

ECOLOGY AND PHYSIOLOGY OF FASTING IN KING PENGUIN CHICKS

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ABSTRACT.—Captive King Penguin (*Aptenodytes patagonica*) chicks can fast for 5 months during the subantarctic winter with a 70% decrease in body mass. To investigate the adaptive value of this remarkable resistance to starvation, we compared captive chicks with free-ranging chicks in their colony at Possession Island, Crozet Archipelago. The chicks in the colony, from mid-April to beginning of September (i.e. all winter) were fed only every 39 days by their parents; some were not fed at all. In spring (October–December) the surviving chicks were fed every 6 days, and their growth was completed. Overall chick mortality in the colony during the winter and subsequent spring was about 50%. Mortality was highest in October, 6 months after the beginning of the winter, and may be attributed mainly to starvation. The decrease in body mass in the free-ranging chicks was remarkably similar to that for captive birds. In both groups, three periods were characterized according to the observed changes in the daily decrease in body mass per unit body mass (dm/mdt): dm/mdt dropped during the first period (I) of 5–6 days, was minimum and steady during period II, which lasted about 4 months, and increased in period III. Blood analysis of the captive chicks indicated the three periods correspond to modifications in protein breakdown. An initial decrease in uricacidemia indicates period I is a short period of transition, marked by a decrease in protein breakdown. In period II a minimum and constant uricacidemia, in parallel with a progressive increase in ketonemia, indicates efficient protein sparing while most of the energy is derived from lipids. Period III is critical because, from a rise in uricacidemia concomitant with a decreasing ketonemia, proteins are no longer spared. The extreme resistance of King Penguin chicks to starvation in winter may be explained partly by the ability to spare proteins for several months (period II). It occurs at a growth stage when the parents' feeding visits are rare. Other laboratory and field investigations of birds suggest that the means by which a wide variety of domestic and wild species adapt to fasting also may be interpreted in terms of three periods corresponding to changes in protein breakdown. Received 6 June 1986, accepted 30 October 1986.

RECENT physiological data show that King Penguin (*Aptenodytes patagonica*) chicks resist starvation in winter remarkably well. At 3–4 months of age they may tolerate a fast of 4–6 months and a 70% decrease in body mass (Cherel and Le Maho 1985). King Penguin chicks are fed infrequently during winter and have a very high mortality due to starvation (Stonehouse 1960). No quantitative information seems to be available on the duration of the fast or the rate of decrease in body mass. The adaptive significance of the extreme resistance to starvation observed in experimental chicks therefore remains poorly understood.

The fledging period of King Penguin chicks

lasts about 11 months. This prolonged down stage may be divided into three parts (Stonehouse 1960, Barrat 1976). First, from hatching in mid-January, the chicks are fed regularly; they grow rapidly and reach a body mass of 10–12 kg in 3–4 months. Then, from May to August during the austral winter, the chicks are left alone for long intervals and not fed. Their body mass falls to about two-thirds or one-half of the autumn maximum. When the parents resume feeding (October–December), growth is completed, and the chicks molt before going to sea.

A wide variety of birds fast and exhibit a decrease in body mass during certain stages of their annual life cycle. Birds fast when food is scarce (Trautman et al. 1939), but also when it is plentiful if they are engaged in other important activities that compete with feeding,

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such as incubation, molting, and migration (Mrosovsky and Sherry 1980). Although there has been recent interest in the energetics of birds fasting during breeding (Croxxall 1982, Le Maho 1984), to our knowledge there are no comparisons of physiological data on fasting in captive birds with similar data on free-ranging animals.

We report here the changes in body mass, rates of feeding, and mortality in free-ranging King Penguin chicks during winter and spring, i.e. during seasons of food shortage and growth, respectively. We measured also fast duration and changes in body mass and plasma concentration of uric acid and β -hydroxybutyrate (β -OHB) in captive chicks. Uric acid is the major nitrogen excretory product in birds (Poulson and MacNabb 1970) and is an index of protein breakdown in penguins (Robin et al. 1983). On the other hand, an increase in plasma concentration of β -OHB, the main ketone body in birds, characterizes the part of a fast during which most energy is derived from lipids (Le Maho et al. 1981).

