The Condor 88:84–90
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VARIATION IN THE COMPOSITION OF THE EGGS AND CHICKS OF AMERICAN COOTS[1]

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Abstract. I evaluated the composition of 97 fresh eggs and 43 one-day-old chicks of the American Coot (*Fulica americana*) to determine if the constituents of eggs or chicks show allometry. Heavier eggs contained proportionately less albumen but proportionately more yolk, and consequently had a higher energy density than lighter eggs. Albumen weight varied more among than within clutches, presumably due to variation in the qualities of coot territories during nesting. Within clutches, the lipid content of eggs declined with laying sequence, but albumen weights remained constant. Moreover, newly hatched chicks contained proportionately more lean dry material if they hatched from large eggs than if they hatched from small ones. These patterns of variation appear to increase the disparities in size of these asynchronously hatching young, and thus result in differential survival probabilities among siblings.

Key words: Allometry; body size; coots; egg weight; energetics; food supply; nutrient reserves; precocity.

INTRODUCTION

Intraspecific variation in egg size has been attributed to a heritable component (Van Noordwijk et al. 1981), to variation in proximate factors which, among other things, include the size (Otto 1979) and nutritional status (Schreiber and Lawrence 1976) of the female, to available food (Quinney 1983), to laying date (Birkhead and Nettleship 1983), to laying sequence in the clutch (see Slagsvold et al. [1984] for a compilation), or to some combination of these factors. Large eggs generally produce large chicks (e.g., Schifferli 1973) that, presumably because they contain more nutrients, show higher rates of survival, at least in the short term (e.g., Ankney 1980).

Alisauskas and Ankney (1985) found that, because the weights of fresh eggs declined as they were laid successively in a clutch by American Coots (*Fulica americana*), the costs of egg production were reduced. It was unknown, however, if the composition of eggs also varied and how such variation affected the chemical constitution of newly hatched chicks. Herein, I (1) show the chemical composition of the eggs and newly hatched chicks of the American Coot (hereafter referred to as coot), (2) analyze the allometric relationship between egg (and chick) composition and egg weight, (3) analyze the effect of interfemale variation, as well as the influence of position in the clutch, on egg composition, and (4) relate my findings to current ideas about the adaptive nature of variation in egg weight among birds.

METHODS

I collected the following from the Delta Marsh, at the southern extremity of Lake Manitoba, Manitoba, in May and June 1981: (1) 97 fresh (i.e., <24 hr old) coot eggs for the analysis of egg composition, and (2) 43 eggs of unknown age which, upon hatching, produced chicks that were subsequently used for the determination of neonatal composition.

Fresh eggs were gathered by removing them from a sample of 17 nests visited daily as part of an experiment dealing with the determinacy of clutch size in coots. After being weighed to the nearest 0.1 g and measured (length and breadth) to the nearest 0.1 mm with calipers, each egg was separated into shell, yolk, and albumen (the albumen weight includes the weight of the shell membrane; see Alisauskas and Ankney 1985:134). Each of these three components was weighed to the nearest 0.01 g, dried to constant weight at 80 to 90°C, and reweighed. Lipids were removed from dried egg yolks using petroleum ether in a Goldfisch apparatus; the lean dry residue is referred to as yolk *LDW*. Romanoff and Romanoff (1949: 315) showed that the *LDW* of chicken egg yolks is 89% protein, so I used the energy equivalent of protein for determining the energy content of yolk *LDW*.

I measured the length and breadth of eggs of unknown age with calipers to the nearest 0.1 mm. These eggs were then placed in a commercial incubator at 37.5°C and 88% relative humidity until they pipped. After each chick hatched, it was left until its plumage had dried (<24 hr), and was then killed by compression of the thorax, weighed (to the nearest 0.01 g), and frozen in a labelled plastic bag. I later

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[1] Received 19 February 1985. Final acceptance 7 September 1985.

TABLE 1. Dimensions (mm) and composition (g) of coot eggs ($n = 97$). Values in the table are means ± one standard deviation ($\bar{x} \pm$ SD).

