TABLE 1.	Adjusted least s	quares means of	f components
of fresh (n =	= 89) and boiled	(n = 21) Starlin	g eggs.

	Adjusted	means (g)	Difference	Signifi-	
Component	Fresh Boiled		(g)	cancea	
Shell					
Dry	0.4657	0.4446	-0.0211	***	
Water	0.2931	0.1058	-0.1873	***	
Total	0.7588	0.5501	-0.2087	***	
Albumen					
Dry	0.5218	0.5501	+0.0283	**	
Water	4.6050	4.4803	-0.1247	***	
Total	5.1268	5.0303	-0.0965	***	
Yolk					
Nonlipid dry	0.1828	0.1862	+0.0034	NS	
Lipid	0.3771	0.3563	-0.0208	*	
Water	0.7035	0.7486	+0.0451	**	
Total	1.2633	1.2911	+0.0278	NS	
Whole egg ^b					
Nonlipid dry	1.1703	1.1810	+0.0107	NS	
Lipid	0.3771	0.3563	-0.0208	*	
Water	5.6015	5.3343	-0.2672	***	
Total	7.1489	6.8716	-0.2773	***	

^a Significance: NS, not significant; *P < 0.05; **P < 0.01; ***P < 0.001. ^b Sum of shell, albumen, and yolk components.

Storage in closed containers in a refrigerator for periods up to two weeks does not appear to affect gross composition. Loss of mass was about 0.1% per day in Starling eggs and this loss, presumably of water, was small compared to the differences in water content among a sample of eggs treated identically (CV about 2%). In addition, eggs stored for longer periods contained no less water than those processed soon after collecting. But significant differences in the composition of the yolk of these eggs, amounting to 6.6% of the average content of nonlipid dry matter and 5.0% of the average content of water, suggest effects related either to season or egg replacement.

The differences observed between fresh and boiled eggs were substantially different from those associated with time of season and preanalysis treatment, suggesting that the differences resulted from method of analysis.

Separating the shell, albumen, and yolk of both fresh and boiled eggs resulted in a loss of about 0.5% of the initial mass. Hard-boiling, which required 7-10 min for the 7-gram Starling egg, resulted in the additional loss of about 4% of the initial mass of the egg, primarily as water

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ESTIMATING THE INITIAL DENSITY OF BIRDS' EGGS

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Three basic physical characteristics of birds' eggs are their volume and initial mass and density at the time of laying. However, the initial values of mass and density change

TABLE 2. Adjusted least squares means of components of fresh eggs from first clutches (n = 69) and replacement clutches (n = 20).

	Adjusted	1 means (g)	Difference	Signifi-	
Component	First ^a	Replacementa	(g)	canceb	
Shell					
Dry	0.4708	0.4487	+0.0221	***	
Water	0.2890	0.3075	-0.0185	NS	
Total	0.7598	0.7562	+0.0036	NS	
Albumen					
Dry	0.5211	0.5251	-0.0040	NS	
Water	4.6191	4.5624	+0.0567	NS	
Total	5.1401	5.0875	+0.0526	NS	
Yolk					
Nonlipid dry	0.1801	0.1924	-0.0123	**	
Lipid	0.3798	0.3680	+0.0118	NS	
Water	0.6955	0.7314	-0.0359	*	
Total	1.2554	1.2917	-0.0363	NS	
Whole egg ^c					
Nonlipid dry	1.1719	1.1662	+0.0059	NS	
Lipid	0.3798	0.3680	+0.0118	NS	
Water	5.6036	5.6012	+0.0024	NS	
Total	7.1553	7.1354	+0.0199	NS	

^a First clutches, 22–28 April 1976; replacement clutches, 3–12 May 1976. ^b Significance: NS, not significant; *P < 0.05; **P < 0.01, ***P < 0.001. ^c Sum of shell, albumen, and yolk components.

from the albumen. Boiling does allow one to separate shell, yolk, and albumen more cleanly than with fresh eggs. Compared to fresh eggs, the shells of boiled eggs had 0.021 g less dry matter, and the albumen 0.28 g more, indicating that in separated fresh eggs about 4.5% of the albumen remained with the shell component. With respect to etherextractible material, boiling may either increase the volatilization of some lipid fractions upon drying or bind some of the lipids to proteins making them difficult to extract.

