

THE ADAPTIVE SIGNIFICANCE OF NUTRIENT RESERVES TO BREEDING AMERICAN COOTS: A REASSESSMENT¹

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Abstract. Female American Coots (*Fulica americana*) lay large clutches of nutrient-rich eggs, and both sexes assist with incubation and brood-rearing. We studied the role of stored fat, protein, and ash reserves in meeting the nutritional demands of reproduction by analyzing carcass composition of 138 male and 181 female coots collected in southwestern Manitoba during 1987-1991. For females, mean reserve levels did not change between prelaying, laying, incubation, early brood-rearing, and late brood-rearing; however, fat reserves of males doubled between early and late brood-rearing (21.1 vs. 45.2 g, respectively). Females with larger fat reserves began nesting earlier, but paradoxically, they did not utilize nutrient reserves for egg laying, and in 1991 females even accumulated fat reserves during laying. Both sexes accumulated fat reserves during incubation and brood-rearing. Coots that had access to supplemental food during laying, incubation, and late brood-rearing had larger fat and protein reserves, but supplemental food did not otherwise alter patterns of nutrient-reserve usage. Nutrient-reserve dynamics of American Coots differed markedly from sympatric populations of breeding ducks, which utilize fat reserves extensively during laying and incubation. We believe that two principal factors contribute to this difference: (1) the nutrient demands of egg formation in coots are about one-half those of comparable-sized ducks, and (2) biparental care in coots allows males and females to share the costs of incubation and brood-rearing, whereas in ducks these costs are incurred entirely by females. We conclude that reproduction in American Coots is not constrained by the availability of endogenous nutrients.

Key words: *American Coot, brood-rearing, clutch size, energetics, Fulica americana, incubation, nutrient reserves, supplemental feeding, timing of breeding.*

INTRODUCTION

Most species of waterfowl produce large clutches of energy-rich eggs (Lack 1968, Sotherland and Rahn 1987). However, clutch size and relative egg size are inversely correlated, which led Lack (1967) to hypothesize that clutch size in waterfowl was limited by the amount of food that females could consume during egg formation. Because some Arctic-nesting geese begin laying eggs before food is generally available, Ryder (1970) modified Lack's hypothesis to include stored energy reserves as an additional source of "food" for the laying female. It is now generally recognized that endogenous reserves constitute an important source of nutrients for laying female waterfowl (reviewed by Ankney and Alisauskas 1991b, Alisauskas and Ankney 1992), although

the extent to which these reserves determine clutch size is still debated (Ankney et al. 1991, Arnold and Rohwer 1991).

Altricial birds generally have small clutches of energy-poor eggs (Lack 1968, Sotherland and Rahn 1987), so the energetic costs of clutch formation are low, relative to waterfowl (Rohwer 1992). Although there have been comparatively few studies of nutrient-reserve dynamics in altricial birds, most have shown that females do not use appreciable amounts of stored nutrients during egg formation (Ankney and Scott 1980, Hails and Turner 1985, Kremenetz and Ankney 1988, Young 1989; but see Jones and Ward 1976). Such findings are consistent with the hypothesis that altricial birds are most likely to be food-limited during the brood-provisioning period (Lack 1947).

American Coots (*Fulica americana*) exhibit a reproductive strategy intermediate between waterfowl and altricial birds. Like waterfowl, they lay large clutches of energy-rich eggs (Arnold et al. 1991, Arnold 1994a), but they invest only about one-half as much energy into clutch