Variable	$\bar{x} \pm 1$ SD	CV (%)[a]
Length	48.15 ± 1.62	3.4
Breadth	33.27 ± 0.97	2.9
Egg weight, fresh	28.88 ± 1.88	6.5
Egg weight, dry	8.88 ± 0.71	8.0
Shell, weight	2.52 ± 0.20	7.9
Shell, thickness	0.175 ± 0.019	10.9
Albumen, wet	17.46 ± 1.25	7.2
Albumen, dry	2.11 ± 0.18	8.5
Albumen, water	15.36 ± 1.13	7.4
Yolk, wet	8.61 ± 1.11	12.9
Yolk, dry	4.24 ± 0.48	11.3
Yolk, lipid	2.56 ± 0.30	11.7
Yolk, *LDW*[b]	1.68 ± 0.26	15.5
Yolk, water	4.37 ± 0.83	19.0

[a] Coefficient of variation.
[b] Lean dry weight.

TABLE 2. Summary of log-log regression analyses of egg components (Y) on fresh egg weight (X), ($n = 97$).

Component	b (95% CI)[a]	r^2
Shell weight	0.832 (0.646–1.018)	0.717
Albumen, total	0.819 (0.662–0.976)	0.531
Albumen, *LDW*[b]	0.881 (0.684–1.078)	0.458
Albumen, water	0.811 (0.644–0.978)	0.496
Yolk, total	1.425 (1.160–1.690)	0.546
Yolk, dry	1.282 (1.049–1.515)	0.557
Yolk, lipid	1.305 (1.060–1.550)	0.541
Yolk, *LDW*[b]	1.244 (0.842–1.646)	0.285
Yolk, water	1.563 (1.097–2.029)	0.319

[a] Slope of regression and 95% confidence interval.
[b] Lean dry weight.

thawed these specimens and measured with calipers their wing, culmen, and tarsal lengths (to the nearest 0.1 mm). I then weighed, dried to constant weight at 85 to 95°C, and reweighed the chick, and placed it in a Soxhlet apparatus for 24 hr to remove neutral lipids, using petroleum ether as a solvent.

Six of the chicks were dissected before determination of their lipid contents. I excised and weighed (to the nearest 0.001 g) the heart, liver, gizzard, esophagus, intestine, and half of each of the breast and leg muscles as defined by Alisauskas and Ankney (1985).

Only those eggs and chicks for which I had complete information were used for statistical analyses. All measures are presented as mm, and all weights as g. All logarithmic transformation of data is to the base 10.

RESULTS

VARIATION IN EGGS

Fresh egg weight (W) can be estimated from egg measurements of length (L), and breadth (B) by the equation

$$W = 3.189 + 0.000482(LB^2) \qquad (1)$$

($n = 97$, $r^2 = 0.93$, $P < 0.001$). The predictability of dry egg weight (D) using these measures is less accurate:

$$D = 0.678 + 0.000154(LB^2) \qquad (2)$$

($n = 97$, $r^2 = 0.66$, $P < 0.001$).

The coefficient of variation (CV) for each measured variable of the fresh eggs shows that characteristics of the yolk were more variable than those of albumen or shell (Table 1).

VARIATION IN EGG COMPOSITION WITH RESPECT TO SIZE

The weights of all constituents of the egg increased significantly with egg weight (Table 2), but shell thickness did not. To determine if egg composition varied allometrically with total egg weight, I regressed the logarithm of each component's weight on the logarithm of fresh egg weight. This procedure yields a value for the slope (b) according to the exponential relationship, $Y = aX^b$. Values of b not different from unity (1.0 within 95% confidence limits of b) indicate that components show isometry as total egg weight varies; + or − values of b for each component show proportional increases or decreases, respectively, relative to increasing egg weight. The results (Table 2) show that larger eggs contained proportionately more yolk ($b > 1.0$) but proportionately less albumen ($b < 1.0$) than smaller eggs.

Absolute energy content of fresh eggs increased with weight (Table 3), but the precision of the relationship was not high ($r^2 = 0.66$). Dry egg weight, however, was highly correlated with estimates of kcal/egg ($r^2 = 0.90$). A log-log regression of kcal/egg on fresh egg weight showed that heavy coot eggs had a higher energy density than light ones (Table 3).

