COMPOSITION OF EGGS OF SEVERAL BIRD SPECIES

ROBERT E. RICKLEFS

ABSTRACT.—This paper presents the lipid, nonlipid dry matter, and water contents of the eggs of the Starling, Coturnix Quail, Mourning Dove, Laughing Gull, and Mallard and compares the data with published accounts of the eggs of other species. The lipid level of the yolk and the percentage of yolk in the egg increase in direct relation to the precocity of the young at hatching. The high lipid content of the eggs of precocial species is related primarily to their long incubation periods, resulting in a larger total metabolic requirement than for the embryos of altricial species. The high water levels of the eggs of altricial species are a direct consequence of the high water levels of the chicks at hatching.—*Department of Biology, University of Pennsylvania, Philadelphia, Pennsylvania 19174.* Accepted 19 November 1975.

THE proportions of yolk, white, and shell in the eggs of birds varies greatly between species (Meyer 1930, Asmundson et al. 1943, Romanoff and Romanoff 1949). The eggs of species with precocial development, particularly waterfowl, have large yolks (about 35% egg weight) compared to the eggs of birds with altricial development (about 20% egg weight). Nice (1962) found a close correspondence between yolk size, expressed as a percent of egg weight, and her categories of development types. At one extreme, the eggs of *Megapodius* have very large yolks (62%) and young *Megapodius* are completely independent of parental care after hatching. At the other extreme, eggs of altricial passerines contain 15 to 27% yolk. Collins and LeCroy (1972) used the ratio of yolk to albumen in the egg as an index to the degree of precocity of development. This index was found to average 0.64 for precocial species, 0.28 for altricial species, and 0.49 for two species of terns with semialtrical (intermediate) development.

Because yolk is more dense than albumen and contains 20–40% lipid, the chemical energy of the contents of fresh eggs varies directly with yolk size. Caloric equivalents of egg contents, summarized by King (1973) from numerous literature sources, were on average about 1.05 kcal/g for altrical species, 1.6 kcal/g for galliform species, and 1.8 kcal/g for anseriform species. These figures were obtained primarily by bomb calorimetry of whole eggs, although energy contents have also been calculated from Romanoff and Romanoff's (1949) chemical analysis of the eggs of many precocial species. Lawrence and Schreiber (1974) and Schreiber and Lawrence (1976) have emphasized that it is more important to determine the chemical constituents of eggs than to calculate the proportions of yolk and albumen or to measure caloric values directly. As proportions of lipid, protein, and water in the yolk vary between species, one cannot reconstruct the chemical composition of an egg solely from the proportions of albumen and yolk, together with the chemical composition of the albumen and yolk in eggs of domesticated precocial species. In addition, caloric values cannot be used to calculate the proportions of lipid, protein, and water in the egg. Schreiber and Lawrence (1976) also point out that neither the Brown Pelican (*Pelecanus occidentalis*) nor the Laughing Gull (*Larus atricilla*) fits particularly well into categories of development pattern based on percent yolk or the yolk/albumen ratio. As a greater variety of species are examined, more exceptions undoubtedly will be found and classifications of development pattern or the relationship of egg contents to development pattern will have to be modified accordingly.

This paper presents the lipid, protein, and water contents of the eggs of the

TABLE 1
COMPOSITION OF THE EGGS OF SEVERAL SPECIES OF BIRDS[1]