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formation as do comparable-sized waterfowl (Arnold and Rohwer 1991). Like waterfowl, hatchling coots exhibit precocial development, but coots are more similar to altricial birds in terms of parental care requirements during the early brood-rearing period. Young coots are fed by their parents for at least the first two weeks post-hatching, but obtain much of their own food for the remaining 5–6 weeks of the fledging period (Ryan and Dinsmore 1979). Thus, a reasonable *a priori* expectation might be that American Coots would rely on endogenous reserves during egg formation, but to a lesser extent than waterfowl. However, Alisauskas and Ankney (1985) estimated that laying female coots obtained 85% of their fat and 28% of their protein requirements from nutrient reserves. This estimated rate of fat use during egg laying was exceeded by only two of 10 species of temperate-nesting ducks, whereas the rate of protein use was exceeded by only one species (Ankney and Alisauskas 1991b). Thus, Alisauskas and Ankney (1985) hypothesized that female American Coots were limited by nutrient availability during clutch formation, and that nutrient reserves were important determinants of clutch size and timing of breeding. However, their hypothesis is not consistent with recent findings that: (1) laying coots can renest rapidly following clutch loss, with some individuals laying greater than 20 eggs almost consecutively (Arnold 1993), and (2) coots respond only slightly to supplemental food, advancing their timing of breeding by about one day and increasing their clutch size by less than one egg, despite having ad libitum access to high-quality food (Arnold 1994a). Thus, in this study, we reassessed the role of nutrient reserves during the breeding cycle of American Coots.

METHODS

STUDY AREA

Our study was conducted at the Minnedosa Substation of the Delta Waterfowl and Wetlands Research Station, located approximately 10 km southeast of Minnedosa, Manitoba (50°16'N, 99°50'W) and 100 km west of Alisauskas and Ankney's (1985) study area at Delta Marsh, Manitoba (50°11'N, 98°19'W). Our study area contained upwards of 40 wetland basins km⁻² and supported high densities of breeding

American Coots during most years (Arnold 1994b).

Supplemental feeding experiments were conducted during 1987–1989 and 1991 (Arnold 1994a). On wetlands where supplemental food was provided, coots had ad libitum access to steam-rolled corn, rabbit chow, layer diet for chickens, oyster shell, and poultry grit (see Arnold 1994a for additional details).

STUDY SPECIES

American Coots are monogamous, and pairs vigorously defend all-purpose territories from spring arrival (15 April–10 May) through the end of brood-rearing (early August). The majority of clutches are initiated between 11 and 24 May (Arnold 1994a), and most pairs will re-nest if early clutches are destroyed (Arnold 1993). Clutch size varies between 3 and 18, but clutches of 8 to 12 eggs are most common. Clutch size also varies among years and typically declines with laying date (Arnold 1994a). Coot eggs are similar to those of waterfowl and other precocial birds in terms of energy density (i.e., 8.3 kJ/g wet weight; Sotherland and Rahn 1987, Arnold et al. 1991), but coot eggs are only about two-thirds the relative size of waterfowl eggs (based on waterfowl of similar adult body mass; Arnold and Rohwer 1991). Both parents assist approximately equally with incubation, brooding, and feeding the young (Ryan and Dinsmore 1979). Adult coots initiate a flightless wing molt during late summer (mid-July through mid-August), which often overlaps with brood-rearing (C. D. Ankney and T. W. Arnold, unpubl. data). During late August to early September, most adults leave their breeding areas and begin staging for fall migration.

FIELD METHODS

We collected adult male and female coots throughout the breeding and molting periods, from the time they arrived at Minnedosa shortly after ice-out (mid-April) until they departed for fall staging areas and/or began southward migration (August to early-September). In this paper, we assess nutrient-reserve dynamics of breeding coots from spring arrival through the end of brood-rearing (Table 1). In a companion paper we will examine nutrient-reserve dynamics of molting coots from the end of brood-rearing through the completion of wing molt. Our analyses overlap during late brood-rearing

because most coots exhibited molt-breeding overlap, and data from this period were therefore essential for both analyses.

