

# INTRACLUTCH VARIATION IN EGG SIZE OF AMERICAN COOTS<sup>1</sup>

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**Abstract.** I measured within-clutch egg-size variability for 3,219 American Coot (*Fulica americana*) eggs from 357 completed clutches, and I determined relative egg volume for 882 eggs of known laying sequence from 233 completed clutches ranging from five to 13 eggs. Within-clutch variation was unrelated to mean egg size, clutch size, laying date, year, and nesting attempt, but was slightly affected by supplemental food. Relative egg size increased with laying sequence for the first two to five eggs, then declined for the remainder of the clutch. Variation in relative egg volume with laying sequence was essentially unaffected by year, laying date, and supplemental feeding, but differed among initial nests, renests, and continuation nests. Most previous work on within-clutch variation in egg size has focused on the last-laid egg, and patterns of variation in the size of this egg typically have been evaluated in the context of hatching asynchrony. However, no single adaptive hypothesis appears capable of explaining the pattern of intraclutch egg-size variation observed in American Coots, and I conclude that this pattern may result from physiological constraints.

**Key words:** American Coot; egg size; *Fulica americana*; hatching asynchrony; supplemental feeding.

## INTRODUCTION

Egg size varies with laying sequence in many species of birds (Parsons 1976, Clark and Wilson 1981, Leblanc 1987, Forbes and Ankney 1988). Intraclutch variation in egg size is usually interpreted in the context of hatching asynchrony (e.g., Howe 1976, O'Connor 1978, Clark and Wilson 1981, Ojanen et al. 1981, Slagsvold et al. 1984; but see Stokland and Amundsen 1988, Slagsvold and Lifjeld 1989). According to the brood-reduction hypothesis (Schüz in Lack 1947), last-laid egg(s) should be relatively small to accentuate size-hierarchies among nestlings, thereby facilitating efficient brood-reduction in the event of food shortages (Slagsvold et al. 1984). Similar reasoning applies to species with obligate siblicide, where the second-laid egg in two-egg clutches presumably serves as "insurance" against hatching failure or early nestling mortality of the first-laid egg (Edwards and Collopy 1983). In contrast, Clark and Wilson (1981; see also Husell 1972, Arnold et al. 1987) hypothesized that selection has favored early onset of incubation to minimize predation risks for first-laid eggs; hatching asynchrony is viewed as an inevitable (and possibly deleterious) byproduct of this be-

havior. According to this hypothesis, last-laid egg(s) should be relatively large to help overcome any disadvantages associated with asynchronous hatching (Clark and Wilson 1981).

These hypotheses may be overly simplistic. They focus on relative size of the last-laid egg (e.g., Slagsvold et al. 1984), but in several bird species the first-laid egg exhibits the most pronounced variation in relative size (e.g., Mead and Morton 1985, Greig-Smith et al. 1987, Leblanc 1987, Forbes and Ankney 1988, Slagsvold and Lifjeld 1989). In addition, intraclutch variation in egg size occurs in several species with self-feeding precocial young (Väisänen et al. 1972; Cooper 1978; Leblanc 1987; C. D. Ankney, pers. comm.), where hatching is highly synchronous and intra-brood competition is presumably low (e.g., Rohwer 1985, Lessells 1986).

Most studies of intraclutch egg-size variation have focused on species with relatively small clutches (e.g., 2-5 eggs; Slagsvold et al. 1984: Appendix). American Coots (*Fulica americana*, hereafter "coots") lay exceptionally large clutches (mean in this study, 9.4 eggs; range, 3-17;  $n = 665$ ) of fairly nutrient-rich eggs (Alisaukas 1986), which hatch over a period of several days (Arnold, unpubl. data). Newly-hatched young are almost completely dependent on parents for food for at least the first week after hatching, but soon gain proficiency at foraging for themselves (Desrochers and Ankney 1986, Driver 1988; see also Horsfall 1984). The purpose of this paper is to

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evaluate intraclutch egg-size variation in coots with respect to laying sequence, clutch size, laying date, and supplemental food availability, and to review potential explanations for this variation.

### STUDY AREA AND METHODS

Coots were studied during six years (1985–1990) at Minnedosa (50°16'N, 99°50'W), Manitoba. The Minnedosa study area consisted of up to 118 semipermanent and permanent wetlands ranging from about 0.1 to 3.0 ha in size. Supplemental food was provided on random subsamples of wetlands during 1987–1989. Food supplements included one or more of the following: steam-rolled corn, trout chow, rabbit chow, layer diet (for chickens), and oystershell (see Arnold 1990 for additional details).