MATERIALS AND METHODS

Field and experimental studies were performed at Possession Island, Crozet Archipelago (46°25'S, 51°45'E), between April and December, during the subantarctic winter and following spring. Two groups of King Penguin chicks were used: free-ranging birds in the breeding colonies of Baie du Marin and chicks caught in these colonies and kept in the nearby station.

Free-ranging chicks.—Fifty-five King Penguin chicks were banded in the breeding colony. Twenty-five were used to determine the beginning of winter starvation, from the time they were no longer fed by their parents. Changes in body mass and rate of feeding were followed in 10 other chicks. Five birds were studied during the austral winter, from June to mid-September, and the other 5 during spring, from mid-October to November. These 10 chicks were weighed daily with a pesola-type balance (accuracy ± 100 g). The remaining 20 banded chicks were observed visually, and every feeding visit of the adults during winter was noted. The parents were banded also to monitor their presence in the colony.

The mortality rate of chicks during winter and spring was estimated by counting those birds apparently dying as a result of weakness because of starvation in a predetermined area of the colony containing 186 chicks at the beginning of April.

Experimental chicks.—Seven King Penguin chicks caught in the second half of May (winter group) and

TABLE 1. Feeding frequency in King Penguin chicks during winter and spring.

	No. of meals ^a	No. of days ^b	Feeding frequency (no. days/no. meals)
Winter			
May	5	227	45.4
June	4	353	88.3
July	10	296	29.6
August	12	330	27.5
Spring			
October	14	103	7.4
November	23	106	4.6
December	10	82	8.2

^a In winter determined by visual observations of 20 chicks; in spring determined by daily weighings of 5 chicks.

^b Total number of days of weighings or visual observations for all chicks.

5 nonmolting chicks in mid-October (spring group) were kept in captivity at the station. Because King Penguin chicks are at thermoneutrality under natural ambient conditions, both in winter and summer (Barré 1984), there was no complication of temperature regime between the colony and the station. Wind velocity was usually higher in the station than at the colony, however, so we protected the captive chicks from the wind. Water was provided *ad libitum*. The animals were weighed daily with a platform balance (accuracy ± 20 g). A 5-ml blood sample was taken from a flipper vein by heparinized syringes every 2 days during the first 10 days of fasting and every 3 days thereafter. The hematocrit of King Penguin chicks was maintained at 42–45% (Cherel and Le Maho 1985). Blood was collected immediately in polyethylene microtubes at 5°C and centrifuged. Plasma was deproteinized in 7% perchloric acid and the supernatant solution neutralized with 10% KOH for the enzymatic determination of β -OHB (Williamson and Mellanby 1974). Uric acid was assayed on whole plasma using the uricase method (Scheibe et al. 1974).

Student's *t*-tests were used for statistical comparisons. Values given in the text are means \pm SE.

RESULTS

FREE-RANGING CHICKS

Winter starvation.—The 25 King Penguin chicks on the colony started winter starvation on 15 April \pm 2.3 days. For 20 banded chicks watched from the beginning of May to the end of August, the mean interval between two successive parental feeding visits was 39 days (Table 1). It is unlikely that this interval was overestimated because of undetected adult feeding

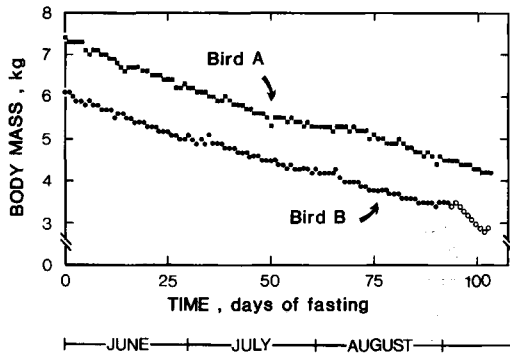


Fig. 1. Rate of decrease in body mass in 2 free-ranging King Penguin chicks fasting during winter. The birds began fasting before time 0. Bird B died from starvation; bird A was still fasting at day 100. See text for explanation of open symbols.

visits because the parents stayed ashore with their offspring for as long as 1.9 ± 0.5 days (range 1–11 days, $n = 20$). Thus, during the winter period of May through August, these King Penguin chicks received on the average only 3 meals.

