# EGG COMPOSITION OF AMERICAN COOTS IN RELATION TO HABITAT, YEAR, LAYING DATE, CLUTCH SIZE, AND SUPPLEMENTAL FEEDING

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ABSTRACT.—Egg composition is generally assumed to influence the viability of hatchlings. We measured composition of 322 American Coot (*Fulica americana*) eggs to determine what factors influenced their variability. Eggs were obtained from 12 sample groups, which varied with respect to location (Delta Marsh or Minnedosa, Manitoba), year (3 yr at each location), and food supply (supplemental food was provided during 1 yr at Delta Marsh and 3 yr at Minnedosa). Egg size did not differ among sample groups, but measures of egg composition varied in both absolute and relative proportions. Egg composition differed between study sites, but only for shell and lean yolk masses. Year effects were pronounced. All variables except shell mass exhibited significant annual variation at one or both locations. Effects of supplemental feeding were generally insignificant, except in one year. In all feeding experiments, however, birds that received food supplements containing corn (high carbohydrate) produced eggs with greater absolute and proportional lipid content and greater energy density. Similar comparisons of birds receiving high-protein food supplements did not reveal any consistent trends in egg protein content. Among females, egg quality increased with clutch size and declined with laying date. Some of the among-group differences in egg composition appeared to be correlated responses to among-group variation in clutch size or laying date. There was no evidence of interwetland variation in egg composition. Although these results illustrate some potential plasticity in egg characteristics, we conclude that egg composition is a relatively inflexible component of the life-history strategy of American Coots. *Received 8 January 1990, accepted 11 December 1990.*

CHICKS hatching from large eggs obtain several potential benefits over small-egg hatchlings, including larger hatchling size, mass, or both (Alisauskas 1986, Hill 1988), faster growth (Schifferli 1973, Rhymer 1983; but see Ricklefs 1984a), enhanced thermoregulation (Rhymer 1988), greater fasting endurance (Krapu 1979, Ankney 1980), and greater nestling survival (Parsons 1970, Lundberg and Väisänen 1979, Quinn and Morris 1986; but see Arcese and Smith 1988). These benefits may be attributed to the greater quantities or proportions of nutrients (fat and protein) present in large versus small eggs (Ankney 1980, Alisauskas 1986), because such benefits would not likely exist if large eggs simply contained more water than did small eggs. Egg size has been a good predictor of nutrient content in most studies (e.g. Ankney 1980, Ankney and Johnson 1985, Alisauskas 1986, Rohwer 1986, Muma and Ankney 1987). For some birds, however, variation in egg size has been primarily due to water content, and egg size has therefore been a rather poor predictor of nutrient content (Ricklefs 1984b, Arnold 1989).

Reproductive rates and population sizes of birds are generally assumed to be food-limited (Lack 1954, 1966; Fretwell 1972; Martin 1987; but see Arnold et al. 1987, George 1987). If food supplies are limiting, but vary geographically or temporally in the extent to which they are limiting, then birds might adjust their reproductive tactics in response to variations in food supply. There is abundant evidence demonstrating that timing of breeding, clutch size, and nestling growth rates may be affected by food availability (reviewed in Martin 1987, Boutin 1990). Egg size may also vary with food supply (e.g. Reid 1987, Hill 1988, Salzer and Larkin 1990), but in most supplemental feeding experiments egg size has been unaffected by food

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availability (Högstedt 1981; Poole 1985; Hochachka and Boag 1987; Arcese and Smith 1988; Korpimäki 1989; Arnold 1990, 1991, unpubl. data; N. E. Langston and S. Rohwer pers. comm.). The influence of food availability on egg composition has been largely ignored, with the exception of domestic birds (but see Hochachka 1988). Among domestic birds, however, diet selection is dictated by human caretakers, and egg composition may be "optimized" with respect to human economics and palatability, rather than to embryo viability. Thus, although feeding experiments with captive birds may illustrate plasticity of egg composition (e.g. Fisher 1969, Begin and Insko 1972, Butts and Cunningham 1972), they shed little light on the adaptive basis for such modifications.

We are unaware of any studies that have examined the heritability of egg composition among wild birds, but within-clutch repeatabilities for egg composition are often as high as for egg size (e.g. Ricklefs 1984b, Alisauskas 1986, Rohwer 1986, Hepp et al. 1987, Arnold 1989), and egg size is highly heritable (reviewed in Lessells et al. 1989). Moreover, egg composition can be highly heritable in domestic chickens (*Gallus gallus*) (e.g. $h^2 = 0.18$ to 0.61; Hill et al. 1966, Washburn 1979). These observations suggest that egg composition might also be highly heritable among wild birds, and therefore relatively insensitive to proximate sources of variation. However, if birds alter the nutritional content of their eggs, and if this can occur without affecting egg size, then studies that rely solely on egg-size information are clearly inappropriate for testing allocational trade-offs among breeding birds.

We assessed several potential sources of variation in egg composition of wild-nesting American Coots (*Fulica americana*, hereafter referred to as coots). We examined habitat variation by comparing eggs between two study areas that differed markedly in wetland productivity, and by comparing eggs among different wetland basins on one of the study areas. Temporal variation was evaluated annually over several years that ranged from extremely dry to fairly wet, and seasonally in relation to among-individual variation in nesting chronology. We also assessed among-individual variation in egg composition in relation to clutch size. Finally, we examined the proximate role of food availability by providing random subsamples of coots with high-quality supplemental food resources.

## STUDY AREAS AND METHODS

We studied coots at two different areas in southwestern Manitoba. The first area, Delta Marsh (50°11'N, 98°19'W), is a large (24,000 ha) palustrine persistent emergent wetland located on the south shore of Lake Manitoba (wetland classification follows Cowardin et al. 1979). The Delta Marsh study area included a series of adjacent bays known locally as Riley Bay, Clair Lake, First Lead, Second Lead, and Third Lead. These bays are permanently flooded and are dominated by cattail (*Typha* spp.), hardstem bullrush (*Scirpus acutus*), and submerged aquatics (*Potamogeton* spp., *Myriophyllum* spp., and *Ceratophyllum* spp.; Anderson and Jones 1976). The second area, Minnedosa (50°16'N, 99°50'W), is located approximately 10 km SE of the town of Minnedosa, and approximately 110 km W of Delta Marsh. The Minnedosa study area comprised numerous small (0.1–3.0 ha) palustrine persistent emergent wetlands that range from semipermanently flooded (water persists in most years) to intermittently exposed (water persists in all but extreme drought years). Wetlands at Minnedosa were dominated by cattail or, rarely, hardstem bullrush.

Other than size, the primary difference between Delta Marsh and Minnedosa wetlands was in water-level fluctuations (both annual and seasonal). Wetlands with a high degree of water-level variation are generally more productive, and hence more attractive to breeding water birds (Weller and Fredrickson 1974, Kantrud and Stewart 1977). At Minnedosa, water levels vary widely in response to annual trends in precipitation (Stoudt 1982), whereas water levels at Delta Marsh are maintained relatively constant by Lake Manitoba, which is regulated by a hydroelectric dam. At Delta Marsh we collected egg composition data during 1981, 1988, and 1989. At Minnedosa we collected egg composition data during 1987 (fairly wet), 1988 (fairly dry), and 1989 (extremely dry) (Arnold 1990).

Coots at Minnedosa initiated nesting approximately 2 weeks earlier than Delta Marsh coots, and laid approximately 2 more eggs per clutch, on average (Alisauskas and Ankney 1985, Arnold 1990, Arnold and Alisauskas unpubl. data). During wet years, Minnedosa also supported substantially higher densities of coots and other wetland birds (except piscivores), which suggests that Minnedosa wetlands were indeed more productive than Delta Marsh (Arnold pers. obs.).

Supplemental feeding experiments were conducted during 1987–1989 at Minnedosa, and during 1989 at Delta Marsh. In 1987, steam-rolled corn and trout chow were provided independently in a 2 × 2 factorial design (±corn, ±trout chow). Corn contains approximately 80% nitrogen-free extract (NFE), and is an excellent diet for lipogenesis (Alisauskas et al. 1988). Trout chow (Martins 84G, Martin Feed Mills, Elmira, Ontario) contains >40% crude protein, and includes a full complement of amino acids (it is also fairly high in fat: ≥10%). Supplemental food was placed on floating platforms located within the territories of breeding coot pairs. Because we did not want supplemental food to influence settling patterns (i.e. high-quality birds selecting territories with feeders), we did not provide food until just after the peak of spring arrival and territory establishment. At Minnedosa, this was determined by regular roadside surveys of 68 wetlands (Arnold 1990, and unpubl. data). Feeding began on 27 April 1987, 10 days before the first freshly laid egg was collected and 20 days before the mean egg-collection date. Feeding continued until no newly initiated nests were discovered. Platforms were refilled every 4 days with approximately 0.5 kg of food. To prevent food piracy among neighboring coot pairs, we provided all pairs on a wetland with the same food supplement (i.e. food supplements were randomly assigned to wetlands rather than coot pairs).