Coot nests were found during systematic searches of emergent wetland vegetation conducted every 4–6 days. Most nests were revisited several times during egg-laying for various objectives; at each visit newly-laid eggs were numbered with a permanent black marking-pen. It was not logistically feasible to visit nests every day in this study, and such frequent disturbance sometimes resulted in nest abandonment. Thus, for a given nest, I usually knew exact laying order for some eggs, but only approximate laying order for the remainder of the clutch. I measured the length (L,  $\pm 0.05$  mm) and maximum breadth (B,  $\pm 0.05$  mm) of eggs using dial calipers. Egg volume was estimated using Hoyt's (1979) equation:  $\text{Volume (cm}^3\text{)} = 0.000507 \cdot \text{LB}^2$ . Estimated egg volume was relatively free of measurement error (0.34% ME,  $n = 76$  eggs measured twice each; Model II ANOVA, PROC NESTED, SAS Institute Inc. [1985]) and was an excellent predictor of fresh egg mass ( $r^2 = 0.96$ ,  $P < 0.0001$ ,  $n = 322$ ). In the following analyses, I used two different measures of intraclutch egg-size variation. For clutches with  $\leq 2$  unmeasured eggs, I used the standard deviation of within-clutch egg volume as a measure of within-clutch egg-size variation. The standard deviation of within-clutch egg volume was independent of the mean ( $r^2 = 0.0005$ ,  $n = 357$  clutches), so no transformation of data was necessary. The second data set included all eggs for which laying order was known exactly, and for which there were  $\leq 2$  unmeasured eggs in the clutch. Because most variation in egg volume occurs among, rather than within, clutches (Alisauskas 1986, Arnold 1990),

I calculated standardized volume for each known-sequence egg by subtracting the within-clutch mean and dividing by the within-clutch standard deviation (e.g.,  $z$  scores). This measure was superior to the previous one because it provided information on egg-size variation with respect to laying sequence; however, sample sizes were quite low for some analyses. Analyses based on the within-clutch standard deviation had larger sample sizes for examining trends in egg-size variation with respect to clutch size, laying date, and supplemental feeding.

Intraspecific nest parasitism was fairly frequent in this population (Arnold, unpubl. data). It was easy to exclude parasitic eggs from the sample of known-sequence eggs because two eggs would be added to a parasitized nest in a single day, and the parasitic egg could usually be identified based on eggshell color and/or spotting pattern (Arnold, unpubl. data). It was more difficult to identify parasitic eggs from among the sample of unsequenced eggs, and in some cases, within-clutch means and standard deviations may have been calculated from samples that included one or more parasitic eggs.

For analyses based on within-clutch standard deviations, I used regressions and ANOVA to analyze variation with respect to clutch size, laying date, supplemental feeding, and year (PROC GLM; SAS Institute Inc. 1985). I compared egg-size variation of re-nests (defined by  $\geq 2$  d lapse in egg laying) and continuation nests (0 or 1 d lapse in laying) with egg-size variation in the original nests using Wilcoxon matched-pairs signed-ranks tests; most data used in these analyses were from 1990, as re-nesting was not well documented in previous years. For analyses based on known-sequence eggs, I pooled data from 5- and 6-egg clutches and deleted clutches of  $\geq 14$  eggs because of low sample sizes. In preliminary analyses, I tested for effects of laying sequence on relative egg volume using one-way ANOVA and polynomial regressions (PROC GLM; SAS Institute Inc. 1985). I elected to use polynomial regressions because they adequately described the data, they explained nearly as much variation as did ANOVA, and they were much less sensitive to low sample sizes than were ANOVA. Effects of year, laying date, nest type (initial, continuation, or re-nest), and supplemental food (all controls vs. all feeding treatments) on relative egg size by laying sequence were analyzed by including appropriate interaction terms in the poly-