Species	Starling	Coturnix Quail	Mourning Dove	Mallard	Laughing Gull
Number of eggs	12	15	4	3	9
Fresh weight (g)	7.2 ± 0.5	9.9 ± 0.95	6.4 ± 0.5	79.96 ± 7.35	42.1 ± 3.87
% shell	12.5 ± 1.2[2]	15.2 ± 2.3[3]	14.9 ± 3.1	10.9 ± 1.6	—
% yolk	17.0 ± 1.7	31.3 ± 1.7	29.3 ± 1.5	35.9 ± 3.4	33.2 ± 1.7
% albumen	70.6 ± 2.0	54.4 ± 2.4	55.8 ± 4.4	51.0 ± 4.0	57.7 ± 1.5
% dry shell	6.3 ± 0.2	7.5 ± 0.6	6.8 ± 0.4	9.6 ± 0.3	6.3 ± 0.4
Yolk					
% water	57.0 ± 0.9	48.6 ± 1.0[4]	61.4 ± 4.0	47.4 ± 5.0	54.5 ± 1.6
% lipid	27.2 ± 2.6	29.6 ± 2.2[4]	21.8 ± 3.2	30.2 ± 2.4	29.1 ± 1.7
% nonlipid dry	15.9 ± 2.4	20.3 ± 2.0[4]	16.9 ± 1.0	21.7 ± 2.1	16.5 ± 1.0
lipid (% dry)	63.1 ± 5.5	57.5 ± 3.4	56.3 ± 2.6	58.2 ± 1.4	63.9 ± 2.3
Albumen					
% water	89.4 ± 0.3	87.6 ± 0.6	88.9 ± 1.3	85.0 ± 0.3	87.5 ± 0.6
% lipid	0.8 ± 0.6	0.3 ± 0.1[5]	0.0 ± 0.2	—	0.004 ± 0.01
% nonlipid dry	9.7 ± 0.6	12.5 ± 0.9	11.1 ± 1.2	15.0 ± 0.3	12.5 ± 0.6
Whole egg contents					
% water	83.1	73.4	79.4	64.5	75.4
lipid (% dry)	35.1	39.0	36.5	41.1	43.2
Yolk/albumen ratio	0.24	0.58	0.53	0.70	0.58
Energy (kcal/g fresh weight including shell)	1.04 ± 0.05	1.63 ± 0.07	1.24 ± 0.07	1.90 ± 0.02	1.60

[1] Mean values ± SD.
[2] Calculated as 100 − % yolk − % albumen.
[3] Based on 5 eggs.
[4] Subsamples of 5 and 10 eggs processed in different years differed significantly.
[5] Based on 10 eggs.

Starling (*Sturnus vulgaris*), Coturnix Quail (*Coturnix coturnix japonica*), Mourning Dove (*Zenaida macroura*), Laughing Gull, and Mallard (*Anas platyrhynchos*). Egg composition is discussed in terms of the water content and yolk reserves of chicks at hatching.

MATERIALS AND METHODS

Starling eggs were taken in 1973 from a breeding colony attracted to nest boxes near Philadelphia, Pennsylvania. Coturnix eggs were obtained from Truslow Farms of Chesterton, Maryland. Mourning Dove eggs were collected in 1972 near Columbia, Missouri. Mallard eggs were obtained from penned birds. Laughing Gull eggs were collected in 1974 near the Rutgers University, Institute for Animal Behavior Field Station at Brigantine, New Jersey. Only fresh eggs were used in the analyses. Starling, quail, and duck eggs were processed immediately after collection. The gull eggs were refrigerated briefly. The dove eggs had been frozen for transport. Although most eggs crack when frozen, these did not.

Yolk, white, and shell were analyzed separately. Each component was dried in a vacuum oven at 50°C. Lipids were extracted in a 5:1 mixture of petroleum ether and chloroform. Ash content was obtained for some of the samples by combustion in a muffle furnace. Lipid content was calculated as the difference between dry weights before and after extraction. In this paper, absolute amounts of components are referred to as "contents" and proportions are referred to as "levels."

RESULTS

Egg composition is summarized in Table 1. Comparable quantities for the eggs of domesticated birds (Brody 1945, Romanoff and Romanoff 1949), the Brown Pelican (Lawrence and Schreiber 1974), and the Laughing Gull (Schreiber and Lawrence 1976) are presented in Table 2. The composition of the Starling egg is similar to that

TABLE 2

COMPOSITION OF THE EGGS OF SEVERAL SPECIES OF BIRDS

	Chicken[1]	Chicken[2]	Turkey[2]	Guinea Fowl[2]	Duck[2]	Goose[2]	Brown Pelican[3]	Laughing Gull[4]
Fresh weight (g)	58.0	57.7	85.0	40.0	80.0	200.0	92.1	39.0
% shell	11.0	10.6	11.8	12.6	12.0	12.4	12.2	8.9
% yolk	30.0	32.4	32.2	32.5	32.8	33.4	26.2	35.8
% albumen	59.0	57.0	52.0	49.8	50.5	55.1	66.0	53.1
Yolk								
% water	49.0	48.6	48.3	49.2	44.8	43.3	66.0	61.1[5]
% lipid	34.0	32.6	33.2	33.0	35.2	36.0	23.0	24.8
% nonlipid dry	17.0	18.7	18.7	17.8	20.0	20.7	11.0	10.9
lipid (% dry)	69.0	63.5	63.9	65.0	63.8	63.5	67.7	69.5
Albumen								
% water	88.0	87.8	86.5	86.6	86.7	86.7	81.0	78.7
% lipid	—	—	0.0	0.0	0.0	0.0	0.0	0.3
% nonlipid dry	12.0	11.9	13.5	13.4	13.3	13.3	17.0	12.0
Whole egg contents								
% water	74.9	73.6	71.9	71.8	70.3	70.3	76.7	63.7
lipid (% dry)	46.0	46.7	48.8	49.5	50.1	49.5	30.0	46.4
Yolk/albumen ratio	0.51	0.57	0.62	0.65	0.65	0.61	0.40	0.67
Energy (kcal/g fresh weight including shell)	1.66	1.65	1.65	1.64	1.75	1.84	1.37	1.44