To avoid causing excessive disturbance on wetlands where we later gathered nesting data, we collected most prelaying coots on wetlands just outside of our intensive study area. We combined the arriving and paired stages used by Alisauskas and Ankney (1985) into a single "prelaying" category because we could not objectively determine the pairing status of most coots that we collected. However, we believe that most coots were paired because they were either alone or with one other coot when collected; only 16% (18/113) of our prelaying sample were in flocks of ≥ 3 coots (definition of arriving category used by Alisauskas and Ankney 1985). Flocked birds were typically observed only during April. However, during 1988 and 1989 we collected 10 "nonbreeders" during May; these birds were in large flocks (≥ 10 coots) on large wetlands and were unlikely to have obtained territories or bred (Arnold 1994b). We therefore excluded nonbreeders (including all 1989 samples) from our data. Most laying and incubating coots were collected from specific nests with known laying histories (i.e., timing of breeding, clutch size, and mean egg volume for these birds were known based on repeated nest visits). Coots in the early brood-rearing category were collected while tending young that were less than two weeks old (< 150 g); nesting histories of most coots in this category were unknown. Most coots in the late brood-rearing category were collected from wetlands where chicks had been individually marked and general nesting information was known (Arnold 1990); however, adults were not marked, so we could not associate these coots with specific nests. Coots were collected by shooting or nest-trapping (Crawford 1977).

CARCASS ANALYSIS

We measured total length, tarsus length, middle toe length, and head length of each coot on the day of collection (Alisauskas and Ankney 1985). We excluded several variables used by Alisauskas and Ankney (1985) because of unacceptably high measurement errors (Lougheed et al. 1991). We also excluded wing measurements because they varied with molting status and bill and claw measurements because they

varied seasonally (T. W. Arnold and C. D. Ankney, unpubl. data). Keel length was measured during dissection (see below).

We assigned age classes based on presence/absence of the bursa of Fabricius, as determined during necropsies. We assumed that coots with a bursal length ≥ 10 mm were yearlings (SY) and coots without a recognizable bursa were after-second-year (ASY) adults; however, this technique has not been evaluated on samples of known-age coots. We did not assign age classes based on tarsal coloration (Crawford 1978) because we found this technique had unacceptably high measurement error (21.2%; Arnold 1990: Appendix 3).

Coots were plucked to remove all flight and contour feathers and to assess molting status. Female coots (and coots of unknown sex) were opened on the day of collection and the ovary and oviduct were removed and stored in 10% formaldehyde. The remaining carcass was sealed in double plastic bags and frozen until subsequent analysis. Thawed carcasses were dissected to remove ingesta contents from the digestive tract. Visible fat deposits were removed from the visceral cavity and individual organs; this fat (referred to as abdominal fat) was weighed and discarded. For male coots, the testes were weighed wet and discarded. The left breast and leg muscles (as defined by Ankney and MacInnes 1978) were excised and weighed wet. The feet were severed just above the tarsometatarsus-tibiotarsus joint and discarded. Alisauskas and Ankney (1985) included the feet with their carcass homogenates, so their estimates of ash reserves are about 1 g larger. All organs, except the liver and breast and leg muscles, were combined with the remainder of the carcass and ground twice in a Hobart meat grinder. This homogenate, or an approximately 300-g subsample of this homogenate for large birds, was dried to constant weight at 90°C (Kerr et al. 1982). The liver, left leg muscle, and left breast muscle were dried separately. Dried samples were weighed and homogenized to a fine powder using an electric coffee grinder.

Fat content of dried liver, leg, breast, and carcass homogenates were determined by petroleum ether extraction in a modified Soxhlet apparatus (Dobush et al. 1985). Lean dry weights (LDW) of the liver, leg, and breast muscles were assumed to consist entirely of protein (Ankney and Afton 1988). Lean dry samples of

TABLE 1. Definitions of reproductive categories and subcategories used in analyses of nutrient-reserve dynamics of adult male (M) and female (F) American Coots.