VARIATION IN EGG COMPOSITION AMONG AND WITHIN CLUTCHES

I used analysis of covariance (ANCOVA, Engelman 1983) to explore how egg composition varied among females, and with respect to laying sequence (Table 4). For this analysis, I used only those clutches for which I had complete information from at least 5 eggs: 4 clutches with 5 eggs, 2 with 6, 1 with 7, and 2 with 8 eggs. There were no interactions between the main effects of female and position in the clutch (Table 4), i.e., the 9 slopes compared in each of the 12 ANCOVAs were parallel indicating that these two effects were additive and independent. Generally, variation in egg composition was due more to differences among clutches (r^2 range: 0.24 to 0.54) than to differences in position within clutches (r^2 range: 0.01 to 0.29). With respect to position effects, all of the regression coefficients were negative suggesting that all constituents of the egg declined

TABLE 3. Estimation and allometry of energy content (kcal/egg)[a] based on fresh and dry egg weights (g), ($n = 97$).

Variables				
X	Y	Y-intercept	b (95% CI)[b]	r^2
Fresh egg weight	kcal/egg	−8.099	1.862 (1.644–2.080)	0.663
Dry egg weight	kcal/egg	−5.207	5.734 (5.355–6.113)	0.904
$\log_{10}$(fresh egg wt)	$\log_{10}$(kcal/egg)	−0.065	1.180 (1.010–1.350)	0.668

[a] Based on energy equivalents of 9.5 $\text{kcal}\cdot\text{g}^{-1}$ of fat and 5.65 $\text{kcal}\cdot\text{g}^{-1}$ of protein (Ricklefs 1977).
[b] Estimated value of slope with 95% confidence interval.

in successive eggs of each clutch. Shell thickness varied little with respect to an egg's position in the clutch, but shells weighed less in lighter eggs (i.e., eggs laid later in the clutch) only because less shell is required to encase the egg's contents. About 45% of the variation in albumen weight was due to differences among females, but the amount of albumen in an egg did not vary with respect to the egg's position in the clutch. A smaller proportion of the variation (about 30%) in yolk composition was due to differences among females. Variation in the protein content of the yolk (as indexed by its *LDW*) was generally similar in magnitude to the variation shown by albumen, both depending on variation among females (r^2 range 0.35 to 0.41) but neither depending on the egg's position in the clutch (r^2 range: 0.01 to 0.03). In contrast, lipid showed less variation from female to female ($r^2 = 0.24$), and unlike protein, it declined significantly in successive eggs of the clutch ($r^2 = 0.23$). Thus female effects on the protein content of the eggs were similar whether the protein was incorporated into albumen or yolk; female effects on the fat content of the egg were less important.

COMPOSITION OF NEWLY HATCHED CHICKS

Chicks showed twice as much variation in fat content as eggs (Table 5). Variability in the water and lean dry weight (*LDW*) was similar between eggs and chicks. On average, embryos metabolized 58% of the fat deposited in eggs, but water loss averaged less and *LDW* changed little.

Since the eggs, from which chicks were subsequently analyzed, were collected at different stages of incubation, I estimated their fresh egg weights from their dimensions and equation (1). The dry weights of chicks increased proportionately faster than the weights of the eggs from which they hatched (Table 6). Slopes for water and lipid were not different from 1.0, although the relationship between lipid and egg size was weak ($r^2 = 0.30$). The slope for *LDW* was >1.0, indicating a proportionately greater increase in chick dry weights relative to increasing egg weights.

The water index ($\text{water}\cdot LDW^{-1}$; *WI*) of a tissue is inversely related to its "functional maturity" (sensu Ricklefs et al. 1980), is an index of the amount of down that a chick possesses, and is therefore a measure of the chick's insulation. I found that the *WI* of coot chicks varied with the fresh weight of the egg from which they hatched, and with the size of the chick (as indexed by chick *LDW*). Water index was inversely related to fresh egg weight as follows:

$$WI = 5.73 - 0.0448(W) \qquad (3)$$

($n = 43$, $r^2 = 0.20$, $P < 0.01$), and more precisely to chick *LDW* as:

TABLE 4. ANCOVA of egg components among clutches corrected for the effects of egg sequence within clutches.

