipelago (46°25′S; 51°45′E) during the 1992 breeding cycle in the colony of La Baie du Marin (40,000 pairs) (Weimerskirch et al., 1992). The egg-laying period of king penguin span 4 months, but only pairs that lay at the beginning of this period are successful (Olsson, 1996). Consequently, chicks of that study are early chicks, i.e., those hatching in January/February. Blood was sampled on breeding adult birds in fall and at 12 different developmental stages according to the chronology of the cycle, i.e., chick growth, acquisition of homeothermy, moult, and departure to sea (Table 1).

Ten king penguins were randomly chosen for each group. Birds were sampled once. Each bird was weighed, and the length (accuracy ± 1 mm) of beak, foot, and flipper was measured according to Stonehouse (1960). Blood samples (usually 5 ml) were taken from a flipper vein (cardiac puncture for hatchlings and 2 weeks old chicks) with heparinized syringes. Blood samples were kept in the field at +5 °C in crushed ice during 1–2 h before being partitioned and centrifuged in the laboratory. Plasma from one microtube was deproteinized in 7% perchloric acid, and the supernatant solution neutralized with 10% KOH. Whole plasma and deproteinized plasma were frozen and kept at −20 °C until assayed. Deproteinized plasma was used for the enzymatic determination of β-hydroxybutyrate (Williamson and Mellanby, 1974) and whole plasma for the determination of uric acid (Scheibe et al., 1974).

Total plasma TH was determined by radioimmunoassays on whole plasma without extraction and

Table 1
Blood sampling schedule in relation to age, development and growth, and moult stages in king penguins (following Barrat, 1976; Barré, 1978; Cherel et al., 1987; Duchamp et al., 2002; Stonehouse, 1960; Weimerskirch et al., 1992)

Season	Months	Age	Abbreviations	Developmental stages	Plumage and moult stages
Chicks					
Summer	End of January	0 week	0	Hatching	Almost unfeathered
	Mid-February	2 weeks	2	Progressive acquisition of homeothermy	Chick down growth
	End of February	~4 weeks	4	Emancipation, end of brooding phase	Chick down growth
	March	~7 weeks	7	Middle of the first growth period	End of chick down growth
Fall	April	~2.5 months	B	End of first growth period and beginning of winter fast: first peak body mass	Chick down
Winter	June–July	~5 months	M	Middle of winter fast	Chick down
	Early September	~7.5 months	E	End of winter fast	Chick down
Spring	Late October	~9 months	Sp	Second peak body mass	Chick down, synthesis of new tail feathers
	Mid-November	~9.5 months	B	Beginning of moult	Chick down, end of synthesis of tail feathers, beginning of synthesis of body feathers
	Late-November	~10 months	M	Mid-Moult	Loss of chick down, synthesis of body feathers
	Early December	~10.5 months	E	End of Moult	End of chick down loss, body feathers fully grown
	Mid-December	~11 months	Sea	Departure to sea	Feathers (= true-adult type waterproof feathers)
Adults					
Summer	Mid-March	>4 years	Adults	Parents returning ashore to feed their offspring (control birds)	Feathers

following the procedure detailed in Chastel et al. (2003). Pooled plasma of different king penguins produced a dose–response curve that paralleled the TH standard curves. These radioimmunoassays were different from those previously used in king penguins (Cherel et al., 1988a,c; Le Ninan et al., 1988). However, the two sets of assays gave similar results for different animals in identical nutritional conditions—fed king penguin chicks at the beginning of the winter fast. The values obtained in Le Ninan et al. (1988) and in the present work were 8.4 ± 3.3 ($n = 9$) and 9.7 ± 2.1 nmol/L ($n = 10$), and 1.2 ± 0.9 and 1.0 ± 0.4 nmol/L for T_4 and T_3, respectively.

Values are means $\pm$ SD. Data were statistically analysed using SYSTAT 9 for WINDOWS (Wilkinson, 1999). Means for each parameter at each developmental stage were compared using a Kruskal–Wallis one-way analysis of variance and Mann–Whitney U tests were used for comparisons between two groups.

