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Daily Body-mass Loss and Nitrogen Excretion During Molting Fast of Macaroni Penguins

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Little is known about the dynamics of protein and energy requirements during avian molt (Murphy and King 1991). In passerine birds, changes in protein requirements appear to resemble those in energy expenditure (Murphy and King 1991). However, no clear relationships have emerged due to the complexity of the metabolic processes. In most species, plumage renewal is a gradual, long-term process. This, combined with the fact that birds feed while molting, makes quantifying the allocation of exogenous and endogenous nutrients to keratin synthesis and energy expenditure difficult.

Unlike other bird species, penguins renew all their feathers over a protracted period (two to five weeks) during which they fast completely (Adams and Brown 1990, Groscolas and Cherel 1992). Thus, penguins rely entirely on their endogenous nutrient stores for both feather synthesis and energy expenditure during molt, and molt is preceded by the buildup of protein and lipid reserves (Cherel et al. 1993). To investigate the dynamics of protein and energy requirements during avian molt, we measured daily changes in body-mass loss and nitrogen excretion in Macaroni Penguins (*Eudyptes chrysolophus*) during their molting fast. In molting King Penguins (*Aptenodytes patagenicus*), the daily loss in body mass follows a pattern similar to that of energy expenditure (Adams and Brown 1990, Groscolas and Cherel 1992) and, therefore, it is a relatively simple way to get a first insight into the energy expenditure of molting penguins.

Methods.—Our study was carried out at the subantarctic Possession Island, Crozet Archipelago (46°25'S, 51°45'E). Six adult Macaroni Penguins were captured when first sighted ashore, at the beginning of their molting fast, in March 1987. Each bird was weighed (accuracy ±10 g) at capture and daily thereafter. Four penguins were kept outdoors in a fenced area. The other two were placed alone in wire-bottomed metabolism cages in a room at external temperature. Guano was collected every day following the procedure of Robin et al. (1987). Fallen old feathers have been carefully discarded from guano. Total nitrogen in the guano was determined by the method of Kjeldahl, using selenium as catalyzer. Values are means and standard errors. Peritz' *F*-test (Harper 1984) was used for statistical comparisons.

Results and Discussion.—The mean body mass of the six Macaroni Penguins was 5.76 ± SD of 0.15 kg at capture. After 31.5 ± 1.4 days of fasting, their mass was 2.56 ± 0.07 kg, which corresponds to a 55.6 ± 0.8% decrease in mass. In birds and mammals, changes in the specific daily body mass loss ($dm/m \cdot dt$) allow the determination of three different phases during long-term fasting (Cherel et al. 1988b). During the first days of the fast, in Macaroni Penguins, $dm/m \cdot dt$ decreased ($P < 0.01$) from 28.5 ± 1.5 (day 1) to 19.7 ± 1.4 $g \cdot kg^{-1} \cdot day^{-1}$ (day 4). However, during the last days, $dm/m \cdot dt$ increased ($P < 0.05$) from 23.0 ± 3.0 (day 30) to 34.1 ± 3.9 $g \cdot kg^{-1} \cdot day^{-1}$ (day 32). These initial and final variations in $dm/m \cdot dt$ characterize, respectively, phases I and III of fasting previously described in molting and nonmolting King Penguins and Emperor Penguins (*A. forsteri*; Groscolas 1990, Groscolas and Cherel 1992).

Phase I of fasting is adaptive because it is marked by a decrease in basal metabolic rate, mobilization of fat stores and a reduction in protein use (Cherel et al. 1988b). In this study, no large decreases in daily body-mass loss and nitrogen excretion occurred during the first days after Macaroni Penguins came ashore (Fig. 1). The main reason for this is probably that

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Macaroni Penguins had already been fasting for hours or even days when they were captured, because pre-fasting adult penguins generally carry no food in their stomachs when they land.

An increase in body protein utilization and a progressive exhaustion of fat reserves characterize phase III of fasting and this phase is critical because birds must refeed at this time (Cherel et al. 1988b). In Macaroni Penguins, the beginning of an increase in daily nitrogen excretion paralleled that in $dm/m \cdot dt$ in late fasting (Fig. 1) and, consequently, birds were released to sea at that time. The duration of the molting fast in the colony is about 25 days (Brown 1986), indicating that naturally fasting birds generally do not reach the point of increased protein utilization (Williams et al. 1992). In the two caged birds, an increase in locomotor activity was apparent during the last days of the experiment. Such an increase has been found in nonmolting male Emperor Penguins, and interpreted as reflecting a stimulation of food foraging behavior before the lethal depletion of nutrient reserves (Groscolas 1990).

