

ON THE COMPOSITION OF BIRD EGGS¹

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Abstract. From data in the literature an attempt is made to provide a general overview of the composition of bird eggs and how individual components are related to the relative yolk content, which varies from about 15% in some Sulidae to 69% in the Kiwi (Apteryx). Regression equations are given for the relative water content of the fresh egg, albumen, and yolk, the solid and lipid fractions of egg content, and the calculated caloric density of egg content as a function of relative yolk content.

As relative yolk content of eggs increases among 127 species representing 44 families, relative water content decreases. These changes are related to a progressive increase in hatching maturity from altricial to precocial birds according to the classification of Nice (1962). Certain exceptions to this rule are discussed, namely, eggs of the pelagic feeding Procellariiformes and offshore-feeding terns. Both groups have reduced their clutch to a single egg, have unusually long incubation and fledging periods, and larger relative yolk content than predicted.

A general model of egg components is presented which relates the ash, carbohydrate, protein, lipid, water, and caloric content to the relative amount of yolk in the freshly laid egg. Lipids make up 58% of all yolk solids, which have an energy content of 33 kJ·g⁻¹; total solids in egg contents have an average energy content of 29 kJ·g⁻¹.

An overview shows how the initial solids and caloric contents are redistributed in the yolk-free neonate and the yolk reserve as well as estimates of the solids and caloric loss during development; energy cost of development is similar in all birds and amounts to ca. 36% of the initial energy content of fresh eggs.

Key words: Bird eggs; yolk content; water content; lipids; proteins; carbohydrates.

INTRODUCTION

One hundred years ago a Russian physician and physiologist, Duke Iwan Romanowitsch Tarchanoff (1884) wrote: "I fully realize that the number of cited samples is fully inadequate to back up my claim: that the relation of egg yolk to egg albumen is significantly smaller in all nidicolous birds than in nidifugous birds (and that this relationship) can be expressed as a general law." The observations were based on 43 eggs of nine nidicolous species where he had weighed yolk and albumen to three or four significant figures which he then compared with 19 eggs of seven nidifugous species. He, furthermore, established that the yolk of nidicolous eggs contained 10 to 16% more water than the yolk of nidifugous species but that the water content of the albumen in each group was similar. Most of the early data of egg composition were limited

to studies of individual species and it was not until much later that Ricklefs (1974, 1977) provided the first attempt to correlate differences in egg composition with different stages of maturity of hatchlings and changes in relative yolk content. Ar and Yom-Tov (1978) surveyed the yolk contents for many species and related these findings to the evolution of parental care, while Carey et al. (1980) attempted to relate the relative yolk content to the specific categories of maturity previously described by Nice (1962) and how the increasing yolk content correlated with the dry mass and caloric density. Since then many other studies have been reported which are reviewed here together with a survey of the older literature in an attempt to describe the relative water content of fresh eggs, their yolk and albumen, as well as their lipid content, and caloric density. All these values have been correlated with the relative yolk content as a common denominator and provide a general overview of egg composition and how these are related to Nice's classification of maturity as well as the exceptions that are found among certain pelagic and offshore feeders with unusually long incubation times.

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METHODS

In Table 1 we have brought together published data on various components of fresh bird eggs, namely, mass of egg contents, the fraction of water in the contents, albumen and yolk, and the fraction of yolk and lipids in egg contents. In addition we have calculated the caloric density of egg content or entered a reported value when it had been obtained by bomb calorimetry. The latter cases have been starred. Also starred are the fractions of lipids which were calculated from the bomb calorimetry values. Equations for these calculations are shown in the section Composition of Solids. An entry from the literature was made in Table 1 only when a value for fraction of water in the contents was available, thereby omitting many data for total content and yolk mass (Ar and Yom-Tov 1978, Carey et al. 1980).

The data are grouped according to the eight categories of hatchling maturity described by Nice (1962) with the exception of the Procellariiformes and offshore-feeding terns, which are shown at the end of Table 1 under the heading Offshore and Pelagic Feeders. The reason for their separation is discussed. Furthermore, we placed the Kiwi, Apteryx, in the precocial 1 and not precocial 2 group as described by Nice.

Using the method of least squares we computed linear relationships between fraction of yolk and each of the following parameters: fraction of water in albumen, fraction of water in yolk, fraction of water in the contents, fraction of lipid in the contents, and energy content per g of egg contents.

RESULTS

The absolute and the relative yolk content of the precocial and altricial eggs listed in Table 1 are plotted by log-log regression against their egg content in Figure 1 with additional values from the tables of Ar and Yom-Tov (1978) and Carey et al. (1980). All data in Table 1, except egg content and caloric density, representing the composition of eggs of 127 species in 44 families of birds are plotted in Figure 2 as a function of the yolk fraction. On the left ordinate all water fractions are expressed as percent, e.g., water in the egg contents, $FWC = 0.91$ is 91%. On the right ordinate the solid and lipid fractions are expressed as percent of egg content, as is the abscissa. Equations for these five relationships graphed in Figure 2 are shown in Table 2. As the fraction of yolk in the contents (FYC) increases,

the fraction of water in the egg contents (FWC) and yolk (FWY) declines, while that of the albumen (FWA) stays relatively constant.

The total water in an egg, FWC, is the sum of the water in the albumen plus the water in the yolk. Thus

$$FWC = FWY \cdot FYC + FWA \cdot (1 - FYC) \quad (6)$$

From this equation it follows that if $FYC = 0$, then $FWC = FWA$, as demonstrated by their common intercept of 91%, Figure 2 and equations 1 and 2. However, for equations 1, 2, and 3 all to be linear and to agree with equation 6, the slopes of the lines described by equations 1 and 3 must be equal, which they are not. Therefore, at least one of the three relationships must be nonlinear. To demonstrate this we substituted equations 1 and 3 into equation 6 and solved for FWC as a function of FYC. This relationship,

$$FWC = 0.908 - 0.209 FYC - 0.283 FYC^2 \quad (7)$$

is plotted as the dashed line in Figure 2. Both equations 2 and 7 appear to fit the empirical data equally well (Fig. 2), and we have henceforth assumed that there is a linear relationship between FWC and FYC (equation 2).

At the bottom of Figure 2 are plotted the fraction of solids, $FSC = (1 - FWC)$, and of lipids (FLC) in egg contents as functions of FYC, which correspond to equations 4 and 5, respectively. The equation for the solid fraction is similar to that described earlier by Carey et al. (1980). Our equation relating the fraction of lipids to the fraction of yolk ($n = 99$), however, has a significantly greater slope than that reported earlier for 21 species (Carey et al. 1980). Thus, we show that as FYC increases from 0.15 to 0.60, for example, the fraction of lipids in the solids approximately doubles, from 0.23 to 0.52 (equations 4 and 5).

DISCUSSION

HATCHLING MATURITY AND RELATIVE YOLK CONTENT

In 1978 Ar and Yom-Tov demonstrated that when yolk mass of precocial and altricial eggs is plotted against egg mass the slopes for both regressions are not significantly different from 1.0, but have different intercepts. In Figure 1 we have extended these observations by including our values and those reported by Carey et al. (1980). The upper regression represents eggs of precocial species (including Nice's category of precocial 1, 2, 3, and 4, semiprecocial, and off-

TABLE 1. Egg contents, fraction of yolk in contents, fraction of water in albumen, fraction of water in yolk, fraction of water in contents, fraction of lipid in contents, and caloric density (kJ/g) in contents of eggs of 127 species of birds in 45 families. See section entitled Composition of Solids for an explanation of starred data in the fraction of lipid and caloric density columns. References: 1. Romanoff and Romanoff 1949; 2. Carey et al. 1980; 3. Ar and Rahn 1980; 4. Reid 1971; 5. Ricklefs and Montevecchi 1979; 6. Ricklefs 1977; 7. Montevecchi et al. 1983; 8. Boersma 1982; 9. Calder et al. 1978; 10. Vleck et al. 1984; 11. Roca et al. 1984; 12. Williams et al. 1982; 13. Drent 1970; 14. Pettit et al. 1984; 15. Bancroft 1985; 16. Warham 1983; 17. Kuroda 1963; 18. Tarchanoff 1884; 19. Ojanen 1983; 20. Rahn et al. 1984; 21. Jones 1979; 22. Nisbet 1978; 23. Birkhead and Nettleship 1984; 24. Reid 1965; 25. Sotherland (unpubl.).