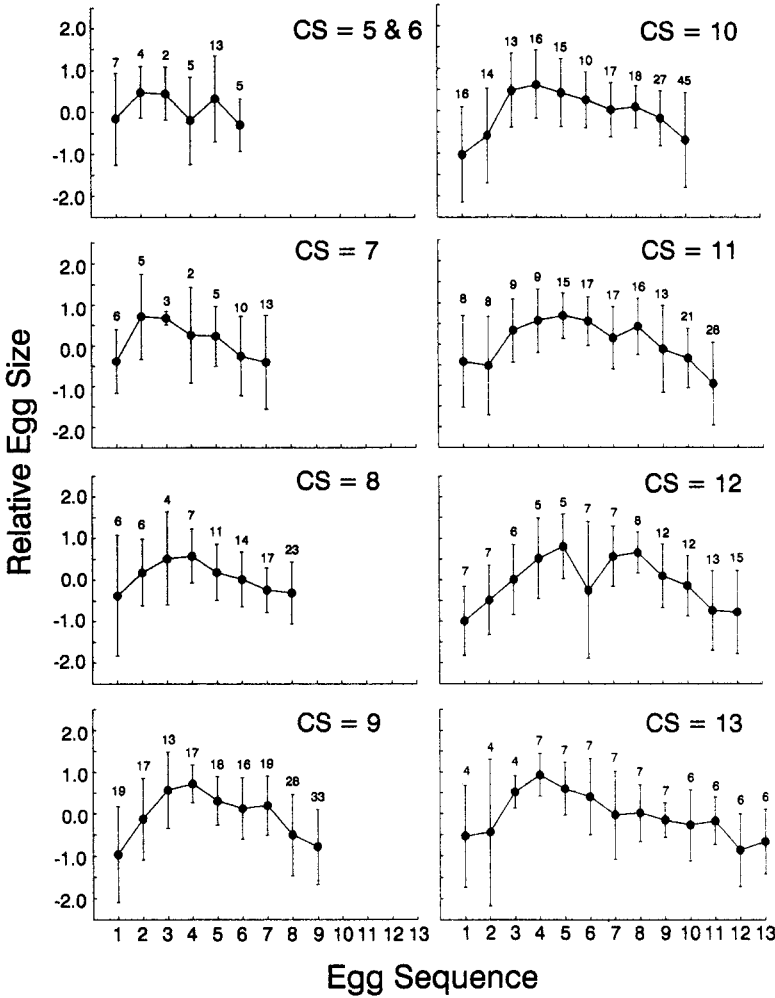


FIGURE 1. Relative egg volume ( $\bar{x} \pm 1$  SD) of American Coots in relation to clutch size (CS) and laying sequence. Relative egg volumes are corrected for within-clutch means and variances (e.g., z scores). Numbers above error bars are sample sizes. Statistical analyses are in Table 1.

nomial regression models (because clutch means were standardized to zero, main effects of these variables should not have been significant, except by chance).

**RESULTS**

**WITHIN-CLUTCH STANDARD DEVIATIONS**

Within-clutch standard deviations were calculated from 3,219 measured eggs in 357 clutches. The average within-clutch mean egg volume was 28.05 cm<sup>3</sup> and the average within-clutch standard deviation was 1.33 cm<sup>3</sup>. Standard deviations did not vary among years ( $F_{5,351} = 0.18, P = 0.97$ ), with clutch size ( $F_{1,355} = 0.13, P = 0.72$ ),

or with laying date ( $F_{1,352} = 2.08, P = 0.15$ ); however, supplementally-fed coots produced slightly less variable clutches than did controls ( $F_{1,355} = 4.17, P = 0.04$ ). This result was only marginally significant ( $F_{1,206} = 3.41, P = 0.07$ ) when 1985, 1986, and 1990 data were deleted (no supplemental food was provided in those years), but the effect size was not reduced (within-clutch standard deviations averaged  $1.39 \pm 0.08$  [1 SE] cm<sup>3</sup> for controls and  $1.22 \pm 0.05$  cm<sup>3</sup> for fed clutches). Egg size was slightly more variable in renests and slightly less variable in continuation nests (SD's averaged 0.26 larger and 0.11 smaller than in the original nests, respectively), but these

TABLE 1. Effects of laying sequence, laying date, and supplemental food on relative size of American Coot eggs.<sup>a</sup>

Clutch size	Sample size		Sequence effects		Date effects		Food effects	
	Ctrl	Fed	Seq	Seq <sup>2</sup>	Date × seq	Date × seq <sup>2</sup>	Food × seq	Food × seq <sup>2</sup>
5-6	22	14	0.23	0.23	0.73	0.76	0.24	0.24
7	22	22	0.23	0.12	0.20	0.14	0.66	0.71
8	82	6	0.04	0.01	0.84	0.83	0.97	0.95
9	116	64	0.0001	0.0001	0.03	0.008	0.61	0.73
10	142	49	0.0001	0.0001	0.17	0.16	0.80	0.91
11	67	94	0.0001	0.0001	0.83	0.73	0.68	0.59
12	70	34	0.0001	0.0001	0.97	0.79	0.13	0.14
13	32	46	0.03	0.004	0.54	0.68	0.67	0.85

<sup>a</sup> Results based on polynomial regressions; models testing for date and food effects included main effects of seq and seq<sup>2</sup>.

differences were not significant ( $T^+ = 272$ ,  $n = 38$ ,  $P > 0.05$ ;  $T^- = 69.5$ ,  $n = 19$ ,  $P > 0.05$ ; respectively).

#### KNOWN-SEQUENCE EGGS

I determined relative egg volume for 882 known-sequence coot eggs from 233 nests. The average within-clutch mean egg volume for these nests was 27.85 cm<sup>3</sup> and the average within-clutch standard deviation was 1.20 cm<sup>3</sup>. Hence, an egg with a standardized volume of  $-1.00$  was, on average, 1.20 cm<sup>3</sup> (4.3%) smaller than the average egg in the clutch. Standardized egg volume ranged from  $-3.80$  to  $2.45$ , and was negatively skewed ( $\text{SQRT}[b_1] = -0.24$ ,  $P = 0.004$ ). There was no annual variation in relative egg volume by laying sequence, except in 7-egg clutches ( $P[\text{year} \times \text{sequence}] = 0.02$ ,  $P[\text{year} \times \text{sequence}^2] = 0.01$ ). Based on inspection of the plotted data, I dismissed this result as an artifact of low and unbalanced sample sizes (sequence effects were not significant by themselves in 7-egg clutches [see below], and annual variation was not apparent in the preceding analysis of within-clutch standard deviations). Data were therefore pooled by year for remaining analyses.