3. Results

3.1. Growth: body mass and structural size

Overall, body mass changed significantly over the chick-rearing period (Kruskal–Wallis; $H_{12,130} = 123$, $p < 0.0001$). It rose from 0.30 ± 0.02 kg at hatching to 6.1 ± 0.2 kg at 7 weeks (Mann–Whitney; $U = 0$, $p < 0.0001$), and to 10.8 ± 0.4 kg ($U = 0$, $p < 0.0001$) at the end of the first growth phase, 2.5 months later (Fig. 1). It then dropped by 44%, to 6.0 ± 0.3 kg ($U = 100$, $p < 0.0001$), at the end of the long winter fast. The second growth phase in spring was marked by an increase in body mass to 13.0 ± 1.5 kg ($U = 0$, $p < 0.0001$), which decreased during moult and until the departure to sea to 8.6 ± 0.6 kg ($U = 0$, $p < 0.0001$). Adult birds rearing chicks in autumn weighed 13.9 ± 1.0 kg (Fig. 1).

Beak, feet, and flippers increased in size during the chick-rearing period ($H_{12,130} = 119$, 83, and 102, respectively, all $p < 0.0001$). Growth of beak, feet, and flippers was most rapid during the first months of life (Fig. 2) (all $U = 0$ and $p < 0.001$, when comparing chicks at hatching and at the beginning of the winter fast). By the end of the first growth phase, feet had reached full adult size ($U = 53.5$, $p = 0.790$), while flippers continued to growth, but at a slower rate, to reach the adult length at the end of the fledging period ($U = 89.5$ and 43, $p = 0.003$ and 0.596, when comparing chicks at the beginning of winter and at their departure to sea, and the latter group with adults, respectively). Beak stopped growing during winter

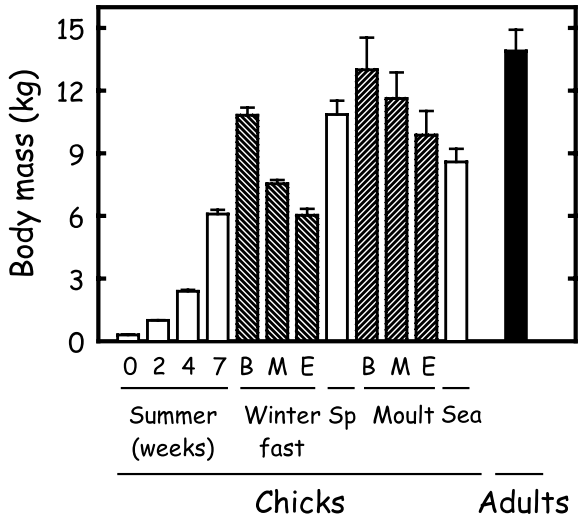

Fig. 1. Body mass measurements of growing king penguin chicks at various developmental stages. Values are means ± SD. Abbreviations: B, beginning; M, middle; E, end; and Sp, Spring. Hatched bars represent winter fast and spring moult.

($U = 30$, $p = 0.130$) but its length increased again in spring ($U = 7$, $p = 0.001$ when comparing chicks at the end of winter and at the beginning of moult). Beak of birds departing to sea is, however, smaller than that of adults ($U = 5$, $p = 0.001$), indicating that beak growth continues after departure to sea. At fledging the length of beak, feet, and flippers had reached 87.5, 98.9, and 99.6% of the adult size, respectively (Fig. 2).

3.2. Nutritional status: plasma β-hydroxybutyrate and uric acid

Plasma metabolite concentrations changed significantly amongst developmental stages ($H_{12,131} = 81$ and $H_{12,129} = 67$, both $p < 0.0001$ for β-hydroxybutyrate and uric acid, respectively). Plasma β-hydroxybutyrate remained at moderate values (0.42–0.81 mmol/L) during the first period of chick growth, as it was in adult birds (Fig. 3). It rose to 1.41 ± 0.92 mmol/L during the winter fast ($U = 7.5$, $p < 0.0001$), and then decreased to 0.59 ± 0.14 mmol/L during the second growth period in spring ($U = 111$, $p = 0.004$). Plasma β-hydroxybutyrate increased progressively thereafter and reached its highest concentration in birds departing to the sea (2.22 ± 0.85 mmol/L; $U = 90$, $p < 0.0001$).