None of the 5 other chicks (which were weighed daily) were fed from 1 June to mid-September, a period of 100 days. Overall, they presumably fasted for about 150 days, because, as indicated above, the chicks in the colony started to fast in mid-April. Thus, they had already been starved for 40–50 days on 1 June. In June these 5 chicks had a mean body mass of 6.6 ± 0.3 kg (range 6.1–7.4 kg); it was 3.4 ± 0.4 kg (range 2.6–3.7 kg) in mid-September. This represents a $49 \pm 3\%$ loss in mass during the 100 days of the study. The decrease in body mass of these chicks was curvilinear (a linear regression through a semi-log plot gave a better fit than a linear regression through the untransformed data), except a terminal sharp drop for two birds (e.g. open symbols for bird B in Fig. 1) that starved to death at body masses of 2.6 and 2.8 kg.

If an animal loses a constant mass dm per 24 h throughout the starvation period, dm represents an increasing proportion of instantaneous body mass m ; therefore, the specific daily change in body mass dm/mdt better expresses the rate of change in mass (Le Maho et al. 1981, Cherel and Le Maho 1985). In each of the five King Penguin chicks, dm/mdt was maintained at a steady value, and ranged from 5.5 to 7.8 $g \cdot kg^{-1} \cdot 24 h^{-1}$ ($\bar{x} = 6.4 \pm 0.4 g \cdot kg^{-1} \cdot 24 h^{-1}$).

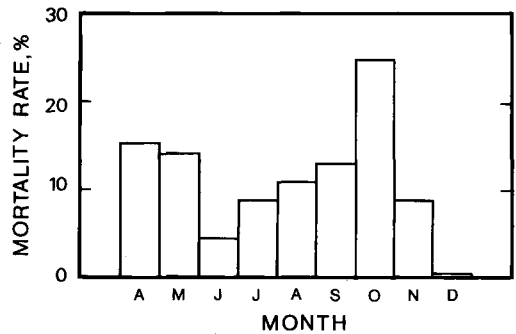


Fig. 2. Mortality during the fledging period in King Penguin chicks, expressed as a percentage of the total number of birds that died from starvation during April through December in a defined colony area.

However, it increased to 33.3 and $37.0 g \cdot kg^{-1} \cdot 24 h^{-1}$ in the two chicks that died.

From the area of the colony demarcated at the beginning of April, only 94 of the 186 chicks left for the sea in December. We estimated the overall mortality during winter and spring to be 49%. The mortality rate was biphasic (Fig. 2). A first peak occurred in April–May, and accounted for one-third of the overall mortality. Mortality was relatively low until October, when it increased greatly; one-fourth of the overall mortality occurred during this month. Mortality dropped thereafter until the end of the fledging period in December.

In a colony of King Penguins, it is difficult to find chicks that have died from starvation, because dying chicks are rapidly consumed by Hall's (*Macronectes halli*) and Antarctic (*M. giganteus*) giant-petrels. The mean body mass of 11 undamaged corpses collected in September was 2.9 ± 0.1 kg, similar to the body masses at death of the 2 birds out of 5 that were weighed daily (see above).

Spring growth.—As previously described (Stonehouse 1960), the King Penguin chicks received considerable food from their parents in spring and began to fatten. From October to December the mean interval between two meals was 6.2 days (Table 1), and until the beginning of molt, the body masses of the 5 free-ranging birds increased 41% from 7.9 ± 0.4 kg (range 6.4–8.6 kg) to 11.1 ± 0.4 kg (range 10.5–12.2 kg).

The pattern in the changes in body mass of each of the 5 free-ranging chicks was a sequence of sharp rises in body mass after every

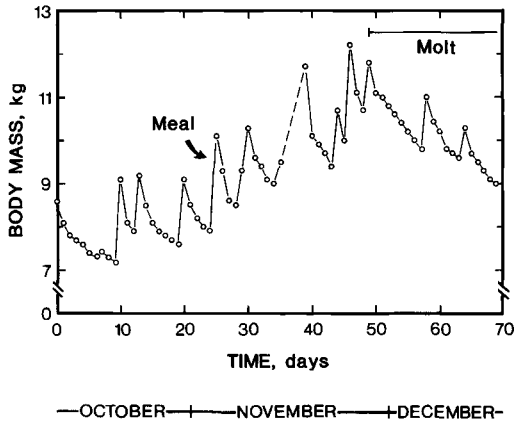


Fig. 3. Change in body mass in a free-ranging King Penguin chick during spring growth and molt.

meal (1.8 ± 0.1 kg, range 0.5–3.6 kg, $n = 47$) followed by a decrease until the next feed (Fig. 3). During the first 24 h of fasting, the mean dm/mdt was 71.6 ± 2.8 $g \cdot kg^{-1} \cdot 24 h^{-1}$ ($n = 47$); it decreased to 33.2 ± 3.2 $g \cdot kg^{-1} \cdot 24 h^{-1}$ ($n = 33$) the third day and stabilized at 14.0 ± 0.4 $g \cdot kg^{-1} \cdot 24 h^{-1}$ ($n = 7$) the sixth day after feeding.