In 1988 and 1989, only one food supplement was provided; fed birds received a mixture of steam-rolled corn, rabbit chow, layer diet, oystershell, and grit in an approximate 20:10:10:1:1 ratio. Rabbit chow (Bunny Booster, Cargill Ltd., Winnipeg, Manitoba) contained >18% crude protein. We replaced trout chow with rabbit chow because coots seemed reluctant to eat trout chow, and we were uncertain if this was due to low palatability or to lack of demand for protein. But because coots are primarily herbivorous, we reasoned that they may be more attracted to a high-protein diet consisting entirely of plant proteins. The layer diet (Co-op Layer Diet 20, Federated Co-operatives Ltd., Saskatoon, Saskatchewan) was a complete diet especially formulated for egg production in domestic chickens, and it therefore provided all essential nutrients for egg formation (≥18% crude protein, ≥3% crude fat, and 3.06% calcium). We also provided oystershell as an additional calcium supplement, and medium poultry grit to assist in mechanical breakdown of natural and supplemental foods (especially corn) in the gizzard. Food was provided similarly to 1987, except that platforms were refilled every third day. At Minnedosa, feeding began on 27 April 1988 and 2 May 1989, 15 and 8 days before the first freshly laid eggs were collected, and 22 and 19 days before the mean eggs were collected, respectively. At Delta Marsh, supplemental feeding began on 6 May 1989, 16 days before the first freshly laid egg was collected, and 22 days before the mean egg was collected. Coots require 5–8 days to produce an egg (including 4–7 days of rapid follicle growth and 1 day of albumen and shell deposition; Alisauskas and Ankney 1985, Arnold 1990), so most coots had adequate time to respond to supplemental food prior to egg formation. Coots were observed feeding from platforms on numerous occasions each year, but no quantitative data were collected on frequency of platform use.

We collected a single fresh (<24 h old) egg per nest for nutrient analysis. Previously laid eggs were identified by marking all eggs with permanent ink 1 day before collections. We attempted to standardize egg sequence by collecting fifth-laid eggs within each clutch; however, when this was not logistically feasible, we collected eggs as near in sequence as possible to the fifth-laid egg. For each egg, we determined fresh mass (±0.1 g), and we measured length and maximum breadth (±0.1 mm) with dial calipers. We determined egg volume (cm$^3$) from Hoyt's (1979) equation: volume = $0.000507 \cdot \text{length} \cdot \text{breadth}^2$. Eggs were then boiled for 5–10 min, bagged individually, and frozen for up to 4 months. In the laboratory, we separated each egg into yolk, albumen, and shell (membranes were removed from the shell and included with the albumen; Alisauskas 1986). Wet components were dried at 80°C for >48 h to obtain dry component masses (Kerr et al. 1982). Most eggs lost considerable water during processing (e.g. from boiling, freezing, and handling; see also Ricklefs 1982, 1984b), and more importantly, the amount of water loss varied significantly among treatment groups (ANOVA: $F_{11,310} = 12.03$, $P = 0.0001$). Because water loss varied among groups, we did not analyze wet component masses, or the water content of specific components. However, total water content was assessed accurately by subtracting dry component masses from fresh egg mass. Dry yolks were analyzed further to determine lipid (yolk fat) and nonlipid (yolk lean) fractions. Neutral lipids were extracted from dried yolks by refluxing the entire yolk for 4 h in a modified Soxhlet apparatus with petroleum ether as solvent (Dobush et al. 1985). We obtained five independent measures of composition for each egg: total water, dry shell, dry albumen, yolk fat, and yolk lean. We also calculated three additional derived variables for each egg. Dry mass was the sum of all previous components except total water. We assumed that dry albumen and yolk lean consisted entirely of protein (Sotherland and Rahn 1987), and we summed these to measure total protein. Finally, we calculated total energy content from the formula: energy (kcal) = $9.5 \cdot$ yolk fat (g) + $5.65 \cdot$ protein (g) (Ricklefs 1984b). Although these three variables were completely derived from the previous five variables, they nevertheless provided valuable auxillary information on egg composition. If, for example, a sample group of eggs contained significantly larger lean-yolk fractions, but nonsignificantly smaller dry-albumen content, the total amount of protein available to developing embryos might not differ between sample groups.

Processing conditions for 1987–1989 eggs were essentially identical (i.e. same laboratory equipment and same chief technician), but 1981 Delta Marsh eggs were processed independently (Alisauskas 1986). Alisauskas' 1981 sample included 97 eggs from 17 nests. We include here data for 1 egg from each of these 17 nests, plus additional previously unpublished data from 8 eggs (all from separate nests). For nests from which Alisauskas (1986) acquired multiple eggs, we selected the egg that was closest in sequence to the fifth-laid egg.

Sample groups are hereafter designated by mnemonics that incorporate study area (M for Minnedosa, D for Delta), year (e.g. 89 for 1989), and supplemental feeding regime (CTRL for unsupplemented controls, CORN for corn, TROUT for trout chow, C+T for corn and trout chow, and MIX for the composite diet used in 1988 and 1989).

All egg composition variables met assumptions of normality (Kolmogorov tests: $W \geq 0.981$, $P \geq 0.26$), so we did not transform variables for general analyses. We examined among-group differences in variances using $F_{max}$ tests (Sokal and Rohlf 1973: 210) and among-group differences in means using one-way ANOVAs. Any such differences are referred to subsequently as differences in *absolute* egg composition. These include both size-dependent and size-independent differences in nutrient content. We examined changes in proportional nutrient content by $\log_{10}$-$\log_{10}$ regressions of component mass versus fresh egg mass (Ankney 1980, Ricklefs 1984b). A regression slope of unity signifies that a component makes up a constant fraction of total egg mass. Slopes significantly less than or greater than one imply that components make up a decreasing or increasing fraction of the total egg as egg mass increasees. We tested for among-group differences in proportional egg composition by including appropriate dummy variables and interaction terms (which tested for differences in intercepts and slopes, respectively) in the log-log regression models (e.g. ANCOVAs). We examined among-group homogeneity of variance in proportional egg composition by conducting $F_{max}$ tests on residuals from the preceding ANCOVAs. Any differences in egg composition that involved fresh-egg mass as a covariate are hereafter referred to as differences in *proportional* egg composition. For each of the specific comparisons, we tested for both absolute and proportional variation in egg composition.

To test for study area effects on egg composition, we used unsupplemented groups only (D81CTRL, D88CTRL, and D89CTRL vs. M87CTRL, M88CTRL, and M89CTRL). Because this comparison was potentially confounded by year effects, we also used only 1988 and 1989 data to test for study-area effects. Using data from control groups only, we examined year effects separately within each study area. Using data from each feeding experiment independently (Minnedosa 1987, 1988, and 1989; and Delta Marsh 1989), we tested for supplemental feeding effects. For the 1987 experiment, we used a 2 × 2 factorial design to assess the independent effects of corn and trout chow, as well as their interaction. We also tested for an overall feeding effect with combined data from 1988 (Minnedosa only) and 1989; 1987 data could not be included due to the different feeding procedures. Because supplemental food was not provided in all study areas and years (or was provided differently in 1987), and because both study areas were not sampled in the exact same years, we had a limited capacity to test for interaction effects. We tested for potential study-area × year interactions with the 1988 and 1989 data from unsupplemented coots (M88CTRL, M89CTRL, D88CTRL, and D89CTRL), study-area × feeding interactions with the 1989 data (M89CTRL, M89MIX, D89CTRL, and D89MIX), and year × feeding interactions with the 1988 and 1989 Minnedosa data (M88CTRL, M88MIX, M89CTRL, M89MIX).

We tested for among-wetland variation in egg composition with the Minnedosa data (the Delta Marsh data were from a single contiguous shoreline). For these analyses, we included data for all wetlands from which two or more eggs had been collected (all from different females). We used nested-ANOVAs to estimate the among- and within-wetland components of variation (e.g. Lessells and Boag 1987). We conducted separate analyses for each year, as well as a combined analysis of all three years. For the separate analyses, wetland effects were nested within supplemental feeding regimes; for the combined analysis, wetland effects were nested within feeding regimes, which were in turn nested within years.

Variations in egg composition with clutch size, laying date, and laying sequence were examined by linear regressions. These effects were examined singly, in concert, and among sample groups by multiple regressions and ANCOVAs.