Relative egg volume varied significantly with laying sequence in clutches of 8 to 13 eggs, but not in smaller clutches (Table 1). Volume tended to increase rapidly over the first two to four eggs, then decline slowly for the remainder of the clutch (Fig. 1). First, second, penultimate, and final eggs were smaller than average, and eggs three through six were larger than average, although this pattern was not always apparent within the smaller clutches (Fig. 1). Relatively small eggs were also relatively variable, as evidenced by negative correlations between the mean and the standard de-

viation of relative egg size (these correlations were significant for clutches of 9, 10, and 11). The number of eggs for which relative volume showed an initial increase was somewhat related to clutch size, with larger clutches exhibiting longer sequences of increase (Fig. 1). Patterns of intra-clutch variation in standardized egg length and standardized egg breadth were virtually identical to the patterns exhibited for volume (Arnold, unpubl. data).

For 29 clutches that were completely or near-completely sequenced (at most, data from one egg were missing), 27 (93%) had initial increases in egg volume and 22 (76%) had terminal declines (1986 and 1987 data only; two clutches of 6, one of 7, three of 8, six of 9, five of 10, five of 11, three of 12, and four of 13). First-laid eggs were  $>1$  SD smaller than the mean in 18 (62%) clutches, second-laid eggs in 1 clutch (3%), penultimate eggs in 9 (32%) clutches, and ultimate eggs in 15 clutches (52%); 12 (41%) clutches had one or more middle sequence eggs that were  $>1$  SD smaller than the mean. Clutches that failed to show the "typical" pattern of an initial increase and a terminal decline in egg size had fairly constant egg volumes over the initial and final sequences, and/or the pattern was obscured by large fluctuations in the volume of middle sequence eggs. The number of eggs over which egg volume showed an initial increase was positively correlated with clutch size ( $r_s = 0.46$ ,  $P = 0.01$ ), but no such relationship existed between clutch size and the length of the terminal decline ( $r_s = 0.25$ ,  $P = 0.18$ ).

Relative egg volume did not vary with laying date except in 9-egg clutches (Table 1). Correlations of relative volume with laying date for each laying sequence revealed that only 9th-laid

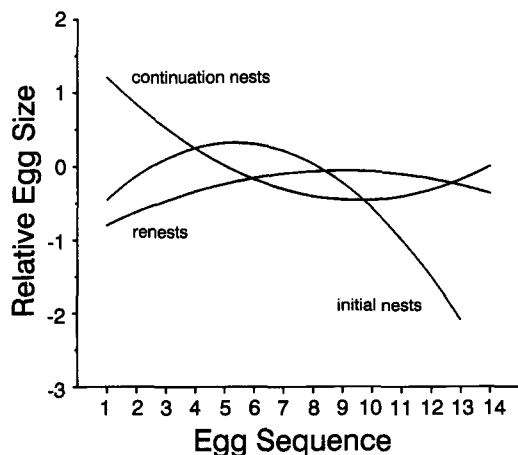


FIGURE 2. Relative egg volume of American Coots in relation to nest type and laying sequence. Curves are second-order polynomial regressions. Statistical differences among nest types are described in the text. Sample sizes are: initial nests, 182 eggs; renests, 36 eggs; and continuation nests, 33 eggs.

eggs varied with date ( $r = 0.48$ ,  $P = 0.004$ ,  $n = 33$ ). Examination of the scatterplot for 9th-laid eggs revealed that this correlation was driven by three late-season eggs; the relationship was not significant with these eggs deleted ( $r = 0.31$ ,  $P = 0.10$ ). Moreover, for other clutch sizes the correlations between laying date and relative egg volume of the last laid egg was both positive and negative, and never significant ( $P > 0.19$ ). I therefore dismissed this result as spurious.

Continuation nests and renests exhibited different patterns of egg-size variation than did initial nests (Fig. 2;  $P[\text{nest} \times \text{sequence}] = 0.0008$ ,  $P[\text{nest} \times \text{sequence}^2] = 0.0002$ ). Continuation nests did not exhibit an initial increase in relative egg size, and neither continuation nests nor renests exhibited as precipitous a decline in late-sequence egg size as did initial nests (Fig. 2). These results should be considered tentative in view of the small sample sizes for reneest and continuation nest eggs.

Supplemental feeding did not affect patterns of relative egg volume by laying sequence for any clutch size (Table 1). Because Horsfall (1984) has shown that supplemental food affected relative egg size of European Coots (*Fulica atra*), I conducted an additional analysis similar to his (Horsfall 1984: Fig. 5) using only the first five eggs of each clutch (clutches of five and six eggs were excluded, remaining clutches were pooled