EXPERIMENTAL CHICKS

Winter group.—Seven King Penguin chicks were captured at the end of their first growth phase, i.e. at their maximal body mass before winter starvation. The initial body mass of the chicks averaged 12.08 kg; after 166 days of fasting the average was 3.35 kg, a loss of 72% in 5–6 months (Table 2). The decrease in body mass of the 7 birds was characterized by three periods (Fig. 4A). During period I, which lasted 6–9 days, there was a rapid decrease in body mass and a decrease in dm/mdt . During the first day of captivity, dm/mdt was 11.5–61.1

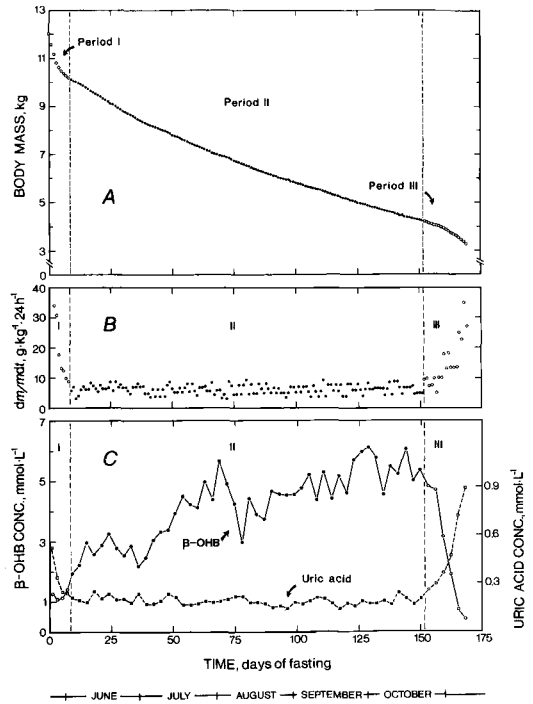


Fig. 4. (A) Rate of body mass decrease during fasting in a captive King Penguin chick. (B) Specific daily change in body mass (dm/mdt) during fasting. (C) Plasma β -hydroxybutyrate (β -OHB) and uric acid concentrations during fasting. See text for definition of periods I, II, and III.

$g \cdot kg^{-1} \cdot 24 h^{-1}$, depending on the bird. This wide range suggests the chicks had begun to fast at different times before being caught. During period II (133 ± 5 days), dm/mdt was maintained at a mean value of 6.3 ± 0.2 $g \cdot kg^{-1} \cdot 24 h^{-1}$ (range 5.7–7.7 $g \cdot kg^{-1} \cdot 24 h^{-1}$). In contrast, period III (24 ± 2 days) was characterized by a sharp increase in dm/mdt that was 21.2 ± 1.5 $g \cdot kg^{-1} \cdot 24 h^{-1}$ on the last day of fasting (Fig. 4B).

TABLE 2. Change in body mass of experimental fasting King Penguin chicks during winter and spring. Values are means \pm SE, with ranges in parentheses.

Season	Duration of fasting (days)	Initial body mass (kg)	Final body mass ^a (kg)	Decrease in body mass (%)
Winter ($n = 7$)	166 ± 5 (152–184)	12.08 ± 0.12 (11.56–12.50)	3.35 ± 0.07 (3.00–3.58)	72 ± 1 (70–76)
Spring ($n = 5$)	10	10.98 ± 0.21 (10.58–11.63)	8.25 ± 0.21 (7.78–9.03)	25 ± 1 (22–28)

^a Final refers to the end of the experiment, i.e. winter birds fasting until period III of fasting, spring birds until the beginning of period II.