Species	Mass (g) Cont	F Yolk Cont	F Wat Alb	F Wat Yolk	F Wat Cont	F Lip Cont	kJ/g Wet	Ref.
Precocial 1								
Apterygidae								
<i>Apteryx australis</i>	411.7	0.611	0.879	0.433	0.607	—	—	4
<i>Apteryx australis</i>	326.7	0.692	0.872	0.471	0.612	0.220*	12.4*	9
Megapodidae								
<i>Alectura lathamii</i>	157.1	0.501	0.874	0.494	0.684	0.141	9.45	10
<i>Leipoa ocellata</i>	169.5	0.526	0.881	0.473	0.665	0.147	9.99	10
Precocial 2								
Anatidae								
Duck	70.4	0.402	0.868	0.448	0.697	—	—	1
<i>Anas moschata</i>	51.5	0.378	0.890	0.466	0.731	0.134	8.28	11
<i>A. platyrhynchos</i>	53.0	0.345	0.900	0.462	0.724	0.132	8.40	11
<i>A. platyrhynchos</i>	72.3	0.413	0.850	0.474	0.645	0.112	9.86	6
<i>A. platyrhynchos</i>	49.4	0.400	0.880	—	0.718	0.141*	8.69*	18, 2
<i>A. platyrhynchos</i>	47.8	0.400	—	—	0.718	0.117	8.29	2
Khaki-Campbell	62.6	0.360	0.870	0.444	0.718	0.114	8.24	17
<i>Tadorna ferruginea</i>	81.9	—	—	—	0.706	—	—	3
Goose	175.2	0.401	0.867	0.433	0.706	—	—	1
Domestic Chinese goose	133.9	0.413	0.892	0.458	0.712	0.138	8.77	17
<i>Anser anser</i>	133.9	0.349	0.866	0.445	0.719	0.106	8.09	11
<i>Branta canadensis</i>	175.0	0.440	—	—	0.719	0.110	8.15	3, 2
<i>Branta canadensis</i>	—	0.440	—	—	0.720	0.132*	8.49*	2
Recurvirostidae								
Himantopus himantopus	17.3	0.500	—	—	0.750	—	—	3, 2
Charadriidae								
Plover	13.7	0.446	—	—	0.747	—	—	1
<i>Vanellus vanellus</i>	22.6	0.380	0.878	0.506	0.740	—	—	18
Scolopacidae								
<i>Actitis macularia</i>	8.7	—	—	—	0.759	—	—	2
<i>Gallinago gallinago</i>	6.7	0.400	0.882	0.460	0.708	0.130	8.73	11
Alcidae								
<i>Alca torda</i>	88.0	0.398	0.871	0.488	0.719	0.133	8.53	23
<i>Ptychoramphus aleuticus</i>	29.3	—	—	—	0.747	—	—	2
<i>Uria aalga</i>	102.7	0.368	0.884	0.487	0.738	0.114	7.79	17
<i>Uria aalga</i>	96.7	0.372	0.870	0.475	0.724	0.126	8.31	23
<i>Cerorhinca monocerata</i>	75.7	0.347	0.890	0.471	0.745	0.111	7.58	17
<i>Fratercula arctica</i>	65.7	0.372	0.841	0.476	0.705	0.126	8.73	23
Precocial 3								
Phasianidae								
Chicken	50.9	0.364	0.879	0.487	0.736	—	—	1
Jungle Fowl	27.9	—	—	—	0.730	—	—	3
Silk Fowl	32.4	—	—	—	0.733	—	—	3
<i>Gallus gallus</i>	51.0	0.347	0.906	0.484	0.763	0.125	7.41	11
<i>Gallus gallus</i>	48.6	0.323	0.881	0.486	0.755	0.100	7.18	17
<i>Gallus gallus</i>	43.7	0.350	0.875	0.496	0.742	—	—	18

TABLE 1. Continued.

Species	Mass (g) Cont	F Yolk Cont	F Wat Alb	F Wat Yolk	F Wat Cont	F Lip Cont	kJ/g Wet	Ref.
<i>Coturnix coturnix</i>	7.9	0.370	0.878	0.467	0.726	0.115	8.08	11
<i>Coturnix coturnix</i>	9.2	0.365	0.876	0.486	0.734	0.098	7.62	6
<i>Phasianus colchicus</i>	27.2	0.371	0.890	0.475	0.738	0.132	8.09	11
<i>Phasianus colchicus</i>	28.3	0.396	—	—	0.739	0.099	7.52	2
<i>Phasianus colchicus</i>	25.6	0.396	—	—	0.728	0.104*	7.86*	3, 2
<i>Chrysolophus pictus</i>	18.3	0.451	0.903	0.499	0.720	0.173	9.17	11
<i>Alectoris rufa</i>	15.9	0.414	0.907	0.494	0.735	0.142	8.32	11
Numididae								
Guinea Fowl	35.0	0.402	0.866	0.492	0.728	—	—	1
<i>Numida meleagris</i>	31.2	0.414	0.901	0.503	0.734	0.148	8.44	11
<i>Numida mitrata</i>	34.6	0.440	0.878	0.487	0.706	—	—	18
Meleagrididae								
Turkey	75.0	0.366	0.865	0.483	0.737	—	—	1
<i>Meleagris gallopavo</i>	77.3	0.375	0.890	0.469	0.733	0.129	8.15	11
Struthionidae								
<i>Struthio camelus</i>	1,202.6	0.378	—	—	0.740	—	—	1
Casuariidae								
<i>Casuaris casuaris</i>	546.0	0.420	—	—	0.730	0.099	7.72	2
Precocial 4								
Podicipedidae								
<i>Podiceps nigricollis</i>	20.3	0.270	0.890	0.520	0.790	—	—	25
<i>Podilymbus podiceps</i>	17.8	—	—	—	0.798	—	—	2
Rallidae								
<i>Gallinula chloropus</i>	20.4	0.320	—	—	0.767	—	—	3, 2
<i>Rallus limicola</i>	10.0	—	—	—	0.790	—	—	2
<i>Porzana carolina</i>	8.0	—	—	—	0.800	—	—	2
<i>Crex crex</i>	12.3	0.370	0.871	0.418	0.700	—	—	18
Semi-precocial								
Stercorariidae								
<i>Catharacta maccormicki</i>	84.3	0.287	0.866	0.510	0.764	—	—	24
<i>C. antarctica</i>	90.8	0.332	0.891	0.522	0.807	0.093	5.89	12
Laridae								
<i>Larus atricilla</i>	39.4	0.365	0.875	0.545	0.754	0.108	7.33	6
<i>Larus atricilla</i>	41.4	0.365	—	—	0.766	0.101*	6.94*	6, 2
<i>Larus atricilla</i>	—	0.365	—	—	0.766	0.082	6.63	6, 2
<i>L. argentatus</i>	75.8	0.265	—	—	0.781	0.076*	6.19*	2
<i>L. argentatus</i>	—	0.265	—	—	0.781	0.066	6.03	2
<i>L. occidentalis</i>	80.8	—	—	—	0.778	—	—	2
<i>L. dominicanus</i>	82.1	0.307	0.899	0.510	0.757	0.076	6.74	12
<i>L. hartlaubi</i>	44.0	0.391	0.884	—	0.800	0.100	6.16	12
<i>L. crassirostris</i>	60.5	0.292	0.883	0.491	0.769	0.086	6.63	17
<i>Sterna bergii</i>	51.2	0.334	0.880	0.509	0.756	—	—	12
<i>S. albifrons</i>	9.2	—	—	—	0.783	—	—	2
<i>S. maxima</i>	65.6	0.300	—	—	0.776	0.079	6.36	2, 20
<i>S. maxima</i>	—	0.300	—	—	0.776	0.092*	6.57*	2
<i>S. sandvicensis</i>	32.2	0.330	—	—	0.764	0.087	6.76	2, 20
<i>S. sandvicensis</i>	—	0.330	—	—	0.764	0.096*	6.90*	2
<i>S. hirundo</i>	19.1	0.286	0.852	0.488	0.748	0.096	7.27	22
<i>Chlidonias leucopterus</i>	11.7	0.300	—	—	0.781	—	—	3, 2
Rynchopidae								
<i>Rynchops niger</i>	25.0	—	—	—	0.780	—	—	2

TABLE 1. Continued.