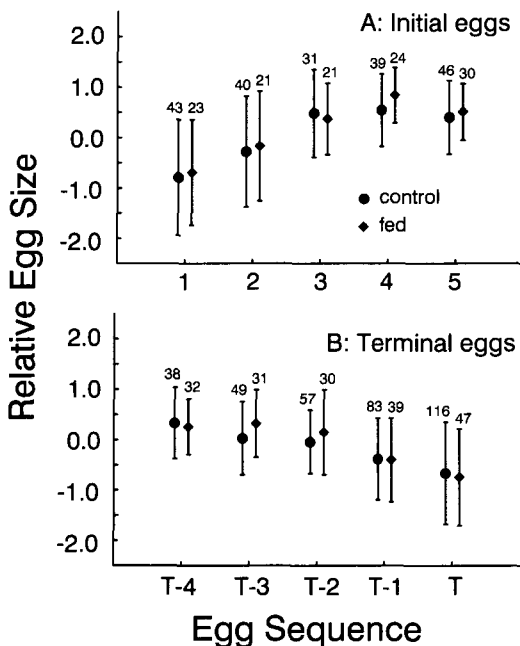


FIGURE 3. Effects of supplemental food and laying sequence on relative egg size ( $\bar{x} \pm 1$  SD) of American Coots for the first (A) and last five eggs (B; T = terminal egg, etc.) in the clutch ( $CS \geq 7$  only). Numbers above error bars are sample sizes. Supplemental feeding effects were not significant (see text).

for analysis). Relative egg size increased in a curvilinear pattern, with the largest increases occurring over the first three sequence positions (Fig. 3A; sequence effect:  $F_{(1,313)} = 38.97$ ,  $P = 0.0001$ ; sequence<sup>2</sup> effect:  $F_{(1,313)} = 20.75$ ,  $P = 0.0001$ ); this was similar to the pattern observed in European Coots (Horsfall 1984: Fig. 5). Unlike European Coots, however, there was no effect of supplemental food on relative egg volume of the first five eggs (Fig. 3A; food  $\times$  sequence effect:  $F_{(1,313)} = 0.15$ ,  $P = 0.70$ ; food  $\times$  sequence<sup>2</sup> effect:  $F_{(1,313)} = 0.02$ ,  $P = 0.90$ ). I conducted a similar analysis using the last five eggs from each clutch. American Coots exhibited a decline in relative egg size at the end of the clutch (Fig. 3B; sequence effect:  $F_{(1,517)} = 23.63$ ,  $P = 0.0001$ ; sequence<sup>2</sup> effect:  $F_{(1,517)} = 3.92$ ,  $P = 0.05$ ) (Horsfall did not present any data on last-laid eggs of European Coots, but stated that last-laid eggs declined in size, p. 94). As in the preceding analysis, supplemental food did not proximately affect this pattern (Fig. 3B; food  $\times$  sequence effect:  $F_{(1,517)} = 1.46$ ,  $P = 0.23$ ; food  $\times$  sequence<sup>2</sup> effect:  $F_{(1,517)} = 1.00$ ,  $P = 1.00$ ).

## DISCUSSION

Relative egg size in this population of American Coots increased rapidly over the first two to four eggs, then declined slowly for the remainder of the clutch. The first-, penultimate-, and last-laid eggs (and sometimes the second-laid) were relatively small, and the third- through fifth-laid eggs were usually relatively large; this pattern was consistent and statistically significant for clutches of 8–13 eggs (sample sizes were generally small for clutches of <8 eggs). I am not aware of any hypothesis that predicts such a pattern, although several other studies have noted a pattern of relatively small first- and last-laid eggs (e.g., Parsons 1976; Cooper 1978; Greig-Smith et al. 1987; Leblanc 1987; C. D. Ankney, pers. comm.).

Supplemental feeding appeared to reduce the amount of within-clutch egg-size variation in coots, but effects of supplemental food on relative egg volume could not be detected for any specific laying sequence, or for first- and last-laid eggs in general. Supplemental feeding affected other variables such as clutch size, adult body condition, and fledgling mass (Arnold 1990, unpubl. data), suggesting that food supplements provided coots with high-quality nutrition. I therefore conclude that sequence-specific patterns of intraclutch egg-size variation in American Coots are not proximately affected by food supply. I attribute the slight reduction in within-clutch egg-size variation of supplementally-fed coots to a proximate food effect; e.g., coots occasionally lay relatively small eggs due to proximate energetic constraints, but these constraints occur randomly (and rarely) throughout the laying sequence, and they do not cause the pattern of initial increase and terminal decline. Consistent with this view, supplemental feeding did not affect mean egg size per se, but laying skips were less frequent among fed coots (laying skips were rare in any case, i.e., food limitation appeared to be an infrequent constraint during egg laying) (Arnold 1990).

Leblanc (1987) compared relative egg sizes of captive Canada Geese (*Branta canadensis*) on ad libitum diets with those of wild geese on natural diets and likewise concluded that food had little proximate effect on patterns of intraclutch egg-size variation. Karlsson (*in* Slagsvold et al. 1984) was able to affect laying date and egg size (among females) of European Starlings (*Sturnus vulgaris*)

by providing supplemental food, but relative egg size of the last-laid egg was unaffected by food availability. Reid (1987), however, was able to affect the relative size of the third-laid (terminal) egg in Glaucous-winged Gulls (*Larus glaucescens*) by providing females with supplemental food. Female Glaucous-winged Gulls appeared to be food-limited during late egg-laying due to reductions in courtship feeding by their mates, and relative size of the third-laid egg was positively correlated with courtship feeding rate (Salzer and Larkin 1990).