Categories	Dates	Definitions
Prelaying	17 Apr–28 May	Male and female coots collected during April or May that had not laid eggs, did not have brood patches, and were not in flocks (≥ 3 coots), except during April ($n = 47$ M, 76 F).
Pre-RFG	17 Apr–24 May	Subcategory of prelaying females where the largest follicle was < 8 mm in diameter ($n = 46$).
RFG	30 Apr–28 May	Subcategory of Prelaying females where the largest follicle was ≥ 8 mm in diameter ($n = 30$).
Early-RFG	30 Apr–24 May	Subdivision of RFG females where the 3rd largest follicle was < 8 mm in diameter ($n = 18$).
Late-RFG	9 May–28 May	Subdivision of RFG females where ≥ 3 follicles were ≥ 8 mm in diameter ($n = 12$).
Laying	11 May–29 May	Females that had laid ≥ 1 egg and had ≥ 1 developing follicle of ≥ 15 mm in diameter or an oviducal egg ($n = 43$). Males collected from laying stage territories ($n = 26$).
Incubation	15 May–11 Jun	Males and females with brood patches and completed clutches ($n = 20$ M, 31 F).
End-of-laying	15 May–10 Jun	Subcategory of incubating females that had laid their last egg ≤ 4 days ago ($n = 17$).
Early brood	21 Jun–23 Jul	Males and females shot while tending chicks less than 2 weeks old (< 150 g) ($n = 10$ M, 8 F).
Late brood	23 Jun–5 Aug	Males and females that had not yet shed their primaries and were collected from known nesting wetlands 40–60 days after the majority of nests had hatched ($n = 35$ M, 19 F).

carcass homogenates were ashed in a muffle furnace at 550°C for 6 hours. All oxidized material was assumed to be protein, and remaining residue was used to calculate total ash content of the carcass. Estimated protein fractions of the carcass, leg, breast, and liver homogenates were summed to obtain total protein, and the fat content of these homogenates were summed with abdominal fat to obtain total fat reserve.

The preserved ovaries of collected females were examined to determine numbers of developing, post-ovulatory, and atretic follicles (Ankney and MacInnes 1978). All developing or atretic follicles ≥ 8 mm in diameter were removed, weighed wet, individually dried at 80°C, and reweighed. Wet and dry weights were also obtained for the remainder of the ovary and the oviduct. Prelaying females with one or more yolky follicles ≥ 8 mm in diameter were considered to have initiated rapid follicle growth (RFG); those with no developing follicles were classified as pre-RFG (Table 1). We further divided RFG females into early- and late-RFG based on numbers of developing follicles (Table 1). We determined fat and protein content of the ovary and developing follicles using petroleum ether extraction; the dried oviduct was assumed

to be 100% protein. We used data on fat and protein content from 45 individual follicles of varying sizes to construct estimates of daily follicle growth. Coots usually laid one egg per day (Arnold 1994a), implying a daily size progression among developing follicles. We used calculated growth rates to estimate the amount of protein and fat that would have been present in follicles that were damaged during collection (Alisauskas and Ankney 1994a). Oviducal eggs were separated into yolk and albumen fractions and analyzed according to Arnold et al. (1991).

Post-ovulatory follicles (POFs) regressed rapidly in coots, such that there was only a moderate correlation ($r = 0.74$, $n = 12$, $P = 0.006$) between microscopic POF counts and known egg production (Arnold et al. 1997). Whenever possible, nutrient expenditures for laying coots were estimated from nesting information, but estimates for 18 of 59 layers and postlayers, including the entire 1987 sample, were based on POF counts. We usually could recognize parasitic eggs (Lyon 1993), and we excluded these eggs from clutch size estimates; this affected 5 of 59 estimates. We collected nine incubating coots that we could not associate with known nests; we have included these birds in analyses involving the general category

of "incubators," but we excluded them from analyses involving number of days incubated or estimated nutrient commitment to egg production (i.e., end-of-layers).

For each prelaying, laying, or end-of-laying female, nutrient commitment to clutch formation was estimated as the sum of each nutrient (fat, protein, and ash) present in the oviduct, ovary, developing follicles, oviducal egg (if present), and any eggs that had already been laid. Estimates of mean nutrient content for eggs in the nest were based on one of the following methods (in descending order of preference): (1) an analyzed egg from the clutch ($n = 12$ females) (Arnold et al. 1991), (2) an analyzed oviducal egg (used for fat and protein [shelled eggs only]; $n = 16$ females), (3) if eggs had been measured but not analyzed, we estimated fat, protein, and ash content based on allometric equations derived from 322 analyzed eggs ($n = 16$ females) (Arnold et al. 1991), and (4) if eggs had not been measured or analyzed, we used the mean nutrient content per egg from the study population at large ($n = 15$ females) (2.66 g fat, 3.89 g protein, 2.64 g ash; Arnold et al. 1991).