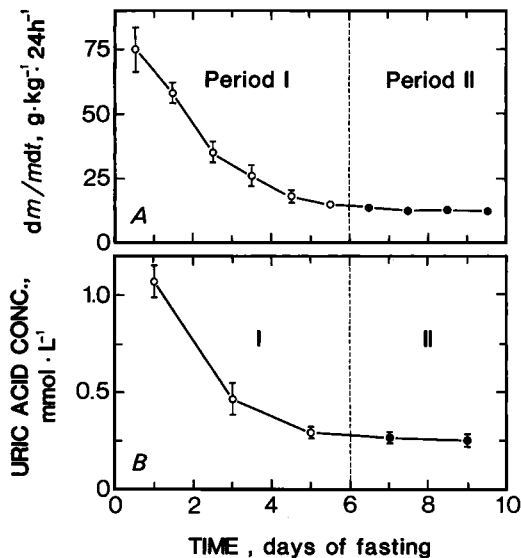


Fig. 5. (A) Specific daily change in body mass (dm/mdt), and (B) plasma uric acid concentration, in 5 captive King Penguin chicks during a 10-day fast in October (spring). See text for definition of periods I and II. Mean values \pm SEM (not drawn when 2 SEM were less than the height of the symbols) are shown.

The changes in plasma uric acid concentration paralleled those in dm/mdt (Fig. 4C). In period I the decrease in plasma uric acid concentration was highly variable in the chicks, presumably because they had started to fast at different times before being caught. During period II plasma uric acid concentration did not vary significantly, and remained at a low value (0.17 ± 0.01 mmol/l). During period III it increased to 0.97 ± 0.08 mmol/l. By contrast, plasma concentration of β -OHB increased progressively during period II (from 1.90 ± 0.22 to 4.51 ± 0.31 mmol/l) and decreased rapidly in period III (to 0.50 ± 0.11 mmol/l).

Spring group.—The mean initial body mass of the 5 King Penguin chicks was 10.98 kg, and after 10 days of fasting their mean body mass was 8.25 kg. They lost about 25% of their initial body mass (Table 2). Period I lasted 6 ± 1 days. dm/mdt was 75.0 ± 7.7 $g \cdot kg^{-1} \cdot 24 h^{-1}$ during the first 24 h of fasting, but declined sharply afterward (Fig. 5A). It reached 34.7 ± 3.8 $g \cdot kg^{-1} \cdot 24 h^{-1}$ the third day and stabilized at 13.6 ± 0.5 $g \cdot kg^{-1} \cdot 24 h^{-1}$ between days 6 and 10 of starvation, i.e. at the beginning of period II (Fig. 5A).

After the initial 24 h of captivity, all plasma

samples were lactescent. For two birds, lactescence was still present in the blood sampled on the third day. This indicates active digestion very soon after the last meal before capture.

In period I, plasma uric acid concentration decreased by 77% from the first to the fifth day of fasting. It then stabilized in period II at 0.25 ± 0.02 mmol/l (Fig. 5B). By contrast, the β -OHB level increased by 60% during the 10 days of starvation.

DISCUSSION

King Penguin chicks tolerate a 72% decrease in body mass during a winter fast. This is comparable to a 63–66% body mass loss in Common Swift chicks (*Apus apus*; Koskimies 1950). We found remarkable similarity in the way body mass decreased in free-ranging and captive chicks during long-term fasting. The rate of decrease in body mass of captive birds has been found previously to reflect protein breakdown; therefore, physiological data obtained on captive King Penguin chicks probably provides reliable information on how free-ranging chicks adapt to starvation.

The growth curve of free-ranging King Penguin chicks in spring was marked by a succession of sharp increases in body mass alternating with more gradual decreases (Fig. 3). The short decreases were similar to those that characterized period I in captive birds. The longer drops (Fig. 3) were similar to period I plus the beginning of period II in the captive birds. Because both groups of winter birds probably had fasted for different periods before the study began, the early responses to starvation cannot be compared. During prolonged fasting in the winter birds, however, the pattern of the change in body mass in free-ranging chicks (Fig. 1) was similar to that defined as periods II and III in the experimental birds (Fig. 4). Thus, the specific daily change in body mass, dm/mdt , was similar over the three periods. Nearly identical values were then observed in each group in spring and winter (Table 3).

The highest rate of decrease in body mass was during the first days of fasting (beginning of period I) in both groups of birds in spring (Table 3). This confirms previous data from experimental King Penguin chicks and adults (Le Maho and Despin 1976, Barré 1984). Much of this initial decrease in body mass was presum-

TABLE 3. Specific daily change in body mass ($\text{g} \cdot \text{kg}^{-1} \cdot 24 \text{ h}^{-1}$) during the three periods of fasting in King Penguin chicks. Values are means \pm SE.