Species	Mass (g) Cont	F Yolk Cont	F Wat Alb	F Wat Yolk	F Wat Cont	F Lip Cont	kJ/g Wet	Ref.
Semi-altricial 1								
Ardeidae								
<i>Bubulcus ibis</i>	25.3	—	—	—	0.818	—	—	2
<i>Bubulcus ibis</i>	—	—	—	—	0.811	—	—	3
<i>Egretta garzetta</i>	24.3	0.247	0.906	0.562	0.822	0.078	5.30	17
<i>E. thula</i>	21.0	—	—	—	0.824	—	—	2
<i>Nycticorax nycticorax</i>	29.6	0.230	0.908	0.539	0.824	0.076	5.22	17
<i>Casmerodius albus</i>	45.0	—	—	—	0.827	—	—	2
<i>Hydranassa tricolor</i>	25.7	—	—	—	0.817	—	—	2
Threskiornithidae								
<i>Eudocimus albus</i>	45.1	—	—	—	0.822	—	—	2
<i>Geronticus eremita</i>	61.4	—	—	—	0.828	—	—	3
Ciconiidae								
<i>Ciconia abdimii</i>	60.7	—	—	—	0.835	—	—	3
<i>C. ciconia</i>	89.9	—	—	—	0.799	—	—	3
Falconidae								
<i>Falco naumanni</i>	9.4	0.240	—	—	0.801	—	—	3, 2
Semi-altricial 2								
Spheniscidae								
<i>Pygoscelis adeliae</i>	87.4	0.253	0.873	0.517	0.783	—	—	24
<i>P. papua</i>	101.0	0.285	0.884	0.512	0.804	0.069	5.56	12
<i>Aptenodytes patagonica</i>	276.0	0.270	0.883	0.493	0.778	0.068	6.13	12
<i>Eudyptes chrysocome</i>	73.5	0.296	0.881	0.509	0.772	0.074	6.36	12
<i>E. chrysolophus</i>	89.5	0.321	0.887	0.519	0.784	0.084	6.26	12
<i>Spheniscus demersus</i>	83.0	0.290	0.885	0.552	0.788	0.078	6.07	12
Strigidae								
<i>Bubo bubo</i>	79.1	0.230	—	—	0.822	—	—	3, 2
Tytonidae								
<i>Tyto alba</i>	18.4	0.240	—	—	0.812	—	—	3, 2
Phaethontidae								
<i>Phaethon rubricauda</i>	63.8	0.244	—	—	0.748	0.069*	6.83*	14
Altricial								
Fregatidae								
<i>Fregata minor</i>	82.2	0.257	—	—	0.775	0.067*	6.18*	14
Sulidae								
<i>Sula sula</i>	52.6	0.158	—	—	0.836	0.032*	4.22*	14
<i>S. bassanus</i>	106.4	0.171	0.884	0.588	0.757	0.042	6.18	5
<i>S. bassanus</i>	103.0	0.176	0.885	0.593	0.834	0.043	4.45	12
<i>S. capensis</i>	83.0	0.212	0.900	0.560	0.828	0.062	4.90	12
Pelecanidae								
<i>Pelecanus onocrotalus</i>	174.0	0.142	0.883	0.524	0.832	0.038	4.42	12
<i>Pelecanus onocrotalus</i>	—	0.195	0.883	0.554	0.819	0.057	5.02	21
Phalacrocoracidae								
<i>Phalacrocorax atriceps</i>	44.0	0.239	0.910	0.619	0.879	0.061	3.74	12
<i>P. capensis</i>	30.0	0.200	0.895	0.622	0.828	0.058	4.84	12
<i>P. carbo</i>	44.0	0.194	0.898	0.589	0.831	0.055	4.72	12
<i>P. coronatus</i>	19.0	0.284	0.906	0.655	0.835	0.074	4.94	12
<i>P. neglectus</i>	41.0	0.202	0.901	0.561	0.833	0.054	4.66	12
Columbidae								
<i>Columba livia</i>	16.3	0.210	—	—	0.804	0.024*	4.81*	3, 2
<i>Columba livia</i>	16.3	0.210	—	—	0.828	0.055	4.79	2, 2

TABLE 1. Continued.

Species	Mass (g) Cont	F Yolk Cont	F Wat Alb	F Wat Yolk	F Wat Cont	F Lip Cont	kJ/g Wet	Ref.
<i>Columba livia</i>	16.2	0.245	0.900	0.566	0.815	0.069	5.31	11
<i>Columba livia</i>	14.5	0.210	0.893	0.577	0.827	—	—	18
Dove	19.9	0.200	0.892	0.579	0.830	—	—	1
<i>Zenaida macroura</i>	6.0	0.344	0.889	0.614	0.794	0.088	6.10	6
<i>Zenaida macroura</i>	5.7	0.350	—	—	0.825	0.070	5.10	2
<i>Zenaida macroura</i>	—	0.350	—	—	0.825	0.065*	5.02*	2
<i>Streptopelia risoria</i>	7.3	0.290	—	—	0.817	—	—	3, 2
<i>S. turtur</i>	7.0	0.318	0.908	0.615	0.818	0.113	5.97	11
Picidae								
<i>Colaptes auratus</i>	8.7	—	—	—	0.862	—	—	2
Alaudidae								
<i>Galerida cristata</i>	3.2	0.240	—	—	0.830	—	—	3, 2
Hirudinidae								
<i>Riparia riparia</i>	1.4	0.230	0.892	—	—	—	—	18
Corvidae								
<i>Pica pica</i>	6.7	0.190	—	—	0.866	0.042	3.72	2
<i>Pica pica</i>	—	0.190	—	—	0.866	0.052*	3.89*	2
Crow	—	0.185	—	—	0.833	—	—	2, 1
<i>Corvus corone</i>	18.0	0.210	0.905	0.571	0.830	—	—	18
<i>C. frugilegus</i>	16.7	0.160	0.896	0.580	0.850	—	—	18
Muscicapidae								
<i>Turdus migratorius</i>	—	0.260	—	—	0.841	0.063	4.63	2
<i>Turdus migratorius</i>	6.3	0.260	—	—	0.841	0.072*	4.77*	2
<i>T. merula</i>	5.6	0.265	—	—	0.801	—	—	1, 2
<i>Catharus guttatus</i>	6.1	—	—	—	0.852	—	—	2
<i>Ficedula hypoleuca</i>	1.6	0.252	0.902	0.565	0.816	0.077	5.42	19
<i>Luscinia megarhynchos</i>	—	—	—	—	0.800	—	—	1
Parulidae								
<i>Dendroica petechia</i>	1.6	—	—	—	0.813	—	—	2
Sturnidae								
<i>Sturnus vulgaris</i>	6.7	0.194	0.894	0.570	0.831	0.061	4.82	6
<i>Sturnus vulgaris</i>	6.5	0.154	0.899	0.566	0.774	—	—	1
<i>Onycognathus tristramii</i>	8.6	—	—	—	0.844	—	—	3
Paridae								
<i>Parus major</i>	1.4	0.224	0.902	0.591	0.832	0.060	4.78	19
Emberizidae								
<i>Emberiza citrinella</i>	1.9	—	—	—	0.814	—	—	1
<i>Melospiza melodia</i>	2.7	—	—	—	0.852	—	—	2
Ploceida								
<i>Passer domesticus</i>	2.4	0.275	0.892	0.564	0.800	0.079	5.82	11
<i>Passer domesticus</i>	2.4	0.210	0.899	0.566	0.829	—	—	18
Icteridae								
<i>Quiscalus major</i>	6.9	0.245	0.907	0.605	0.784	0.063	5.91	15
<i>Q. quiscula</i>	6.4	—	—	—	0.844	—	—	2
<i>Molothrus ater</i>	2.7	—	—	—	0.852	—	—	2
<i>Euphagus carolinus</i>	6.3	—	—	—	0.841	—	—	2
<i>E. cyanocephalus</i>	4.7	0.210	—	—	0.851	0.064	4.42	2
<i>Agelaius phoeniceus</i>	4.3	—	—	—	0.860	—	—	2
<i>Xanthocephalus xanthocephalus</i>	4.3	—	—	—	0.837	—	—	2
Fringillidae								
<i>Carpodacus mexicanus</i>	2.3	—	—	—	0.826	—	—	2

TABLE 1. Continued.

Species	Mass (g) Cont	F Yolk Cont	F Wat Alb	F Wat Yolk	F Wat Cont	F Lip Cont	kJ/g Wet	Ref.
Offshore and pelagic feeders								
Diomedeiidae								
<i>Diomedea exulans</i>	458.0	0.300	0.882	—	0.765	0.074	6.52	12
<i>D. nigripes</i>	284.0	0.330	—	—	0.749	0.086*	7.09*	14
<i>D. immutabilis</i>	261.0	0.350	—	—	0.742	0.085*	7.23*	14
<i>Phoebetria fusca</i>	220.0	0.310	0.879	—	0.755	0.080	6.85	12
<i>P. palpebrata</i>	229.0	0.340	0.882	—	0.783	0.090	6.38	12
Procellariidae								
<i>Macronectes giganteus</i>	230.0	0.350	0.882	—	0.783	0.084	6.28	12
<i>M. halli</i>	222.0	0.390	0.876	—	0.782	0.096	6.50	12
<i>Pterodroma mollis</i>	44.0	0.390	0.861	—	0.785	—	—	12
<i>P. macroptera</i>	72.0	0.420	0.875	—	0.776	—	—	12
<i>P. hypoleuca</i>	36.0	0.400	—	—	0.706	0.120*	8.61*	14
<i>Procellaria aequinoctialis</i>	113.0	0.440	0.852	—	0.787	—	—	12
<i>Puffinus pacificus</i>	54.0	0.400	—	—	0.732	0.117*	7.98*	14
<i>Bulweria bulwerii</i>	21.0	0.380	—	—	0.722	0.083*	7.64*	14
Hydrobatidae								
<i>Oceanodroma leucorhoa</i>	9.7	0.410	0.873	0.570	0.717	0.115	8.28	7
<i>Oceanodroma leucorhoa</i>	9.7	0.390	—	—	0.758	0.113	7.32	2
<i>Oceanodroma leucorhoa</i>	—	0.390	—	—	0.758	0.153*	7.99*	2
Laridae								
<i>Sterna fuscata</i>	34.5	0.377	—	—	0.717	0.098*	8.01*	14
<i>S. lunata</i>	26.8	0.365	—	—	0.746	0.082*	7.09*	14
<i>Gygis alba</i>	21.0	0.380	—	—	0.711	0.125*	8.59*	14
<i>Anous stolidus</i>	37.4	0.353	—	—	0.747	0.080*	7.03*	14
<i>A. minutus</i>	23.4	0.349	—	—	0.749	0.089*	7.13*	14

shore and pelagic feeders). The lower regression represents eggs of altricial birds (including the category of semialtricial 1 and 2). The slopes of both regressions, as previously noted by Ar and Yom-Tov, are not significantly different from 1.0. The regression for the precocial group is based on 111 species ($n = 181$) with an intercept of 0.35, while the altricial egg regression is based on 72 species ($n = 88$) with an intercept of 0.24. Both relationships indicate that within these ma-

turity categories the relative yolk content is independent of egg mass, that egg mass of altricial birds is generally smaller, and that, on the average, precocial eggs contain (0.35/0.24) or 46% more yolk than altricial eggs.