Horsfall (1984) showed that supplemental food resulted in greater relative masses of first- and second-laid eggs in European Coots. Horsfall interpreted this as an adaptation to minimize size-disparities among broodmates, and hence minimize the likelihood of brood-reduction, given the availability of predictable, superabundant food. This interpretation was likely incorrect, however, because first-laid eggs of supplementally-fed European Coots were relatively larger (Horsfall 1984: Fig. 5) and therefore produced relatively larger chicks (Horsfall 1984: Fig. 6) which also hatched earlier (Horsfall 1984: Fig. 3) and therefore attained even greater body size than did chicks from later-laid eggs; these factors would all serve to *exacerbate* brood hierarchies and *increase* the likelihood of brood reduction among supplementally-fed European Coot broods (e.g., Stokland and Amundsen 1988). To have reduced size disparities among broodmates, supplementally-fed European Coots would either have had to delay the onset of incubation and/or have produced relatively smaller first eggs; they appeared to do neither. Although the functional explanation for Horsfall's results remain obscure, the different responses by European and American coots to supplemental food are nevertheless intriguing.

American Coots use both endogenous nutrient reserves and exogenous food resources during egg formation (Alisauskas and Ankney 1985; but see Arnold 1990). Although my supplemental feeding experiments suggested that patterns of relative egg size were not proximately affected by food availability, these patterns might still correspond to ultimately predictable patterns of nutrient availability during egg formation.

Alisauskas and Ankney (1985) noted that egg size of American Coots declined with laying sequence (they did not detect an initial increase),

and they interpreted this result in terms of nutrient reserve "savings" for the laying female. But endogenous reserves represent a fixed amount of nutrients that are available for egg formation, and there is no reason why egg size need decline with sequence to "save" reserves; coots need only lay consistent-sized eggs of the same average size and composition. Coots might, however, be rate-limited in their ability to mobilize body reserves for egg synthesis. This should not affect albumen synthesis, because the albumen of a given egg is produced in a single day and therefore represents a constant daily investment provided that eggs are of similar size and composition (e.g., Alisauskas and Ankney 1985: Fig. 5). Yolks, on the other hand, overlap in development and the largest daily nutrient costs for yolk synthesis are incurred during the formation of middle-sequence eggs (Alisauskas and Ankney 1985: Fig. 5). Coots, however, obtained their highest "estimated savings" on the last day of laying, when their costs were lowest, and many of these birds possessed substantial remaining lipid reserves at clutch completion (Alisauskas and Ankney 1985: Fig. 3). Because "estimated savings" do not overlap with "estimated costs," it suggests that intra-clutch variation in egg size is not the result of ultimate constraints imposed by endogenous nutrient reserves. Furthermore, given that late-sequence egg size declined less rapidly among continuation nests and renests (Fig. 2), where coots had presumably already utilized much of their endogenous reserves to produce an initial clutch, it seems even less likely that declining late-sequence egg size is a function of proximate nutrient reserve constraints.

Coots apparently meet most of their protein and maintenance energy requirements through daily foraging (Alisauskas and Ankney 1985, Arnold 1990). Any factor(s) which consistently affected the availability of dietary food resources during egg laying could ultimately affect patterns of egg-size variation. In most temperate wetland systems, availabilities of aquatic invertebrates and submerged vascular plants are increasing during the period when coots are producing eggs (Arnold 1990; see also Daan et al. 1989), suggesting that egg size should increase with laying sequence due to more abundant food. However, egg-size variation was unaffected by laying date; moreover, mean size and nutrient content of eggs declined seasonally, contrary to food availability

(Arnold 1990; Arnold et al., unpubl. MS). Although food abundance is likely increasing during the laying period, the amount of time available for foraging is probably declining due to increasing incubation constancy (Arnold, unpubl. data). However, digestive tract contents (g) of laying female coots did not vary with number of eggs laid ( $r = -0.03$ ,  $P = 0.89$ ,  $n = 25$ ; Arnold, unpubl. data), suggesting that food consumption was fairly constant throughout laying. Hence, ultimately predictable patterns of endogenous and exogenous nutrient availability are not consistent with observed patterns of intraclutch egg-size variation.

Alternatively, coots may invest differentially in eggs based on their probability of producing surviving chicks. This hypothesis requires that reproductive value of eggs should vary with laying or hatching order and with relative egg size (e.g., Parsons 1970, Schifferli 1973, Ankney 1980, Horsfall 1984). This hypothesis predicts two very different patterns of egg-size variation depending on whether brood reduction is the adaptive goal, or a maladaptive consequence, of hatching asynchrony (e.g., Clark and Wilson 1981, Slagsvold et al. 1984): (1) in species for which food resources frequently limit brood size, late-sequence eggs might be smaller to facilitate brood-reduction, and (2) in species where brood-reduction is a maladaptive consequence of selection for early incubation onset (e.g., Clark and Wilson 1981, Arnold et al. 1987), late-sequence eggs might be larger to offset the competitive disadvantage of late-hatched young. Prediction 1 is weakened by three general observations: (1) egg size is unimportant, relative to hatching order, in determining nestling size hierarchies (Stokland and Amundsen 1988), (2) many birds appear capable of rearing larger than normal broods (reviewed in Lessells 1986, Ydenberg and Bertram 1989), and, most importantly, (3) in almost all cases where nestling size hierarchies have been experimentally reduced, synchronous broods have fledged more young than asynchronous broods (reviewed in Amundsen and Stokland 1988). If brood-reduction is a deleterious and inevitable by-product of selection for early onset of incubation, then egg size might also be smaller in late-sequence eggs if increased egg size did little to offset survival disadvantages of late-hatched chicks (e.g., Bancroft 1984, Arcese and Smith 1988) and if nutrients could be invested more