Season	Status	Period of fasting		
		Beginning of period I	Period II	End of period III
Spring	Free-ranging	71.6 \pm 2.8 (n = 47)	14.0 \pm 0.4 (n = 7)	
	Experimental	75.0 \pm 7.7 (n = 5)	13.6 \pm 0.5 (n = 5)	
Winter	Free-ranging		6.4 \pm 0.4 ^a (n = 5)	35.2 \pm 1.9 (n = 2)
	Experimental		6.3 \pm 0.2 ^a (n = 7)	21.2 \pm 1.5 ^b (n = 7)

^a $P < 0.001$ compared with spring birds.

^b $P < 0.005$ compared with free-ranging chicks.

ably related to the production of urine and feces (Koskimies 1950, Ricketts and Prince 1984). The early reduction of the plasma concentration of uric acid (Fig. 5), suggests that the observed drop in dm/mdt also was due in part to a decrease in protein utilization.

Digestion in King Penguins occurs over less than 2 days (Copestake et al. 1983), but there was still a 3–4-fold decrease in dm/mdt in the following days, until the end of period I. This additional decrease may be attributed principally to reduced protein catabolism, as there was a parallel decrease in plasma uric acid concentration (Fig. 5). Thus, in their colony King Penguin chicks reduce protein utilization within only a few days of fasting.

In spring and winter the minimum, steady values of dm/mdt characterizing period II in the captive chicks were similar to those for the free-ranging chicks (Table 3). The progressive increase in ketonemia in captive birds, while uricacidemia remained minimum and constant, is consistent with earlier experimental data (Cherel and Le Maho 1985) indicating that period II is a long phase of protein sparing and lipid mobilization. In spring, however, the chicks lost mass at twice the rate of period II in the winter fast (Table 3). If body mass at the end of period II is similar for both spring and winter birds, period II probably lasts only about 62 days in spring vs. 133 days in winter. This difference might be due to more efficient protein sparing in the winter, because plasma uric acid concentration during period II was lower in winter than in spring (Figs. 4C and 5B). Such seasonal differences were observed in adult

Emperor Penguins (*Aptenodytes forsteri*; Robin et al. 1986).

The period III decrease in the plasma concentration of β -OHB of experimental birds, as uricacidemia increased abruptly (Fig. 4), accords with earlier data (Cherel and Le Maho 1985) indicating that this period is marked by an increase in protein catabolism. There is a characteristic increase in dm/mdt . The final, rapid decrease in body mass in chicks that starved to death (Fig. 1) indicates they died while in this period of increased protein utilization. These chicks presumably would have survived if their parents had returned earlier, as period III is reversible in Emperor Penguins (Le Maho 1984).

The values of dm/mdt reached near death in the free-living chicks were higher than those at the end of the fast in the experimental birds (Table 3). In captive birds the fast was always interrupted before it endangered the life of the animal.

Adaptive significance of winter fasting in King Penguin chicks.—King Penguin chicks are fed infrequently during the austral winter because of the uncertain and erratic availability of food in the sea (Stonehouse 1960). The high adaptive value of the ability of chicks to resist starvation is clearly related to the low feeding rate in winter. We estimated only one meal every 5–6 weeks. A 2–4-week interval had been indicated previously, but it was an underestimate because none of 10 King Penguin chicks kept during the winter in a pen accessible to the parents was fed during a 12-day period. Two other chicks, observed daily for one month in

their colony, fasted continuously (Stonehouse 1960). A large proportion of King Penguin chicks probably fast all winter (Fig. 1). This failure to feed did not seem to result from the disturbance caused by weighings: the 5 free-ranging chicks that were weighed daily in spring were fed normally, and grew and molted like other chicks in the colony.

The ability of King Penguin chicks to fast all winter in their colony is consistent with the previous observation (Stonehouse 1960) that the largest peak in mortality occurs in October, about 6 months after the beginning of winter. Stonehouse (1960) indicated that only birds weighing at least 6 kg at the beginning of winter can fast the entire period. The smaller peak in mortality observed at the beginning of winter (Fig. 2) may be attributed to the smallest chicks, which are either inadequately fed or too young, and therefore unable to starve for a long time.