HATCHLING MATURITY AND RELATIVE WATER CONTENT

In a previous study (Carey et al. 1980) it was demonstrated that for 149 species there was a

TABLE 2. Summary table of equations for linear regressions between dependent variables and fraction of yolk in contents.

Equation number	1	2	3	4	5
Dependent variable	FWA	FWC	FWY	FSC	FLC
Slope	-0.066	-0.458	-0.349	0.458	0.332
Intercept	0.906	0.917	0.631	0.083	-0.015
r^2	0.203	0.696	0.444	0.696	0.890
$S_{y,x}$	0.013	0.028	0.040	0.028	0.014
SSX	0.869	1.16	0.769	1.16	0.770
SES	0.014	0.026	0.046	0.026	0.016
n	89	137	75	137	99

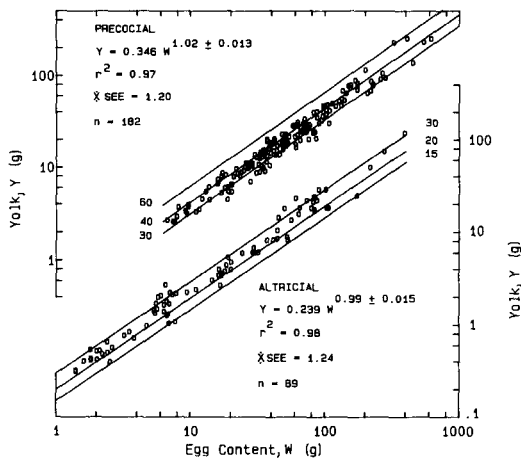


FIGURE 1. Regression of yolk mass against egg content. Upper curve—precocial birds (including precocial 1, 2, 3, and 4, semiprecocial birds, and offshore and pelagic feeders). Lower curve—altricial birds (including semialtricial 1 and 2). Data from Table 1 and from tables of Ar and Yom-Tov (1978) and Carey et al. (1980). Lines indicate isopleths for relative yolk content from 15 to 60%.

progressive increase in relative yolk content of fresh eggs with increasing physiological and behavioral maturity of hatchlings (Nice 1962). Although based on relatively few species ($n = 21$), the study also showed an inverse relationship between the fractional water and yolk content. This relationship (equation 2) for 127 species is shown in Figure 3, as are the mean value and SD of FWC and FYC for various maturity groups (Table 1). The key and number of observations for each group are shown in the inset. No. 7 represents the offshore and pelagic feeders and will be discussed below. Whether or not the average value for six eggs of *Apteryx australis* (No. 6) belongs to the precocial 1 group with Megapodidae is debatable and will be dealt with later; Nice placed *Apteryx* in the precocial 2 group. Thus with the exception of groups 6 and 7 all other groups demonstrate a progressive increase in yolk content and a decrease in water content with increasing maturity as originally shown by Carey et al. (1980).

Maturation is a continuous process starting with the formation of the early embryo and ending at the adult stage where at any stage of development the degree of maturity is reflected by the relative water content of the organism, or as Needham (1963) stated: "A decreasing water-content is a universal accompaniment of growth."

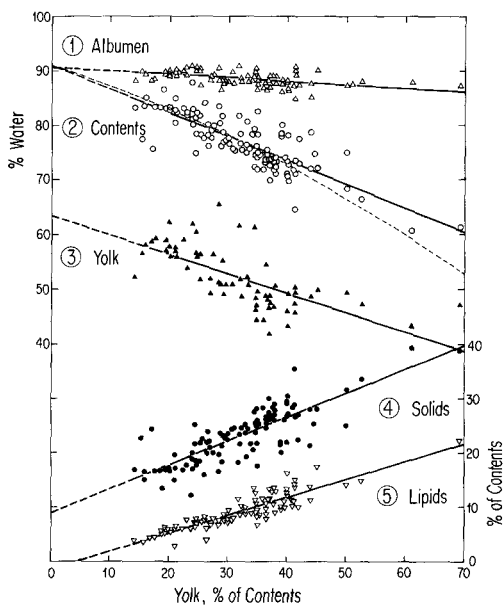


FIGURE 2. Percent water in albumen, egg contents, and yolk as well as percent solids and lipids in egg contents plotted as functions of percent yolk in egg contents. (Data from Table 1.) The numbers 1-5 correspond to the numbers of the linear regression equations (Table 2) for the solid lines. The dashed line is a curvilinear relationship between FWC and FYC—see Results for explanation.

In birds (Needham 1963, Romanoff 1967), reptiles (Packard et al. 1983), and mammals (Needham 1963, Altman and Dittmer 1974) early embryos have a relative water content of ca. 92 to 95%; with development and maturation, water content gradually declines to about 60% of whole body mass in adult birds (Skadhauge 1981, Mahoney and Jehl 1984) and to similar levels in mammals.

Figure 4 illustrates the general process of xerogenic maturation in birds by plotting the relative water content of embryos against their relative incubation period. The triangular symbols are the average of six precocial species (Romanoff 1967) and the other symbols represent values for two species of terns (Pettit et al. 1984). Ricklefs (1979) reported that the relative water content of altricial hatchlings was significantly higher than that of precocial hatchlings. Similar observations have now been made by Ar and Rahn (1980), Carey (1983), and also by Vleck et al. (1984) for two species of megapods. The mean values of FWC in hatchlings for five maturity groups are shown in Figure 4. The dotted lines show pos-

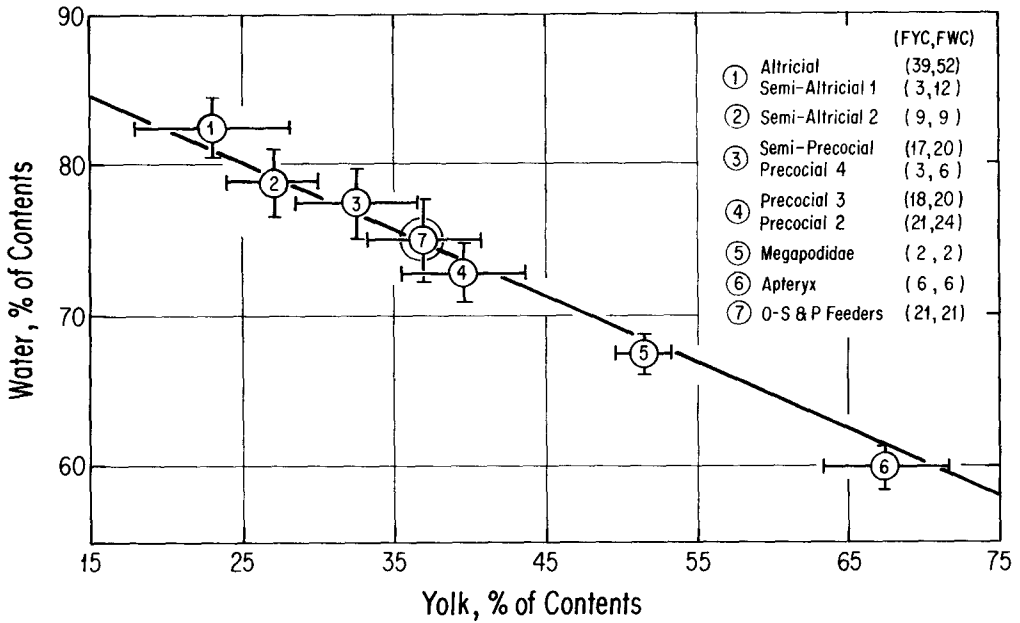


FIGURE 3. Relationship between percent water and percent yolk in contents of fresh eggs for seven groups of birds (see inset for key to the numbers). The solid line was plotted using equation 2 (Table 2). Means and standard deviations for the seven groups were computed from data in Table 1; sample sizes of the groups, or subgroups, for FYC and FWC are shown in the inset.

