# BODY MASS CHANGES AND ENERGETICS OF THE KIWI'S EGG CYCLE*

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## ABSTRACT

The disproportionately large kiwi egg and its formation were studied by following the increase in body mass of a hen through an egg cycle. Indirect calorimetry of the hen and bomb calorimetry of a kiwi egg were used with body mass data to estimate the rate of energy expenditure, the peak energy demand during egg production and the extent of fasting at laying time. The energy content of whole fresh egg was 11.55 Kj per g. The yolk, containing 91% of the energy of the kiwi egg, was completed during the first 7½ days of the cycle, adding 174 to 203% to her standard metabolic budget.

## INTRODUCTION

The kiwis have attained the extreme in the proportion of egg size to adult body size (Huxley 1927), approximately 1:5 for the Brown Kiwi, *Apteryx australis* (cf Reid 1971a). This is of considerable interest both mechanically and energetically. Such a large egg apparently precludes significant overlap in production of consecutive eggs, so that changes in body mass between eggs can be more clearly attributed to specific stages in egg formation.

The kiwis are thus important, both as interesting birds in their own rights, and because of their broader implications for constraints upon evolution and function in class Aves. In his review of reproduction energetics, Rickleffs (1974) cited water contents of kiwi yolk and albumen from Reid (1971b), but apparently overlooked the significance of the unusually large, energy-rich yolk, 61% of egg contents (Reid 1971a). Compounded with the absolute size of the kiwi egg, this suggests an energy content that is very large in proportion to the bird's metabolic rate. Reid (1971b) estimated this energy content, but calorimetric data were not available for the kiwi egg, so he used published values for caloric content of typical bird yolk and albumen. Discussing the effect of egg-laying on adult weight, Rickleffs (1974) did not consider the possible extreme in this respect, represented by the kiwis.

We report here the changes in body mass of a female Brown Kiwi during the cycle between two consecutive egg-layings, and the energy content of a Brown Kiwi egg. This information is related to the metabolism of female Brown Kiwis, and may suggest advantages

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of kiwis for the study of basic avian reproduction, further justifying the propagation and protection of these unique birds.

## MATERIALS AND METHODS

A North Island Brown Kiwi hen *(A. australis mantelli)*, 2 years of age, was obtained in 1974 from the Mt Bruce Native Bird Reserve and paired with a 14 month old male. These are the youngest ages for which kiwis are known to breed. She laid 4 eggs in 1974, 6 in 1975, and has laid 7 in the 1976-77 season. She was weighed at two day intervals, from the time that the first egg was laid in 1976 until the laying of the second egg, on a pan balance readable to $\frac{1}{8}$ oz. (Lyssese infant model). Mass and other values have been converted to S.I. units following Mechtly 1969. Mass was measured at approximately the same time, between 1700 and 1800 hr.

The bird and her mate were maintained and weighed in a 250 $m^2$ outdoor aviary of the Otorohanga Zoological Society, Otorohanga, North Island. Natural foraging was supplemented by a diet of raw ox heart double-cut in julienne strips mixed with cooked rolled oats, wheat germ, soya oil and nutritional premix (No. 178, Tasman Vaccine Laboratories). Breeding has occurred in both artificial burrows and burrows dug by the birds. Further details of the programmes have been submitted to the Wildlife Division, Department of Internal Affairs (Rowe, unpubl. ms).

Standard metabolic rates were determined as oxygen consumption, employing a paramagnetic oxygen analyser (Servomex OA 272) with read-out on a potentiometric recorder (Esterline Angus " Mini-Servo ") and a digital multi-meter (Hewlett-Packard 3465A). Air was passed through the metabolic chamber (20.7 1. rectangular tin or 134 1. refrigerator compartment) with a diaphragm pump (Charles Austen Mk II) and measured with a calibrated rotameter (Matheson 603) traceable to U.S. National Bureau of Standards (USNBS). Oxygen volumes were corrected to standard temperature and pressure, dry, and used to estimate metabolic energy requirements using routinely accepted assumptions of a respiratory quotient ($CO^2/O^2$) of 0.8, at which 1 ml of oxygen consumed would be equivalent to 20.1 joules or 4.8 calories of energy released (Calder 1974). Temperatures in an underground metabolic bunker or within the refrigerator were monitored with thermocouples and electronic thermometer (Bailey Instruments BAT-4), calibration traceable to USNBS.

So as not to disrupt the breeding programme or make unauthorized sacrifice of an egg, an infertile egg of slightly smaller size (357 vs 432 g) was separated into yolk and albumen and submitted for bomb calorimetry to the Laboratory of Animal Nutrition at the Ruakura Agricultural Research Centre. The mass of this egg had decreased 9.71 g between laying and calorimetry. Carbon loss was estimated from four determinations of oxygen uptake spaced over a 35 day period in controlled environments and subtracted from mass decrease to estimate water loss by evaporation, assumed to have come from the albumen and therefore added to albumen mass for calculating energy content per unit fresh mass.

