

ESTIMATION BY USE OF FIELD WEIGHINGS OF METABOLIC RATE AND FOOD CONVERSION EFFICIENCY IN ALBATROSS CHICKS

C. RICKETTS AND P. A. PRINCE

British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, Cambridge CB3 0ET, United Kingdom

ABSTRACT.—A knowledge of the assimilation of food and of the energetic demands of chicks at different stages in the growth period can provide a basis for understanding growth strategies of seabirds. We have developed a simple model of chick weight loss between feeds that allows an estimation of metabolic costs and food-conversion efficiency in albatross chicks. The data required to provide these estimates are a series of frequent weights of a chick following a meal and the weight of food delivered in the meal. Preliminary results show a considerable variation in both food-conversion efficiency, which may reflect variation in the composition of meals delivered to chicks, and in the metabolic demands of individual chicks. Received 19 October 1983, accepted 26 March 1984.

PATTERNS of growth of seabird chicks reflect a delicate balance between the ability of the adults to provide food and the metabolic demands of the chick for existence and development. Growth curves for samples of chicks indicate a steady increase in weight but obscure the underlying growth patterns of individual chicks. In Procellariiformes, these patterns are typified by relatively large and infrequent weight gains as a result of feeding, followed by weight loss as a result of the metabolic demands of the chick between feeds. A knowledge of the assimilation of food and of the energetic demands at different stages of the growth period can provide a basis for understanding differences among growth strategies.

Two approaches to the measurement of metabolic costs in Procellariiformes have been used. The first is more direct, but essentially laboratory oriented, and involves the measurement of oxygen consumption over a short period of time (e.g. Ricklefs and Matthew 1983). The second approach is more field oriented and involves the estimation of rates of weight loss during prolonged periods of fasting (Prince et al. 1981). This latter method is technically simpler and potentially causes less disturbance and stress. The conversion of weight loss to energy, however, requires a knowledge of the composition and energy content of the material lost. We have developed a technique for estimating the rate of weight loss of chicks between meals and, from a knowledge of individual feed sizes, the proportion of the meal assimilated.

METHODS

The data collected were successive weights of individual chicks of Grey-headed (*Diomedea chrysostoma*) and Black-browed (*Diomedea melanophris*) albatrosses at Bird Island, South Georgia (54°S, 38°W). Weights were collected by two different methods in two different breeding seasons.

Three-hour weights.—Thirteen Black-browed and 11 Grey-headed albatross chicks of known ages were weighed at 3-h intervals from 0600 to 2100 each day for a 2-week period in early February and for a 1-week period in early March 1978. The chicks were observed continuously during daylight (0500–2200) so that the arrival of adults bringing food could be noted. Chicks were weighed immediately before and after delivery of a meal, and the timing of feeds for each chick was recorded.

Ten-minute weights.—Because collection of weights at 3-h intervals was extremely labor intensive, artificial nests incorporating an automatic weighing device and recorder were developed (Prince and Walton in press) and deployed to obtain the weights of two Grey-headed Albatross chicks at 10-min intervals for 26 days from 23 February to 21 March 1982. The weighing device was accurate to within 15 g, and its correct calibration was checked on alternate days by using known weights.

A MODEL OF CHICK WEIGHT LOSS

Immediately after the chick receives a feed, the total weight of a chick is comprised of two components: the weight of the chick's body and the weight of the meal (Fig. 1). Thereafter, three processes occur simultaneously: metabolism, assimilation, and defecation. The chick's body

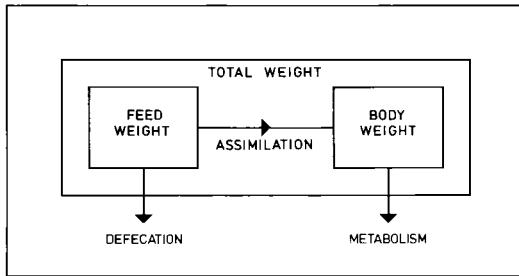


Fig. 1. Diagrammatic representation of a chick's total weight as the sum of its body weight and the weight of food in the gut. Weight is lost as a result of metabolism and defecation of nonassimilated food.

weight increases as a result of assimilation and decreases as a result of metabolism. The weight of food within the chick decreases as a result of both assimilation and defecation. The simultaneous occurrence of these processes produces a complex curve, the general form of which is shown in Fig. 2A: the total weight decreases as a result of two processes, defecation and metabolism. The later part of the curve, after assimilation and defecation are completed, represents weight loss simply as a result of metabolism. An alternative breakdown of the total weight-loss curve can be made by extrapolating this later part of the curve back to the weight axis (Fig. 2B). This is equivalent to as-

suming that assimilation is instantaneous and that the chick's metabolic rate is that which would pertain after assimilation is completed. Then, the two components of the chick's total weight are the weight of the chick's body plus assimilated food and the weight of the unassimilated food. In this case, any energy costs incurred by the process of assimilation are excluded from the chick's metabolic rate and the assimilated food.