	Equality of slopes		Among clutches			With position		
Variable	$F_{(8,37)}$	P^{a}	$F_{(8,45)}$	P^{a}	% Var[b]	$F_{(1,45)}$	P^{a}	% Var[b]
Fresh egg weight	1.59	NS	8.08	***	44	25.98	***	18
Dried egg weight	0.59	NS	4.73	***	32	20.55	***	18
Shell weight	1.58	NS	7.88	***	47	38.43	***	29
Shell thickness	1.49	NS	6.99	***	54	7.23	*	7
Albumen, wet	0.69	NS	6.07	***	48	1.25	NS	1
Albumen, *LDW*[c]	1.02	NS	4.62	***	41	0.90	NS	1
Albumen, water	0.75	NS	5.80	***	48	1.12	NS	1
Yolk, wet	0.87	NS	3.63	**	30	18.42	***	19
Yolk, dry	0.66	NS	4.66	***	32	19.26	***	17
Yolk, lipid	0.67	NS	4.00	**	24	31.83	***	23
Yolk, *LDW*[c]	0.67	NS	3.30	**	35	2.33	NS	3
Yolk, water	0.72	NS	2.29	*	26	8.67	**	12

[a] Probability that F-value is significant; * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, NS indicates that $P > 0.05$.
[b] Percentage of variance explained; for "clutches," among-clutch sum of squares (SS)/total SS; for "position," within-clutch SS/total SS; these proportions of variance are additive.
[c] Lean dry weight.

TABLE 5. Comparison of the variation and the change in composition from the egg stage (excluding shell, n = 97) to the chick stage (n = 43) in coots.

Variable	Eggs	Chicks	% Change
Water	19.73[a]	15.32	−22
	6.7%[b]	10.8%	
	(F = 1.61, $P > 0.05$)[c]		
Fat	2.56	1.07	−58
	11.7%	23.6%	
	(F = 2.02, $P < 0.05$)		
LDW[d]	3.79	3.53	−7
	9.4%	12.8%	
	(F = 1.36, $P > 0.10$)		
Water·LDW^{-1}	5.2	4.3	−17
Fat·LDW^{-1}	0.68	0.30	−56

[a] Mean.
[b] Coefficient of variation.
[c] F-value for test of equality of C.V.'s for egg and chick components.
[d] Lean dry weight.

$$WI = 5.48 - 0.320(LDW) \qquad (4)$$

(n = 43, $r^2 = 0.36$, $P < 0.001$). Thus, larger chicks, originating from heavier eggs, hatched with tissues that were also relatively more mature. The fat index (fat·LDW^{-1}, as defined by Ricklefs 1977) did not vary with fresh egg weight (n = 43, $r^2 = 0.01$, $P > 0.05$) or with chick *LDW* (n = 43, $r^2 = 0.03$, $P > 0.05$), indicating that the proportion of fat stored in a newly hatched chick was independent of its weight.

A comparison of the growth increments required for individual muscles and organs of chicks to achieve adult size (Table 7) showed that structures associated with flight were less developed than those used for walking and swimming (tarsus and leg muscle). The heart and digestive organs would have required the least postnatal development to attain adult size.

DISCUSSION

The values for characteristics of freshly-laid coot eggs are remarkably similar to those given by Carey et al. (1980) for eggs in their "semi-precocial" category; e.g., solids as a % of egg contents—24.3 vs. 23.5, lipids as a % of egg contents—9.7 vs. 9.5, energy expressed as kcal·egg^{-1} (wet weight)—1.58 vs. 1.63, and lipids as a % of dry egg weight—40.3 vs. 40.3, for coots and "semi-precocial" birds respectively.

TABLE 6. Log-log regressions of constituents of newly hatched coot chicks (Y) on egg size (X), (n = 43).

Constituent	Y-intercept	b (95% CI)[a]	r^2
Body weight	−0.484	1.197 (0.948–1.446)	0.696
Dry body weight	−1.530	1.471 (1.156–1.786)	0.684
Water	−0.478	1.117 (0.856–1.378)	0.645
Fat	−2.537	1.717 (0.899–2.535)	0.304
LDW[b]	−1.551	1.409 (1.129–1.689)	0.716

[a] Slope of regression and 95% confidence interval.
[b] Chick lean dry weight.

TABLE 7. Dimensions and organ weights of newly hatched coots and increments of growth required to attain adult size.

Variable	Chick	Adult[a]	Growth increment[b]
Lengths (mm)			
Wing	15.0	189.0	12.6
Tarsus	17.1	54.2	3.2
Culmen	14.7	48.0	3.2
Weights (g)			
Body	19.9	534.5	26.9
Heart	0.126	4.6	36.5
Liver	0.577	16.1	27.9
Gizzard	1.009	35.7	35.4
Esophagus	0.295	5.7	19.3
Intestine	0.684	26.0	38.0
Breast muscle	0.195	58.0	297.4
Leg muscle	1.143	79.0	69.1

[a] Values are averages for 108 male and 93 female adults used in Alisauskas and Ankney (1985).
[b] (Adult value)·(neonate value)$^{-1}$.