Plasma uric acid concentration was moderate (0.47–0.68 mmol/L) in chicks during the first period of growth and in adult birds (Fig. 3). It then dropped to low values during the winter fast (0.21 ± 0.20 mmol/L; $U = 95$, $p = 0.005$). The second growth phase was marked by high concentrations that peaked at that time (0.96 ± 0.24 mmol/L; $U = 2$, $p < 0.0001$, when comparing chicks in the middle of winter and in spring). Plasma uric acid thereafter decreased progressively and reached its lowest values at the end of moult and in birds departing to sea (0.15–0.16 mmol/L; $U = 90$ and 0, respectively, both $p < 0.0001$).

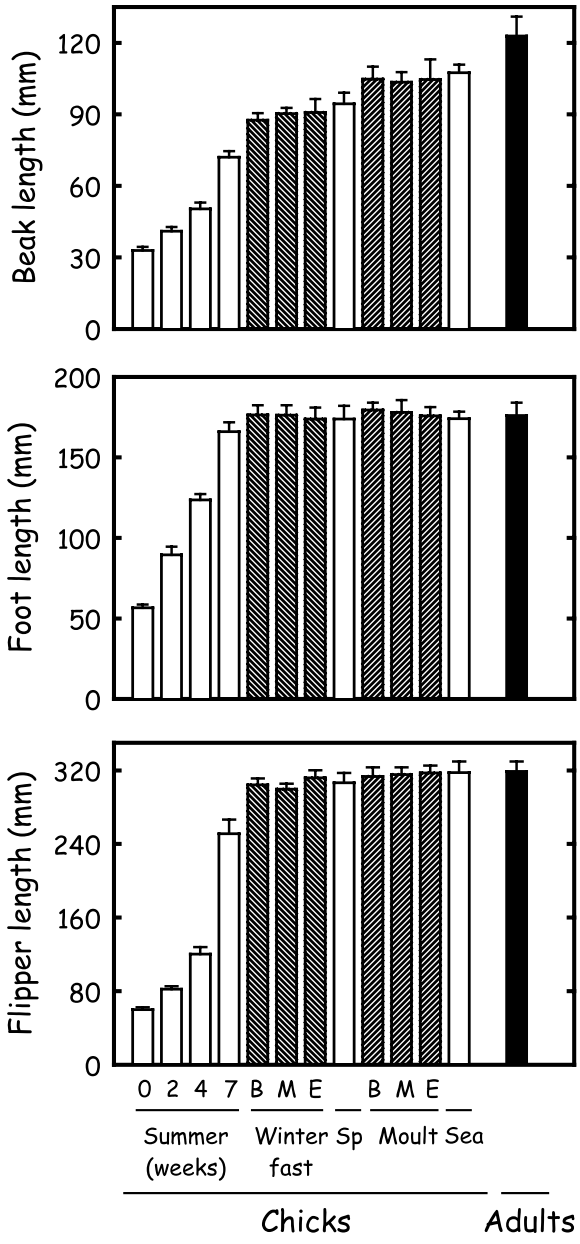

Fig. 2. Structural size in growing king penguins chicks. Beak, foot, and flipper measurements at various developmental stages. Values are means ± SD. Abbreviations: B, beginning; M, middle; E, end; and Sp, Spring. Hatched bars represent winter fast and spring moult.

