Condor, 82:335–343

CALORIES, WATER, LIPID AND YOLK IN AVIAN EGGS

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ABSTRACT.—The contents of fresh eggs of altricial, semi-altricial, semi-precocial, and precocial birds were compared with values for yolk content gathered from the literature. The continuum of developmental maturity at hatching from altricial to precocial eggs is correlated with an increase in yolk, solids, and caloric contents (per gram wet mass) and a decrease in water content. The proportion of lipid in dry matter and caloric content per gram dry mass does not vary significantly among the four developmental groups. The progressively higher caloric content on a wet mass basis with increasing precocity is a result of a larger solid content and lower water content, rather than variation in caloric value of the dry matter itself. Comparison of values within the same developmental group discloses no significant correlation between relative yolk content and egg mass. The total amount of calories in eggs is more importantly determined by egg mass than by yolk content.

A freshly laid avian egg contains the necessary nutrients and raw materials that will eventually produce a hatchling. Although it has been recognized since the study of Tarchanoff (1884) that the initial proportions of yolk and albumen differ considerably in the eggs of altricial and precocial birds, the relations between the energetic and chemical contents of eggs and developmental mode are not completely understood (see Ricklefs 1974, Kendeigh et al. 1977, for review). We report here new values for lipid, water, and caloric contents of eggs of precocial, semi-precocial, semi-altricial, and altricial species. These results are combined with previously published caloric and yolk contents to provide an overview of the variation among these values as a function of embryonic maturity at hatching.

METHODS

Whenever possible, eggs of each species were gathered from more than one nest. Freshly laid eggs were taken or shipped to the laboratory and stored in a refrigerator before processing. The initial egg mass at laying was determined by injecting water into the air cell with a syringe to replace water that had evaporated from the egg. The egg was blotted dry and weighed to the nearest 0.001 g on a Mettler balance. The shell was gently cracked open, the contents were drained into a previously weighed container and then homogenized by rapid stirring with a glass rod. The washed eggshell was dried to constant mass in an oven at 60°C. The difference between the initial egg mass and dry shell mass represented the mass of the egg contents. The entire contents of the egg were dried to constant mass by lyophilization. Water content of the egg was determined by substracting the dry mass from the initial egg content. Neutral lipid was removed with petroleum ether from an aliquot of the dry egg content in a Soxhlet extraction apparatus. The caloric content of another aliquot of the dry mass was analyzed using a Phillipson microbomb calorimeter, using benzoic acid as a standard. Triplicate samples of each egg were assayed.

Eggs of each species were classified as to their developmental maturity at hatching with the aid of the scheme presented by Nice (1962). The species designated Precocial 1–Precocial 4 were all lumped into a single Precocial category because of the small number of species. Nice (1962) listed Procellariiformes in three categories (Semi-Altricial 1, 2 and Semi-Precocial); we lumped them in Semi-Precocial due to their large yolk content and thermoregulatory abilities. Statistical comparisons among groups of average values for egg characteristics were made with one-way analysis of variance. Regression equations were calculated by the method of least squares.

We attempted to gather all existing information on the relative yolk content of avian eggs by consulting literature dating from the first description of egg contents by Valenciennes and Fremy (1857), Davy (1863), and Tarchanoff (1884). We employed recent systematic texts of France, England, and Germany to replace common names used in these early papers with current scientific names. If the relative egg contents gathered from the literature were expressed as percent egg mass, we have used the dry shell mass for each species provided by Schönwetter (1960–1978) to recalculate the yolk portion as percent egg content. The data from the literature are grouped according to the eight classes of developmental types described by Nice (1962). The only exception we made was to place the Brown Kiwi (*Apteryx australis*) into the P1 (the most precocial) rather than the P2 category owing to its exceptionally large yolk content and unusually advanced maturity at hatching (Thomson 1964).

RESULTS

Mean values for masses and contents of eggs collected for this study and those derived from the literature are presented in

TABLE 1. Mean ± S. E. values for egg mass and various characteristics of egg contents in 56 avian species obtained in this study or derived from the literature. References: 1. Lawrence and Schreiber (1974); 2. Ricklefs (1977); 3. Mertens, unpubl. data*; 4. Kale (1965)*; 5. Tangl (1903)*; 6. Pinowski (1967)*; 7. El-Wailly (1966)*; 8. Drent (1970); 9. Schreiber and Lawrence (1976); 10. Calder et al. (1978); 11. Romanoff and Romanoff (1949); 12. Cain (1976)*; 13. Case and Robel (1974)*; 14. Brody (1945)*; 15. Norton (1973)*. *Cited in Kendeigh et al. (1977).