To minimize extensive Type I errors, we adopted a two-step statistical protocol: (1) For each of the comparisons described above, a single multivariate test (MANOVA for comparisons involving absolute egg composition, MANCOVA for comparisons involving proportional composition) was conducted with the five independent egg components as response variables (total water, dry shell, dry albumen, yolk fat, and yolk lean). In addition to providing a single powerful test of all simple ANOVAs (or ANCOVAs), this analysis also tested for among-group differences in covariances. (2) If the overall MANOVA or MANCOVA was significant ($P \leq 0.05$), or nearly significant ($P \leq 0.10$), we interpreted individual ANOVAs or ANCOVAs for each of the five response variables, and we also conducted additional ANOVAs or ANCOVAs for dry mass, total protein, and total energy. Statistical tests were performed using the GLM and NESTED procedures of SAS (SAS Institute Inc. 1985). For analyses with more than one predictor variable (e.g. multiple regressions and ANCOVAs), we began our analysis with full statistical models and deleted nonsignificant ($P > 0.05$, based on partial sums of squares [SAS Type III SS]) effects from the models and recalculated significance levels for the remaining variables. Significance levels for MANOVAs and MANCOVAs were based on the Wilk's Lambda approximation to the $F$ distribution (SAS Institute Inc. 1985). $F$ values and $P$ values for nested ANOVAs were obtained from the GLM procedure (the SAS NESTED

TABLE 1. Sample size, laying sequence, estimated volume (cm$^3$), fresh mass (g), clutch size, and laying date of American Coot eggs (values are $\bar{x} \pm 1$ SD).

| Group[a] | Size | Laying sequence | Estimated volume | Fresh mass | Clutch size | Laying date[b] |
|---|---|---|---|---|---|---|
| D81CTRL | 25 | 4.7 ± 1.3 | 27.3 ± 1.9 | 29.1 ± 1.8 | —[c] | 144.6 ± 6.7 |
| D88CTRL | 30 | 5.1 ± 0.3 | 27.6 ± 1.8 | 29.1 ± 2.1 | 7.1 ± 1.7 | 157.0 ± 4.3 |
| D89CTRL | 9 | 5.1 ± 2.8 | 27.6 ± 3.1 | 29.6 ± 3.5 | 8.0 ± 2.0 | 154.0 ± 6.6 |
| D89MIX | 23 | 5.5 ± 1.8 | 27.4 ± 2.4 | 29.2 ± 2.3 | 8.1 ± 1.5 | 147.8 ± 5.1 |
| M87CTRL | 24 | 5.8 ± 1.4 | 27.2 ± 2.7 | 29.1 ± 2.8 | 9.0 ± 1.6 | 137.3 ± 5.0 |
| M87CORN | 24 | 5.9 ± 2.2 | 28.3 ± 1.6 | 30.3 ± 1.8 | 10.5 ± 1.9 | 136.5 ± 5.4 |
| M87TROUT | 21 | 6.0 ± 1.6 | 28.4 ± 2.3 | 30.3 ± 2.4 | 9.9 ± 1.8 | 136.9 ± 5.5 |
| M87C+T | 24 | 5.8 ± 2.0 | 28.1 ± 2.5 | 29.9 ± 2.8 | 10.6 ± 1.8 | 135.7 ± 3.9 |
| M88CTRL | 42 | 5.2 ± 0.7 | 28.2 ± 2.2 | 30.1 ± 2.4 | 9.2 ± 2.1 | 139.9 ± 4.6 |
| M88MIX | 47 | 5.3 ± 0.8 | 28.1 ± 2.3 | 30.0 ± 2.3 | 10.2 ± 2.1 | 139.1 ± 3.4 |
| M89CTRL | 34 | 4.4 ± 2.2 | 27.8 ± 2.2 | 29.5 ± 2.5 | 8.9 ± 1.9 | 138.8 ± 4.6 |
| M89MIX | 19 | 4.8 ± 1.9 | 27.2 ± 2.4 | 28.9 ± 2.6 | 9.9 ± 3.1 | 140.6 ± 6.1 |
| Combined | 322 | 5.3 ± 1.6 | 26.8 ± 2.3 | 29.6 ± 2.4 | 9.3 ± 2.2 | 141.6 ± 7.9 |

[a] Sample group mnemonics: M designates Minnedosa, D designates Delta Marsh; numerals designate year; terminal letters designate supplemental feeding regime (CTRL = unfed controls, CORN = corn, TROUT = trout chow, C+T = corn and trout chow, MIX = mixed diet of 1988 and 1989).

[b] Julian date.

[c] Multiple eggs were removed from clutches without replacement (Alisauskas 1986); hence clutch size data are inappropriate.

procedure does not provide these parameters for unbalanced statistical designs).

## RESULTS

We determined nutrient composition of 322 American Coot eggs; sample sizes ranged from 9 to 47 per sample group (Table 1). Two or more eggs were obtained from 52 Minnedosa wetlands during the 3 yr (160 total eggs); these data were used in the analysis of among-wetland variation in egg composition.

Although we attempted to minimize sequence effects on egg composition by collecting the fifth-laid egg from each clutch, there were nevertheless significant differences in egg sequence among sample groups (ANOVA: $F_{11,310} = 2.86, P = 0.001$). This was primarily a function of many late-sequence eggs in the 1987 Minnedosa groups (Table 1). Because laying order can affect egg composition among coots (Alisauskas 1986), we conducted additional analyses using egg sequence as a potential covariate. Sample groups also differed significantly in mean clutch size ($F_{10,224} = 7.30, P \leq 0.0001$) and mean laying date ($F_{11,305} = 46.88, P = 0.0001$) (Table 1). Delta Marsh coots had smaller clutches and began nesting later than Minnedosa coots (Arnold and Alisauskas unpubl. data). In addition, there was significant annual variation in clutch size and laying date at each study area (Alisauskas and Ankney 1985, Arnold 1990, Arnold and Alisauskas unpubl. data). Finally, clutch size, but not laying date, was affected by supplemental food (Arnold 1990 unpubl. data).

Mean egg size did not differ among sample groups (ANOVAs, $P \geq 0.37$), although variances were significantly heterogeneous for both fresh mass and volume ($F_{max} = 3.61$ and $3.78$, respectively; $P \leq 0.05$); D89CTRL eggs were the most variable, and M87CORN eggs the least variable (Table 1). In additional analyses of egg-size variation among Minnedosa and Delta Marsh coots (based on much larger samples of measured clutches), mean egg volume did not differ in relation to supplemental food (Arnold 1990). There was significant annual variation in egg size at Minnedosa, and Minnedosa eggs were larger, on average, than Delta Marsh eggs (Arnold 1990; Arnold and Alisauskas unpubl. data). However, most of these differences could be attributed to large average egg volumes in the 1981 and 1986 Minnedosa samples. Data from 1981 and 1986 were excluded from this study because no eggs were collected for composition analysis.

*Among-group variation in egg composition.*—Variances of most egg components differed significantly among sample groups ($F_{max}$ tests, Table 2). Homogeneity of variance was rejected at the 5% level for 5 of 8 variables and at the 1% level for three of these variables (Table 2). Eggs from the D89CTRL, M87CTRL, and M87C+T groups were particularly variable, whereas M87CORN and D88CTRL eggs showed the most consistency within-groups (Table 3). Patterns of

TABLE 2. Sources of variation in absolute and proportional composition of American Coot eggs.[a] Levels of significance: * = $P < 0.05$; ** = $P < 0.01$; NS = $P > 0.05$.

| | Absolute composition | | | | Proportional composition | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | $F_{max}$ test | | 1-way ANOVA | | $F_{max}$ test[b] | | Egg size effect[c] | | | | Group effect | | Inter-action | | Model[d] | |
| Variable | $F_{max}$ | $P$ | $F$ | $P$ | $F_{max}$ | $P$ | log($a$) | $b$ | SE($b$) | $F$ | $F$ | $P$ | $F$ | $P$ | $F$ | $r^2$ |
| Total water | 3.34 | NS | 1.15 | 0.32 | 3.41 | * | −0.15 | 1.00 | 0.01 | 7,816 | 6.58 | 0.0001 | 1.12 | 0.34 | 679.3 | 0.96 |
| Egg dry mass | 3.62 | * | 2.60 | 0.004 | 3.41 | * | −0.53 | 1.01 | 0.03 | 1,603 | 6.42 | 0.0001 | 1.14 | 0.33 | 147.5 | 0.85 |
| Shell | 7.56 | ** | 2.20 | 0.01 | 1.85 | NS | −0.90 | 0.90 | 0.04 | 348 | 1.30 | 0.22 | 1.39 | 0.18 | 377.5 | 0.54 |
| Albumen | 5.71 | ** | 2.41 | 0.007 | 3.70 | * | −1.39 | 1.19 | 0.05 | 511 | 3.12 | 0.0005 | 1.63 | 0.09 | 47.7 | 0.65 |
| Yolk fat | 3.02 | NS | 2.40 | 0.007 | 2.17 | NS | −1.03 | 0.99 | 0.06 | 276 | 4.12 | 0.0001 | 1.48 | 0.14 | 27.4 | 0.52 |
| Yolk lean | 6.84 | ** | 3.49 | 0.0001 | 9.00 | ** | −1.30 | 1.02 | 0.07 | 229 | 4.21 | 0.0001 | 1.29 | 0.22 | 24.6 | 0.49 |
| Protein | 2.97 | NS | 2.65 | 0.003 | 12.64 | ** | −1.05 | 1.12 | 0.03 | 1,236 | 5.12 | 0.0001 | 1.34 | 0.20 | 114.0 | 0.82 |
| Energy | 3.63 | * | 2.54 | 0.004 | 3.65 | * | 0.14 | 1.05 | 0.04 | 937 | 6.35 | 0.0001 | 1.43 | 0.16 | 87.3 | 0.77 |
| MANOVA | — | | 3.43 | 0.0001 | — | | — | — | — | 966,284 | 2.58 | 0.0001 | 0.96 | 0.60 | — | — |

[a] $N = 322$ eggs, $k = 12$ groups.

[b] $F_{max}$ test based on variance of residuals from the common regression of $\log_{10}$ component mass on $\log_{10}$ egg mass.