[1] Brody (1945).
[2] Romanoff and Romanoff (1949).
[3] Lawrence and Schreiber (1974).
[4] Schreiber and Lawrence (1976).
[5] Totals do not add to 100% because nonlipid dry was estimated independently by protein assay.

of other altrical species; the composition of the Coturnix Quail egg resembles that of domesticated precocial species. Eggs of the Mallard closely resemble those of the domestic duck and goose. The size of the yolk of the Mourning Dove egg resembles that of precocial species more closely than that of altricial species. Laughing Gull eggs also have large yolks.

The water level of yolk varies greatly between species, from 43–48% in anseriforms, to 48–50% in galliforms, 55% in the Laughing Gull, and 57–66% in altricial species. The proportion of water in the yolk of one Kiwi (*Apteryx australis*) egg, 43.3%, is at the lower end of the scale (Reid 1971). The percent lipid in the dry weight of the yolk is more uniform (most levels are between 55 and 65%); the lipid level does not bear any consistent relationship to the mode of development.

The composition of albumen is more uniform than that of yolk: water level varies between 85 and 90%. The low water levels reported by Lawrence and Schreiber (1974) for the Brown Pelican (81%) and by Schreiber and Lawrence (1976) for the Laughing Gull (79%) are inconsistent with other species owing to the expression of some water from the albumen with freezing and its loss when egg components were separated (Lawrence pers. comm.). The standard deviation of percent water in the albumen of Laughing Gull eggs (5.4%) in Schreiber and Lawrence's study was much greater than that obtained in this study (0.6%). Mourning Dove eggs, which were also frozen before analysis, had the most variable albumen water content of the species analyzed in this study.

Because uncontaminated albumen contains virtually no lipid, measured amounts of lipid (up to 0.8% in the Starling) undoubtedly reflect the extraction of nonlipid material rather than the presence of lipid.

The nonlipid dry component of the yolk or albumen contains small amounts of carbohydrates and inorganic compounds. Carbohydrates were not determined in this study, but Romanoff and Romanoff (1949) reported levels of 0.8–1.22% of yolk wet weight and 0.7–1.3% albumen wet weight. Inorganic materials were found to constitute 1.0–1.6% of the wet weights of the yolk and 0.6–0.8% of the white. Ash levels in Starling eggs, after combustion in a muffle furnace, were 0.9% of the wet weight of the albumen and 1.8% of the yolk, representing 9.2 and 7.5% of the nonlipid dry weights. Ash levels in five Coturnix Quail eggs averaged 0.9% of the wet weight of the albumen and 1.2% of the yolk, representing 6.9% and 6.2% of the nonlipid dry component.

Energy per gram of fresh eggs (including shell) was calculated utilizing energy equivalents of 9.5 kcal/g lipid and 5.65 kcal/g nonlipid dry weight. These constants exceed the energy levels of egg components to the extent that inorganic matter and carbohydrate are included in the nonlipid dry component, but they nonetheless provide a basis for a useful index of comparison between species. Among the species presented in Tables 1 and 2, energy levels vary between 1.04 kcal/g for the Starling and 1.75–1.90 kcal/g among waterfowl. Galliforms uniformly fall within the range of 1.63–1.66 kcal/g. The energy level of Laughing Gull eggs was 1.60 kcal/g in this study, but only 1.44 kcal/g in Schreiber and Lawrence's (1976) study. The discrepancy, resulting from a slightly lower lipid level and higher water level of the yolk in the latter study, may reflect differences between Florida and New Jersey populations. Loss of water from the eggs with freezing would have increased the energy level of the contents and reduced the difference between the Florida and New Jersey samples. Drent (1970) obtained an energy level of 1.52 kcal/g for two Herring Gull (*Larus argentatus*) eggs by direct calorimetry. The energy level of eggs of the Mourning Dove (1.24 kcal/g) and Brown Pelican (1.37 kcal/g) are intermediate between precocial species and altricial passerines, including the Long-billed Marsh Wren (*Telmatodyles palustris*), 1.11 kcal/g (Kale 1965), European Tree Sparrow (*Passer montanus*), 1.02 kcal/g (Mackowicz et al. 1970), House Sparrow (*Passer domesticus*), 1.10 kcal/g (Tangl 1903), and House Wren (*Troglodytes aedon*), 1.05 kcal/g (Kendeigh et al. 1956).