Ricklefs (1977) compared lipid and water indices of the eggs and chicks of several species that differed in precocity. The average *WI* of coot eggs (5.2) is in the range of precocial (3.9 to 5.5) vs. non-precocial species (5.4 to 7.6), but the *WI* of newly hatched coots (4.3) is intermediate between values for precocial (3.3 to 4.7) and non-precocial species (4.1 to 7.3). The lipid indices of coot eggs (0.68) and chicks (0.30), however, are more similar to non-precocial eggs (0.54 to 0.76) and chicks (0.29 to 0.34) than to precocial eggs (0.70 to 0.85) and chicks (0.57 to 0.75). Thus, coot chicks are non-precocial in that they possess relatively little lipid when hatching, resulting in the need to be fed by their parents for up to 15 days thereafter (see Ryan and Dinsmore 1979). However, the young are precocial in that 5-day-olds regularly follow their parents on foraging excursions; some do so as 2-day-olds (Gullion 1954). The high mobility and low *WI* of coots indicate that they have higher "functional maturity" and greater insulation than the non-precocial species described by Ricklefs (1977).

Coot embryos on average metabolized about 60% of the egg's lipid during 23 days of incubation (Table 5). At hatching, however, the proportionate lipid content of the chicks did not vary with respect to weights of the eggs from which they hatched, although heavier chicks possessed absolutely more lipid than did lighter chicks (Table 6). Egg weight and egg-lipid weight were more highly correlated ($r = 0.74$) than were chick weight and chick-lipid weight ($r = 0.23$), indicating that coot embryos vary in the rate at which they metabolize lipid. A heritable component of embryonic growth rates (but see Ricklefs and Smeraski 1983) or differences in the incubation constancy among pairs of attending parents may be responsible for variation observed in the relative amounts of lipid reserves at hatching.

Alisauskas and Ankney (1985) found that female coots use stored somatic fat to produce egg lipids; they argued that the likelihood that a female would nest depended on the size of these fat reserves. If females begin to lay eggs only when their fat reserves reach a specific threshold level, then differences among females should explain less variation in the lipid content of eggs than if they did not rely on nutrient reserves. Conversely, protein requirements of egg synthesis were met primarily through exogenous sources (Alisauskas and Ankney 1985), and because the "quality" of a coot territory must in part be related to the availability of protein, "among-female" effects can be more broadly interpreted as "among-territory" effects. My results are consistent with that reasoning, as differences among females explained more of the variation in albumen (41 to 48%) and yolk protein (35%) than of the variation in the amount of yolk lipids (24 to 26%, Table 4). These same arguments apply to "among-female," i.e., "among-territory," effects on the deposition of coot eggshells: eggshell calcium comes directly from the diet without long-term storage (Alisauskas and Ankney 1985), and consequently the amount of variation in shell weight and thickness due to differences among females was correspondingly high (47 and 54%, respectively).

ANCOVA revealed that the order in which eggs were laid did not affect the amount of albumen or yolk protein (Table 4) but was responsible for variations in their lipid and fresh weights, which declined in successive eggs of a clutch. One explanation for the constancy of albumen weight within clutches is related to the physico-chemical properties of albumen. Some albumen proteins inhibit microbial activity (Freeman and Vince 1974:168) so that the yolk is protected. The central location of the yolk contributes to its defense (Board and Hornsey 1978:58), but if the distance between the yolk surface and the shell is small, the aseptic qualities of the amniotic fluid may be compromised. The lytic properties of albumen are presumably very important as, in domestic fowl, they persist well into incubation, that is, until the dry matter of the albumen begins to be absorbed by the embryo (Romanoff 1967: 180).