## RESULTS

The first egg, in her third year of laying at Otorohanga, was laid by this bird on the night of 16 June 1976. Weighings commenced at 1730 hr, 17 June. Her body mass increased 0.397 kg in the next 17 days, then stabilized for a week (Figure 1). After laying the second egg, her mass had decreased 0.51 kg. The egg weighed 0.432 kg, so 0.078 kg was lost from the body of the hen during the two days centred around laying.

The standard metabolic rate of this hen measured in a later egg cycle (No. 6), 5.18 W (Watts: = 4.46 kcal/hr) at 2.19 kg (day 12) and 4.54 W (3.91 kcal/hr) at 2.22 kg body mass (day 15 of a 23-day cycle). She was lighter by 8-9% in this cycle, and the egg was, in similar proportion, 7% lighter. The increase in body mass between days 6 and 18 during egg cycle 7 was the same as in cycle 2 studied in more detail, though the absolute or basal mass of the bird was running lower, possibly reflecting a seasonal mass cycle.

The egg yolk of another Brown Kiwi egg had an energy content of 18.16 kilojoules/g wet (4.34 kcal/g). The albumen yielded 3.15 kilojoules/g wet (0.75 kcal/g). The yolk contributed 63% of the extrapolated fresh mass of the contents (assuming water loss was from the albumen), and the albumen 37%. The energetic density of the whole fresh egg, including the 25.5 shell and membranes was therefore 11.55 kilojoules/g (2.76 kcal/g). This value applied to the mass of the egg analysed by Reid (1971b) gives an energy content of 1202 kcal, which is remarkably similar to his 1100 kcal estimate.

## DISCUSSION

With information on body mass changes of the hen, composition and energy content of the kiwi egg, and published knowledge of function of the female reproductive tract in birds, it is possible to piece together significant information on the energetics of egg-formation, a proportionately great energy demand for the female kiwi.

The mean interval between eggs of this female in 3 years of laying 17 eggs at Otorohanga has been 33.2 days ± 14.3 (1 s.d.) with a range of 24 days (twice) to 75 days. One half of the intervals were 24 to 27 days long. Kinsky (1971) has summarized published time intervals between eggs of the Brown Kiwi of 11 to 57 days with a mean of 33 days also. He reported that successive ovulations occur alternately from two ovaries, and that maximum development of a second ovum continues only to a diameter of 40 to 50 mm. Calculated as a sphere this is a volume of 33.5 to 65.5 $cm^3$, which, at the specific gravity of yolk from the domestic hen's egg, 1.035 g $cm^3$ (Romanoff & Romanoff 1949), would weigh 34.7 to 67.7 g.

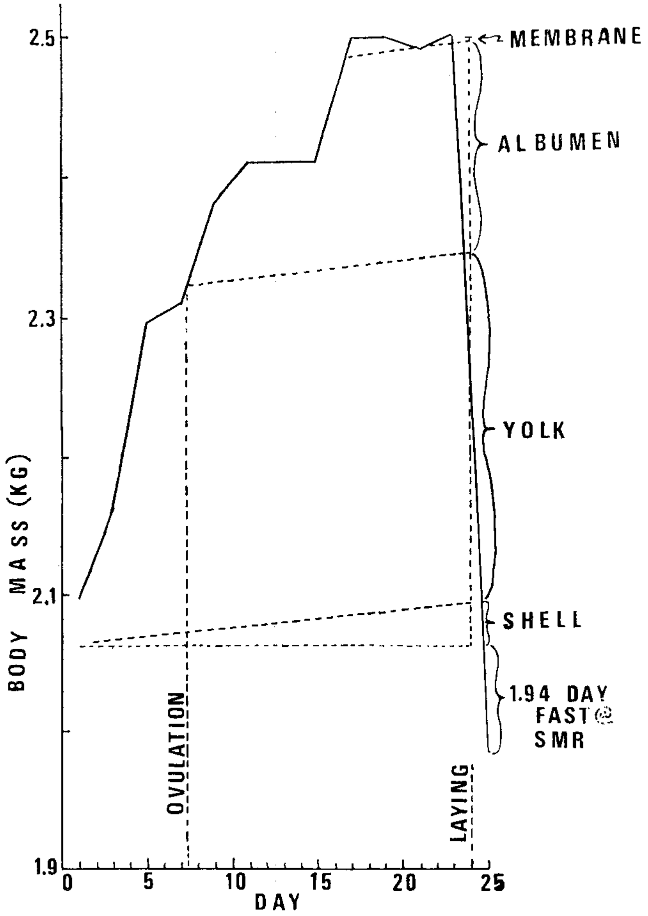

FIGURE 1 — The body mass changes of a female North Island Brown Kiwi between layings of successive eggs (day 0 and day 24) is shown by the solid line. The vertical line on day 24 shows the mass of the second egg, subdivided by brackets according to the composition of kiwi eggs (Reid 1971b and this study). We assume that the shell material is accumulated linearly through the egg cycle. Since the yolk is formed prior to ovulation, the increment due to yolk mass can be ascribed (3rd dashed line from bottom) to female mass change and at date of ovulation estimated thereby. At ovulation, 91% of the energy content of the egg has been incorporated. The contribution of albumen follows (4th from bottom). The difference between decrease in female associated with egg-laying and mass of egg laid probably represents fasting or reduced food intake at this time of obvious discomfort, and is equivalent to the energy requirement of 1.94 days at the standard (basal) 3 rate.