The proportions of water, lipid, and nonlipid dry material in the entire egg, irrespective of their distribution between yolk and albumen, are presented in Tables 1 and 2. These quantities represent the total resources upon which the developing embryo can draw. Levels of water fall uniformly between 70 and 75% in the eggs of precocial and semiprecocial species, and above 79% in the eggs of altricial species. The level of lipid in the dry matter of the egg varies between 46 and 50% for precocial species excepting the Mallard (41.1%) and Coturnix Quail (39.0%), the only species that have not been altered greatly under domestication. The lipid level is, of course, lower in altricial species (35–37%, not including the Brown Pelican). Among charadriiforms, the dry matter of the Herring Gull's egg contains about 33% lipid, that of the Laughing Gull 43–46% lipid, and that of two *Calidris* sandpipers 43 and 51% lipid (Norton 1973, Ricklefs 1974).

Discussion

Because the composition of albumen is fairly constant, one can distinguish the eggs of various species by the proportion of yolk in the egg and the proportion of lipid in the yolk (Fig. 1). The eggs of three altrical species contain 4–7% lipid. Although the

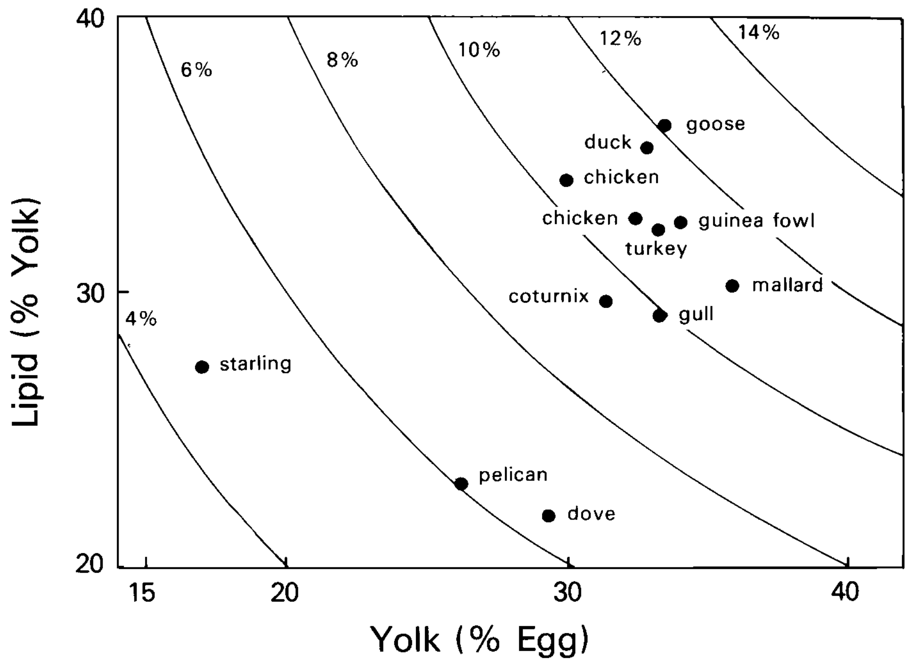

Fig. 1. Scatter diagram showing the relative size of the yolk and proportion of lipid in the yolk for eggs of species listed in Tables 1 and 2. The diagonal curves represent different levels of lipid as a percent of the whole egg, defined by the relationship

$$\frac{\text{lipid}}{\text{egg}} = \frac{\text{yolk}}{\text{egg}} \times \frac{\text{lipid}}{\text{yolk}}.$$

sizes of the yolks in pelican and dove eggs are intermediate between those of the Starling and those of precocial species, the yolks have low lipid levels. Nonetheless the eggs of these altricial species contain more lipid than the egg of the Starling whose yolk, while relatively richer, is smaller.

The yolks of the eggs of precocial and semiprecocial species are relatively large and rich, which results in a high total lipid level (9–12%). Among this group of species, the Laughing Gull and Coturnix Quail have the smallest proportion of lipid in their eggs, and domesticated waterfowl the largest.