The inverse relationship between egg weight and laying sequence leads to a prediction concerning the survival of young coots. Coots often start incubation before the clutch is completed (Gullion 1954 and references therein), and thus siblings hatch asynchronously. Lack (1968) proposed that this asynchrony functioned to create age and therefore size disparities among siblings in those species where parents must feed the brood. The major foods of young coots are aquatic invertebrates (Jones 1940, Sooter 1941, Fitzner et al. 1980), which are unpredictable in occurrence and which the parents must feed to the young whose demands peak about 10 days after hatch (Ryan and Dinsmore 1979). Fredrickson (1969) found that 25 to 30% of mortality in large broods occurred within a week of hatch. It seems plausible, especially in years when food is scarce, that a feeding hierarchy is established in which the largest and oldest brood members would survive best. I propose that in coots there are additional ways in which disparities in size, and therefore survival, are enhanced. First, because egg and chick weights are correlated (Table 6), the production of successively lighter eggs within a clutch would increase existing age-related differences in offspring size. Second, the slope relating the logarithms of chick *LDW* to egg weight was >1.0 (Table 6), indicating that these size-related differences are disproportionate with respect to the eggs from which the chicks orginated. In addition to competitive advantages, larger size confers the advantage of a smaller surface : volume ratio, thereby reducing heat loss on nights when temperatures drop below the zone of thermoneutrality. Larger chicks with better thermoregulatory abilities would not rely on energy reserves as greatly as smaller chicks. Third, although the heaviest coot eggs contained proportionately the most fat, the proportionate fat reserves of the chick did not vary with egg or chick weight. However, as Ankney (1980) has shown for Lesser Snow Goose (*Chen caerulescens*) goslings, absolutely larger, rather than proportionately larger, fat reserves can extend survival of starving young. Finally, coot chicks from heavier eggs have a lower *WI*, and therefore higher "functional maturity" (sensu Ricklefs et al. 1980) than chicks from smaller eggs. Another interpretation, more conservative than the one given by Ricklefs et al. (1980), of the *WI* for the whole body is that it should be inversely related to the amount of plumage present on the chick. Thus, in addition to being larger, chicks from larger eggs are also better insulated than chicks from smaller eggs. In summary, coot siblings that emerged from the first eggs laid in a clutch were larger, more developed, and perhaps better able to follow the parents or to beg for food than chicks that hatched from eggs laid later. These differences would remain even in the absence of asynchronous hatching. These disparities may enable nesting coots to reduce brood size more easily than would otherwise be possible.

The patterns of variation in the composition of eggs found here differ from those reported for the Lesser Snow Goose (Ankney 1980), Japanese Quail, *Coturnix coturnix* (Ricklefs et al. 1978), and European Coot, *Fulica atra* (Horsfall 1984) in which all of the eggs' components varied isometrically with fresh egg weight. On the other hand, the eggs of Laughing Gulls, *Larus atricilla* (Ricklefs et al. 1978) and some altricial species (European Starling, *Sturnus vulgaris* [Ricklefs 1984], Brown-headed Cowbird, *Molothrus ater* [Ankney and Johnson 1985]) showed proportionate declines in yolk weight and proportionate increases in albumen weight with increasing fresh egg weight. Of the intraspecific comparisons available, only those involving American Coots (this study) and Mute Swans, *Cygnus olor* (Birkhead 1984) showed proportionate increases and declines in the weights of yolk and albumen, respectively, with increasing egg weight. From this comparison, no consistent pattern of variation in the relative allocation of egg components over a continuum of total egg weight is apparent, at least from the standpoints of ecological relevance or taxonomic grouping. As most of the above studies involved only one breeding season, facultative adjustments in the allocation of nutrients by individual females could obviously not be demonstrated. However, such adjustments in response to annual variation in available food are predictable in species in which the parents feed the young. Studies spanning several seasons, particularly in breeding habitats that vary considerably in quality (see Pospahala et al. 1974), are needed to more fully evaluate the importance of intraspecific variation in egg composition.

ACKNOWLEDGMENTS

I thank the Canadian Wildlife Service for permission to collect eggs; P. Kehoe, D. MacLaughlin, M. Madore, R. Titman, and A. Young for helping to collect them; and K. Bedford for assistance in the laboratory. D. Ankney, D. Scott, and R. C. Bailey commented on early drafts of the manuscript; and I thank J. J. Dinsmore and an anonymous reviewer for their additional comments. The study was funded by the North American Wildlife Foundation through grants to the Delta Waterfowl and Wetlands Research Station, and by the Natural Sciences and Engineering Research Council (Canada) through operating grants to D. Ankney.

LITERATURE CITED

Alisauskas, R. T., and C. D. Ankney. 1985. Nutrient reserves and the energetics of reproduction in American Coots. Auk 102:133–144.

Ankney, C. D. 1980. Egg weight, survival, and growth of Lesser Snow Goose goslings. J. Wildl. Manage. 44: 174–182.