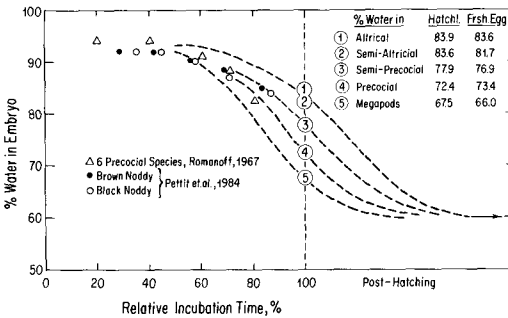


FIGURE 4. A model of xerogenic maturation in birds. The dashed curves are proposed time courses for dehydration during development of embryonic and post-natal birds that hatch at varying levels of physiological and behavioral maturity. Relative water content of early embryos is ca. 92 to 95% and falls to ca. 60% at maturity. Data points, from literature (see inset), show the relationship between measured percent water in embryos and relative incubation time. The large, numbered circles at hatching time indicate average values for different groups of hatchlings. The numbers correspond to different stages of hatchling maturity, shown in inset, which were determined by Ar and Rahn (1980) and Carey (1983).

sible time courses of dehydration for each of these groups during development. It is interesting to note that the “altricial” rat is born with a relative water content of 86.6% ($n = 177$) and the “precocial” guinea pig with 71% water content ($n = 11$) (Altman and Dittmer 1974), whereas painted and snapping turtle hatchlings have relative water contents of ca. 80% and 79%, respectively, (Packard et al. 1983, Morris et al. 1983).

Therefore, avian embryos begin development by creating their own hydric environment, which is similar in all species regardless of the initial water fraction of the fresh egg. By the end of incubation they have incorporated into their bodies the remaining solids within the egg and hatch with a relative water content similar to that of the fresh egg (see insert of Fig. 4). This similarity between the state of hydration of the fresh egg and that of the hatchling is achieved during incubation by a continuous loss of water from the egg which equals the amount of additional water generated by the metabolism of the embryo (Ar and Rahn 1980). Thus, the initial relative water content of the fresh egg is not only correlated with a given state of hatchling maturity, but is also similar to that of the hatchling

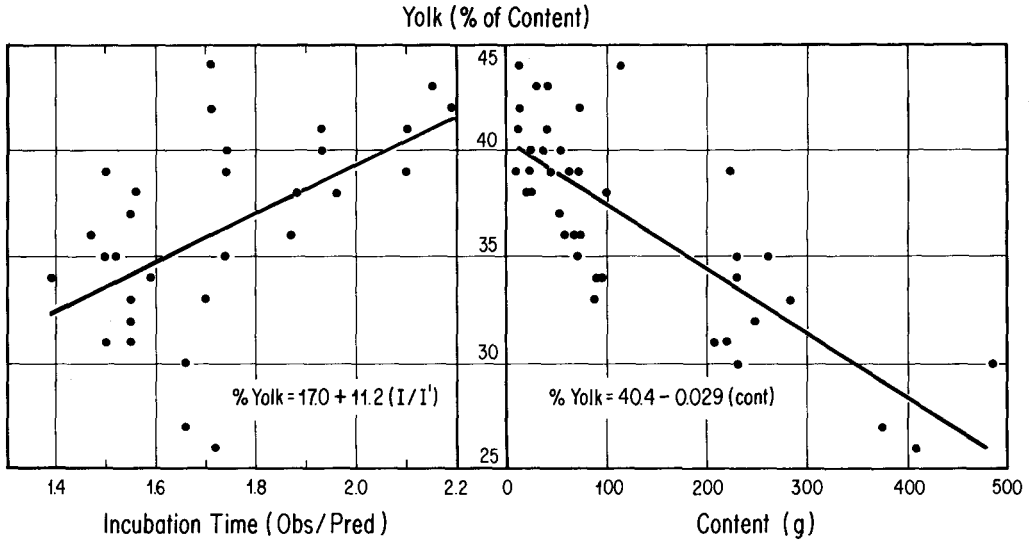


FIGURE 5. Relative yolk content of eggs of Procellariiformes plotted as functions of relative incubation time (observed length/predicted length) and mass of egg contents (g). Data from Table 4.

itself. For these reasons we suggest that in general the relative water content of eggs is perhaps a better guide for assessing maturity than the relative yolk content, because the maturation process continues after hatching.

OFFSHORE AND PELAGIC FEEDERS

Discrepancy between the position of the Procellariiformes in Nice's (1962) classification of maturity at hatching and their relative yolk content has always been troublesome and has invited much discussion. Nice suggested that "albatrosses and perhaps petrels are really more semi-precocial than semi-altricial." Ricklefs (1974) and Skutch (1976) considered them altricial or semi-altricial, but later Ricklefs et al. (1980) suggested that Leach's Petrel chicks are semiprecocial. In 1984 Pettit et al. reported the egg yolk content of five species of Procellariiformes and considered the hatchlings to be semiprecocial. As

Boersma (1982) and Williams et al. (1982) again emphasize, there is no simple relationship between relative yolk content and hatchling maturity in this group. We have, therefore, taken the position of Warham (1983) and Boersma (1982) that Procellariiformes "seem to form a special category of their own" and suggest that so-called offshore-feeding terns fall into a similar category.

Compared with an inshore-feeding tern, such as *Sterna hirundo*, Lack (1968) described *S. fuscata* as an offshore feeder with a reduced clutch, longer incubation and fledging periods, longer incubation spells, and less frequent visits with food for the young. As he pointed out, similar attributes can be found among other terns, although in these cases the modifications can also be attributed to the scarcity of food in tropical waters. For convenience we have labeled all of them offshore feeders and compare five of these, *S. fuscata*, *S. lunata*, *Anous stolidus*, *A. tenuirostris* (*minutus*), and *Gygis alba*, with nine so-called inshore-feeding terns in Table 3. These two groups are most easily separated by their clutch size, but also differ in incubation time, fledging time, and relative yolk mass. It is suggested that the extended incubation period of offshore feeders, which is 50% longer than that of the inshore feeders, requires extra maintenance energy during development and that this is supplied by the yolk lipids. The large yolk may also provide for

TABLE 3. Comparison of onshore- and offshore-feeding terns. Average values and SE (parentheses) from the tables of Rahn et al. (1984).

Feeders	Clutch size	Egg mass g	Incub. days	Fledging days	Yolk %	n
Onshore	2-3	29	23 (1.1)	26 (1.7)	31 (0.6)	9
Offshore	1	30	34 (1.3)	51 (4)	37 (0.7)	5

TABLE 4. Egg content (g), relative yolk content, FYC, and observed/predicted incubation time, I/I', among Procellariiformes.

	Cont.	FYC	I/I'	Ref.
Diomedeiidae				
<i>Diomedea exulans</i>	375	0.27	1.66	1
<i>Diomedea exulans</i>	485	0.30	1.66	2
<i>Diomedea epomorpha</i>	409	0.26	1.72	1
<i>Diomedea nigripes</i>	247	0.32	1.55	1
<i>Diomedea nigripes</i>	284	0.33	1.55	3
<i>Diomedea immutabilis</i>	261	0.35	1.52	3
<i>Diomedea bulleri</i>	230	0.30		1
<i>Phoebetria fusca</i>	220	0.31	1.55	2
<i>Pheobetria palpebrata</i>	229	0.34	1.59	2
Procellariidae				
<i>Macronectes giganteus</i>	230	0.35	1.50	2
<i>Macronectes giganteus</i>	208	0.31	1.50	4
<i>Macronectes giganteus</i>	222	0.39	1.50	5
<i>Macronectes halli</i>	222	0.39		2
<i>Fulmarus glacialis</i>	92	0.34	1.39	4
<i>Fulmarus glacialis</i>	87	0.33	1.70	1
<i>Daption capense</i>	59	0.36	1.47	4
<i>Pagodroma nivea</i>	52	0.37	1.55	4
<i>Pterodroma solandri</i>	73	0.36	1.87	1
<i>Pterodroma mollis</i>	44	0.39		2
<i>Pterodroma macroptera</i>	72	0.42	1.71	2
<i>Pterodroma neglecta</i>	64	0.39		1
<i>Pterodroma nigripennis</i>	40	0.43		1
<i>Pterodroma hypoleuca</i>	39	0.41	1.93	1
<i>Pterodroma hypoleuca</i>	36	0.40	1.93	3
<i>Pachyptila turtur</i>	23	0.39		1
<i>Pachyptila turtur</i>	23	0.40		2
<i>Pachyptila vittata</i>	29	0.43	2.15	2
<i>Procellaria aequinoctialis</i>	113	0.44	1.71	2
<i>Puffinus carneipes</i>	68	0.36		1
<i>Puffinus pacificus</i>	71	0.35	1.74	1
<i>Puffinus pacificus</i>	54	0.40	1.74	3
<i>Puffinus bulleri</i>	61	0.39		1
<i>Puffinus gravis</i>	99	0.38	1.56	1
<i>Puffinus griseus</i>	96	0.34		1
<i>Puffinus tenuirostris</i>	71	0.39	1.74	1
<i>Puffinus lherminieri</i>	24	0.38	1.96	1
<i>Bulweria bulwerii</i>	21	0.38	1.88	3
Hydrobatidae				
<i>Pelagodroma marina</i>	12	0.42	2.19	1
<i>Oceanodroma leucorhoa</i>	9.7	0.39	2.10	6
<i>Oceanodroma leucorhoa</i>	9.7	0.41	2.10	7
<i>Oceanodroma furcata</i>	11.6	0.44		8

References: 1. Warham (1983); 2. Williams et al. (1982); 3. Pettit et al. (1984); 4. Etchécopar and Prévost (1954); 5. Conroy (1972); 6. Unpubl.; 7. Montevecchi et al. (1983); 8. Boersma (1982).

a larger hatchling yolk reserve, particularly if parent birds have less frequent feeding bouts than inshore feeders.