Fitting a mathematical curve with two components of appropriate form to the weight-loss data should provide estimates of the following parameters:

- C: the sum of the chick's body weight and assimilated portion of the food after the additional energetic costs of assimilation have been met. This is the intercept of the slower component of the weight-loss curve on the weight axis (Fig. 2B).
- m*: the rate of weight loss of the chick as a result of resting (post-absorptive) metabolism. This is the slope of the slower component of the weight loss curve (Fig. 2B).
- F: the weight of food that is not converted to chick body weight. This includes the weight of food used to fuel assimilation. This is the intercept of the faster component of the weight-loss curve on the weight axis (Fig. 2B). Independent measurement

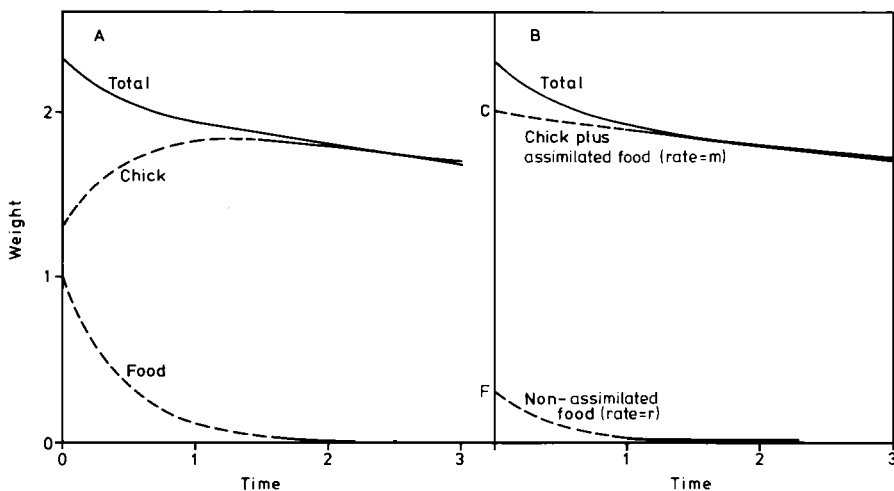


Fig. 2. Two possible breakdowns of the total weight-loss curve. (A) Changes in chick body weight and food weight following a feed; (B) changes in chick body weight and food weight if assimilation were instantaneous.

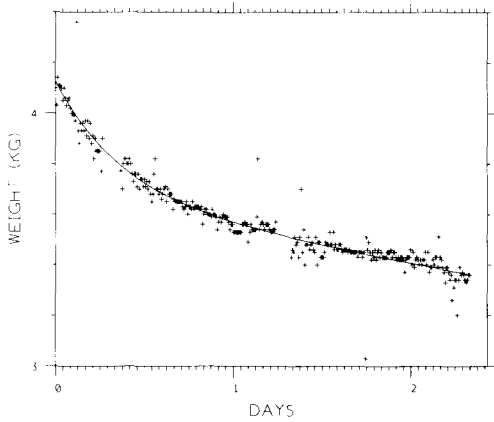


Fig. 3. Weight loss of a Grey-headed Albatross measured at 10-min intervals following a feed and the fitted double exponential curve.

of feed weight then provides the fraction converted to chick body weight.

r : the rate of defecation of the food. This is the slope of the faster component of the weight-loss curve.

We have investigated the possibilities that the two components of the weight-loss curve may be either linear or exponential. The linear case represents constant absolute weight loss per unit time (a zero-order process). The exponential case represents a constant proportional weight loss per unit time (a first-order process). The data used for this investigation were four weight-loss curves with weights at 10-min intervals extending for more than 2 days.

The weight-loss curve (Fig. 3) is clearly not a straight line, which precludes the possibility

that both defecation and metabolism are linear (zero-order) processes. Moreover, the faster component (defecation) was not linear. Therefore, the two possible descriptions of the data both have exponential defecation rates and either linear or exponential rates of body weight loss. The mathematical form of these curves is then either

$$W(t) = Fe^{-rt} + C - mt$$

or

$$W(t) = Fe^{-rt} + Ce^{-mt},$$

where $W(t)$ represents the chick's total weight at time t after a feed. The estimated parameters for these curves are given in Table 1, together with a measure of goodness of fit for the curves (the residual sum of squares). Both curves fitted the data well and gave virtually identical parameter estimates and residual sums of squares and so could not be separated statistically on the basis of these data. Metabolic costs in most species, however, decrease as weight decreases, and weight loss in incubating adults of these species, where fasts continue for considerably longer, follows an exponential decay (Prince et al. 1981). For these reasons, we have used the double exponential curve as the description of the pattern of weight loss.