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with incubation, because of the large loss of water vapor, and have rarely been reported. A simple field method for determining initial egg mass at any stage of incubation was recently described by Grant et al. (1982). In this study we report an equation for predicting initial egg density based upon egg dimensions published by Schönwetter (1960-1981). Our predictions of initial egg density are compared with direct measurements in 44 species.

METHODS

To derive a predictive equation for initial egg density it was first necessary to establish a common value for the density of egg content. For this purpose we collected fresh eggs in the field (Alaska, Marshall Islands, Gulf of California) and at the Zoological Garden in Buffalo, New York,

TABLE 1. Basic measurements (Columns 1–6) of egg mass (M_{egg}), egg volume (V_{egg}), shell mass (M_{shell}), shell thickness (T), and shell volume (V_{shell}) in 23 species of birds. From these measurements are derived (Columns 7–9) the initial density of the egg's contents (d_{cont}), the initial density of the egg (d_{egg}), and the volume of the egg (V_{egg}), as explained in the text.

	EGG		SHELL			CONTENT	E	EGG	
	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)
Order	N	Megg	Vegg	M _{shell}	T	V _{shell}	d _{cont}	d _{egg}	Vegg
Species		g	cm ³	g	cm	cm ³	g · cm ⁻³	g∙cm ⁻³	cm ³
Tinamiformes									
Eudromia elegans	10	35.81	33.28	2.58	0.023	1.19	1.036	1.076	33.42
Pelecaniformes									
Pelecanus occidentalis	10	111.2	103.5	10.4	0.054	5.91	1.033	1.074	103.7
Phaethon rubricauda	2	67.74	62.92	5.41	0.036	2.84	1.037	1.077	63.30
Sula leucogaster	4	57.79	53.36	5.75	0.039	2.77	1.029	1.083	53.25
Anseriformes									
Cygnus buccinator	1	348.6	315.7	43.3	0.086	20.04	1.033	1.104	316.2
Anser fabalis	3	142.6	129.9	15.7	0.047	6.06	1.025	1.098	129.1
Aix sponsa	5	43.29	39.91	3.93	0.030	1.76	1.032	1.085	39.94
Falconiformes									
Buteo jamaicensis	2	74.78	69.73	6.04	0.039	3.28	1.034	1.072	69.95
Galliformes									
Pavo muticus	9	100.1	90.97	12.2	0.054	5.51	1.029	1.100	90.77
Chrysolophus pictus	10	32.12	29.91	2.77	0.026	1.25	1.024	1.074	29.72
Syrmaticus soemmerringii	10	31.49	29.36	2.38	0.024	1.14	1.032	1.073	29.38
Chrysolophus amherstiae	10	29.51	27.32	2.55	0.026	1.18	1.031	1.080	27.33
Charadriiformes									
Larus glaucescens	8	99.69	93.83	6.94	0.035	3.56	1.027	1.062	93.52
L. occidentalis	12	97.69	91.65	6.54	0.033	3.31	1.032	1.066	91.72
L. heermanni	11	53.37	50.16	3.52	0.027	1.82	1.031	1.064	50.17
L. canus	13	49.93	47.27	2.89	0.024	1.54	1.029	1.056	47.17
Rissa tridactyla	9	51.35	48.54	3.10	0.026	1.71	1.030	1.058	48.51
Anous stolidus	15	37.29	35.35	2.29	0.023	1.22	1.025	1.055	35.17
Lunda cirrhata	3	95.75	89.61	6.89	0.036	3.57	1.034	1.069	89.76
Uria aalge	10	113.7	103.4	14.6	0.066	7.33	1.032	1.100	103.5
Ptychoramphus aleuticus	6	29.08	27.50	1.91	0.023	1.04	1.027	1.057	27.39
Passeriformes									
Turdus migratorius	16	6.667	6.29	0.38	0.011	0.19	1.031	1.060	6.29
Agelaius phoeniceus	19	4.111	3.91	0.21	0.010	0.12	1.032	1.055	3.90
						x	1.031		·
						S.D.	0.003		