3.3. Thyroid hormones: plasma T_4 and T_3

Plasma TH concentrations and the ratio T_3/T_4 changed significantly amongst developmental stages ($H_{12,133} = 108$, 63, and 90 for T_4, T_3, and T_3/T_4,

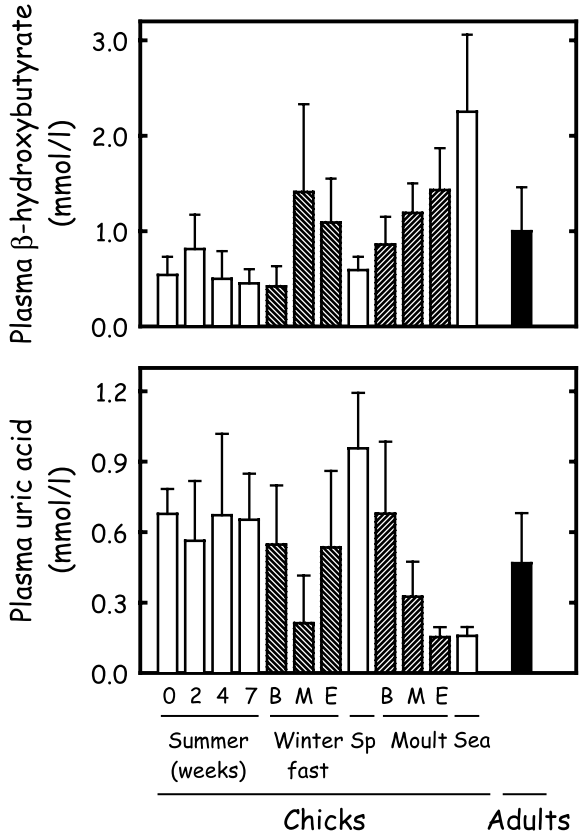

Fig. 3. Nutritional status during growth of king penguin chicks. Plasma concentrations of β-hydroxybutyrate and uric acid at various developmental stages. Values are means ± SD. Abbreviations: B, beginning; M, middle; E, end; and Sp, Spring. Hatched bars represent winter fast and spring moult.

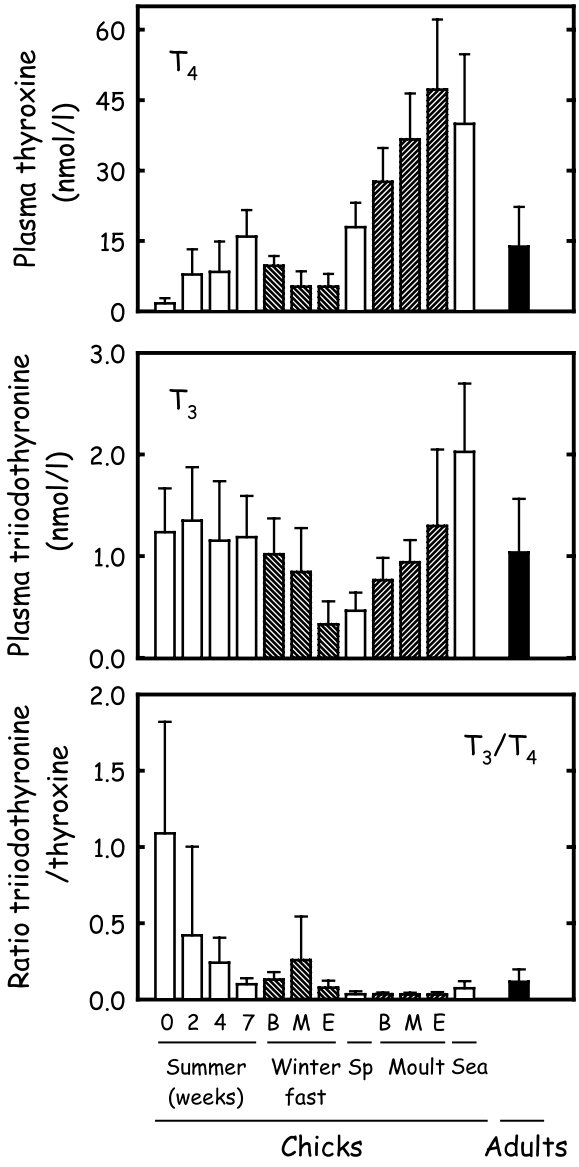

Fig. 4. Plasma concentrations of thyroid hormones (thyroxine and triiodothyronine) and their molar ratio in growing king penguin chicks at various developmental stages. Values are means ± SD. Abbreviations: B, beginning; M, middle; E, end; and Sp, Spring. Hatched bars represent winter fast and spring moult.