SPECIES	Ref.	*n*	EGG MASS	EGG CONTENT				
			g	Mass g	Dry Mass g	Lipid g	kcal·g⁻¹ Dry Mass	kcal·g⁻¹ Wet Mass
ALTRICIAL								
Pelecanus occidentalis	(1)	6	92.1 ± 3.2	80.9	-	-	-	1.56
Columba livia		1	17.4	16.3	2.8	0.9	6.89	1.15
Zenaida macroura		4	6.0 ± 0.4	5.7	1.0 ± 0.1	0.4 ± .03	7.25 ± 0.10	1.20 ± 0.03
"	(2)	4	6.4 ± 0.3	6.0	1.2	0.5	6.98	1.33 ± 0.03
Colaptes auratus		3	8.8 ± 0.3	8.7	1.2 ± 0.2	0.3 ± 0.06	6.39 ± 0.15	0.80 ± 0.15
Sayornis phoebe		2	2.5 ± 0.03	2.4	0.4 ± 0.01	0.2 ± 0.01	7.34 ± 0.11	1.28 ± 0.02
Pica pica		1	7.2	6.7	0.9	0.28	6.77	0.93
Parus major	(3)	-	1.6	1.5	-	-	-	1.22
Cistothorus palustris	(4)	-	1.1	1.1	-	-	-	1.15
Turdus migratorius		6	6.7 ± 0.1	6.3	1.0 ± 0.2	0.4 ± 0.1	7.25 ± 0.05	1.14 ± 0.01
Catharus guttatus		1	6.5	6.1	0.9	0.2	6.72	0.99
Sturnus vulgaris	(2)	12	7.2 ± 0.1	6.8	1.1	0.4	6.57	1.11
Dendroica petechia		3	1.7 ± 0.2	1.6	0.3 ± 0.01	0.1 ± 0.01	6.96 ± 0.09	1.17 ± 0.03
Passer domesticus	(5)	-	2.7	2.5	-	-	-	1.27
P. montanus	(6)	-	2.2	2.1	-	-	-	1.14
Xanthocephalus xanthocephalus		3	4.6 ± 0.1	4.3	0.7 ± 0.03	0.2 ± 0.02	6.98 ± 0.21	1.06 ± 0.07
Agelaius phoeniceus		5	4.5 ± 0.2	4.3	0.6 ± 0.04	0.2 ± 0.02	7.07 ± 0.07	1.04 ± 0.03
Euphagus carolinus		3	6.8 ± 0.1	6.3	1.0 ± 0.02	0.4 ± 0.02	7.14 ± 0.04	1.14 ± 0.02
E. cyanocephalus		3	4.9 ± 0.1	4.7	0.7 ± 0.03	0.3 ± 0.02	7.08 ± 0.04	1.08 ± 0.03
Quiscalus quiscula		3	6.8 ± 0.1	6.4	1.0 ± 0.02	0.5 ± 0.03	7.52 ± 0.14	1.19 ± 0.03
Molothrus ater		4	2.9 ± 0.1	2.7	0.4 ± 0.02	0.1 ± 0.01	6.73 ± 0.06	0.94 ± 0.06
Carpodacus mexicanus		5	2.4 ± 0.1	2.3	0.4 ± 0.01	0.2 ± 0.01	7.34 ± 0.05	1.18 ± 0.02
Poephila guttata	(7)	-	1.0	0.9	-	-	-	1.37
Melospiza melodia		2	2.9 ± 0.1	2.7	0.4 ± 0.03	0.1 ± 0.03	6.57 ± 0.03	0.89 ± 0.01
SEMI-ALTRICIAL								
Bubulcus ibis		4	26.9 ± 0.3	25.3	4.6 ± 0.1	1.4 ± 0.1	6.81 ± 0.12	1.25 ± 0.03
Casmerodius albus		3	48.5 ± 0.2	45.0	7.7 ± 0.1	3.2 ± 0.2	7.26 ± 0.10	1.25 ± 0.02
Egretta thula		3	22.5 ± 0.2	21.0	3.7 ± 0.1	1.5 ± 0.1	7.22 ± 0.05	1.27 ± 0.02
Hydranassa tricolor		1	27.5	25.7	4.7	0.8	7.33	1.25
Eudocimus albus		3	49.2 ± 0.7	45.1	8.0 ± 0.2	2.6 ± 0.1	6.94 ± 0.05	1.23 ± 0.04

Table 1. Caloric values are presented in kcal units. Conversion to the SI equivalent, kJ, is accomplished by multiplying the caloric value by 4.187. Since the variation in egg mass and absolute values for egg contents makes comparisons among developmental groups difficult, the trends in these features are most evident when averages of relative values are compared among the developmental modes (Table 2). Solids and water, expressed as percent egg contents, significantly ($P < 0.01$) increase and decrease, respectively, with progressive precocity (Table 2). The increase in the proportion of solid material and decrease in water results in a significant ($P < 0.01$) increase in the calories (expressed as $kcal \cdot g^{-1}$ wet mass) in fresh eggs of more highly developed hatchlings. Although the relative lipid content of eggs is significantly ($P < 0.01$) greater in more precocial eggs, the proportion of lipid in the dry solids does not significantly vary ($P = 0.13$) among the four developmental groups. Consequently, the caloric content of the dry matter ($kcal \cdot g^{-1}$ dry mass) is not significantly variable ($P = 0.12$) among the developmental types.