[c] Egg size = fresh egg mass (g); $\log_{10}$(component mass) = $\log_{10}(a) + b[\log_{10}$(fresh egg mass)]. $P < 0.0001$ for all egg size effects.

[d] Model includes significant parameters only; $P < 0.0001$ for all models.

within-group variation showed no obvious relationships with study area, year, or supplemental food, and they showed no consistent relationships with group means (i.e. mean and variance were not correlated, as might be expected if, for example, supplemental feeding affected egg composition in only part of the population).

Absolute egg composition differed significantly among the 12 sample groups (Table 2; MANOVA: $P < 0.0001$). Total water was the only component that did not vary among groups ($P = 0.32$). Egg quality (e.g. lipid, protein, and energy content) was generally highest among M87CORN, M87TROUT, and M87C+T groups, and quality was lowest for D88CTRL, M89CTRL, and M89MIX groups (Table 3).

Proportional composition also differed among sample groups, as would be expected because egg size did not differ among groups, but most measures of absolute egg composition did (e.g. Table 2). There was no significant sample group × egg-mass interaction effect (i.e. slopes from the regressions of egg component masses on total egg mass were essentially parallel; MANCOVA: $P = 0.60$). With the interaction effect removed, main effects of sample group and egg mass were both highly significant (Table 2; MANCOVA: $P < 0.0001$). Individual ANCOVAs explained from 41 to 96% of the variation in measures of egg composition (Table 2). Effects of egg mass were highly significant for each ANCOVA (Table 2; $P < 0.0001$), and group effects were significant for all variables except shell mass ($P = 0.22$).

Most components varied isometrically with egg mass. For example, log-log regression slopes did not differ from unity, thus component masses made up a constant proportion of total egg mass. The log-log regression slope, however, was significantly less than one for shell mass ($b = 0.90 \pm 0.04$ [1 SE]), and significantly greater than one for albumen mass ($b = 1.19 \pm 0.05$). Because these components were not isometric, it would be inappropriate to use ratio variables to describe proportional egg composition among sample groups (Packard and Boardman 1988). Therefore, to calculate proportional component masses, we used residuals from the common regression of component mass on egg mass (Table 2). These residuals were standardized to a fresh egg mass of 29.65 (the grand mean for all 322 eggs) and converted to percentages (Table 3).

Variance in proportional egg composition was significantly heterogeneous for dry mass, total water, albumen, yolk lean, protein, and energy content (Table 2), but within-group variance showed no obvious patterns with respect to supplemental feeding, study area, or year (Table 3).

*Study area effects on egg composition.*—Eggs differed significantly in absolute composition between Delta Marsh and Minnedosa (Table 4: MANOVA, $P = 0.004$). Dry masses of shell and albumen were heavier among Minnedosa eggs, whereas lean dry yolk was heavier among Delta Marsh eggs (Table 3). When egg mass was included as a covariate using log-log regression analyses, study area effects remained significant

TABLE 3. Among-sample group variation in egg composition of American Coots. Data in top half of table are absolute component masses (g) and energy content (kcal); data in bottom half of table are proportional composition (percentage of fresh egg mass)[a] and energy content (kcal/g fresh egg mass) (values are $\bar{x} \pm$ SD).

| Group | Total water | Egg dry mass | Shell dry mass | Albumen dry mass | Yolk fat | Yolk lean dry | Protein dry mass | Total energy |
|---|---|---|---|---|---|---|---|---|
| **Absolute composition** | | | | | | | | |
| D81CTRL | 19.9 ± 1.3 | 9.18 ± 0.79 | 2.58 ± 0.19 | 2.15 ± 0.18 | 2.71 ± 0.31 | 1.75 ± 0.34 | 3.90 ± 0.45 | 47.7 ± 5.0 |
| D88CTRL | 20.2 ± 1.5 | 8.86 ± 0.66 | 2.53 ± 0.22 | 2.24 ± 0.22 | 2.52 ± 0.26 | 1.57 ± 0.17 | 3.81 ± 0.32 | 45.5 ± 3.7 |
| D89CTRL | 20.4 ± 2.3 | 9.15 ± 1.16 | 2.67 ± 0.44 | 2.22 ± 0.34 | 2.68 ± 0.38 | 1.59 ± 0.26 | 3.81 ± 0.50 | 47.0 ± 5.6 |
| D89MIX | 20.2 ± 1.8 | 9.00 ± 0.62 | 2.55 ± 0.19 | 2.17 ± 0.26 | 2.73 ± 0.26 | 1.55 ± 0.13 | 3.72 ± 0.32 | 46.9 ± 3.7 |
| M87CTRL | 19.9 ± 1.8 | 9.16 ± 1.06 | 2.64 ± 0.29 | 2.36 ± 0.34 | 2.63 ± 0.40 | 1.54 ± 0.24 | 3.89 ± 0.46 | 47.0 ± 6.0 |
| M87CORN | 20.6 ± 1.3 | 9.68 ± 0.61 | 2.75 ± 0.23 | 2.40 ± 0.24 | 2.83 ± 0.23 | 1.71 ± 0.15 | 4.10 ± 0.30 | 50.0 ± 3.2 |
| M87TROUT | 20.7 ± 1.7 | 9.54 ± 0.81 | 2.73 ± 0.34 | 2.37 ± 0.22 | 2.75 ± 0.32 | 1.68 ± 0.16 | 4.05 ± 0.29 | 49.1 ± 4.4 |
| M87C+T | 20.3 ± 2.0 | 9.52 ± 0.93 | 2.71 ± 0.34 | 2.39 ± 0.43 | 2.81 ± 0.29 | 1.61 ± 0.18 | 4.00 ± 0.50 | 49.3 ± 4.8 |
| M88CTRL | 20.9 ± 1.7 | 9.20 ± 0.79 | 2.68 ± 0.24 | 2.30 ± 0.26 | 2.60 ± 0.30 | 1.63 ± 0.17 | 3.93 ± 0.37 | 46.8 ± 4.5 |
| M88MIX | 20.7 ± 1.7 | 9.29 ± 0.82 | 2.68 ± 0.27 | 2.29 ± 0.27 | 2.65 ± 0.30 | 1.67 ± 0.22 | 3.95 ± 0.40 | 47.5 ± 4.5 |
| M89CTRL | 20.6 ± 1.7 | 8.93 ± 0.79 | 2.63 ± 0.24 | 2.21 ± 0.26 | 2.57 ± 0.33 | 1.51 ± 0.19 | 3.72 ± 0.36 | 45.5 ± 4.5 |
| M89MIX | 19.9 ± 1.8 | 8.95 ± 0.86 | 2.54 ± 0.16 | 2.20 ± 0.29 | 2.65 ± 0.37 | 1.56 ± 0.20 | 3.76 ± 0.42 | 46.4 ± 5.5 |
| Combined | 20.4 ± 1.7 | 9.20 ± 0.84 | 2.64 ± 0.26 | 2.28 ± 0.28 | 2.66 ± 0.32 | 1.62 ± 0.21 | 3.89 ± 0.40 | 47.3 ± 4.7 |
| **Proportional composition** | | | | | | | | |
| D81CTRL | 68.5 ± 1.6 | 31.5 ± 1.6 | 8.9 ± 0.5 | 7.4 ± 0.4 | 9.3 ± 0.8 | 6.0 ± 1.0 | 13.4 ± 1.1 | 1.64 ± 0.12 |
| D88CTRL | 69.5 ± 1.0 | 30.5 ± 1.0 | 8.7 ± 0.5 | 7.7 ± 0.4 | 8.7 ± 0.7 | 5.4 ± 0.4 | 13.1 ± 0.3 | 1.57 ± 0.07 |
| D89CTRL | 69.1 ± 0.9 | 30.9 ± 0.9 | 9.0 ± 0.7 | 7.5 ± 0.6 | 9.1 ± 0.9 | 5.4 ± 0.6 | 12.9 ± 0.6 | 1.59 ± 0.08 |
| D89MIX | 69.1 ± 0.9 | 30.9 ± 0.9 | 8.7 ± 0.6 | 7.5 ± 0.5 | 9.4 ± 0.7 | 5.3 ± 0.3 | 12.8 ± 0.4 | 1.61 ± 0.07 |
| M87CTRL | 68.5 ± 1.2 | 31.5 ± 1.2 | 9.0 ± 0.5 | 8.2 ± 0.8 | 9.0 ± 0.8 | 5.3 ± 0.6 | 13.4 ± 0.7 | 1.62 ± 0.08 |
| M87CORN | 68.0 ± 1.0 | 32.0 ± 1.0 | 9.1 ± 0.5 | 7.9 ± 0.5 | 9.3 ± 0.7 | 5.6 ± 0.4 | 13.5 ± 0.4 | 1.65 ± 0.07 |
| M87TROUT | 68.5 ± 1.0 | 31.5 ± 1.0 | 9.0 ± 0.7 | 7.8 ± 0.5 | 9.1 ± 0.8 | 5.6 ± 0.4 | 13.4 ± 0.4 | 1.62 ± 0.08 |
| M87C+T | 68.1 ± 1.1 | 31.9 ± 1.1 | 9.1 ± 0.8 | 8.0 ± 0.8 | 9.4 ± 0.9 | 5.4 ± 0.5 | 13.4 ± 0.7 | 1.65 ± 0.08 |
| M88CTRL | 69.4 ± 1.0 | 30.6 ± 1.0 | 8.9 ± 0.5 | 7.6 ± 0.4 | 8.6 ± 0.7 | 5.4 ± 0.4 | 13.1 ± 0.6 | 1.56 ± 0.07 |
| M88MIX | 69.1 ± 1.4 | 30.9 ± 1.4 | 9.0 ± 0.7 | 7.6 ± 0.5 | 8.8 ± 0.8 | 5.5 ± 0.5 | 13.1 ± 0.6 | 1.58 ± 0.08 |
| M89CTRL | 69.7 ± 0.9 | 30.3 ± 0.9 | 9.0 ± 0.5 | 7.6 ± 0.7 | 8.6 ± 0.6 | 5.1 ± 0.4 | 12.7 ± 0.6 | 1.54 ± 0.06 |
| M89MIX | 69.0 ± 1.0 | 31.0 ± 1.0 | 8.8 ± 0.4 | 7.7 ± 0.5 | 9.2 ± 0.9 | 5.4 ± 0.4 | 13.0 ± 0.4 | 1.61 ± 0.09 |
| Combined | 69.0 ± 1.2 | 31.0 ± 1.2 | 8.9 ± 0.6 | 7.7 ± 0.6 | 9.0 ± 0.8 | 5.5 ± 0.6 | 13.1 ± 0.7 | 1.60 ± 0.09 |