and weighed them both in air and in water for determination of egg volume by Archimedes' principle. Gas in the air cell was then replaced by water injected with a hypodermic syringe, and the eggs were reweighed to obtain initial egg mass (Grant et al. 1982). Finally, the eggs were emptied, their shells dried in a desiccator, and shell mass and thickness measured as previously described (Rahn et al. 1976). Volume of the shell was calculated from the product of shell thickness and surface area, the latter derived from the relationship

$$A = 4.835 M_{egg}^{0.662}$$
(1)

where A is the surface area (cm²) and $M_{\mbox{\tiny CBB}}$, the initial egg mass (g) (Paganelli et al. 1974).

RESULTS AND DISCUSSION

Density of egg contents. Basic measurements of eggs from 23 species appear in Columns 1–6 of Table 1. From these measurements we calculated for each species the initial



FIGURE 1. Initial egg densities for 44 species of birds predicted from the egg dimensions published by Schönwetter (1960–1981) plotted against initial egg densities directly measured in this study and those reported in the literature. The line of identity is shown.

density of the egg contents based on the following considerations. By definition, the initial density of egg content (d_{conl}) is M_{conl}/V_{cont} , where $M_{cont} = mass$ of the content and $V_{cont} = volume$ of the content. Since $M_{cont} = M_{egg} - M_{shell}$ and $V_{cont} = V_{egg} - V_{shell}$, this equation can be rewritten as $d_{cont} = (M_{egg} - M_{shell})/(V_{egg} - V_{shell})$, or using the data in Table 1, $d_{cont} = (Col. 2 - Col. 4)/(Col. 3 - Col. 6)$.

The initial density of the egg content so calculated is shown in Column 7. There is remarkably little variation among the 23 species, and the mean value is $1.031 \text{ g} \cdot \text{cm}^{-3}$ (SD = ±0.003), similar to $1.035 \text{ g} \cdot \text{cm}^{-3}$ cited by Romanoff and Romanoff (1949:408) for the chicken.

Egg volume. By definition, the total volume of an egg (V_{egg}) is $V_{shell} + V_{cont}$. These terms can be expanded since from equation (1) $V_{shell} = 4.835 \ M_{egg}^{0.662} \times T$, where T = shell thickness, and $V_{cont} = (M_{egg} - M_{shell})/1.031$, where 1.031 = the initial density of the egg's contents. Thus, the general equation for egg volume is:

$$V_{egg} = [4.835 M_{cgg}^{0.662} \times T] + [(M_{egg} - M_{shell})/1.031] (2)$$

Egg volumes calculated on the basis of equation (2) are shown for each species in Column 9 of Table 1 and may

be compared with those measured by immersion shown in Column 3. The mean percent difference for the 23 species is 0.05% (SD = ± 0.3). The largest individual difference is 0.6%.

Initial egg density. Equation (2) enables us to calculate egg volume if the initial egg mass, shell thickness, shell mass, and the density of the egg content are known. Since Schönwetter (1960–1981) has provided the first three of these dimensions for more than 5,000 species and subspecies of birds, it now becomes possible to predict the initial density of their eggs by dividing his values of M_{egg} by V_{egg} from equation (2).

In Figure 1 initial egg density predicted from Schönwetter's data is plotted against initial egg density directly determined for 23 species shown in Column 8 of Table 1 and for 21 additional species reported by others (Westerkov 1950, Reid 1965, Evans 1969, Brown 1973, Manning 1979, D. F. Hoyt, pers. comm.). The percent difference between measured and predicted densities for these 44 species ranged from $\pm 1.3\%$ to $\pm 1.2\%$, with a mean difference of 0.1% (SD = ± 0.7).

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