Ankney, C. D., and S. L. Johnson. 1985. Variation in weight and composition of Brown-headed Cowbird eggs. Condor 87:296–299.

Birkhead, M. 1984. Variation in the weight and composition of Mute Swan (*Cygnus olor*) eggs. Condor 86:489–490.

Birkhead, T. R., and D. N. Nettleship. 1983. The adaptive significance of egg size and laying date in Thick-billed Murres *Uria lomvia*. Ecology 63:300–306.

Board, R. G., and D. J. Hornsey. 1978. Plasma and egg white proteins, p. 37–74. *In* M. Florkin and B. T. Scheer [eds.], Chemical zoology, Vol. X. Aves. Academic Press, New York.

Carey, C., H. Rahn, and P. Parisi. 1980. Calories, water, lipid and yolk in avian eggs. Condor 82:335–343.

Engelman, L. 1983. One-way analysis of variance and covariance, p. 347–358. *In* W. J. Dixon [ed.], BMDP statistical software. Univ. of California Press, Berkeley.

Fitzner, R. E., E. T. Shapiro, and R. G. Schrekhise. 1980. American Coot nesting and feeding habits in southeastern Washington. Northwest Sci. 54:244–252.

Fredrickson, L. H. 1969. An experimental study of clutch size of the American Coot. Auk 86:541–550.

Freeman, B. M., and M. A. Vince. 1974. Development of the avian embryo. Chapman and Hall, London.

Gullion, G. W. 1954. The reproductive cycle of American Coots in California. Auk 71:366–412.

Horsfall, J. 1984. Food supply and egg mass variation in the European Coot. Ecology 65:89–95.

Jones, J. C. 1940. Food habits of the American Coot with notes on distribution. U.S. Dep. Inter. Wildl. Res. Bull. 2.

Lack, D. 1968. Ecological adaptations for breeding in birds. Metheun, London.

Otto, C. 1979. Environmental factors affecting egg weight within and between colonies of Fieldfare *Turdus pilaris*. Ornis Scand. 10:111–116.

Pospahala, R. S., D. R. Anderson, and C. J. Henny. 1974. Population ecology of the Mallard. II. Breeding habitat conditions, size of breeding populations, and production indices. U.S. Fish Wildl. Serv. Resour. Publ. No. 115.

Quinney, T. E. 1983. The relation between food abundance and reproductive performance in Tree Swallows. Ph.D.diss., Univ. Western Ontario, London, Ontario, Canada.

Ricklefs, R. E. 1977. Composition of eggs of several bird species. Auk 94:350–356.

Ricklefs, R. E. 1984. Variation in the size and composition of eggs of the European Starling. Condor 86: 1–6.

Ricklefs, R. E., D. C. Hahn, and W. A. Montevecchi. 1978. The relationship between egg size and chick size in the Laughing Gull and Japanese Quail. Auk 95:135–144.

Ricklefs, R. E., S. White, and J. Cullen. 1980. Postnatal development of Leach's Storm Petrel. Auk 97: 768–781.

Ricklefs, R. E., and C. A. Smeraski. 1983. Variation in incubation period within a population of the European Starling. Auk 100:926–931.

Romanoff, A. L. 1967. Biochemistry of the avian embryo. Wiley, New York.

Romanoff, A. L., and A. J. Romanoff. 1949. The avian egg. J. Wiley and Sons, New York.

Ryan, M. R., and J. J. Dinsmore. 1979. A quantitative study of the behavior of breeding American Coots. Auk 96:704–713.

SCHIFFERLI, L. 1973. The effect of egg weight on the subsequent growth of nestling Great Tits *Parus major.* Ibis 115:549–558.

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

SLAGSVOLD, T., J. SANDVIK, G. ROFSTAD, O. LORENTSEN, AND M. HUSBY. 1984. On the adaptive value of intraclutch egg-size variation in birds. Auk 101:685–697.

SOOTER, C. A. 1941. Ecology and management of the American Coot, *Fulica americana americana* Gmelin. Ph.D.diss., Iowa State Univ., Ames.

VAN NOORDWIJK, A. J., J. H. VAN BALEN, AND W. SCHARLOO. 1981. Genetic and environmental variation in clutch size of the Great Tit, *Parus major.* Neth. J. Zool. 31:342–372.

Attendees of the June 1985 Joint Meeting of the Cooper and Wilson Ornithological Societies, Boulder, Colorado.