The main difference in changes in $dm/m \cdot dt$ between molting and nonmolting King and Emperor penguins occurs during phase II of fasting (Groscolas and Cherel 1992). In nonmolting birds, $dm/m \cdot dt$ remains steady at low values during the long phase II that lasts weeks and even months (Cherel et al. 1987, Groscolas 1990). In contrast, phase II of molting in King and Emperor penguins can be divided into three stages (Groscolas 1978, Cherel et al. 1988a, Groscolas and Cherel 1992); these also are seen in molting Macaroni Penguins (Fig. 1). During the first stage (days 4–7 of fasting; Fig. 1), $dm/m \cdot dt$ remains constant at about 19–20 $g \cdot kg^{-1} \cdot day^{-1}$. In the longer second stage (days 8–24), it peaks at up to 33 $g \cdot kg^{-1} \cdot day^{-1}$, and it stabilizes at lower values (about 23 $g \cdot kg^{-1} \cdot day^{-1}$) during the third stage (days 25–30). Unlike previous studies on molting penguins (Cooper 1978, Brown 1986, Gales et al. 1988), we found the decrease in mass of Macaroni Penguins was not linear during molt. This discrepancy probably results from the fact that penguins were not weighed daily in previous studies, and $dm/m \cdot dt$ was not calculated (i.e. body mass and not specific body-mass loss was plotted versus time of molt). Our data on two large (King and Emperor) and one small (Macaroni) penguin species, therefore, suggest that the peak in daily body mass loss during the molting fast is a general trend in penguins.

The comparison of molt events (new feather synthesis and old feather loss) with daily body-mass loss in Emperor and Macaroni penguins (Groscolas 1978, Brown 1986, this study) shows that feather growth is not involved in the peak of daily body-mass loss (Fig. 1). However, the chronology of molt changes indicates that the increase in body-mass loss was associated with the reduction in thermal insulation. This phenomenon, previously described in the Little Penguin (*Eudyptula minor*; Baudinette et al. 1986), probably begins when new feathers protrude more and more through the skin while old feathers still remain connected to them. The reduction in thermal insulation then peaks because the heavily vascularized skin is exposed while new feathers are small and old feathers are lost. Thermal insulation is progressively restored until new feathers reach their maximum external length (molt end). The existence of this link between thermal insulation, old-feather loss and the peak in $dm/m \cdot dt$ is strongly supported by the concomittant rise in specific metabolic rate observed at this time and interpreted as an increase in thermoregulatory demands when insulation is reduced (Brown 1985, Adams and Brown 1990). The mass of old feathers is a minor component (5–8%, calculated from Adams and Brown 1990) of total body-mass loss and, therefore, cannot alone explain the peak in $dm/m \cdot dt$.

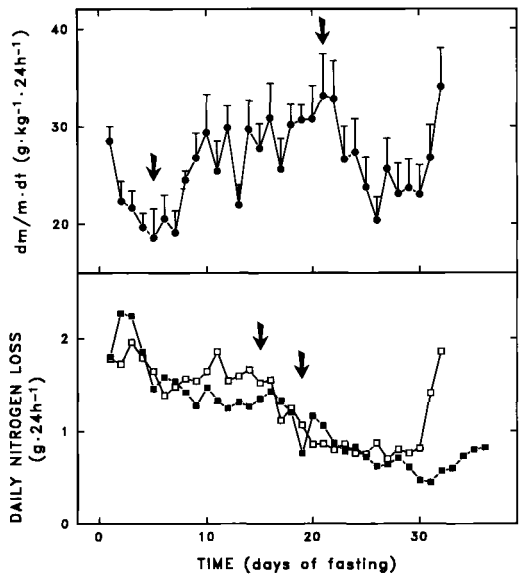

Fig. 1. Changes in specific daily loss in body mass ($dm/m \cdot dt$) for six Macaroni Penguins and in daily nitrogen excretion for two birds during a molting fast. Upper panel: at first arrow, new feathers begin to protrude through skin; at second arrow, new feathers reach their maximum external length (end of molt per se). Lower panel: at first arrow, feather-synthesis rate begins to decrease; at second arrow, feather synthesis ends (following Brown 1986).

The pattern of daily nitrogen excretion was very similar in the two caged birds (Fig. 1), and their cumulative nitrogen losses during the first 30 days of fasting were similar (36.7 and 38.5 g N). Therefore, we consider them to be representative of the normal pattern of nitrogen excretion in Macaroni Penguins during molting fast. In phase II, nitrogen excretion stabilizes at 1.5 g N·24 h^{-1} until day 16 when a sharp

decline to 0.9 g N·24 h^{-1} (day 19) occurs within a few days. Afterwards, daily nitrogen excretion decreases slowly, remaining at low levels until the end of phase II (Fig. 1). Such a slow decrease may be related to the continual reduction in body protein mass. The comparison of daily changes in body-mass loss, nitrogen excretion, feather growth, and metabolic rate in molting Macaroni Penguins (Brown 1986, Adams and Brown 1990, this study) clearly shows that the peaks in $dm/m \cdot dt$ and in energy expenditure are not associated with an increase in nitrogen loss. However, high levels of nitrogen excretion occur when feather growth is active, and nitrogen loss decreases when the rate of feather synthesis declines (Fig. 1).