respectively, all $p < 0.0001$). Plasma T_4 was very low at hatching (1.7 ± 1.2 nmol/L) (Fig. 4). It then increased during the first weeks of life, peaking in the middle of the first growth period (15.9 ± 5.6 nmol/L; $U = 0$, $p < 0.0001$), during which it reached adult values (13.8 ± 8.4 nmol/L; $U = 64$, $p = 0.290$). Concentrations dropped thereafter to low values during the winter fast (5.3 ± 2.7 nmol/L; $U = 97$, $p < 0.0001$). They increased again during the second growth period and moult ($U = 2$ and 0 when comparing chicks at the end of winter with those in spring and at the end of moult, respectively, both $p < 0.0001$), and reached their highest values at the end of moult and before juveniles initiated foraging at sea (40.0–47.3 mmol/L).

Plasma T_3 concentration had already reached adult values at hatching (1.24 ± 0.43 and 1.04 ± 0.53 nmol/L for hatchlings and adult king penguins, respectively; $U = 71$, $p = 0.112$) (Fig. 4). It did not change during the first period of chick growth, but it decreased to low values at the end of the winter fast (0.33 ± 0.23 nmol/L, $U = 95$, $p < 0.0001$ when comparing chicks at the beginning and the end of winter). Plasma T_3 then increased progressively during the whole spring, reaching its highest concentration before chicks departed to sea in December (2.03 ± 0.67 nmol/L; $U = 100$, $p < 0.0001$).

The molar ratio T_3/T_4 was elevated at hatching and it was nine times higher than in adult plasma (1.09 ± 0.73 and 0.12 ± 0.08, respectively; $U = 90$, $p < 0.0001$). It then decreased during the first period of chick growth ($U = 90$, $p < 0.0001$ when comparing chicks at hatching and at the beginning of winter) and remained at these low values during the winter fast (0.10–0.26). In spring, there was a further initial decline of the ratio to very low values (<0.10; $U = 82$, $p = 0.015$ when comparing chicks at the end of winter and in spring), which stabilized thereafter (Fig. 4).

4. Discussion

4.1. The first growth phase of king penguin: thyroid hormone pattern in a semi-precocial bird

To our knowledge, this work is the first to investigate the developmental TH pattern of a semi-altricial bird. In the few altricial species so far investigated, both plasma T_4 and T_3 concentrations are very low at hatching and increase steadily thereafter (McNabb and Olson, 1996; McNabb et al., 1998). In king penguin chicks, plasma T_4 followed this general pattern (with a different time scale, here in weeks, not in days, due to the long developmental period of this large species), rising from hatching to the middle of the first growth period (~7 weeks). In contrast with that pattern, plasma T_3 had already reached adult values at hatching and did not change during the first growth phase. This also contrasts with the peak in TH at hatching observed in precocial birds (McNabb and Olson, 1996; McNabb et al., 1998). Hence, circulating TH of king penguin chicks follow an original pattern, thus highlighting the need for more information on hormonal changes in species belonging to different orders and families and with different patterns of development.

A consequence of low T_4 and high T_3 plasma concentrations at hatching is that the molar ratio T_3/T_4 was extremely high at that time, ninefold higher than in adult plasma. Such values have been rarely encountered in birds, in which T_4 concentrations normally exceed those of T_3 in plasma by severalfold (T_4: 6–19 nmol/L, T_3: 0.7–1.5 nmol/L; McNabb, 2000). The elevated ratio in king penguin chicks may result from both an increase rate of extrathyroidal conversion of T_4 to T_3 together with decreasing rates of T_3 inactivation and degradation at hatching, as previously described in precocial birds (McNabb and Olson, 1996; McNabb et al., 1998). Alternatively, a high T_3/T_4 ratio may be a consequence of a high secretion rate of T_3 directly from the thyroid gland. Clearly, the biochemical mechanisms responsible for the high T_3/T_4 ratio at hatching together with its subsequent decline to adult values (see also Olson et al., 1999) merit further functional investigation.