The yolk contents, expressed as percent egg content, of 149 species are presented in Table 3 and the averages calculated for the eight developmental groups are shown in Table 4. The mean yolk content increases from 24% in altricial eggs to 65% in the most precocial (Precocial 1) eggs. The averages for yolk content are recalculated in Table 4 to correspond to the four developmental

SPECIES	Ref.	*n*	EGG MASS	EGG CONTENT				
			g	Mass g	Dry Mass g	Lipid g	kcal•g⁻¹ Dry Mass	kcal•g⁻¹ Wet Mass
SEMI-PRECOCIAL								
Larus argentatus		3	81.1 ± 2.1	75.8	16.6 ± 0.7	5.0 ± 0.5	6.76 ± 0.08	1.48 ± 0.10
"	(8)	-	95	86	-	-	-	1.67
L. occidentalis		4	86.8 ± 2.6	80.8	17.9 ± 0.6	6.8 ± 0.2	7.11 ± 0.03	1.57 ± 0.01
L. atricilla		3	44.2 ± 1.4	41.4	9.7 ± 0.4	3.4 ± 0.2	7.13 ± 0.15	1.66 ± 0.06
"	(2)	-	42.1 ± 1.3	39.4	-	-	-	1.71
"	(9)	-	38	35	-	-	-	1.76
Sterna albifrons		1	9.8	9.2	2.0	2.1	6.52	1.45
S. maxima		3	70.2 ± 2.3	65.6	14.7 ± 0.4	5.2 ± 0.3	7.03 ± 0.10	1.57 ± 0.05
S. sandvicensis		3	34.6 ± 0.7	32.2	7.6 ± 0.2	2.8 ± 0.2	7.09 ± 0.10	1.65 ± 0.04
Rynchops nigra		1	26.6	25.0	5.5	2.0	7.00	1.55
Oceanodroma leucorhoa		6	10.2 ± 0.3	9.7	2.5 ± 0.1	1.1 ± 0.1	7.29 ± 0.05	1.91 ± 0.03
PRECOCIAL								
Casuarius casuarius		2	623 ± 16.8	546	147 ± 7.1	52.4 ± 1.3	6.97 ± 0.04	1.87 ± 0.05
Apteryx australis	(10)	5	351 ± 21.3	314	-	-	-	3.05 ± 0.06
Podilymbus podiceps		2	19.7 ± 1.1	17.8	3.6 ± 0.2	1.5 ± 0.1	7.19 ± 0.06	1.48 ± 0.03
Branta canandensis		2	197 ± 4.3	175	49.0 ± 2.9	19.3 ± 0.7	7.24 ± 0.05	2.03 ± 0.08
Goose	(11)	-	200	175	-	-	-	2.10
Dendrocygna autumnalis	(12)	-	41	37.8	-	-	-	2.87
Anas platyrhynchos		3	51.9 ± 0.2	47.8	13.5 ± 0.1	5.6 ± 0.1	7.37 ± 0.02	2.08 ± 0.08
"	(2)	3	79.9 ± 4.2	72.3	-	-	-	2.10
Duck	(11)	-	80	70.4	-	-	-	1.99
Phasianus colchicus		5	31.2 ± 1.0	28.3	7.4 ± 0.3	2.8 ± 0.1	7.12 ± 0.02	1.88 ± 0.05
Colinus virginianus	(13)	-	8.7	8.4	-	-	-	1.93
Coturnis sp.	(2)	15	9.9 ± 0.1	9.1	-	-	-	1.76
Turkey	(11)	-	85	75	-	-	-	1.87
Guinea fowl	(11)	-	40	35	-	-	-	1.87
Domestic fowl	(5)	-	56	51.4	-	-	-	1.87
"	(14)	-	58	53.4	-	-	-	1.85
Rallus limicola		1	10.8	10.0	2.1	0.9	7.13	1.50
Porzana carolina		1	8.7	8.0	1.6	0.6	7.05	1.37
Actitis macularia		3	9.1 ± 0.2	8.7	2.1 ± 0.1	1.0 ± 0.1	7.39 ± 0.17	1.79 ± 0.12
Calidris alpina	(15)	-	10.0	9.3	-	-	-	1.83
C. bairdii	(15)	-	12.3	10.5	-	-	-	2.13
Ptychoramphus aleuticus		3	31.4 ± 1.0	29.3	7.4 ± 0.3	3.4 ± 0.4	7.43 ± 0.11	1.87 ± 0.06

groups used in Table 1. For this purpose, the megapode and kiwi eggs have been separated from the values of other precocial birds due to their extremely high yolk content.

Comparing relative values within each developmental group shows no significant correlation between egg mass and caloric or solid content. Similarly, no significant relation exists between egg mass and relative

TABLE 2. Summary of mean ± S.E. values describing egg characteristics derived from data presented in Table 1. Caloric values (kcal·g⁻¹ wet mass) for the Brown Kiwi (*Apteryx australis*) were omitted from the calculation of the mean value for kcal·g⁻¹ wet mass of the Precocial group due to the bird's excessively high yolk content. Number of species and sample sizes in each category are the same as shown in Table 1.