High endogenous protein mobilization is the only way to provide amino acids for feather synthesis in penguins that are fasting and molting simultaneously. However, high nitrogen excretion at that time indicates that a portion of the amino acids is not used for keratin synthesis. High protein mobilization and nitrogen excretion rates are explained by the mismatch of amino acids between keratin and other body proteins. As in other species of birds, penguin feather proteins are notably rich in sulfur amino acids, containing proportionately more cystine than proteins from other body tissues (Murphy et al. 1990). The dominant bottleneck in keratin synthesis during the penguin molting fast is therefore the availability of cystine, and it has been calculated that at least 2.9 to 3.6 g of tissue protein must be mobilized to produce 1 g of feather protein (Murphy et al. 1990). Consequently, amino acids in excess are used for energy production through direct and/or indirect (gluconeogenesis) oxidation, resulting in an increased production of uric acid and, thus, in an increase in nitrogen excretion.

Daily nitrogen excretion was measured in only two birds and, thus, data on protein metabolism must be interpreted with caution. The picture emerging from this study on penguin molt, however, is that high protein requirements are linked to new feather growth, and high energy requirements to old feather loss, respectively. Such results contrast with those obtained for well-nourished passerine birds that suggest a positive relationship between protein and energy requirements (Murphy and King 1991).

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Can Avian Distribution Patterns in Northern Argentina be Related to Gallery-forest Expansion-Retraction Caused by Quaternary Climatic Changes?

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Nores (1992) presented an analysis of two bird distribution patterns in subtropical South America. The first is comprised of disjunct distribution of pairs of species and subspecies between the southern Yungas and the Paranaense forests, which are separated by 700 km of xerophytic Chaco vegetation. The second is a supposed zone of secondary contact located in the central Chaco, where some "nonforest" species and subspecies interact.

Nores proposed that both patterns were produced by vegetational changes in the central Chaco associated with the well-supported global climate changes during the Quaternary. He suggested that, when this region was more humid than today (possibly during interglacial periods), forests advanced from the Yungas and the Paranaense regions along the Pilcomayo and Bermejo rivers, forming a wide and continuous forest bridge. Forest birds from both regions presumably expanded their distributions during this epoch, whereas the ranges of nonforest birds were interrupted by this same ecological barrier. The opposite occurred when the forest bridge was fragmented during the following drier period. As the forest and nonforest species sharing the same distribution pattern show different "speciation" levels, Nores proposed that these vegetational shifts occurred several times in the recent past.

There are, however, several fundamental problems with the analysis of Nores that cause me to question the validity of his conclusions. These problems can be grouped in the following major topics: (a) problems with habitat classification; (b) the authenticity of a secondary contact zone in the central Chaco; (c) questionable assumptions; (d) lack of paleoecological support.

Habitat classification.—The first problem with Nores' analysis is the lack of a precise definition for forest and nonforest birds. This is an important point because his hypothesis can be considered as an application of the refuge model (for review, see Lynch 1988) to a specific point in the subtropical region of South America. Therefore, it must require that the taxa involved present distributional concordance as well as rigid ecological fidelity (Vanzolini 1981, Lynch 1988). This problem is even bigger in Chaco, which comprises several different types of forests and woodlands (see Ramella and Spichiger 1989). Since Nores did not make a clear distinction between the different types of forests in the Chaco region, I assume that his "forest" within the Chaco region means only "tall humid gallery forest."

It is implicit in Nores' hypothesis that the present-day Chaco vegetation represents a major barrier to the dispersion of his forest birds. If this is correct, one would expect to find forest birds in this region only in gallery forests along the rivers. Nores convincingly showed that this is the case for many of his forest species (see Nores 1992:fig. 3).

However, he included in his list of forest birds some species that did not fit entirely this situation. *Nystalus chacuru* is a savanna species (Sick 1985, Silva 1992, Davis 1993). Some species are absent from the Argentine Chaco, but occur throughout Paraguayan and/or Bolivian Chaco and, thus, would not require belts of humid forests along the Pilcomayo and Bermejo rivers to reach the Yungas forests. This category of birds includes *Pionus maximiliani* (Smith 1960, Short 1975), *Piaya cayana* (Short 1975), *Veniliornis paserinus* (Short 1975, 1982), *Xenops rutilans* (Vaurie 1980), *Cyanocorax cyanomelas* (Short 1975), *Basileuterus culicivorus* (Short 1975, Ridgely and Tudor 1989, Davis 1993), and *Hemithraupis guira* (Short 1975, Isler and Isler 1987).

Other species (*Philydor rufus* and *Pipraeidea melanonota*) avoid the Chaco region, but are distributed almost continuously from the Yungas forests to the Paranaense forests throughout central Brazil and southern Bolivia. In fact, this distribution pattern is shown so clearly in different groups of birds that