The significance of variation in the lipid reserves of eggs may be found in patterns of embryonic and postembryonic development. Precocial species have long incubation periods and the embryos presumably expend energy at a higher rate for metabolic purposes than the embryos of altricial species. Moreover the young of precocial species hatch with a large reserve of yolk to supplement their own feeding during the first few days after hatching (Romanoff 1944, Schmekel 1961, Kear 1965, Marcström 1966, Ricklefs 1974). Development pattern does not explain differences in the relative size and lipid content of the yolk. Why, for example, do doves and pelicans have large yolks with low lipid levels, when the same lipid content could be obtained with a smaller, denser yolk?

Egg contents may be portrayed by the ratios of water and lipid to the nonlipid dry material of the whole egg (the water index and lipid index, respectively). Because the nonlipid dry component is used primarily for synthesis rather than respiration, it is the most conservative fraction of the egg. That is, except for material in the egg

TABLE 3

COMPARISON OF THE WATER, NONLIPID DRY, AND LIPID CONSTITUENTS OF EGG CONTENTS (EXCLUDING SHELL) AND NEWLY HATCHED CHICKS

Species[1]	Component[2]	Constituent (grams)		
		Water	Nonlipid dry	Lipid
Starling	Egg (12)	5.223	0.690	0.373
	Hatchling (3)	4.773	0.607	0.095
	Yolk sac (3)	0.361	0.094	0.102
	Net change	−0.089 (−2%)	+0.011 (+1%)	−0.176 (−47%)
Coturnix Quail	Egg (15)	6.050	1.356	0.866
	Hatchling (8)	4.428	1.027	0.374
	Yolk sac (8)	0.282	0.087	0.072
	Net change	−1.340 (−22%)	−0.242 (−18%)	−0.420 (−48%)
Laughing Gull	Egg (9)	28.207	5.22	3.97
	Hatchling (17)	18.744	4.086	1.063
	Yolk sac (17)	2.133	1.074	0.709
	Net change	−7.330 (−26%)	−0.060 (−1%)	−2.20 (−55%)
Mallard	Egg (3)	46.65	12.36	8.62
		39.68[3]	10.18[3]	7.69[3]
	Hatchling (2)	25.96	6.95	3.06
	Yolk sac (2)	3.75	1.98	2.06
	Net change	−16.94	−3.43	−3.50
		−9.97[3] (−25%)	−1.25[3] (−12%)	−2.57[3] (−33%)
Mourning Dove	Egg (4)	4.325	0.714	0.411
	Hatchling (1)	3.323	0.717	0.211
	Yolk sac (1)	—	—	—
	Net change	−1.002 (−23%)	+0.003 (+0%)	−0.200 (−49%)

[1] Egg data from this study; samples of newly hatched chicks as in Table 4.
[2] Sample size in parentheses.
[3] Values for one egg whose size was nearly identical to the eggs from which the chicks were hatched.

membranes and in the yolk reserve of the newly hatched chick, the nonlipid dry material in the egg is assimilated by the embryo (Table 3). Water and lipid contents of the egg decrease during the incubation period owing to evaporation and to the metabolism of lipid during respiration. As one would expect, the water and lipid

TABLE 4

COMPARISON OF WATER AND LIPID INDICES OF EGGS AND CHICKS

Species	Water index			Lipid index		
	Egg[1]	Chick[2]	Diff.	Egg[1]	Chick[2]	Diff.
Mallard	3.9	3.3[3]	−0.6	0.70	0.57[3]	−0.13
Coturnix Quail	4.5	4.2[4]	−0.3	0.64	0.40[4]	−0.24
Duck	4.7			1.00		
Goose	4.7			0.98		
Turkey	5.0			0.95		
Guinea Fowl	5.0			0.98		
Chicken[5]	5.2			0.88		
		4.7[7]	−0.7		0.75[7]	−0.12
Chicken[6]	5.5			0.85		
Laughing Gull	5.4	4.1[8]	−1.3	0.76	0.34[8]	−0.42
Mourning Dove	6.1	4.6[9]	−1.5	0.57	0.29[9]	−0.28
Starling	7.6	7.3[10]	−0.3	0.54	0.29[10]	−0.25