The characteristics Lack (1968) ascribed to off-shore feeders can also be used to describe the rather homogeneous group of pelagic-feeding birds in the order Procellariiformes. Within this group, however, there are no inshore feeders, with the possible exception of the Pelecanoides (the

diving petrels), with which comparisons can be made. This invites comparison with non-Procellariiform birds.

Whittow (1980) and Grant et al. (1982) pointed out that the ratio (I/I') of the observed incubation time (I) of Procellariiformes over the predicted incubation times (I') of "other birds" decreases as eggs get larger, e.g., I/I' varies from 2.1 for 10-g eggs to 1.5 for 400- to 500-g eggs.

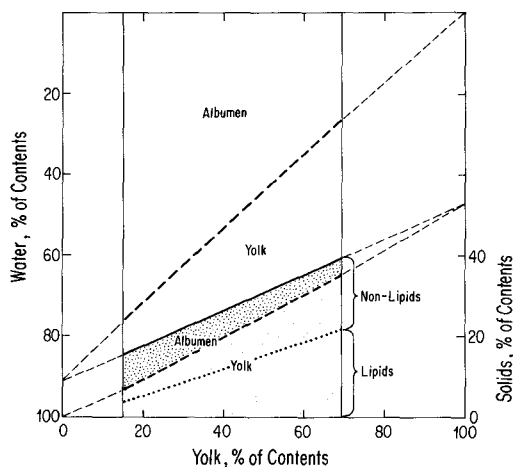


FIGURE 6. Partitioning of water and solids between yolk and albumen in avian eggs as a function of percent yolk in contents. The two vertical lines delineate the range of percent yolk for avian eggs listed in Table 1. Between these two lines the solid line, separating water (unshaded) from solids (shaded), was drawn using equation 2 (Table 2); the dashed lines, separating yolk from albumen in both the water and solid portions, were drawn using the equation

$$(\text{albumen water/content water}) = \frac{\text{FWA}/\text{FWC}}{(1 - \text{FYC})}$$

where FWA and FWC were computed using equations 1 and 2 (Table 2); the dotted line, separating lipids from nonlipids in the solids, was drawn using equation 5 (Table 2).

Values for the ratio I/I' for the eggs of various species of Procellariiformes are listed in Table 4 as well as their content and FYC. Incubation time, I , values were obtained from Rahn et al. (1984), and I' values were calculated from the relationship $I = 12 W^{0.22}$ (Rahn and Ar 1974) where I = incubation time (d) and W = egg mass (g). The general trend of relative yolk content as a function of I/I' and egg size (content) is shown in Figure 5. The inverse relationship between egg size and yolk content was first described by Warham (1983). Thus, in general, the smaller the egg, the longer the relative incubation time and the larger the relative yolk content.

As Lack (1968) emphasized, increased fledging time is usually associated with increased incubation time. When fledging time of various orders (Anseriformes, Sphenisciformes, Falconiformes, Passeriformes, and family Laridae) are regressed against egg mass ($n = 320$), the fledging times for 35 species of Procellariiformes (Rahn et al. 1984) are 40 to 60% longer for a given egg mass than for the other groups. Thus so-called

offshore and pelagic feeders are similar in having their clutches reduced to one egg, prolonged incubation and fledging times, and increased yolk content. That other egg functions are modified to cope with prolonged incubation time in the offshore-feeding terns and Procellariiformes has been amply demonstrated by Whittow (1984). For example, shell conductance and incubation water loss are reduced so that at the end of incubation the relative water loss and air cell O_2 and CO_2 tensions are similar to those of other birds but the total energy expended during development is greater. From these points of view the discrepancy between maturity at hatching and relative yolk content in offshore and pelagic feeders can be accounted for as an adaptation to the various factors which contribute to a prolonged incubation-fledging time as a way to compensate for the greater maintenance cost and/or to provide larger yolk reserves in the postnatal period.

On this basis one might predict that many other exceptions to the maturity-yolk content rule will be found. For example, the Bridled Tern, *Sterna anaethetus*, and the Crested Tern, *S. bergii*, lay single eggs and have incubation and fledging periods similar to the offshore feeders listed in Table 3 (Langham 1984). *Creagrus furcatus*, the Swallow-tailed Gull of the Galapagos, lays a single egg and has an incubation and a fledging period of 32 and 60 days, respectively, while *Rissa brevirostris*, the Red-legged Kittiwake of the Pribilof Islands, lays one egg, with incubation and fledging periods of 31 and 37 days, respectively (G. L. Hunt, pers. comm.). One might also predict a relatively larger yolk content for the Lyrebird, *Menura superba*, of Australia which lays a single 60-g egg, incubated for 42 days. Comparable clutch size and incubation time for passerines of similar body mass (Corvidae) are 4 to 5 eggs and 18 to 20 days, respectively (see Rahn et al. 1985).

Nice (1962) classifies the Kiwi hatchling as precocial 2 (ducks and shorebirds) because it is not independent of parents as are the megapods, which are in the precocial 1 group. On the other hand, Kiwi eggs have the longest incubation time known (74 to 84 days, Reid and Williams 1975), the chicks hatch fully feathered with an adult plumage and are confined to the burrow for 7 to 10 days before they emerge and feed by themselves (Reid 1977). The very large yolk reserve (95 to 125 g, Reid 1977) probably provides the required energy during the postnatal period before feeding is initiated.

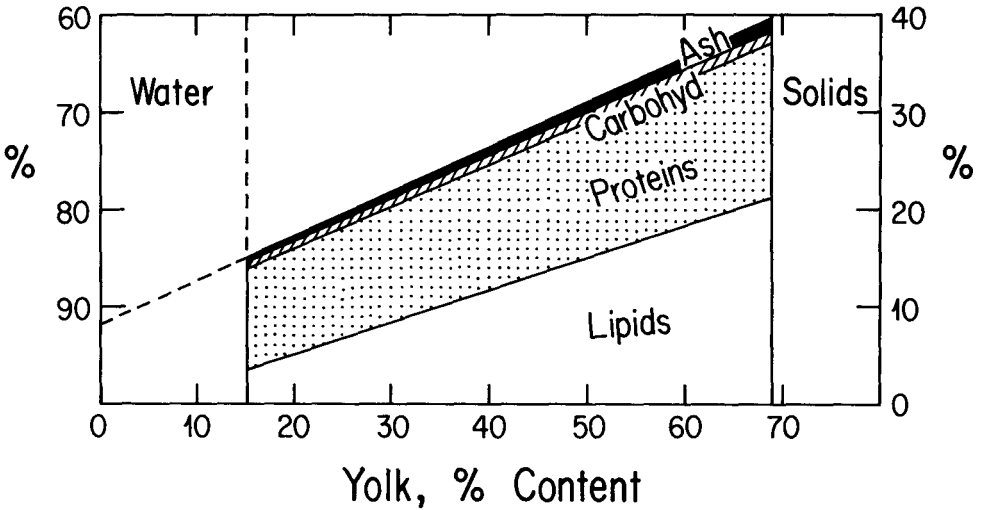
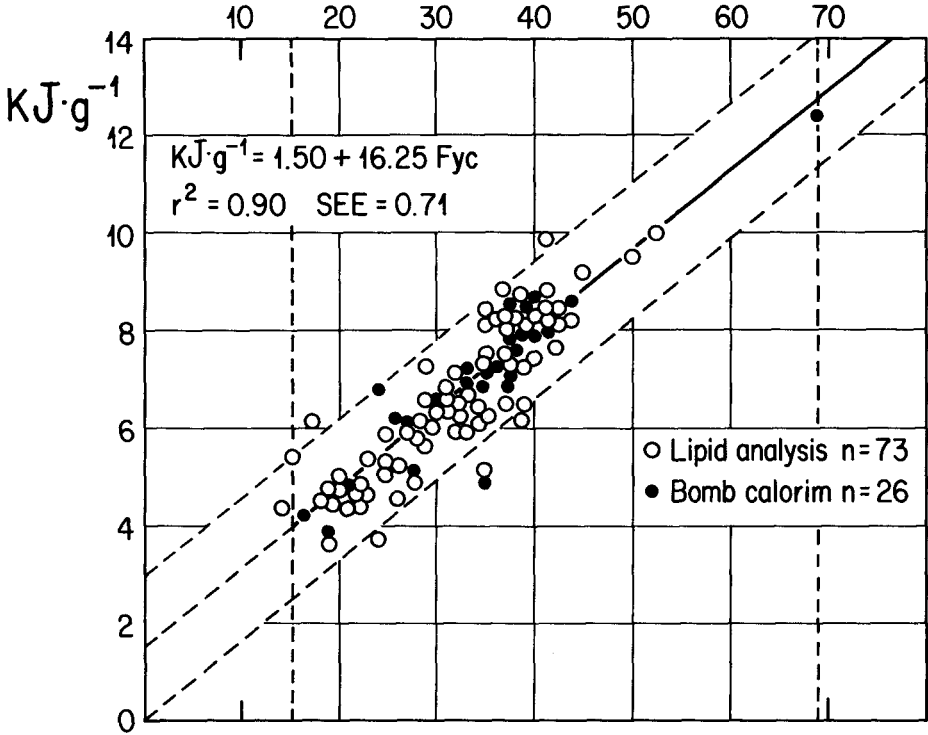


FIGURE 7. Lower graph: A model showing the distribution of lipids, proteins, carbohydrates, and ash in egg solids as a function of relative yolk content. Upper graph: Caloric density of egg content as a function of relative yolk content. The solid dots represent values determined by bomb calorimetry, the open dots represent values calculated using equation 8 (see text) and measured values of FLC.

