**Title:** Feet First: Adaptive Growth in Magellanic Penguin Chicks

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**Keywords**

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**Abstract:**

Growing animals should allocate their limited resources in ways that maximize survival. Seabird chicks must balance the growth of features and fat reserves needed to survive on land with those needed to successfully fledge and survive at sea. We used a large, 34-year dataset to examine energy allocation in Magellanic penguin chicks. Based on the temporal trends in the selective pressures that chicks faced, we developed predictions relating to the timing of skeletal feature growth (Prediction 1), variation in skeletal feature size and shape (Prediction 2), and responses to periods of high energetic constraint (Prediction 3). We tested our predictions using descriptive statistics, generalized additive models, and principal component analysis.

Nearly all of our predictions were supported. Chicks grew their feet first, then their flippers. They continued to grow their bill after fledging (Prediction 1). Variance in feature size increased in young chicks but declined before fledging; this variance was largely driven by overall size rather than by shape (Prediction 2). Chicks that died grew slower and varied more in feature size than those that fledged (Prediction 2). Skeletal features grew rapidly prior to thermoregulation and feet and flippers were 90% grown prior to juvenile feather growth; both thermoregulation and feather growth are energetically expensive (Prediction 3). To avoid starvation, chicks prioritized storing mass during the first 10 days after hatching, then the body condition of chicks began to decline (Prediction 3). In contrast to our prediction of mass prioritization in young chicks, chicks that were relatively light for their age had high skeletal size to mass ratios. Chicks did not show evidence of reaching physiological growth limits (Prediction 3). By examining energy allocation patterns at fine temporal scales and in the context of detailed natural history data, we provide insight into the trade-offs faced by growing animals.

**Data Files**

Statistics\_ByFeatureAge.txt

Description:

This text file includes basic statistics (average, standard deviation, coefficient of variation) for Magellanic penguin chicks that fledged and for chicks that died, as both absolute values and relative to the average adult male size [,1:16]. The four skeletal features (foot length, flipper length, bill length, bill depth) were all measured in cm and mass was measured in kg. The data represent 9,491 unique chicks measured from when they hatched until they died or fledged. Also included are results of allometric models for log-transformed skeletal feature size and overall body size versus log-transformed mass [,17:28]. There are outputs for three types of models: linear models, generalized additive models, and third-order polynomial models. Overall body size was the first principal component (PC1) of a principal component analysis run on all four skeletal features at each age of growth.

Columns [, column number(s)]:

* Age [,1]: Chick age in days.
* Feature [,2]: The name of the feature.
* AverageSize\_Died [,3]: The average size of that feature at that age for chicks that later died; skeletal feature in cm, mass in kg.
* SD\_Died [,4]: The standard deviation of that feature at that age for chicks that later died.
* CV\_Died [,5]: The coefficient of variation of that feature at that age for chicks that later died.
* n\_Died [,6]: The sample size of that feature at that age for chicks that later died.
* [,7:9]: Same [,3:5], but units are percent of average adult male size rather than measurements.
* [,10:16]: The columns above are all repeated for chicks that eventually fledged and are demarcated by \_Fledged.
* [,17:28]: For each model, several outputs are included; see package mgcv (Version 1.8-33; Wood 2020) documentation for further details. Models are differentiated using the following terms: \_gam = generalized additive model; \_lm = linear model; \_poly = third-order polynomial model.
  + df = model degrees of freedom
  + logLik = log-likelihood of the fitted model
  + AIC = Akaike Information Criterion (AIC) of the fitted model
  + df.residual = effective residual degrees of freedom of the model

Wood, S. 2020. Package 'mgcv'. Version 1.8-33.

PCAOutputs\_ByAge.txt

Description:

This data file includes age-specific information on two types of principal component analyses that were run on the centered and scaled skeletal features of chicks (foot length, flipper length, bill length, bill depth). The first ([,2:3]) was run for all chicks of all ages and was used to calculate an overall index of body size for each chick at each age that they were measured (first principal component). We used the residuals of the relationship between log-transformed mass and overall body size to indicate the body condition of chicks. The second type of analysis was used to quantify variance in feature size attributed to size (first principal component) versus shape (higher-order principal components) among chicks of the same age ([,4:15]). For this question, a principal component analysis was run separately for each age of the chick period.

Columns [, column number(s)]:

* Age [,1]: Chick age in days.
* Average\_BodyCondition [,2]: The average value of the residuals for chicks of that age.
* BodyConditionChange [,3]: The absolute change in average body condition from one day of the chick period to the next.
* PC1\_varexp, PC2\_varexp, PC3\_varexp, PC4\_varexp [,4:7]: Percent variance in skeletal measurements for chicks of that age described by the first principal component, second principal component, third principal component, and fourth principal component.
* PC1\_flipper, PC1\_foot, PC1\_BillDepth, PC1\_BillLength [,8:11]: Loading values of each skeletal feature (flipper, foot, bill depth, bill length) for the first principal component.
* PC2\_flipper, PC2\_foot, PC2\_BillDepth, PC2\_BillLength [,12:15]: Loading values of each skeletal feature (flipper, foot, bill depth, bill length) for the second principal component.