[1] Values calculated from data in Tables 1 and 2: ratio of weight of water and lipids to nonlipid dry weight.
[2] Including yolk sac.
[3] Averages of two incubator-hatched chicks.
[4] Averages of eight incubator-hatched chicks.
[5] From Brody (1945).
[6] From Romanoff and Romanoff (1949).
[7] Calculated from data in Medway and Kare (1957).
[8] Based on 17 incubator-hatched chicks.
[9] Based on one chick collected on the day of hatching but exact age unknown.
[10] Based on three chicks collected on day of hatching and known to be less than 6 h old.

indices of newly hatched chicks correspond closely to these indices in fresh eggs (Table 4). Explanation of the variation in proportions of lipid, nonlipid dry matter, and water in freshly laid eggs therefore should be sought in terms of the body composition of the newly hatched chick and its metabolic needs during the incubation period and the first few days after hatching.

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LITERATURE CITED

ASMUNDSON, V. S., G. A. BAKER, AND J. T. EMLEN. 1943. Certain relations between the parts of birds' eggs. Auk 60: 34–44.

BRODY, S. 1945. Bioenergetics and growth. New York, Reinhold.

COLLINS, C. T., AND M. LECROY. 1972. Analysis of measurements, weights and composition of Common and Roseate Tern eggs. Wilson Bull. 84: 187–192.

DRENT, R. H. 1970. Functional aspects of incubation in the Herring Gull (*Larus argentatus* Pont.). Behav. Suppl. 17.

KALE, H. W., II. 1965. Ecology and bioenergetics of the Long-billed Marsh Wren *Telmatodytes palustris griseus* (Brewster) in Georgia salt marshes. Publ. Nuttall Ornithol. Club No. 5.

KEAR, J. 1965. The internal food reserves of hatching Mallard ducklings. J. Wildl. Mgmt. 29: 523–528.

KENDEIGH, S. C., T. C. KRAMER, AND F. HAMERSTROM. 1956. Variations in egg characteristics of the House Wren. Auk 73: 42–65.

KING, J. R. 1973. Energetics of reproduction in birds. Pp. 78–107 *in* Breeding biology of birds (D. S. Farner, Ed.). Washington, Natl. Acad. Sci.

LAWRENCE, J. M., AND R. W. SCHREIBER. 1974. Organic material and calories in the egg of the Brown Pelican, *Pelecanus occidentalis*. Comp. Biochem. Physiol. 47(A): 435–440.

MACKOWICZ, R., J. PINOWSKI, AND M. WIELOCH. 1970. Biomass production by House Sparrows (*Passer d. domesticus*) and Tree Sparrows (*Passer m. montanus* L.) populations in Poland. Ekol. Polska 18: 465–501.

MARCSTRÖM, V. 1966. Mallard ducklings (*Anas platyrhynchos* L.) during the first days after hatching. A physiological study with ecological considerations and a comparison with Capercaillie chicks (*Tetrao urogallus* L.). Viltrevy 4: 343–370.

MEDWAY, W., AND M. R. KARE. 1957. Water metabolism of the domestic fowl from hatching to maturity. Amer. J. Physiol. 190: 139–141.

MEYER, O. 1930. Untersuchungen an den Eiern von *Megapodius eremita*. Ornitol. Monatsber. 38: 1–5.

NICE, M. M. 1962. Development of behavior in precocial birds. Trans. Linnaean Soc. New York 8: 1–211.

NORTON, D. W. 1973. Ecological energetics of calidrine sandpipers breeding in northern Alaska. Unpublished Ph.D. dissertation, College, Univ. Alaska.

REID, B. 1971. Composition of a Kiwi egg. Notornis 18: 250–252.

RICKLEFS, R. E. 1974. The energetics of reproduction in birds. Pp. 152–292 *in* Avian energetics (R. A. Paynter, Jr., Ed.). Publ. Nuttall Ornithol. Club No. 15.

ROMANOFF, A. L. 1944. Avian spare yolk and its assimilation. Auk 61: 235–241.

———, AND A. J. ROMANOFF. 1949. The avian egg. New York, Wiley.

SCHMEKEL, L. 1961. Datem uber des Gewicht des Vogeldottersackes von Schlupftag vis zum Schwinden. Rev. Suisse Zool. 68: 103–110.

SCHREIBER, R. W., AND J. M. LAWRENCE. 1976. Organic material and calories in Laughing Gull eggs. Auk 93: 46–52.

TANGL, F. 1903. Beitrage zur Energetik der Ontogenese. 1. Mittheilung die Entwicklungsarbeit in Vogelei. Pflugers Arch. Gesampt Physiol. 93: 327–376.