[a] Proportional composition based on residuals from regressions of component mass on fresh egg mass (Table 2); standardized to fresh egg mass = 29.65 (the grand mean for all eggs; Table 1).

overall (MANCOVA: $P = 0.006$), as well as for shell mass and yolk lean, but albumen mass no longer differed between areas (Table 4). For a given egg mass, Minnedosa eggs contained significantly more shell, but Delta Marsh eggs contained more lean-yolk mass and more total energy (Table 3).

Differences between study areas were diminished if year effects were included in these analyses [nested MANOVA: $P(\text{area}) = 0.02$, $P(\text{yr}) \leq 0.0001$; nested MANCOVA: $P(\text{area}) = 0.09$, $P(\text{yr}) \leq 0.0001$, $P(\text{egg mass}) \leq 0.0001$; year effects nested within study area effects], but study area effects remained significant for absolute ($P = 0.04$) and proportional ($P = 0.004$) lean yolk content, and for proportional shell content ($P = 0.02$). If analyses were confined to 1988 and 1989 (the only two years in common), study area effects were no longer significant overall (MANOVA: $F_{5,109} = 1.54$, $P = 0.18$; MANCOVA: $F_{5,108} = 1.41$, $P = 0.23$), but Minnedosa eggs still had absolutely and proportionately greater shell masses ($P = 0.04$ for both).

*Annual variation.*—At Minnedosa, absolute measures of egg composition varied significantly among years (Table 4; MANOVA: $P \leq 0.0001$), but the only variable individually affected was yolk lean ($P = 0.02$; $P = 0.06$ for protein). Proportional composition also varied among years (MANCOVA: $P \leq 0.0001$), and in this case all variables except shell and yolk fat were significantly affected (Table 4).

Among Delta Marsh eggs, year effects were nearly significant in the analysis of absolute variation in egg composition (MANOVA: $P = 0.09$), and were marginally significant for proportional composition (Table 4; MANCOVA: $P = 0.05$). Individual effects were significant for water, yolk fat, yolk lean, dry mass, and energy.

*Supplemental feeding effects.*—For the 1987 feeding experiment, there was a significant corn × trout-chow interaction effect on absolute egg composition (Table 5; MANOVA: $P = 0.02$), but the only variable individually affected by this interaction was yolk lean ($P = 0.003$). Presumably, yolk lean was significantly higher among

TABLE 4. Between-study-area and among-year variation in absolute (ABS) and proportional (PROP) composition of American Coot eggs.[a] For analyses of proportional composition, effects of egg mass were always significant ($P < 0.0001$). Interactions with egg mass were not significant (MANCOVAs: $F < 1.11$, $P > 0.36$).

| | Study area effect | | | | Year effect: Minnedosa | | | | Year effect: Delta Marsh | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | ABS | | PROP | | ABS | | PROP | | ABS | | PROP | |
| Variable | *F* | *P* | *F* | *P* | *F* | *P* | *F* | *P* | *F* | *P* | *F* | *P* |
| Egg mass | 1.12 | 0.29 | — | — | 1.39 | 0.26 | — | — | 0.21 | 0.81 | — | — |
| Total water | 1.55 | 0.21 | 1.03 | 0.31 | 2.27 | 0.11 | 7.97 | 0.0006 | 0.45 | 0.64 | 4.81 | 0.01 |
| Egg dry mass | 0.29 | 0.59 | 0.97 | 0.33 | 1.06 | 0.35 | 7.68 | 0.0008 | 1.26 | 0.29 | 4.68 | 0.01 |
| Shell | 4.74 | 0.03 | 5.17 | 0.02 | 0.45 | 0.64 | 0.38 | 0.68 | 1.13 | 0.33 | 1.09 | 0.34 |
| Albumen | 3.75 | 0.05 | 2.44 | 0.12 | 1.96 | 0.15 | 6.03 | 0.003 | 0.99 | 0.38 | 2.92 | 0.06 |
| Yolk fat | 0.15 | 0.70 | 2.48 | 0.12 | 0.21 | 0.81 | 2.33 | 0.10 | 2.77 | 0.07 | 3.83 | 0.03 |
| Yolk lean | 4.37 | 0.04 | 11.07 | 0.001 | 4.11 | 0.02 | 3.60 | 0.03 | 3.21 | 0.05 | 4.42 | 0.02 |
| Protein | 0.00 | 0.94 | 2.44 | 0.12 | 2.88 | 0.06 | 9.83 | 0.0001 | 0.36 | 0.70 | 1.76 | 0.18 |
| Energy | 0.04 | 0.83 | 4.35 | 0.04 | 0.97 | 0.38 | 5.93 | 0.004 | 1.70 | 0.19 | 4.19 | 0.02 |
| MANOVA[b] | 3.65 | 0.004 | 3.37 | 0.006 | 4.80 | 0.0001 | 4.57 | 0.0001 | 1.71 | 0.09 | 1.90 | 0.05 |

[a] Sample sizes: study area effects, 164; Minnedosa year effects, 100; Delta Marsh year effects, 64.

[b] MANOVA based on total water, shell, albumen, yolk fat, and yolk lean.

eggs laid by birds receiving either corn or trout chow, but not among birds that received both supplements (Table 3). Main effects of corn and trout chow were not significant (MANOVAs: $P \geq 0.43$), although the ANOVA for corn effect on yolk fat was individually significant ($P = 0.05$; this "effect" was ignored based on our MANOVA criterion).

For proportional composition in 1987, the three-way interaction among egg mass, corn, and trout chow was significant (Table 5; MANCOVA: $P = 0.02$). However, this effect was individually significant only for protein content ($P = 0.02$). Because visual inspection of the plotted regression lines did not reveal any intuitively obvious relationship (e.g. Arnold 1990: fig. 4.1), we deleted this three-way interaction and fit reduced models to each variable. For most variables, corn effects were significant (Table 5: albumen, yolk fat, yolk lean, and energy), but yolk lean and protein were also affected by trout chow and the interaction between corn and trout chow. Small eggs produced by corn-fed coots contained greater quantities of lipid and energy than did small eggs produced by control birds, but large eggs were not more nutrient rich than control eggs (Fig. 1). Albumen content was lower among small eggs of corn-fed birds (Fig. 1).

Supplemental feeding had no effect on absolute or proportional egg composition at Minnedosa in 1988 (MANOVA: $P = 0.75$; MANCOVA: $P = 0.06$ [$P \geq 0.13$ for all ANCOVAs]), or at Delta Marsh in 1989 (MANOVA: $P = 0.77$; MANCOVA: $P = 0.44$). In 1989 at Minnedosa, the MANOVA indicated a significant feeding effect on absolute composition, but this effect was not obvious for any single variable (Table 6), nor could we find evidence of significant differences in covariances among albumen, yolk fat, and yolk lean, or between dry mass and total water. For proportional composition in 1989, the MANCOVAs for feeding effect and feeding × egg-size interaction effect were both suggestive ($P = 0.09$ and $0.08$), and feeding effects were individually significant, or nearly significant, for water, dry mass, yolk lean, protein, and energy (Table 6). Eggs from fed birds contained more nutrients, and less water, than did control eggs (Table 3). The feeding × egg-size interaction was individually significant for shell mass ($P = 0.04$); large control eggs had relatively larger shells. For the combined 1988 and 1989 data, supplemental food affected overall absolute egg composition (Table 6; MANOVA: $P = 0.02$), but no single variable was affected. For proportional composition, feeding effects were significant overall (MANCOVA: $P = 0.01$), and for total water, yolk fat, yolk lean, dry mass, and energy content (Table 6).

*Among-wetland variation.*—For the Minnedosa eggs, there was no significant among-wetland variation in absolute or proportional egg composition in any year, or for the three years combined (Table 7: $P \geq 0.07$, % Var. $\leq 23.1$, $k = 48$ comparisons).