profitably elsewhere (e.g., towards additional eggs, incubation, or renesting; De Laet and Dhondt 1989, Moreno 1989, Rohwer and Eisenhauer 1989). By combining this "egg value hypothesis" with the nutrient limitation hypothesis, Alisauskas and Ankney's (1985) hypothesis of nutrient "savings" might become a tenable explanation of declining egg mass among late-sequence coot eggs, although it still cannot explain the relatively small size of first-laid eggs. The combined effects of incubation onset, brood reduction, nest loss, and hatching failure might conceivably produce a pattern of sequence-specific egg values that was consistent with observed patterns of egg-size variation, but I lack the quality of empirical data necessary to attempt this.

Leblanc (1987) suggested that the smaller size of first-laid and last-laid eggs in Canada Geese might be physiological responses to changing hormonal levels associated with onset of egg-laying and onset of incubation, respectively (see also Mead and Morton 1985). Although this does not represent an adaptive hypothesis, it can be formulated as such by supposing that the costs of a more refined physiological control system outweigh any benefits of uniform egg size. In coots, onset of incubation typically occurred between the third and sixth eggs, with onset occurring earlier among late-season and small clutches (Arnold, unpubl. data). Although variation in incubation onset with respect to clutch size was somewhat consistent with patterns of egg-size variation (e.g., Fig. 1; duration of initial increase is positively correlated with clutch size), the lack of laying date effects on relative egg size was not consistent with this hypothesis. The small size of first- and second-laid eggs might be attributable to "gearing up" physiologically for egg production (Parsons 1976), and the lack of early egg effects in continuation nests is certainly consistent with this hypothesis (this is based on only three eggs, however). Finally, I note that the length of the terminal decline among larger clutches is five to seven eggs (Fig. 1), which is coincidentally similar to the number of simultaneously-developing follicles in laying coots ( $\leq 7$ , Alisauskas and Ankney 1985; typically 4–6, Arnold, unpubl. data). Perhaps the hormonal mechanism used to suppress development of additional follicles as coots near clutch completion also affects yolk deposition of currently developing follicles. Given the inability of current adaptive hypotheses

to explain the full range of intraclutch egg-size variation in coots and other birds, these physiological explanations may warrant additional consideration.

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#### LITERATURE CITED

- ALISAUSKAS, R. T. 1986. Variation in the composition of the eggs and chicks of American Coots. *Condor* 88:84–90.
- ALISAUSKAS, R. T., AND C. D. ANKNEY. 1985. Nutrient reserves and the energetics of reproduction in American Coots. *Auk* 102:133–144.
- AMUNDSEN, T., AND J. N. STOKLAND. 1988. Adaptive significance of asynchronous hatching in the Shag: a test of the brood reduction hypothesis. *J. Anim. Ecol.* 57:329–344.
- ANKNEY, C. D. 1980. Egg weight, survival and growth of Lesser Snow Goose goslings. *J. Wildl. Manage.* 44:174–182.
- ARCESE, P., AND J. N. M. SMITH. 1988. Effects of population density and supplemental food on reproduction in Song Sparrows. *J. Anim. Ecol.* 57:119–136.
- ARNOLD, T. W. 1990. Food limitation and the adaptive significance of clutch size in the American Coot (*Fulica americana*). Ph.D. diss., University of Western Ontario, London.
- ARNOLD, T. W., F. C. ROHWER, AND T. ARMSTRONG. 1987. Egg viability, nest predation, and the adaptive significance of clutch size in prairie ducks. *Am. Nat.* 130:643–653.
- BANCROFT, G. T. 1984. Patterns of variation in size of Boat-tailed Grackle *Quiscalus major* eggs. *Ibis* 126:496–510.
- CLARK, A. B., AND D. S. WILSON. 1981. Avian breeding adaptations: hatching asynchrony, brood reduction and nest failure. *Q. Rev. Biol.* 56:253–277.
- COOPER, J. A. 1978. The history and breeding biology of the Canada Geese of Marshy Point, Manitoba. *Wildl. Monogr.* No. 61.
- DAAN, S., C. DIJKSTRA, R. DRENT, AND T. MEIJER. 1989. Food supply and the annual timing of avian