King penguins are essentially ectothermic at hatching, but newly hatched chicks show small, but significant regulatory thermogenesis, which improved during the first two to three weeks of life (Duchamp et al., 2002). These changes can be related to the relatively high T_3 plasma concentrations at that time, in agreement with the hypothesis that circulating T_3 controls thermogenesis in penguins (Groscolas and Cherel, 1992). Full thermal emancipation in king penguins is, however, a two-step process, the end of the period of maturation of thermogenic mechanisms being overlapped and followed by an improvement of thermal insulation due to rapid down growth (Barré, 1978; Duchamp et al., 2002). It is noteworthy that changes in plasma T_4 during the first growth period paralleled those in down length (Barré, 1978; Duchamp et al., 2002) and in the lengths of beak, feet, and flippers, i.e., high growth rates during the first 2 months of life that slow down thereafter. Data thus suggest a major role for circulating T_4 in the control of down and structural growth during early development in king penguin chicks.

4.2. Nutritional status and winter fast

During the first period of growth, plasma β-hydroxybutyrate and uric acid remained at moderate levels, i.e., at intermediate concentrations between those characterizing the fed and fasting states (Cherel and Le Maho, 1985, 1988; Cherel et al., 1988c; Le Ninan et al., 1988). This indicates that king penguin chicks were on average in a physiological situation of short-term fast and is in agreement with birds receiving meals at various time intervals (Stonehouse, 1960). By contrast, winter is a long period of undernutrition during which chicks are rarely and irregularly fed (Cherel et al., 1987; Descamps et al., 2002). Accordingly, Plasma β-hydroxybutyrate was elevated and plasma uric acid low in mid-winter, indicating that chicks were using their lipid stores and sparing their body proteins at that time.

Plasma TH concentrations decreased to low levels during the long-term winter fast of king penguins in the colony. This is in agreement with previous results obtained on captive fasting chicks (Le Ninan et al., 1988) and adults (Cherel et al., 1988c). A decrease in thyroid activity with food deprivation was also found in various species of birds including quail, chicken, and eider (Criscuolo et al., 2003; Sharp and Klandorf, 1985). Such a decrease was generally interpreted in terms of energy conservation in a metabolic situation during which animals rely on their endogenous nutrient reserves (Cherel et al., 1988b). Structural growth, an energy-consuming process, stopped in winter. Accordingly, plasma T_4 was low, thus supporting again the hypothesis that circulating T_4 controls growth in penguins.

4.3. Spring moult and departure to sea

Chicks' moult is unique in penguin's life because, unlike adults that fast ashore while renewing their whole plumage at the expense of muscle protein (Cherel et al., 1994; Williams, 1995), chicks are fed by their parents during their spring moult (Groscolas and Cherel, 1992). The high amino acid requirement resulting from keratin synthesis and muscle maturation occurring at the same time is the most likely explanation why penguin chicks must be fed while moulting (Barré, 1977; Vaucoulon et al., 1985). In king penguins, no chicks with a body mass lower than 10 kg moult their body feathers (Vaucoulon et al., 1985). Accordingly, chicks from the

present study weighed on average 11.6 kg at the beginning of moult, and plasma metabolite levels of spring chicks and birds beginning to moult indicate that they were well fed. However, there were concomitant and progressive decreases in body mass and plasma uric acid together with an increase in plasma β-hydroxybutyrate throughout moult and until departure to sea, thus indicating that chicks were fasting. This suggests that adults stop feeding chicks at that time, an hypothesis that is in agreement with the visual observation of successful breeders engage in moulting fast while their healthy chicks are still in the colony (Stonehouse, 1960).