*Effects of laying sequence.*—Egg composition was affected by laying sequence (MANCOVA: $F_{5,303}$

TABLE 5. Effects of supplemental food on absolute and proportional egg composition of American Coots at Minnedosa in 1987.

| Variable | Absolute composition | | | | | | Proportional egg composition[a] | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Corn | | Trout | | C·T | | Corn | | Trout | | C·T | | C·ES | | T·ES | | C·T·ES | | Model |
| | *F* | *P* | *F* | *P* | *F* | *P* | *F* | *P* | *F* | *P* | *F* | *P* | *F* | *P* | *F* | *P* | *F* | *P* | $r^2$ |
| Total water | 0.25 | 0.62 | 0.64 | 0.43 | 2.22 | 0.14 | 3.59 | 0.06 | 0.31 | 0.58 | 0.01 | 0.93 | 3.33 | 0.07 | 1.10 | 0.30 | 1.59 | 0.21 | 0.97 |
| Egg dry mass | 2.12 | 0.15 | 0.32 | 0.58 | 2.12 | 0.15 | 3.57 | 0.06 | 0.31 | 0.58 | 0.00 | 0.95 | 3.46 | 0.07 | 1.21 | 0.27 | 1.77 | 0.19 | 0.88 |
| Shell | 0.73 | 0.40 | 0.19 | 0.67 | 1.05 | 0.31 | 0.12 | 0.74 | 0.17 | 0.68 | 0.06 | 0.80 | 0.30 | 0.59 | 0.05 | 0.83 | 0.45 | 0.50 | 0.59 |
| Albumen | 0.22 | 0.66 | 0.01 | 0.94 | 0.02 | 0.90 | 7.52 | 0.007 | 0.30 | 0.58 | 1.54 | 0.22 | 7.44 | 0.008 | 0.01 | 0.91 | 2.28 | 0.14 | 0.65 |
| Yolk fat | 3.79 | 0.05 | 0.58 | 0.45 | 1.17 | 0.28 | 11.93 | 0.0008 | 0.00 | 0.95 | 0.03 | 0.86 | 11.56 | 0.001 | 0.95 | 0.33 | 0.78 | 0.38 | 0.58 |
| Yolk lean | 9.76 | 0.002 | 6.62 | 0.01 | 1.17 | 0.003 | 7.77 | 0.007 | 4.70 | 0.03 | 7.62 | 0.007 | 1.02 | 0.32 | 3.35 | 0.07 | 0.53 | 0.47 | 0.49 |
| Protein | 0.98 | 0.32 | 0.09 | 0.77 | 2.33 | 0.13 | 0.34 | 0.56 | 5.07 | 0.03 | 5.67 | 0.02 | 0.33 | 0.57 | 5.08 | 0.03 | 5.62 | 0.02 | 0.86 |
| Energy | 2.94 | 0.09 | 0.39 | 0.53 | 2.04 | 0.16 | 6.29 | 0.01 | 0.09 | 0.76 | 0.00 | 1.00 | 6.02 | 0.02 | 1.92 | 0.17 | 3.06 | 0.08 | 0.80 |
| MANOVA | 0.99 | 0.43 | 0.30 | 0.91 | 2.87 | 0.02 | 1.99 | 0.06 | 1.97 | 0.06 | 2.43 | 0.02 | 1.98 | 0.06 | 1.96 | 0.06 | 2.42 | 0.02 | — |

[a] Egg size effect was significant for all models ($P < 0.0001$).

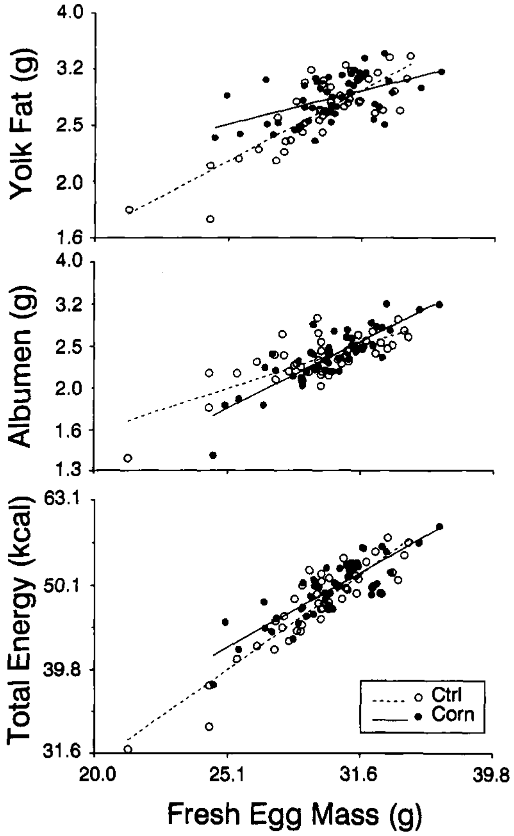

Fig. 1. Effects of supplemental corn on proportional content of yolk fat, albumen, and total energy of American Coot eggs in 1987. Controls (Ctrl) include birds that received either no supplements or trout chow only; corn-fed birds include some individuals that received both corn and trout chow (e.g. M87C+T). Slope differences are significant for each component (see Table 5).

= 1.87, $P = 0.05$), but sequence effects were small and were significant only for shell and yolk lean (partial $r^2 = 0.01$, $P = 0.05$ for each). In both cases, component masses declined with egg sequence. Adjusting for sequence effects did not alter the significance or magnitude of previously described differences among sample groups.

Egg sequence also affected proportional egg composition (MANCOVA: $F_{5,302} = 2.42$, $P = 0.02$), but this effect was significant only for albumen mass (partial $r^2 = 0.007$, $P = 0.01$), which increased marginally with laying sequence. Correcting for sequence effects did not affect the significance or magnitude of previously described differences in proportional composition among sample groups.

TABLE 6. Effects of supplemental food on absolute and proportional egg composition of American Coots, 1988 and 1989.[a]

| | 1989 Minnedosa | | | | | | 1988 & 1989, Minnedosa & Delta | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Absolute | | Proportional[b] | | | | Absolute | | Proportional[b] | | | |
| | Food effect | | Food effect | | Food·ES[c] | | Food effect | | Food effect | | Food·ES[c] | |
| Variable | *F* | *P* | *F* | *P* | *F* | *P* | *F* | *P* | *F* | *P* | *F* | *P* |
| Egg mass | 0.41 | 0.53 | — | — | — | — | 0.20 | 0.66 | — | — | — | — |
| Water | 0.89 | 0.35 | 3.39 | 0.07 | 0.28 | 0.60 | 0.67 | 0.42 | 4.73 | 0.03 | 0.33 | 0.56 |
| Egg dry mass | 0.01 | 0.92 | 3.42 | 0.07 | 0.26 | 0.61 | 0.19 | 0.67 | 4.43 | 0.04 | 0.31 | 0.58 |
| Shell | 2.41 | 0.13 | 2.35 | 0.13 | 4.43 | 0.04 | 1.31 | 0.25 | 1.36 | 0.25 | 3.90 | 0.05 |
| Albumen | 0.03 | 0.87 | 0.18 | 0.67 | 0.71 | 0.40 | 0.19 | 0.66 | 0.04 | 0.84 | 0.55 | 0.46 |
| Yolk fat | 0.67 | 0.42 | 2.68 | 0.11 | 0.45 | 0.50 | 2.77 | 0.10 | 6.56 | 0.01 | 0.24 | 0.62 |
| Yolk lean | 0.80 | 0.37 | 3.78 | 0.06 | 0.27 | 0.61 | 1.41 | 0.24 | 4.09 | 0.04 | 0.78 | 0.38 |
| Protein | 0.12 | 0.73 | 4.84 | 0.03 | 2.46 | 0.12 | 0.09 | 0.76 | 2.37 | 0.13 | 0.29 | 0.59 |
| Energy | 0.49 | 0.49 | 5.78 | 0.02 | 1.56 | 0.22 | 1.52 | 0.22 | 10.34 | 0.002 | 0.68 | 0.42 |
| MANOVA[d] | 2.66 | 0.03 | 1.88 | 0.09 | 2.14 | 0.08 | 2.80 | 0.02 | 3.09 | 0.01 | 1.34 | 0.25 |

[a] Feeding effects were not significant in 1988, or at Delta Marsh in 1989; see text for statistical tests.

[b] Egg size was included as a main effect in all proportional models, and it was always highly significant ($P < 0.0001$).

[c] Food·egg size interaction (F·ES).

[d] MANOVA on total water, shell, albumen, yolk fat, and yolk lean.