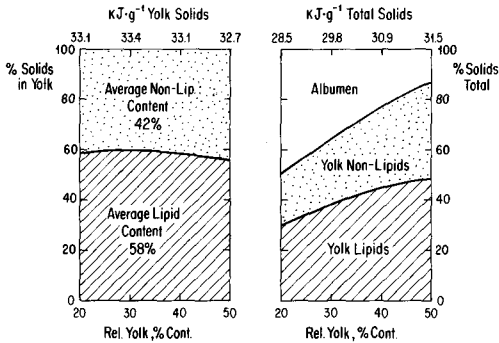


FIGURE 8. Left: Relative distribution of lipids and nonlipids in yolk solids as a function of relative yolk content. Caloric density of yolk solids is shown at the top. For details see text. Right: Relative distribution of albumen and yolk in total solids as a function of relative yolk content. Caloric density of total solids is shown at the top. For details see text.

DISTRIBUTION OF WATER AND SOLIDS

Figure 6 shows the average distribution of water and solids between yolk and albumen as a function of FYC, generated from equations 1 and 2 (Table 2). The vertical lines denote the span of relative yolk, from 15% (some species of *Pelecaniformes*) to 50% for the *Megapodidae* to 69% for the *Kiwi* (*Apterygidae*), although most of the species are confined to the 15 to 45% range (see Fig. 3). Whereas albumen is the principal carrier of water in the lower range of FYC, at 62% relative yolk, similar to that of a *Kiwi* egg, the water in the yolk equals that in the albumen. At a relative yolk content of 20% the albumen carries 85% of the total water and half of the total solid.

The distribution of lipids and nonlipids between the yolk and albumen solids is of interest. Albumen carries essentially no lipids; as the relative amount of yolk in eggs increases, progressively more nonlipids are carried by the yolk. At a yolk content of 34% about half the nonlipids are contained in the yolk, but at a relative yolk content of 69% nearly 80% of the nonlipid solids are contained therein.

COMPOSITION OF SOLIDS

The nonlipid fraction. Subtracting the lipid and ash fractions from the total solids provides an estimate of the nonlipid fraction. For the ash fraction we used an average value of 4% of solids based on the studies of Needham (1963), Romanoff (1967), Calder et al. (1978), Ricklefs and Montevecchi (1979), Pettit et al. (1984), Vleck et al. (1984), and Bancroft (1985). The mean

TABLE 5. Percent protein and carbohydrate in the ash-free, lipid-free, solid content of avian eggs. Data are for eight species in five orders.

Species	% Protein	% CHO	Ref.
Khaki Campbell	97.2	2.8	1
Domestic Chinese Goose	94.6	5.4	1
<i>Uria aalga</i>	93.4	6.6	1
<i>Cerorhinca monocerata</i>	94.4	5.6	1
<i>Gallus gallus</i>	97.0	3.0	1
<i>Gallus gallus</i>	94.9	5.1	2
<i>Larus crassirostris</i>	95.1	4.9	1
<i>Egretta garzetta</i>	94.5	5.5	1
<i>Nycticorax nycticorax</i>	95.7	4.3	1
Average	95.2	4.8	
SD	1.2	1.2	
n	9	9	

References: 1. Kuroda (1963); 2. Romanoff (1967).

value was 3.85%, SD = 0.70%, n = 27, and represents 23 species in seven orders.

The distribution of carbohydrates and proteins within the nonlipid, ash-free fraction was calculated from the values shown in Table 5. In all cases both the protein and the carbohydrate fractions were reported. The average values (Table 5) were 95% proteins and 5% carbohydrates. We have assumed these to be reasonable estimates for all species, and their relationships to relative yolk content are plotted in Figure 7.

Calculation of caloric density. For all species in Table 1 where the fractions of water and lipids in the content were reported we obtained the nonlipid fraction, FNLC, by subtracting FLC from the ash-free solids, 0.96 (1 - FWC), and calculated the caloric density of the content with the following relationship:

$$\text{kJ}\cdot\text{g}^{-1} \text{ content} = \text{FLC}\cdot(40 \text{ kJ}\cdot\text{g}^{-1}) + \text{FNLC}\cdot(23.5 \text{ kJ}\cdot\text{g}^{-1}) \quad (8)$$

assuming the following energetic equivalent: 40 $\text{kJ}\cdot\text{g}^{-1}$ lipids, 17.6 $\text{kJ}\cdot\text{g}^{-1}$ carbohydrates, and 23.8 $\text{kJ}\cdot\text{g}^{-1}$ proteins (King and Farner 1961, Kleiber 1961). The protein and carbohydrate proportions of 95 and 5%, respectively, (Table 5) yield an average caloric value of 23.5 $\text{kJ}\cdot\text{g}^{-1}$ nonlipids. Starred values for FLC in Table 1 were obtained by substituting (0.96 FSC - FLC) for FNLC in equation (8) and solving for FLC, as follows:

$$\text{FLC} = [\text{kJ}\cdot\text{g}^{-1} - (0.96 \text{ FSC} \times 23.5)]/16.5 \quad (9)$$

where $\text{kJ}\cdot\text{g}^{-1}$ = caloric content obtained by bomb calorimetry, FSC = (1 - FWC) and 16.5 = difference between caloric equivalents of lipids and nonlipids.

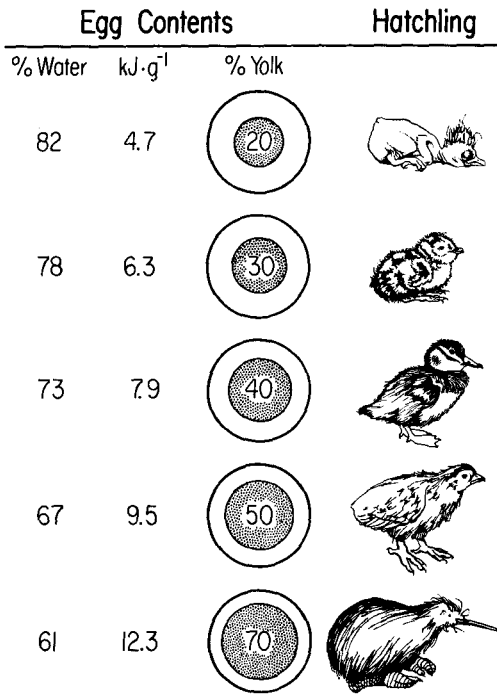


FIGURE 9. Simple overview of differences in egg composition as a function of relative yolk content and sketches of typical hatchlings for each group. For details see text.

In the upper portion of Figure 7 values for the calculated caloric densities, obtained using equation 8, are shown as circles; and the measured caloric densities, obtained directly by bomb calorimetry, solid symbols, are plotted against relative yolk content. The lowest values are close to $4 \text{ kJ}\cdot\text{g}^{-1}$ of content, corresponding to relative yolk contents between 15 and 20%. The two species of megapods with yolk contents of ca. 50% have ca. $10 \text{ kJ}\cdot\text{g}^{-1}$, while the Kiwi with ca. 69% yolk has a value of ca. $12 \text{ kJ}\cdot\text{g}^{-1}$.

CALORIC DISTRIBUTION IN SOLIDS

What is the distribution of lipids and nonlipids in dry yolk? From equations 3 and 5 (Table 2) one can calculate their relative distribution which is plotted against the relative yolk content of fresh eggs in Figure 8. There is a remarkable constancy, namely, in all eggs over this range the lipids constitute on average 58% of the dry yolk. Using equation 8 the caloric density of dry yolk is shown at the top of the figure, giving an average value of $33.1 \text{ kJ}\cdot\text{g}^{-1}$ dry yolk and can be compared with an average value of $33.4 \text{ kJ}\cdot\text{g}^{-1} \pm 1.1 \text{ SD}$ dry yolk determined by Ar et al. (in press) by

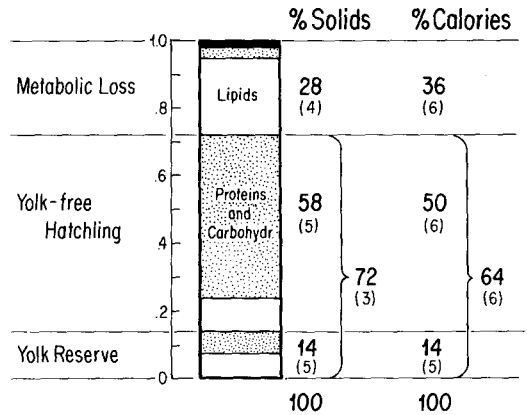


FIGURE 10. The column represents the total initial solids in fresh eggs. It shows how the solids, lipids and nonlipids, as well as initial caloric density are partitioned between the yolk-free hatchling, the yolk reserve, and the portion lost by metabolism. This partitioning is based on averages (SD in parentheses) of 12 species with an average yolk content of 39%. See text for details.

direct calorimetry of 35 species comprising 12 altricial, 5 semialtricial, 4 semiprecocial, and 14 precocial types. Their average value for albumen was $22.5 \text{ kJ}\cdot\text{g}^{-1} \pm 1.6$ dry albumen.