Three periods of fasting in birds.—The three periods that characterize the changes in protein utilization during fasting in captive King Penguin chicks (Cherel and Le Maho 1985), captive adult Emperor Penguins (Le Maho et al. 1976, Groscolas and Clement 1976), and domestic geese (Le Maho et al. 1981) also occur naturally in King Penguin chicks in their colony.

Early reports indicated that pheasants and domestic fowl and geese adapt to experimental fasting by initially decreasing their rates of body mass loss and nitrogen excretion. These rates are maintained at a reduced level for several days and then increase (Schimanski 1879, Phillips et al. 1932, Benedict and Lee 1937, Errington 1939). These early data demonstrate the three periods of fasting more recently described in captive birds (Le Maho et al. 1976, 1981; Cherel and Le Maho 1985). Period I, a short period of transition, is marked by a considerable decrease in the relative rate of body mass loss and by high fat mobilization. Period II, a long phase of economy, exhibits a low relative rate of decrease in body mass; most of the energy expenditure derives from lipids, and proteins are spared. Period III, the critical period, is characterized by an increase in the relative rate of body mass loss and coincides with a rise in protein utilization while there still are available lipid stores.

Field data on the Wandering Albatross (*Diomedea exulans*) have shown that the chicks' growth curves resemble those of King Penguin

chicks (Fig. 3). There are large changes in body mass from day to day, depending on the amount of food received and the duration of each bout of fasting (Tickell 1968). Chicks of Gray-headed (*D. chrysostoma*) and Black-browed (*D. melanophris*) albatrosses also respond to fasting by an initial drop in body mass followed by a steady curvilinear decline, like the adults during incubation shifts (Prince et al. 1981, Ricketts and Prince 1984). All of these observations are consistent with periods I and II.

Incubating female ducks and geese eat little or nothing, and generally lose about 40% of their prebreeding body mass. Carcass analyses indicate significant amounts of pectoral muscle and gizzard protein are used regularly during this spontaneous fast, but most of the energy is derived from fat, and lipid stores are essentially exhausted by the time of hatching (Milne 1976, Korschgen 1977, Ankney and MacInnes 1978, Raveling 1979). In late incubation, however, some females leave their nests to feed while others starve to death (Korschgen 1977, Ankney and MacInnes 1978). Failed nesters still have a relatively high muscle protein content, but dead birds have depleted both fat and protein stores (Ankney and MacInnes 1978). This suggests the females are usually at the end of period II at hatching, whereas those that leave their nest before chicks hatch may have entered period III. Some birds die on the nest while in prolonged period III. The protein depletion described in seabirds after long storms (Duron et al. 1984) and in waterfowl during prolonged cold weather (Trautman et al. 1939) may correspond to period III.

The high rate of energy expenditure of migrating birds due to the cost of flying contrasts with the fasting birds achieving the lowest possible energy expenditure. It has been suggested that it is beneficial for a migrating bird to lose protein mass (pectoral muscles). The supposition is that flight muscles work at a power output near maximum efficiency early in the flight and, because of the decrease in transported mass, well below maximum efficiency toward the end of the flight. By constantly using surplus muscle as a fuel reserve, the working conditions for the remaining muscle would be maintained nearer to those for maximum efficiency (Pennycuik 1975). It is then remarkable that during migration body mass in passerines is lost through losses of dry lipids,

and the nonfat body mass remains constant (Odum et al. 1964, Odum 1965). This may correspond to an extreme situation of period II in which proteins are totally spared. However, protein depletion has been described in birds that have encountered unfavorable winds (Odum et al. 1964, Odum 1965), suggesting they are in period III.

Our findings on King Penguin chicks accord with data available for a wide variety of birds either starving under natural conditions or experimentally fasted. Such data may provide an understanding of the strategy of wild species for surviving long-term fasting.

ACKNOWLEDGMENTS

We are indebted to Dr. S. Dejours for help in editing. We thank Mrs. O. Frain and Mr. S. Liess for their technical contribution. This study was supported by grants from Terres Australes et Antarctiques Françaises and from CNRS (Action Thématique Programmée No. 4584, "Réponses physiologiques et biochimiques à des situations vitales critiques," and Recherche Coopérative sur Programme No. 764, "Ecosystèmes terrestres subantarctiques et antarctiques").

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