*Covariation with clutch size and laying date.*— Absolute egg composition varied with clutch size and laying date (MANOVAs: $F_{5,229} = 11.27$, $P \leq 0.0001$; $F_{5,311} = 6.39$, $P \leq 0.0001$; respectively), with all components increasing with clutch size and declining with laying date. There was significant among-group variation in the slopes of the relationships between egg composition and laying date (MANOVA: date × group effect, $F_{55,1341} = 1.39$, $P = 0.03$), but the only variable affected was total water content (water declined or showed no relationship with date in most groups, but increased within the small D89CTRL sample [$n = 9$]). Among-group variation in absolute egg composition remained significant when laying date was used as a covariate (MANOVAs: date effect, $F_{5,300} = 3.02$, $P = 0.01$; group effect, $F_{55,1392} = 3.12$, $P \leq 0.0001$), but only yolk fat, yolk lean, and protein varied significantly among groups ($P = 0.04$, 0.0001, and 0.03, respectively; $P = 0.07$ for total energy). Before controlling for laying date, all variables except total water had exhibited significant among-group variation (Table 2). Among-group variation in absolute composition remained significant when clutch size was included as a covariate (MANCOVA: group effect, $P \leq 0.0001$; clutch size effect, $P \leq 0.0001$), but group effects were not significant for any single variable ($P > 0.13$).

Proportional egg composition varied with clutch size (MANCOVA: $F_{5,228} = 6.94$, $P \leq 0.0001$) and laying date (MANCOVA: $F_{5,310} = 3.36$, $P = 0.006$). Proportions of most solid components

TABLE 7. Among-wetland variation in absolute (ABS) and proportional (PROP) egg composition of American Coots. Percentages of explained variation (% Var.) are from nested-ANOVAs (PROC NESTED; SAS Institute Inc. 1985), and *P* values are from PROC GLM. Analyses based on proportional composition used residuals from common regressions of component masses on total egg mass.

| | 1987-ABS | | 1987-PROP | | 1988-ABS | | 1988-PROP | | 1989-ABS | | 1989-PROP | | All data-ABS | | All data-PROP | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Variable | % Var. | *P* | % Var. | *P* | % Var. | *P* | % Var. | *P* | % Var. | *P* | % Var. | *P* | % Var. | *P* | % Var. | *P* |
| Water | 0.0 | 0.54 | 0.0 | 0.51 | 9.0 | 0.30 | 13.6 | 0.20 | 5.4 | 0.28 | 0.0 | 0.74 | 2.2 | 0.37 | 4.2 | 0.26 |
| Egg dry mass | 0.0 | 0.53 | 0.0 | 0.52 | 0.0 | 0.53 | 13.6 | 0.20 | 9.2 | 0.23 | 0.0 | 0.75 | 0.4 | 0.46 | 4.4 | 0.26 |
| Shell | 0.0 | 0.60 | 0.0 | 0.59 | 11.2 | 0.26 | 23.1 | 0.10 | 1.2 | 0.53 | 0.7 | 0.44 | 0.3 | 0.51 | 7.2 | 0.20 |
| Albumen | 0.0 | 0.77 | 0.0 | 0.84 | 9.8 | 0.29 | 0.0 | 0.93 | 0.0 | 0.44 | 4.2 | 0.36 | 0.0 | 0.64 | 0.0 | 0.93 |
| Yolk fat | 1.8 | 0.43 | 0.0 | 0.79 | 0.0 | 0.52 | 8.0 | 0.32 | 11.4 | 0.19 | 0.0 | 0.67 | 3.0 | 0.34 | 0.0 | 0.71 |
| Yolk lean | 0.0 | 0.76 | 0.0 | 0.86 | 0.0 | 0.93 | 0.0 | 0.53 | 1.5 | 0.39 | 0.0 | 0.82 | 0.0 | 0.90 | 0.0 | 0.87 |
| Protein | 0.0 | 0.60 | 13.6 | 0.15 | 0.0 | 0.53 | 0.0 | 0.61 | 7.3 | 0.26 | 16.1 | 0.07 | 0.0 | 0.53 | 7.6 | 0.12 |
| Energy | 3.3 | 0.38 | 1.4 | 0.43 | 0.0 | 0.53 | 9.1 | 0.28 | 10.5 | 0.20 | 0.0 | 0.90 | 3.1 | 0.33 | 0.0 | 0.50 |

increased with clutch size and declined with laying date, whereas the opposite was true of relative water content. Group effects remained insignificant for shell mass, and remained significant for all other variables, when clutch size or laying date was included as a covariate with sample group. Only one significant interaction involved clutch size, laying date, sample group, and egg mass (MANCOVAs: clutch-size × date effect, $F_{5,224} = 4.19$, $P = 0.001$; all others, $P \geq 0.07$). Large clutches initiated late in the year had relatively smaller solid components, and relatively more water, than did large early clutches or small late clutches. This interaction remained significant only for water content ($P = 0.05$) when sample group was included in the analysis. With the interaction effect removed, egg composition was affected by clutch size and sample group, but not by laying date (MANCOVAs: clutch size effect, $F_{5,215} = 3.40, P = 0.006$; egg mass effect, $F_{5,215} = 327{,}007$, $P = 0.0$; date effect, $F_{5,215} = 1.61$, $P = 0.16$).

Including clutch size and laying date as covariates eliminated the statistical significance of annual variation in egg composition at Delta Marsh ($P \geq 0.14$), and of feeding effects on egg composition in the combined 1988 and 1989 data ($P \geq 0.13$), but all other previously described effects of location, year, and supplemental food remained significant when clutch size and laying date were used as covariates.

## DISCUSSION

Based on analysis of single eggs from 322 American Coot nests, our results differed only slightly from those of Alisauskas (1986), who analyzed multiple eggs from 17 nests in the D81CTRL group (97 total eggs). Mean egg mass in our sample was significantly heavier (by 0.7 g) than in Alisauskas' (1986) sample, and hence most of our mean component masses were also heavier, but proportional composition was similar for all components except yolk lean (Table 3). We suspect that this variation stems from the potentially different procedures used to extract lipids from D81CTRL yolks (see Methods).

Log-log regression analysis of component masses versus egg mass for our data indicated that yolk components displayed isometry ($b = 1.0$), albumen displayed positive allometry ($b > 1.0$), and shell displayed negative allometry ($b < 1.0$). Alisauskas (1986) found that shell and albumen showed negative allometry, whereas yolk components exhibited positive allometry. We observed virtually identical trends as Alisauskas (1986) within the subset of D81CTRL data analyzed for this study, but covariance analyses (ANCOVAs) detected no differences in slope estimates among sample groups (including Alisauskas' D81CTRL sample). We conclude this variation was either weak or was due to sampling error. Indeed, in reviewing regression coefficients from all 12 sample groups, we can find examples of isometry, positive allometry ($b > 1.2$), and negative allometry ($b < 0.8$) for all components except total water (because this component makes up such a large part of total egg mass, it is usually always isometric). However, none of this variation was significant. Thus, on average, large coot eggs do not contain proportionately more nutrients than do small eggs, as suggested previously by Alisauskas (1986), but they do contain absolutely more nutrients, and therefore are of better quality than are small eggs (Ankney 1980).

*Among-group variation in egg composition.*—Egg composition showed little variation between study areas. This was somewhat surprising to us, because our major incentive for initiating a comparative study of egg composition was the large difference we observed between Delta Marsh coots and Minnedosa coots in other aspects of their breeding biology (e.g. mean clutch size = 7.2 and 9.5, mean initiation date = 26 May and 13 May, respectively; Alisauskas and Ankney 1985, Arnold and Alisauskas unpubl. data). Minnedosa eggs had absolutely and proportionately heavier shells than did Delta Marsh eggs, and this effect remained significant when only common years (1988 and 1989) were analyzed. If Delta Marsh coots normally encountered difficulties obtaining adequate calcium for eggshell production, one might predict that they would draw on stored calcium reserves during laying (e.g. Ankney and MacInnes 1978). They did not do so in 1981 when nutrient reserve dynamics of laying females were assessed (Alisauskas and Ankney 1985). Site variation in yolk lean content may have been related to different processing procedures for the 1981 Delta Marsh eggs (see Methods), because site effects were not significant when data were analyzed for common years only. Yolk lean represents the insoluble residue remaining after ether extraction, so determination of this fraction could be affected by subtle variation in extraction procedures (see below).

Annual variation in egg composition was significant for several components, and in many cases this effect seemed to overshadow variation associated with study area or supplemental feeding effects (e.g. Fig. 2). It was not possible to test statistically the relative contributions of study area, year, and supplemental feeding with our unbalanced study design. Because supplemental feeding effects and among-wetland variation were generally nonsignificant, we do not attribute these year effects to annual variation in resource levels on nesting territories. Perhaps these differences (if they are indeed real) reflected annual variation in population age-structure (e.g. Davis 1975, Crawford 1980), or in the quality of nutrient reserves that female coots carried with them to the breeding grounds (e.g. Heitmeyer and Fredrickson 1981, Alisauskas and Ankney 1985). Arnold (1990) found significant positive correlations between female age (as indexed by tarsus color; Crawford 1978) and yolk fat, between carcass fat and yolk fat, and between carcass protein and yolk lean; but these relationships were weak ($r^2 = 0.12$ to 0.18). Alternatively, year effects at Delta Marsh may have represented correlated responses with annual variation in clutch size or laying date, because among-year variation was no longer significant when clutch size or laying date were included as covariates.