	Altricial	Semi-Altricial	Semi-Precocial	Precocial
Solids, % content	15.7 ± 0.3	18.3 ± 0.5	23.5 ± 0.4	25.3 ± 0.6
Water, % content	84.3 ± 0.3	81.7 ± 0.5	76.5 ± 0.4	74.7 ± 0.6
Lipids, % content	5.9 ± 0.3	6.3 ± 0.3	9.5 ± 0.7	10.3 ± 0.3
Kcal·g⁻¹ wet mass	1.14 ± 0.01	1.24 ± 0.04	1.63 ± 0.04	1.91 ± 0.07
Kcal·g⁻¹ dry mass	7.06 ± 0.05	7.09 ± 0.08	7.07 ± 0.05	7.23 ± 0.05
Lipids, % dry mass	37.2 ± 1.0	34.8 ± 1.9	40.3 ± 2.9	41.0 ± 0.9

		W (g)	Content (g)	Yolk (%)	Ref
P1	*Galliformes*				
	Megapodiidae				
	Megapodius freycinet	108	99	67	16
	Apterygiformes				
	Apterygidae				
	Apteryx australis	435	412	61	14
	"	350	-	65	20
P2	*Anseriformes*				
	Anatidae				
	Cygnus atratus	235	202	57	15
	C. olor	312	271	39	15
	Anser anser	158	136	50	15
	"	200	175	40	3
	"	173	155	47	5
	"	160	140	38	6
	"	172	151	51	8
	Domestic Chinese Goose	147	137	41	18
	Anser caerulescens	119	105	45	15
	"	120	109	38	6
	Khaki Campbell Coose	70	62.5	36	18
	Branta c. canadensis	163	145	44	6
	"	198	176	47	15
	B. c. atlanticus	113	98	41	15
	B. sandvicensis	141	128	41	15
	Anas platyrhynchos	55.7	49.6	44	15
	"	80	70.4	40	3
	"	54	49.6	36	6
	"	80.0	69.5	41	21
	"	56.7	49.4	40	8
	"	72	63	49	5
	A. undulata	49.1	42.2	47	15
	A. clypeata	40	37	54	6
	"	-	-	41	15
	A. aucklandica	52.5	48.3	48	15
	A. specularis	69.4	61.8	47	15
	Tadorna tadorna	-	-	43	15
	"	76.9	69.0	43	2
	"	78	70.8	47	6
	Alopochen aegyptiacus	82.6	73.5	48	15
	Cereopsis novaehollandiae	137	122	38	6
	Somateria mollissima	108	98.3	48	15
	"	117	104	46	2
	Netta rufina	49.1	42.2	48	15
	Aythya fuligula	-	-	41	15
	A. nyroca	43	39	44	6
	Aix sponsa	43.5	39.6	45	15
	A. galericulata	44.9	40.4	47	15
	"	41	37.5	42	6
	Melanitta fusca	-	-	44	15
	Bucephala clangula	57	51	45	6
	"	65.4	58.2	49	15
	Cairina moschata	68.4	60.2	48	15
	"	74	67.2	37	6
	Plectropterus gambensis	115	98.9	47	15
	Dendrocygna bicolor	42.4	36.5	52	15
	Mergus serrator	-	-	45	15
	"	69.1	62.5	45	2
	Charadriiformes				
	Charadriidae				
	Vanellus vanellus	26	24.5	37	6
	"	26.0	22.6	38	8
	Plover	15.0	13.7	45	3
	Recurvirostridae				
	Himantopus himantopus	18.3	17.3	50	5
	Recurvirostra avosetta	31.7	29.7	36	6
	Alcidae				
	Alca torda	90	81.3	41	6
	Uria aalge	120	103	37	18
	Cerorhinca monocerata	82	75.6	35	18
	Galliformes				
	Tetraoninae				
	Tetrao tetrix	35.5	32.9	42	6
	Lagopus lagopus	19.2	17.0	47	5
P3	*Phasianidae*				
	Gallus gallus	55.8	50.2	34	11
	"	49.3	43.7	35	8
	"	58	50.9	36	3
	"	58	51.6	34	4
	"	58	51.6	36	4
	"	53.3	48.2	37	6
	"	54	48.9	32	18
	"	31.4	28.8	38	5
	Perdix perdix	18	15.8	42	3
	"	15.0	13.1	42	2
	Alectoris graeca	17.5	15.7	46	5
	Lophortyx californicus	10.3	9.35	34	11
	"	9	8.1	46	18
	Phasianus colchicus	31.5	28.6	36	6
	"	32	28.6	41	3
	Phasianus colchicus	26.7	23.9	37	11
	"	29.2	26.3	43	5
	"	24	20.6	41	18
	Lophura nycthemera	44	38.9	45	11
	"	47.0	42.2	49	6
	"	36.7	32.9	44	6
	Chrysolophus pictus	26	22.4	44	18
	Syrmaticus reevesi	32.2	29.6	46	6
	Pavo cristatus	101	88.4	46	6
	P. muticus	112	99	45	6
	Coturnix coturnix	9.9	8.49	37	21
	Numidinae				
	Numida meleagris	40	35.0	40	3
	"	39.4	32.9	38	6
	" *(mitrata)*	40.5	34.6	44	8
	"	41	33.0	40	18
	Meleagridinae				
	Meleagris gallopavo	80.5	72.5	36	2
	"	85	73.2	33	6
	"	57.9	50.6	40	8
	"	81.8	73.2	36	11
	Struthioniformes				
	Struthionidae				
	Struthio c. camelus	1367	1096	32	2
	"	1400	1203	38	3
	S. c. massaicus	1600	1280	33	2
	Casuariiformes				
	Casuariidae				
	Casuarius casuarius	644	562	42	6
	Dromaiidae				
	Dromaius novae-hollandiae	710	619	40	3
P4	*Charadriiformes*				
	Haematopodidae				
	Haematopus ostralegus	46.5	43.1	32	6
	"	47.5	41.8	44	5
	Scolopacidae				
	Philomachus pugnax	21.5	20.0	33	2
	Limosa limosa	39.0	36.7	31	6
	Burhinidae				
	Burhinus oedicnemus	33.5	31.0	28	5
	Esacus magnirostris	50	46.1	30	6
	Glareolidae				
	Glareola pratincola	8.45	7.63	34	5
	Podicipediformes				
	Podicipedidae				
	Podiceps cristatus	39.5	35.9	25	6
	P. nigricollis	21	19.3	24	6
	P. grisegena	30.5	27.6	25	6
	Gruiformes				
	Rallidae				
	Fulica atra	36.5	33.3	27	6
	Porphyrio porphyrio	41.5	38.5	27	6
	Gallinula chloropus	22.3	20.4	32	6
	Porzana parva	7.9	7.37	35	6
	Crex crex	13.2	12.3	37	6
SP	*Charadriiformes*				
	Stercorariidae				
	Catharacta maccormicki	-	-	29	10
	Laridae				
	Larus marinus	116	108	28	2
	L. argentatus	92	85.8	24	6
	"	93	82	29	5
	L. ridibundus	37.5	35.3	28	6
	"	36.2	33.6	30	2
	L. atricilla	42.1	38.3	37	21
	Sterna hirundo	21.0	18.8	32	1
	"	20.2	19.1	29	6
	S. dougallii	20.6	18.4	33	1
	S. paradisaea	18.4	17.2	31	2
	Chlidonias nigra	11.4	10.8	30	6
	C. hybrida	15	14.2	32	6
	C. leucoptera	14.0	11.7	40	5
	Hydroprogne caspia	65	60.5	27	6
	Procellariiformes				
	Procellariidae				
	Macronectes giganteus	234	208	31	9
	Fulmarus glacialoides	106	94.6	34	9
	Pagodroma nivea	56.9	51.4	38	9
	Daption capense	67.8	60.1	36	9
	Puffinus pacificus	61.8	56.3	40	23
	Hydrobatidae				
	Oceanodroma leucorhoa	10.0	9.32	39	22