Welty (1975: 301) gave a table of intervals between eggs for various kinds of birds. The listing of the kiwi as 5 days is obviously incorrect, and assuming that the other data are correct, the kiwi exceeds significantly all other birds, the longest interval of which is represented by the megapodes in a 4 to 8 day category. Note that egg mass as per cent of adult mass, divided by interval between eggs, makes the kiwi more comparable to other birds.

The interval during which the hen's mass was monitored in the present study was 24 days. A maximum of 2.495 kg was maintained essentially stable between days 17 and 24. The egg weighed 0.432 kg, which subtracted from maximum body mass gives a value 0.035 kg below the mass at the start of the interval. We assume from this failure to " break even " on the one egg that the maximum mass of a second ovum calculated above from Kinsky (1971) would be related to the shortest intervals of 11 to 19 days between eggs. Thus we will neglect the minor contribution of egg 3 to the hen's mass changes between layings of eggs 1 and 2.

The yolk of a bird's egg is formed within the ovary, with the albumen added in the magnum of the oviduct and finally the shell membranes and the shell in the isthmus and the uterus respectively (Welty 1975).

The dry shell of a Brown Kiwi's egg contributes 5.3% of the total mass, the shell membranes 0.9%, the yolk 57.4% (61.1% of contents), and the albumen 36.5% (calculated from Reid 1971b). The infertile egg of this analysis had proportionately slightly more yolk (63.3% of contents), but we will use Reid's values, because the egg he analysed was so similar in size to the egg laid in the cycle reported here (434.6 g vs. 432 g). This egg would have had an estimated 23 g shell, 4 g membranes, 248 g yolk, and 157 g of albumen.

The shell of a domestic hen's egg is mostly calcium carbonate, the calcium for which is obtained from the diet over the entire cycle and an additional amount is reabsorbed from her bones (Welty 1975; Peaker 1975). In the kiwi, the mass of these bones is greater, being solid, amounting to 130 g to 168 g or about 6 times the mass of an eggshell (calculated from Reid & Williams 1975). While the shell is formed last, the mass of material involved is absorbed earlier and transferred internally (note the essentially unchanging body mass in the last week before laying). Thus we have assumed (Fig. 1) that this component of the mass increase is distributed linearly through the interval. To the bottom sloped line we add the 248 g yolk, which increment, parallel to the incremental increase in eventual shell material, intercepts the hen's mass curve during day 7 of the cycle.

This has profound implications. The yolk must have been completed by 7½ days into the cycle. The yolk contains 6.3 times as much energy per gram as the albumen, and there is 1.6 to 1.7 times as much yolk as albumen. The product of yolk size and energy content thus is 91% of the energy content of the egg. If this was acquired and deposited only in the one interval, 600.4 kilojoules (143.5 kcal) of energy would have to be stored per day, a power requirement of 6.95 watts. Rickleffs (1974, Table 12) assumes that the energy content of an egg must be multiplied by 1.33 to cover the cost of synthesis, so the power requirement of egg formation becomes 9.24 W.

On the other hand, the 35 g difference between her maximum mass less the egg (2.063 kg) and her starting mass for this cycle (2.098 kg) could represent yolk formed at the end of the previous cycle. This mass is similar to that estimated above for a 40 mm ovum, and at 18.16 kilojoules/g represents 636 kilojoules of energy which could be subtracted to give a lower value (4503 – 636 = 3867 kilojoules), or 516 kilojoules/day to complete the yolk during days 1-7½ of the cycle. This is equivalent to a 5.97 W incorporation or 7.94 W synthesis cost rate.

These estimated rates of synthesis of 7.94 to 9.24 W give a possible range, the magnitude of which can be appreciated by comparison to the standard metabolic rate of this hen, 4.55 W, or of 3 hens averaged, 4.27 W, which represents minimum maintenance cost. In addition to her maintenance, she must process energy at a rate of an additional 174 to 203% while forming yolk during the first week of a new egg cycle. Such a requirement should be reflected in the ecology and feeding behaviour of female kiwis. If intake and stored reserves are inadequate, egg-formation would, obviously, be inhibited.

Note that in the 48 hour period between weighings when the egg was laid, the decrease in mass exceeded the mass of the egg by 78 g. This could be the result of fasting during the period of discomfort just before laying and the observed behaviour of kiwi hens to remain with the egg for a period after laying, when they would be unable to feed.

King (1974) gave a figure of 2.09 kcal (= 8.74 kilojoules) metabolized per gram of body weight loss during fasting. Applying this factor to the loss in mass beyond egg mass, we have 690.8 kilojoules, which if " burned " at the standard metabolic rate of this bird would last 1.94 days, a reasonable approximation to the fasting period.

In conclusion, we feel that the combination of body mass changes, egg mass, and egg calorimetry can provide useful insight into the energetics of reproduction in kiwis.

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