On the right of Figure 8 the distribution for total solid (albumen and yolk) is shown as a function of relative yolk content of fresh eggs. At the top of this figure the caloric density of dry total solids is indicated, which increases slightly with increasing relative yolk content. When these values are multiplied by the corresponding value of total solids, $(1 - \text{FWC})$ (equation 2, Table 2), one obtains the caloric density $\cdot\text{g}^{-1}$ of wet content, which does not differ significantly from the regression of caloric density as a function of relative yolk content shown in Figure 7.

Carey et al. (1980) showed that the energy content per g of dry mass obtained by direct calorimetry did not vary significantly among developmental groups (i.e., as a function of percent yolk) and that the average value was $29.8 \text{ kJ}\cdot\text{g}^{-1}$ ($n = 40$). This observation is corroborated by Ar et al. (in press), who also showed that the average value for the energy content of eggs, determined by direct calorimetry, is $29.2 \pm 1.3 \text{ kJ}\cdot\text{g}^{-1}$ dry mass ($n = 45$). Using data from Table 1, energy content per g wet mass ($\text{kJ}\cdot\text{g}^{-1}$ wet) divided by the fraction of solids in egg contents $(1 - \text{FWC})$, there is statistically a slight but significant increase in the energy per g dry mass of eggs as a function of FYC. The equation relating the energy content per g solids (EGS) to the fraction of

TABLE 6. Egg content (g), egg solids = dry mass (g), and caloric content of solids (kJ) of fresh eggs, yolk-free hatchling, yolk reserve, and metabolic loss obtained and calculated from data of Ricklefs (1977), ref. 1; Vleck et al. (1984), ref. 2; and Pettitt et al. (1984), ref. 3.

Species	Ref.	Fresh egg			Yolk-free hatch		Yolk reserve		Metabolic loss	
		Content	Solids	kJ	Solids	kJ	Solids	kJ	Solids	kJ
Black-footed Albatross <i>Diomedea nigripes</i>	3	284	71.2	2,016	40.7	1,025	13.5	424	17.0	567
Laysan Albatross <i>Diomedea immutabilis</i>	3	261	67.4	1,886	39.9	962	11.0	338	16.5	586
Mallee Fowl <i>Leipoa ocellata</i>	2	156	52.1	1,594	31.4	853	5.70	168	15.0	574
Brush Turkey <i>Alectura lathamii</i>	2	170	53.6	1,663	35.3	1,000	6.48	198	11.8	465
Mallard Duck <i>Anas platyrhynchos</i>	1	67.6	21.0	629	10.0	282	4.04	128	6.93	219
Wedge-tailed Shearwater <i>Puffinus pacificus</i>	3	53.5	14.4	428	7.13	157	3.20	97	4.10	174
Laughing Gull <i>Larus atricilla</i>	1	37.4	9.19	279	5.15	137	1.78	53	2.97	89
Brown Noddy <i>Anous stolidus</i>	3	37.4	9.45	263	5.58	124	0.92	30	2.95	109
Bonin Petrel <i>Pterodroma hypoleuca</i>	3	36.0	10.6	310	6.16	143	1.53	48	2.91	119
Black Noddy <i>Anous minutus</i>	3	23.5	5.89	167	3.82	88	0.48	15	1.59	64
White Tern <i>Gygis alba</i>	3	21.0	6.07	181	3.60	81	0.48	16	1.99	84
Japanese Quail <i>Coturnix coturnix</i>	1	8.27	2.22	66	1.40	39	0.16	5	0.66	22

yolk is $EGS = 25.9 + 9.6 FYC$, $n = 99$, $r^2 = 0.34$, which predicts a 10% increase as FYC increases from 0.20 to 0.50, the common range for most birds. However, as a first approximation, the average EGS is a useful constant; for our data EGS is $29.1 \pm 1.5 \text{ kJ} \cdot \text{g}^{-1}$ solids ($n = 99$), which agrees well with the above cited data of Carey et al. (1980) and Ar et al. (in press).

Thus, we see a remarkable constancy in the energy content of egg solids. All yolk solids have a lipid content of 58% and a caloric density of $33 \text{ kJ} \cdot \text{g}^{-1}$, while total solids have a caloric density of $29 \text{ kJ} \cdot \text{g}^{-1}$ in spite of differences in yolk-albumen ratio. This suggests that reasonably accurate values of caloric content of fresh eggs can be obtained by simply determining their dry content and factoring this value by $29 \text{ kJ} \cdot \text{g}^{-1}$.

OVERVIEW

Figure 9 presents a simple overview of fresh egg composition of five arbitrarily chosen yolk contents of 20, 30, 40, 50, and 70%, shown schematically as cross sections of spheres, and their typical hatchlings. The water content (%) is from the regression (equation 2) plotted in Figure 3

and the caloric density from the regression in Figure 7. The first three hatchling sketches are taken from figures of Harrison (1978) and depict, in order, the altricial Brown Creeper (*Certhia familiaris*), a semiprecocial Least Tern (*Sterna albifrons*), and a precocial Ruddy Duck (*Oxyura jamaicensis*). The sketch of the neonate Mallee Fowl (*Leipoa ocellata*) at 50% yolk content was reproduced from photographs courtesy of C. and D. Vleck and R. S. Seymour; the sketch of the neonate Kiwi (*A. australis*) was reproduced from photographs courtesy of W. A. Calder. As relative yolk content increases, so does the caloric density and maturity of hatchling accompanied by a large decrease in the relative water content.

DISTRIBUTION OF SOLIDS AND CALORIES IN THE NEONATE

How are the initial solids, proteins, carbohydrates, lipids, and calories of the fresh egg redistributed by the time the hatchling emerges from its shell? This can be calculated from the studies of Ricklefs (1977), Pettitt et al. (1984), and Vleck et al. (1984) who determined the solids and caloric content in the fresh egg, the yolk-free hatch-

ling, and the yolk reserve for a total of 12 species. These data are shown in Table 6 and are arranged according to the initial mass of egg contents. Also shown are data for solids and calories lost during development, which for convenience have been labeled Metabolic Loss. All values were then converted to percentages of the initial solids and calories of the fresh egg. The averages of these relative values are shown in Figure 10 and provide a general overview of the fate of the initial solids and calories in species whose average yolk content was 39% (range 33–53%).

Of the initial solids, indicated by the column in Figure 10, 28% are lost; 1.6% represents the meconium and membranes which are left behind (Romanoff 1967) and are shown as a solid black bar at the top of the column. The remaining 26.4% constitute solids that are metabolized. Thus 72% of the initial solids are retained by the hatchling, including the yolk reserve. The latter varies greatly among these species, with no particular relationship with the initial yolk content of the egg.

Furthermore, it is of interest to look at the average distribution between the lipid and nonlipid (protein and carbohydrate) fractions. These were calculated for each species in Table 6 using equation (9) and averaged. Of the total solids lost by metabolism the lipid fraction was 88%, indicated by the white area, while the nonlipid fraction is shown by the shaded area. This mean value for the lipid fraction is similar to 85% estimated by Romanoff (1967) for the chick embryo. Thus approximately 88% of the initial nonlipids are retained by the hatchling plus yolk reserve. If one adds up all the lipids, they constitute 42% of the initial solids, which agrees well with the distribution of lipids and nonlipids at a relative yolk content of 39% as shown in Figure 7.

ENERGETIC REQUIREMENTS DURING DEVELOPMENT

Whereas about 28% of the initial solids is actually lost during development, 36% of the initial caloric content is lost because lipids constitute the major metabolic fuel during this period. This leaves 64% of the initial caloric content for the hatchling and its yolk reserve with its relatively large nonlipid fraction (Fig. 10). While our analysis (Table 6) is based on 14 precocial species, Vleck and Vleck (in press) reported the cost of development in 17 precocial and 7 altricial species and state that "all bird species expend about the same percentage of the energy stored in the egg

before they hatch." From their tables one calculates an average expenditure of 33% of the original energy content of the egg. A similar analysis by Ar et al. (in press) for 16 altricial, 7 semialtricial, 12 semiprecocial, and 14 precocial species showed that the average gross production efficiency (hatchling energy/egg energy) is $63.7\% \pm 7.8$ SD and "does not differ significantly among maturity types." The gross production efficiency of our analysis (Fig. 10) is identical, namely, $64\% \pm 6$ SD. The general agreement of these studies suggests that among birds in general the energy cost of development is similar, namely, ca. 36% of the initial energy content of the fresh egg.

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