TABLE 3. Egg mass, content mass and yolk mass expressed as percent of egg content for 149 species listed according to the 8 stages of maturity at hatching as proposed by Nice (1962): **P**recocial 1, 2, 3 and 4; **S**emi-**P**recocial; **S**emi-**A**ltrical 1 and 2; and **A**ltrical. References: 1. Collins and LeCroy (1972); 2. Groebbels (1932); 3. Romanoff and Romanoff (1949); 4. Ricklefs (1974); 5. Ar and Yom-Tov (1978); 6. Heinroth (1922); 7. Diamond (1975); 8. Tarchanoff (1884); 9. Etchécopar and Prevost (1954); 10. Reid (1965); 11. Asmundson et al. (1942); 12. Lawrence and Schreiber (1974); 13. Davy (1863); 14. Reid (1971); 15. Lack (1968); 16. Meyer (1930); 17. Hammel (pers. comm.); 18. Kuroda (1963); 19. Valenciennes and Fremy (1857); 20. Calder et al. (1978); 21. Ricklefs (1977); 22. Rahn (unpubl.); 23. Whittow and Paganelli (pers. comm.).

← ↓

	W (g)	Content (g)	Yolk (%)	Ref
SA-1				
Ciconiiformes				
Ardeidae				
Egretta garzetta	30.0	7.84	28	5
"	27	24.2	25	18
Nycticorax nycticorax	34	31.8	19	6
"	33	29.6	23	18
Ardea cinerea	50.0	44.8	32	5
Ciconiidae				
Ciconia ciconia	75.1	61.1	38	5
Threskiornithidae				
Threskiornis aethiopicus	-	-	27	19
Falconiformes				
Falconidae				
Falco naumanni	10.8	9.41	24	5
Accipitridae				
Aquila rapax	92.8	83.7	20	5
Buteo rufinus	60.7	55.7	24	5
Circus cyaneus	31	28.6	21	6
C. aeruginosus	40	36.6	22	6
C. pygargus	-	-	22	19
Gyps fulvus	244	218	23	5
SA-2				
Pelecaniformes				
Phaethontidae				
Phaethon rubricauda	72.5	65	28	7
P. aethereus	56	50.1	36	7
Sphenisciformes				
Spheniscidae				
Aptenodytes forsteri	469	395	30	9
Pygoscelis adeliae	118	-	29	10
Strigiformes				
Tytonidae				
Tyto alba	19.6	18.1	24	5
Strigidae				
Bubo bubo	69.3	63.4	23	5
Strix aluco	36.1	33.6	25	5
Asio flammeus	21.3	19.9	24	6
A *Pelecaniformes*				
Pelecanidae				
Pelecanus occidentalis	92.1	84.9	28	12
Phalacrocoracidae				
Phalacrocorax carbo	58	51.8	17	6
Columbiformes				
Columbidae				
Columba livia	17.8	16.4	24	2
"	17.0	15.6	19	3
"	17.8	16.7	21	6
"	16.7	14.5	21	8
"	18.0	16.6	20	13
Zenaida macroura	6.41	5.45	35	4
Streptopelia senegalensis	6.63	6.29	22	5
S. risoria	8.18		29	5
Geopelia humeralis	7.0	6.55	27	6
Apodiformes				
Trochilidae				
Archilochus colubris	0.5	.475	27	3
Psittaciformes				
Cacatuidae				
Nymphicus hollandicus	5.68	5.31	27	6
Melopsittacus undulatus	2.15	2.01	21	6
"	2.25	2.13	25	5
Coraciiformes				
Alcedinidae				
Halcyon smyrnensis	11.5	10.7	22	5
Meropidae				
Merops apiaster	6.39	5.47	31	5
Piciformes				
Picidae				
Jynx torquilla	2.7	2.5	16	6
Passeriformes				
Alaudidae				
Galerida cristata	2.93	2.64	24	5
Hirundinidae				
Riparia riparia	1.53	1.4	23	8
Hirundo rustica	1.90	1.75	30	12
Pycnonotidae				
Pycnonotus capensis	3.05	2.58	22	5
Mimidae				
Mimus polyglottos	4.10	3.78	19	11
Turdinae				
Erithacus rubecula	3.65	3.51	24	13
E. megarhynchos	2.05	1.83	24	8
Phoenicurus phoenicurus	2.04	1.86	23	8
Turdus merula	5.97	5.4	25	8
"	6.36	5.80	28	5
T. viscivorus	8.07	7.66	14	13
Sylviinae				
Regulus regulus	0.93	.88	25	13
Prinia gracilis	1.12	1.04	26	5
Prunellidae				
Prunella modularis	2.24	2.16	22	13
Nectariniidae				
Nectarinia fusca	0.877	.822	32	5
Corvidae				