RESULTS

Weight-loss curves extending for more than 3 days were selected from the 3-h weight data. Those for which the chick had received another meal during the previous 24 h were excluded to minimize the effect of residual food in the gut on measured feed sizes. There was some

TABLE 1. Fitted parameters of the weight-loss curves $W(t) = Fe^{-rt} + C - mt$ and $W(t) = Fe^{-rt} + Ce^{-mt}$, where $W(t)$ = total weight of chick at time t after feed, F = nonassimilable weight of feed, r = defecation rate, C = weight of chick's body plus assimilable portion of feed, and m = rate of weight loss of chick. The column headed RSS gives the residual sum of squares of the data from the fitted curve.

Curve number	$W(t) = Fe^{-rt} + C - mt$					$W(t) = Fe^{-rt} + Ce^{-mt}$				
	F (kg)	r (d^{-1})	C (kg)	m ($kg \cdot d^{-1}$)	RSS	F (kg)	r (d^{-1})	C (kg)	m (d^{-1})	RSS
6/2	0.89	2.96	3.77	0.097	0.94	0.89	2.96	3.77	0.027	0.94
6/3	0.86	1.97	3.80	0.087	0.86	0.85	2.00	3.81	0.025	0.86
7/1	0.45	2.70	3.67	0.135	0.74	0.44	2.75	3.68	0.039	0.74
7/2	0.70	3.37	3.93	0.135	1.12	0.70	3.38	3.93	0.036	1.12

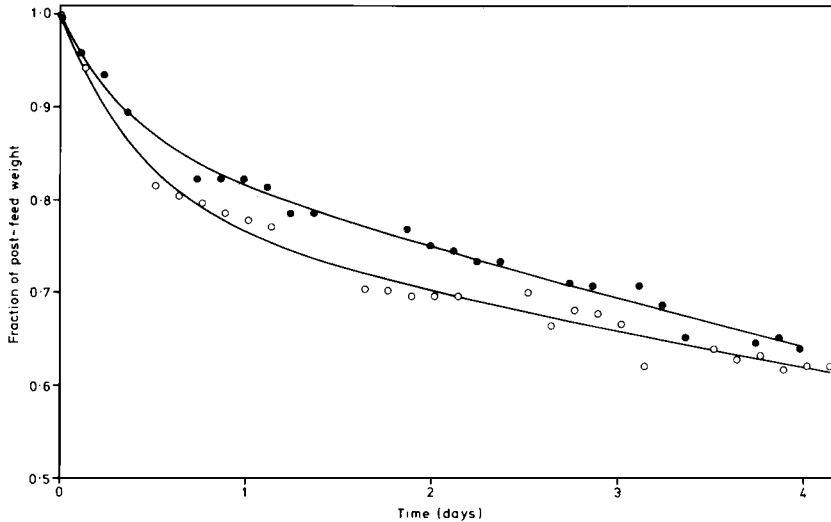


Fig. 4. Observed weights of two Grey-headed Albatross chicks and fitted weight-loss curves expressed as a fraction of the post-feed weight for a chick with 51% food conversion (upper curve, ●) and a chick with 19% food conversion (lower curve, ○). In both cases the feed was approximately 28% of the post-feed weight.

variation in the shape of the weight-loss curve (Fig. 4), and this was reflected in the parameters of the fitted curves. The values of metabolic costs, proportion of feed assimilated, and defecation rate are given in Table 2 in relation to the chick's age and body weight before the feed. The results from the 10-min weights are given for comparison.

Metabolic costs varied from 2.5 to 9.9% of body weight per day and defecation rate from 1.02 to 3.38 per day. The differences in weight-loss curves were mainly reflected in the range of food converted to chick body weight, which varied from 7 to 55% of the feed. Neither defecation rate nor the assimilated portion of the feed had a significant correlation with either age of chick or feed size ($P > 0.10$ for all). Although there was no significant change in metabolic costs with age in the sample as a whole ($P > 0.10$), 4 of the 5 chicks for which more than one estimate was available had a decrease in metabolic costs with age.