There is considerable evidence that thyroid hormones are involved in the control of moult in many species of birds (Kuenzel, 2003; Payne, 1972). In penguins, circulating T_4 appears to be the main regulatory factor, because it is elevated during feather synthesis, while plasma T_3 remains at low levels at that time (Groscolas and Cherel, 1992; Otsuka et al., 1998). Our data indicate that plasma T_4 concentration was already elevated in the spring group and that it continued to increase thereafter. The criterion used for the determination of moult onset was the beginning of synthesis of body feathers. However, the first sign of moult in spring is the beginning of tail feather synthesis that precedes and overlaps with body moult. Accordingly, birds from the spring group were already moulting their tail feathers. Measurement of body feather length showed that feather growth occurred in the first two groups of moulting birds, while it was over in the last moulting group that had external length of new feathers close to that of adult penguins (data not shown). Elevated plasma T_4 concentrations in spring birds and in the two first groups of moulting chicks are thus in agreement with T_4 controlling feather synthesis in penguins. However, very high plasma T_4 levels at the end of moult were unexpected, because circulating T_4 decreases to low values after the end of feather growth in adult penguins (Cherel et al., 1988a; Groscolas and Leloup, 1986). In fact, chicks showed their highest plasma concentrations in both T_4 and T_3 at the end of the fledging period, while they were fasting. This markedly contrasts with the low circulating TH hormones usually associated with long-term fasts in birds, including king penguins (Cherel et al., 1988c; Le Ninan et al., 1988; present study).

The more likely explanation of this discrepancy is that TH are involved in maturation of physiological processes anticipating marine life. Juvenile penguins face an intensive energetic demand in order to maintain homeothermy when going to sea for the first time to swim and dive for food in cold waters. After moulting, juvenile king penguins undergo a series of very short journeys to and from the sea before leaving the colony permanently. Physiological investigations have shown that an improved resistance to cold waters is partly obtained by an increase of the thermogenic capacities through these successive immersions (Barré and Roussel, 1986). It is thus noticeable that T_3 plasma concentration was at its highest during that period, suggesting a role for circulating T_3 in the process of cold acclimatization in anticipation of the marine life of juvenile king penguins.

Passage to a marine life also implies many morphological, anatomical, and biochemical adaptations of skeletal muscles, such as well-developed pectoral muscles with a high myoglobin content. Direct and indirect evidences indicate that maturation of these adaptations take place during the second period of growth in spring. For example, structural growth is almost complete at the end of the first growth phase, but body composition analysis shows that pectoral girdle is mainly cartilaginous, and pectoral muscles are underdeveloped and have a pinkish colour, thus indicating a low myoglobin content (Cherel et al., 1993). On the other hand, in spring, breastbone is more developed and calcified, and pectoral muscles are larger and dark reddish. Swimming muscles of spring chicks are nevertheless still smaller and lighter than adult muscles (Cherel et al., 1993), indicating that muscle and skeletal growth continues during the subsequent moulting period and probably thereafter.

In birds, TH hormones are required for both growth and maturation of muscles, and, in skeletal tissues, they trigger cartilage differentiation and ossification (McNabb, 2000). Moreover, it has been hypothesized that they are involved in hypertrophy of the pectoral muscles prior to migration in adult geese (John and George, 1978). Accordingly, goslings show elevated circulating levels of T_4 in the premigratory period, a time also marked by the development of pectoral muscles and an increase in their oxidative capacities (Bishop et al., 1998). Experimental investigations support the hypothesis that tissue-specific levels of TH are needed for the maturation process of the locomotor muscles to be completed (Deaton et al., 1997, 1998). For example, hypothyroidism results in lower mass of pectoral muscles, a lowering of bone growth and a delay in plumage development of goslings (Deaton et al., 1998). In king penguin chicks, the high plasma levels of T_4 may thus be associated not only with moult but also with skeletal and pectoral muscle development and maturation, which occur in spring, before birds initiate their first foraging trip at sea.

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