Corvus corone	20.2	18.0	21	8
C. frugilegus	18.6	16.7	16	8
Garrulus glandarius	8.25	7.84	28	13
Pica pica	-	-	19	19
Sturnidae				
Sturnus vulgaris	7.46	6.92	15	13
"	7.20	6.30	19	4
Icteridae				
Euphagus cyanocephalus	4.58	4.24	21	11
Agelaius tricolor	3.67	3.39	22	11
Fringillidae				
Carduelis chloris	2.07	1.95	26	5
Estrildidae				
Peophila guttata	0.805	.770	27	22
Ploceidae				
Passer domesticus	2.87	2.42	21	8
"	2.76	2.55	26	5
"	-	-	26	19
P. moabiticus	1.50	-	20	5

TABLE 4. Summary of means, standard errors, and sample sizes of relative yolk values presented in Table 3 arranged according to the classification of Nice (left) or to the grouping of species used in Table 1 (right). In the classification on the right, the data from Precocial 1 birds (megapods and kiwi) have been separated from the other precocial values.

Nice's classification	n	$\bar{X}$	S.E.	Reclassification	n	$\bar{X}$	S.E.
Precocial 1	2	65		Precocial 1	2	65	2.0
Precocial 2	38	44	2.0	Precocial 2, 3, 4	71	40	0.6
Precocial 3	19	41	0.8	Semi-Precocial	18	33	1.0
Precocial 4	14	30	1.0	Semi-Altricial 1, 2	20	26	1.1
Semi-Precocial	18	33	1.2	Altricial	38	24	0.8
Semi-Altricial 1	12	25	1.0				
Semi-Altricial 2	8	27	1.5				
Altricial	38	24	0.8				

yolk content. Therefore, a larger egg would not necessarily be expected to have a greater caloric content (g^{-1} wet mass) or yolk content when compared to a smaller egg of the same developmental type.

It was possible to match the values for dry mass, caloric content, and lipid content of 21 species listed in Table 1 with the yolk content of the same species or genus in Table 3. The regression equations for each of these relations are:

$$L = 0.749 + 0.232\,Y \qquad (1)$$
$$n = 21 \quad r^2 = 0.81 \quad S_{y\cdot x} = 1.19$$

$$D = 8.02 + 0.420\,Y \qquad (2)$$
$$n = 21 \quad r^2 = 0.77 \quad S_{y\cdot x} = 2.34$$

$$C = 0.473 + 0.33\,Y \qquad (3)$$
$$n = 21 \quad r^2 = 0.79 \quad S_{y\cdot x} = 0.17$$

where L = lipid content (percent of dry mass), D = dry mass (percent of content), C = $kcal \cdot g^{-1}$ wet mass, and Y = yolk (percent of content). The mean values for dry mass and caloric content are presented as a function of yolk content in Figures 1 and 2.

DISCUSSION

YOLK CONTENT

In Table 3 we have compiled the original data on relative yolk content starting with the observations of Valenciennes and Fremy (1857) and Davy (1863) who each examined ten species. They found that the yolk/albumen ratio varied among species and that the water content of the albumen was relatively constant, very nearly 89%. The difference in relative yolk content between altricial and precocial eggs, however, was not recognized until Tarchanoff (1884) observed that the relative yolk content of eggs of eight altricial species was 22%, while that of eggs of seven precocial species averaged 41%. His findings led him to propose a general law "that the relation of egg yolk to albumen is significantly less in altricial birds than in precocial birds" (p. 360). By 1922, Heinroth stated that "it is well known that altricial birds' eggs have relatively small yolk content" but did not cite any previous authors.