DISCUSSION

The results we have presented here exemplify a new approach to the simultaneous estimation of metabolic costs and food-conversion efficiency in seabird chicks. Although the data suggest some interesting physiological

comparisons, we shall deliberately refrain from speculating about the biological significance of the results because of the limited sample sizes and because the 1978 breeding season was one of a relative food shortage during which chicks of below average weight for their age were produced. Rather, we wish to emphasize the potential usefulness of the technique. Thus, by using a simple series of frequent chick weights, combined with pre- and post-feed weights, we have been able to provide estimates of some of the primary variables that may underlie the evolution of growth strategies.

First, resting metabolic costs of individual chicks can be estimated at different stages in the growth period. The metabolic costs, expressed as percentage of body weight per day, are consistently higher than those of adults of the species (Prince et al. 1981). Moreover, there is an indication, from a few chicks, that metabolic costs may decline with age. The conversion of these metabolic costs to absolute rates of energy consumption requires a knowledge of the composition—water, fat, and protein—of the material lost. It seems likely, however, that metabolic costs expressed as percentage of body weight will provide a useful relative basis for comparison.

Second, the proportion of the feed weight that is converted into chick body weight can

TABLE 2. Estimates of metabolic costs, food-conversion efficiency, and defecation rate in Black-browed (BBA) and Grey-headed albatrosses (GHA). The age, chick weight before the feed, and feed weight are also given.

Chick number	Age (days)	Metabolic costs (% body weight/day)	Food converted (%)	Feed weight (kg)	Chick weight (kg)	Defecation rate (d ⁻¹)
1978 3-h weights						
BBA 20	33	4.3	39	0.65	1.85	2.47
BBA 17	35	5.7	30	0.72	1.73	1.55
BBA 20	41	5.5	45	0.66	1.92	1.02
BBA 16	67	6.7	49	0.69	1.89	1.82
Mean	44	5.5	41	0.68	1.85	1.72
1978 3-h weights						
GHA 13	37	7.3	34	0.84	1.78	1.49
GHA 4	41	8.1	51	0.78	1.28	2.24
GHA 5	43	4.6	43	0.48	1.30	1.27
GHA 1	43	9.9	45	0.55	1.70	2.41
GHA 4	45	7.6	55	0.49	1.23	2.82
GHA 6	46	8.5	7	0.37	1.50	3.16
GHA 1	50	6.0	19	0.72	1.95	2.23
Mean	44	7.4	36	0.60	1.53	2.23
1982 10-min weights						
GHA 7/1	—	3.9	24	0.58	3.54	2.75
GHA 7/2	—	3.6	20	0.88	3.78	3.38
GHA 6/2	—	2.7	—	—	—	2.96
GHA 6/3	—	2.5	27	1.16	3.50	2.00
Mean	—	3.2	24	0.87	3.61	2.77

be calculated, provided feed weight is known. This estimate of conversion efficiency represents the proportion of the feed that is converted to chick body weight after the energetic costs of assimilation have been taken into account. Meals delivered to the chicks of these species have a high (mean 50%) and variable water content (Prince 1980), and it seems likely that this accounts for much of the variation in food-conversion efficiency.

Finally, the rate of defecation of the feed can be estimated. Again, the variation in this parameter may reflect variation in meal composition. The range of values found indicates that 90% of the feed is defecated or assimilated within 0.7 to 2.3 days (mean 1.2 days). Grey-headed Albatross chicks are fed, on average, every 1.1 days. This suggests that the chick's ability to process the food may be closely linked to the parents' ability to supply food.

The technique we have developed is applicable to many pelagic seabirds, particularly Procellariiformes, that typically rear one chick. Even in such species, useful weight-loss curves

must include a period for which the chick is simply metabolizing and not assimilating its food. Our experience suggests that only about one-tenth of the data collected will be useful in this context. Moreover, while weighing at 3-h intervals was adequate in these albatrosses, which feed their chicks approximately every 1.1 days, the sampling frequency would need to be increased in species that feed their chicks more frequently.

The application of this technique for estimating metabolic costs and food-conversion efficiency in seabirds will depend largely on the deployment of devices that record weights at frequent intervals: such a device has been developed for albatross chicks (Prince and Walton in press) and adult Herring Gulls (*Larus argentatus*) and Barnacle Geese (*Branta leucopsis*) (Sibly and McCleery 1980). The value of techniques such as this is clear: they enable changes in metabolic costs through the growth period and variation in food-conversion efficiency with age and meal composition to be investigated. The measurement of these parameters should

enhance our understanding of the evolution of the variety of growth strategies exhibited by seabirds.

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