Annual variation in absolute egg composition was due primarily to variation in the yolk lean fraction. There was also significant annual covariation between yolk fat and yolk lean (ANCOVA: $P = 0.009$), the two variables most likely to be affected by measurement error. We have no estimate of the accuracy or precision of our yolk extractions, but Rohwer (1986) found relatively small absolute errors [3.0% for yolk protein determination and 1.6% for yolk fat determination based on replicated extractions of half-fractions of Blue-winged Teal (*Anas discors*) yolks]. Among-individual coefficients of variation for yolk fat and yolk lean averaged approximately 12% among samples of coot eggs. The measurement error of these variables might be rather high, but it is not excessive.

Typically, investigators have focused on lipid content when evaluating the quality of egg yolks (e.g. Ankney 1980, Alisauskas 1986). Duncan (1988) suggested recently that the nonlipid fraction of the egg yolk may constitute a more critical resource for newly hatched Northern Pintails (*Anas acuta*). If Duncan's suggestion proves true for other birds, then the variation in yolk lean we observed, if biologically real, might have important fitness implications for newly hatched coots.

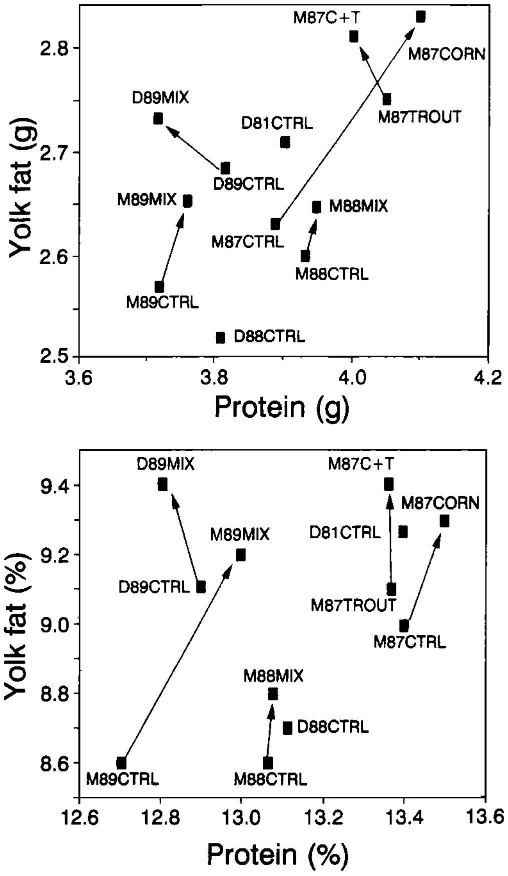

Fig. 2. Mean absolute (top) and proportional (bottom) fat and protein content of American Coot eggs in relation to study area, year, and supplemental feeding. Proportional values are based on adjusted means of residuals obtained from ANCOVAs (Table 3: bottom). Arrows connect treatment pairs differing in access to supplemental corn (plus other foods, see Methods). For sample group mnemonics, see Table 1.

Annual variation in egg composition has also been recorded for Herring Gulls (*Larus argentatus*; Meathrel et al. 1987) and Common Murres (*Uria aalge*; Birkhead and Nettleship 1984). For the most part, these effects involved the wet component masses, water fractions of specific components, or both. Estimations of water content are especially prone to procedural biases (Ricklefs 1982, 1984b; this study), and it therefore seems possible that these differences are not valid. Further assessment of accuracy and precision in egg-composition analyses are clearly needed.

Timing of nest initiation, clutch size, and fledgling mass were all significantly affected by supplemental feeding (Arnold 1990), which demonstrates that food availability can influence breeding success in coots (see also Martin 1987, Arcese and Smith 1988, Boutin 1990). Despite consistent effects on these variables, supplemental feeding had no influence on egg size (Arnold 1990, 1991; this study; but see Hill 1988). Absolute and proportional masses of several components were influenced by supplemental feeding in the 1987 and 1989 Minnedosa experiments, but these effects were generally small. In all cases where supplemental corn was added to the diet, corn-fed coots produced eggs of greater absolute and proportional lipid and energy content than did control coots (Fig. 2; sign tests, $P = 0.03$). No such trend was apparent for high-protein food supplements and protein content of eggs.

Few investigators have examined the effects of food supply on egg composition. Hochachka (1988) analyzed nutrient composition of Black-billed Magpie (*Pica pica*) eggs and observed a significant interaction effect of supplemental feeding and egg size on proportional water content. His results appear to be influenced heavily by a single outlying data point from a control clutch (Hochachka 1988: fig. 1), although similar results were apparently obtained in another study of Black-billed Magpies (Clarkson 1984, *in* Hochachka 1988). Measures of egg composition more closely linked with egg quality, such as dry mass of the yolk and albumen, were unaffected by supplemental feeding (Hochachka 1988). Studies with either captive or domestic birds have documented changes in egg composition in response to experimental manipulations of diet (Fisher 1969, Begin and Insko 1972, Butts and Cunningham 1972, Krapu and Swanson 1975, Krapu 1979, Beckerton and Middleton 1982, Eldridge and Krapu 1988), but many of these studies employed extremely deficient diets (e.g. only wheat in the Krapu studies).

*Among-wetland variation.*—There was no evidence of among-wetland variation in egg composition for any egg component in any year. Thus, our results do not support earlier suggestions that egg quality of American Coots should vary among terriories in response to local variation in food supply (Alisauskas 1986, Hill 1988). Although we did not measure food abundance in this study, casual observations suggested that there was substantial variation among wetlands, both in numbers of invertebrates and in standing crops of submerged macrophytes (Arnold pers. obs.). Moreover, there was significant among-wetland variation in clutch size and laying date (Arnold 1990), which suggests that at least some components of the life history varied among wetlands, for whatever reasons.

*Variation with clutch size and laying date.*—By far the strongest sources of variation in egg composition were covariation with clutch size and laying date; egg quality increased with clutch size and declined with laying date. Clutch size and laying date are strongly negatively correlated themselves (e.g. Alisauskas and Ankney 1985), and after taking this into account, clutch size had the most influence on egg composition. Similar effects of laying date and clutch size on egg composition were found for wild-nesting Blue-winged Teal (Rohwer 1986) and semicaptive Barnacle Geese (*Branta leucopsis*; Owen and West 1988). Both of these correlations are opposite of predictions based on life-history tradeoffs: birds investing in larger clutches should have fewer nutrients available for each egg (Lessells et al. 1989, Rohwer and Eisenhauer 1989), and birds that initiate laying before food becomes plentiful should have less exogenous resources available for egg production (e.g. Daan et al. 1988). However, empirical observations almost unanimously indicate that life-history traits are positively correlated (e.g. Clutton-Brock 1988), despite theoretical arguments for negative correlations (e.g. Smith and Fretwell 1974). We suggest that most of the observed individual variation in egg quality in these coots was inherent, and that "quality" females nested earlier, laid larger clutches of bigger and better-quality eggs, and probably even survived better than "inferior" females (e.g. Smith 1981). The extent to which such individual variation may be attributed to heritable versus nonheritable sources is still largely unknown (e.g. Boag and van Noordwijk 1987, Price et al. 1988).

We conclude that variation in egg composition can probably be ignored in most intraspecific studies. From our sample of analyzed eggs, we estimated total energy invested per clutch as the product of clutch size and energy per egg (we ignored intra-clutch variation in egg composition, which we did not assess; but see Alisauskas 1986). Clutch size accounted for 85.1% of the variation in total energy per clutch, egg size 10.3%, and energy density (kcal/g fresh mass) only 4.6%. The pattern was reflected in the coefficients of variation of these three variables (clutch size = 23.7%, egg size = 8.2%, and energy density = 5.6%). Similarly, egg size accounted for 70.0% of the variation in total energy per egg, whereas energy density explained 30.0%. Measurement error is negligible for clutch size and egg size (Arnold 1990), but is perhaps high for egg composition (see Discussion). The variance we attributed to egg composition may be an overestimate.

Although our analyses detected many significant differences in egg composition among different samples of coot eggs, the results were often inconsistent across study areas, years, or supplemental feeding regimes, and were therefore difficult to interpret. Responses were generally modest. For example, the "highest quality" eggs (M87CORN) contained only 10–12% more lipid, protein, and energy, on average, than the "lowest quality" eggs (D88CTRL and M89CTRL). For comparisons of interest (e.g. location, year, and supplemental feeding), significant differences among absolute component masses averaged ca. 8%. Among-group differences in proportional composition were even smaller. Among studies that documented potential survival advantages in relation to egg size, "big eggs" have averaged 15–60% larger than "small eggs" (Schifferli 1973, Nisbet 1978, Lundberg and Väisänen 1979, Ankney 1980, Rhymer 1988; differences based on fresh egg mass, egg volume, or hatchling mass). It is difficult to interpret the fitness consequences of subtle variation in egg composition, because the process of determining egg composition necessarily reduces the embryo's fitness to zero. Ricklefs (1984a, b) used within-clutch repeatability of egg composition to infer the effect of egg quality on growth characteristics in European Starlings (*Sturnus vulgaris*) (i.e. he analyzed one egg per clutch and measured growth rates for the remaining eggs in the clutch). Although Ricklefs (1984a) found little effect of egg quality on offspring growth and survival, it would be instructive to repeat this experiment on other birds, such as larids, where egg quality is more likely to be important (e.g. Parsons 1970, Lundberg and Väisänen 1979, Hébert and Barclay 1988).

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