The relation between developmental mode and yolk content was first fully characterized by Nice (1962). She described eight categories of developmental maturity at hatching "according to the manner of getting food, amount of down, activity, and development of sight" (p. 26). While this classification is a convenient tool, Nice recognized that there is actually a continuum of maturational characteristics from the most mature hatchling (Precocial 1) to the most immature and helpless chick (Altricial). On the basis of her data, she similarly noted a continuous reduction in the relative yolk content of eggs from precocial to altricial species. Our compilation of published data (Table 3) confirms her observations when the averages are arranged according either to her classification or to our reclassification of developmental stages (Table 4).

Several exceptions to the general trends are noteworthy. As Nice (1962) pointed out, the relationship between yolk content and maturity does not hold in certain groups, such as the semi-precocial Procellariiformes, whose eggs contain as much yolk as those of precocial birds. Although mourning doves (*Zenaida* spp.) are altricial, their eggs have relatively much more yolk (35%) than those of other Columbidae. Their large yolk content is matched by a higher caloric content than that of eggs of most altricial birds (Table 1). One further exception to the general pattern of altricial birds is the exceptionally high caloric value reported for the Brown Pelican (*Pelecanus occidentalis*; Lawrence and Schreiber 1974). This value does not correspond to an equally elevated yolk content (Tables 1 and 3).

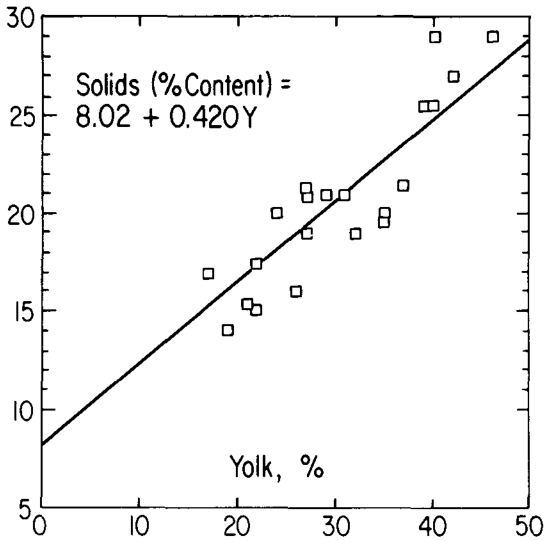

FIGURE 1. Relation of mean dry matter (solids as percent egg content) to mean yolk (as percent egg content) in eggs of 21 avian species.

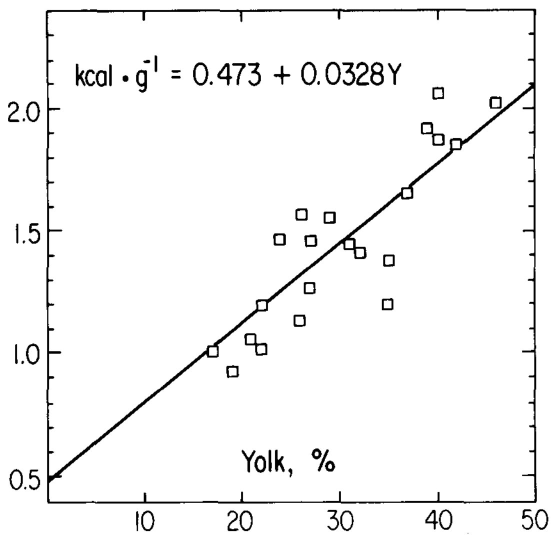

FIGURE 2. Relation of mean caloric content (as $kcal \cdot g^{-1}$ wet mass) to mean yolk (as percent egg content) in eggs of 21 avian species.

SOLIDS, LIPIDS, WATER, AND CALORIC CONTENT

Previous reviews concerning the constituents of avian eggs have shown that lipids, solids, water, and calories differ significantly between precocial and altricial eggs (Ricklefs 1974, 1977). The additional information on the intermediate semi-altricial and semi-precocial eggs provided by this study shows that the continuum of both developmental maturity at hatching and yolk contents noted above correlates with continuous variation of egg contents (Table 2). In general, relative water and solid contents decrease and increase, respectively, with increasing yolk content. The continuum in water, solid, and lipid content can be viewed as a function of relative yolk content rather than developmental mode (Fig. 3). Equations 1 and 2, the regressions describing the relations between dry matter and lipid, respectively, to relative yolk content, were used to construct this figure. It is proposed as a model with which the relative water, solid, and lipid contents can be approximated for any egg if the initial yolk content is known. This method could reduce the error in such an approximation caused by use of an arbitrary system of classification based on developmental maturity at hatching. A second axis is provided, constructed on the basis of the relations between relative yolk content and solid and caloric contents (Eq. 2 and 3), which can be used to estimate the caloric content (g^{-1} wet mass) from the relative yolk content. The yolk contents reported so far range from 14 to 67% (Table 3), but values of caloric content of eggs containing more than 50% yolk are available only for the kiwi. This value, 3.05 $kcal \cdot g^{-1}$ wet mass (Calder et al. 1978) is 19% higher than the value predicted in Figure 3.