- reproduction. Pp. 392–407 in Proc. XIX Intern. Ornithol. Congr., Ottawa, Canada.
- DE LAET, J. F., AND A. A. DHONDT. 1989. Weight loss of the female during the first brood as a factor influencing second brood initiations in Great Tits *Parus major* and Blue Tits *P. caeruleus*. *Ibis* 131: 281–289.
- DESROCHERS, B. A., AND C. D. ANKNEY. 1986. Effect of brood size and age on the feeding behavior of adult and juvenile American Coots (*Fulica americana*). *Can. J. Zool.* 64:1400–1406.
- DRIVER, E. A. 1988. Diet and behaviour of young American Coots. *Wildfowl* 39:34–42.
- EDWARDS, T. C., JR., AND M. W. COLLOPY. 1983. Obligate and facultative brood reduction in eagles: an examination of factors that influence fratricide. *Auk* 100:630–635.
- FORBES, M.R.L., AND C. D. ANKNEY. 1988. Intra-clutch variation in egg weights of Pied-billed Grebes. *Condor* 90:709–711.
- GREIG-SMITH, P. W., C. J. FEARE, E. M. FREEMAN, AND P. L. SPENCER. 1987. Causes and consequences of egg-size variation in the European Starling *Sturnus vulgaris*. *Ibis* 129:1–10.
- HORSFALL, J. A. 1984. Food supply and egg mass variation in the European Coot. *Ecology* 65:89–95.
- HOWE, H. F. 1976. Egg size, hatching asynchrony, sex, and brood reduction in the Common Grackle. *Ecology* 57:1195–1207.
- HOYT, D. F. 1979. Practical methods of estimating volume and fresh weights of bird eggs. *Auk* 96: 73–77.
- HUSSELL, D.J.T. 1972. Factors affecting clutch size in arctic passerines. *Ecol. Monogr.* 42:317–364.
- LACK, D. 1947. The significance of clutch-size. Parts I and II. *Ibis* 89:302–352.
- LEBLANC, Y. 1987. Intraclutch variation in egg size of Canada Geese. *Can. J. Zool.* 65:3044–3047.
- LESSELLS, C. M. 1986. Brood size in Canada Geese: a manipulation experiment. *J. Anim. Ecol.* 55: 669–689.
- MEAD, P. S., AND M. L. MORTON. 1985. Hatching asynchrony in the Mountain White-crowned Sparrow (*Zonotrichia leucophrys oriantha*): a selected or incidental trait? *Auk* 102:781–792.
- MORENO, J. 1989. Strategies of mass change in breeding birds. *Biol. J. Linn. Soc.* 37:297–310.
- O'CONNOR, R. J. 1978. Growth strategies in nestling passerines. *Living Bird* 16:209–238.
- OJANEN, M., M. ORELL, AND R. A. VÄISÄNEN. 1981. Egg size variation within clutches: effects of ambient temperature and laying sequence. *Ornis Fenn.* 58:93–108.
- PARSONS, J. 1970. Relationship between egg size and post-hatching chick mortality in the Herring Gull *Larus argentatus*. *Nature* 228:1221–1222.
- PARSONS, J. 1976. Factors determining the number and size of eggs laid by the Herring Gull. *Condor* 78:481–492.
- REID, W. V. 1987. Constraints on clutch size in the Glaucous-winged Gull. *Stud. Avian Biol.* 10:8–25.
- ROHWER, F. C. 1985. The adaptive significance of clutch size in prairie ducks. *Auk* 102:354–361.
- ROHWER, F. C., AND D. I. EISENHAUER. 1989. Egg mass and clutch size relationships in geese, eiders, and swans. *Ornis Scand.* 20:43–48.
- SALZER, D. W., AND G. J. LARKIN. 1990. Impact of courtship feeding on clutch and third-egg size in Glaucous-winged Gulls. *Anim. Behav.* 39:1149–1162.
- SAS INSTITUTE INC. 1985. SAS user's guide: statistics. Version 5 edition. SAS Institute Inc., Cary, NC.
- SCHIFFERLI, L. 1973. The effect of egg weight on the subsequent growth of nestling Great Tits *Parus major*. *Ibis* 115:549–558.
- SLAGSVOLD, T., AND J. T. LIFJELD. 1989. Constraints on hatching asynchrony and egg size in Pied Flycatchers. *J. Anim. Ecol.* 58:837–849.
- SLAGSVOLD, T., J. SANDVIK, G. ROFSTAD, O. LOR-ENSTEN, AND M. HUSBY. 1984. On the adaptive significance of intra-clutch egg variation in birds. *Auk* 101:685–697.
- STOKLAND, J. N., AND T. AMUNDSEN. 1988. Initial size hierarchy in broods of the Shag: relative significance of egg size and hatching asynchrony. *Auk* 105:308–315.
- VÄISÄNEN, R. A., O. HILDÉN, M. SOIKKELI, AND S. VUOLANTO. 1972. Egg dimension variation in five wader species: the role of heredity. *Ornis Fenn.* 49:25–44.
- YDENBERG, R. C., AND D. F. BERTRAM. 1989. Lack's clutch size hypothesis and brood enlargement studies on colonial seabirds. *Colonial Waterbirds* 12:134–137.