The difference in relative water content of altricial and precocial eggs (Table 2) is due not only to the relative proportion of yolk and albumen in these eggs, but also to the water contents of these substances. The composition of albumen does not vary

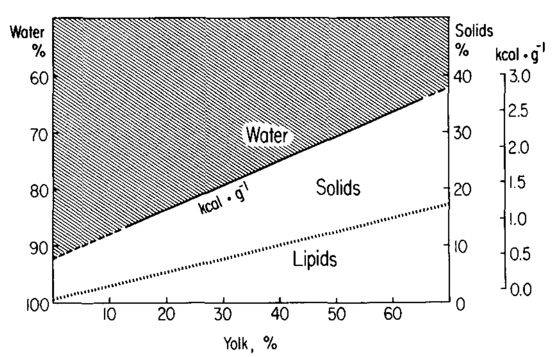

FIGURE 3. Relations between solids, water, and lipid constituents of avian eggs with varying yolk contents. All values are expressed as percent of egg content. Solid line represents the regression between dry mass and yolk content (Eq. 2); the dotted line is the regression between lipid content and yolk content (Eq. 1). The solid line may also be used to predict an approximate caloric value ($kcal \cdot g^{-1}$ wet mass) using the ordinate on the right.

widely among species; water content varies between 85 and 90% (Ricklefs 1977). The water content of yolk is significantly lower than that of albumen in all eggs and increases in precocial eggs (43–50%) to altricial eggs (57–66%) (Ricklefs 1977). Therefore, the larger yolk content of precocial eggs results in a lower relative water content because a volume of fairly dilute albumen is replaced with a drier volume of yolk.

The importance of the variation in initial water content among developmental groups is unclear, but the differences are maintained throughout incubation and are matched by equivalent differences in water content of pipped embryos (Ricklefs et al. 1978, Carey and Rahn, unpubl. data). The high relative water content of altricial eggs has been proposed to provide an extra water reserve for altricial hatchlings that may be fed dry food (Ar and Yom-Tov 1978). In this context, it is interesting that eggs of pigeons and doves, which feed their hatchlings a liquid diet, have a relative water content that is indistinguishable from that of other altricial eggs (Table 1).

Although other studies have indicated that the amount of lipid in yolk increases slightly with precocity (Ricklefs 1974, 1977), analysis of variance of our data indicates that lipid content, as percent dry mass, does not vary significantly among developmental types (Table 2). Although the increase in yolk in precocial eggs undoubtedly provides additional calories for maintenance and growth (Ricklefs 1977), the augmented yolk content also clearly represents a proportional increase in other materials, especially protein which is used in the construction of feathers, muscles, and other advanced tissues typical of precocial hatchlings. The caloric content, expressed as $kcal \cdot g^{-1}$ dry mass, similarly does not vary significantly among developmental groups, but does vary significantly when expressed as $kcal \cdot g^{-1}$ wet mass. This result is due to the variation in water and solid content of the egg rather than to the caloric value of the dry matter itself.

Tables 1 and 3 present data for certain species that were gathered from more than one study. In these instances, some of the variation in the data is undoubtedly due to methods employed by different investigators. However, numerous studies have shown that size, calories, and yolk vary not only within a species, as shown in eggs of Gannets (*Morus bassanus*; Ricklefs and Montevecchi 1979), but also among eggs of the same clutch. The variation in egg size and caloric content for eggs of the same clutch may not only reflect the physiological state of the female prior to laying each egg, but also may have important consequences for differential survival of hatchlings (Howe 1976).

This study shows that the larger yolk content associated with greater precocity results in a higher caloric content per gram wet mass of egg content. It should be remembered, however, that the important factor determining the total amount of calories and material in eggs is egg mass rather than yolk content alone. Certainly, a precocial egg will contain a greater total amount of calories than an equally sized altricial egg owing to differences in yolk content. However, a larger egg obviously will contain more and therefore provide more calories and materials for growth and maintenance than a smaller egg. For example, the caloric content, 1.87 $kcal \cdot g^{-1}$ wet mass of the largest egg in this study, that of a cassowary, is 36% higher than the 1.37 value of the smallest egg, that of an estrildid finch (Table 1). Multiplying these values by the masses of their respective egg contents results in a total of 1,021 kcal in the cassowary egg, over 830 times as great as the 1.2 kcal in the finch egg. This result is due in large part to the approximately 600-fold differences in the masses of the egg contents. Therefore, although variation in yolk content certainly does influence the relation of solids to water in the egg, the more effective means of increasing or decreasing total calories and materials available to the embryo is by varying egg size. Not only would such variation affect the development of the embryo, but also the cost of manufacturing the egg. The evolution of altricial eggs was accompanied by a reduction in egg size and yolk content that diminished the cost of manufacture to about one-fifth that of a typical precocial egg (Rahn, unpubl. data).

CONCLUSIONS

An analysis of fresh egg contents provides only the beginning of the story of avian development and merely hints about the changes in these contents as growth proceeds toward hatching. The differences in the egg contents among the four developmental groups represent differential provisioning that is ultimately reflected in the developmental maturity at hatching.

ACKNOWLEDGMENTS

This study was supported in part by a Summer Research Initiation Faculty Fellowship and Council on

Research and Creative Work Grant-in-Aid from the University of Colorado, BRSG Grant RR07013 awarded to the University of Colorado by The Biomedical Research Support Grant Program (NIH), and NSF PCM-7620947 to H. R. We thank the Denver Zoological Garden, Carol and David Vleck, Robert Putnam, Albert Bennett, and Tom Roudybush for supplying certain eggs used in this study.

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