STATISTICAL ANALYSIS

We assessed body size (Alisauskas and Ankney 1987) by conducting principal components analysis (PROC PRINCOMP; SAS Institute Inc. 1985) on the correlation matrix of the following five morphometric variables: total length, head length, keel length, tarsus length, and middle toe length. This analysis was performed separately for each sex, and the data set included the entire pool of adult birds from this paper plus 199 additional molting adults (C. D. Ankney and T. W. Arnold, unpubl. data). Resulting scores from the first principal axis ($PC1_{sex}$) were used as an index of overall body size. For each sex, we determined whether endogenous reserves (i.e., fat, protein, and ash reserves) varied with body size by regressing each reserve against $PC1_{sex}$:

$$\text{Reserve} = a + b \cdot PC1_{sex}$$

Because $PC1$ scores were normally distributed ($\bar{x} = 0$, $SD = 1$) for each sex, we could correct for body size variation by subtracting $b \cdot PC1_{sex}$ from the observed reserve mass:

$$\text{Corrected mass} = \text{observed mass} - b \cdot PC1_{sex}$$

We used these corrections for all analyses except female fat reserves (see Results).

We used t -tests ($P < 0.05$) to determine if nutrient reserves differed between temporally-adjacent breeding categories (i.e., prelaying, laying, incubation, early brood-rearing, and late brood-rearing), using separate analyses for each sex.

We used analysis of covariance (PROC GLM; SAS Institute Inc. 1985) to determine if nutrient reserves varied according to reproductive investment, year, date, age (SY vs. ASY), and supplemental feeding (FED vs. CTRL). For prelaying females, we conducted an additional analysis comparing pre-RFG females (no developing follicles) with early-RFG females (1–2 developing follicles; late-RFG females were excluded) to determine whether coots require some minimum threshold of nutrient reserves to initiate egg formation (see Ankney and Alisauskas 1991a).

To determine how nutrient reserves varied during egg formation, we included data from RFG, laying, and end-of-laying females, and we used the amount of reproductive nutrient (R-Nutrient) that had been invested in oviduct, ovary, follicle, and egg tissues as a covariate (Ankney and Alisauskas 1991a). For example, if fat reserve (FAT) was negatively correlated with R-FAT, it would indicate that coots utilized fat reserves during egg formation (Alisauskas and Ankney 1985). For females nearing clutch completion (i.e., ≥ 4 eggs laid, ≤ 4 developing follicles), we regressed number of developing follicles on fat reserve, protein reserve, and ash reserve (Ankney and Afton 1988). We performed a similar analysis for females that had completed their clutch within the last 0 to 4 days by comparing number of atretic follicles with nutrient reserves. For each of these analyses, we also included year, date, age, supplemental food, and number of previously-laid eggs as potential covariates. These analyses tested whether follicle development and/or resorption by late-laying females was based on levels of nutrient reserves; i.e., did females modify clutch size based on levels of remaining reserves?

For incubating males and females, we used the number of days since clutch completion as a covariate to measure the amount of time spent incubating; this measure was not strictly accurate because most coots began incubation midway through clutch completion. Additional details of individual analyses are provided in the

TABLE 2. Nutrient reserves and body mass (g) of male and female American Coots throughout the breeding cycle. Data are least-squared means ($\bar{x} \pm \text{SE}$) controlling for body size ($\text{PC}_{1\text{sex}}$) and annual variation. Supplementally-fed coots and 1989 samples were excluded.

Reserve	Prelaying	Laying	Incubation	Early brood	Late brood
Males					
Fat	32.6 \pm 4.0 ^a	24.0 \pm 5.0 ^a	32.0 \pm 6.1 ^a	21.1 \pm 6.2 ^a	45.2 \pm 4.3 ^b
Protein	112.7 \pm 2.4	115.0 \pm 3.0	115.0 \pm 3.6	110.5 \pm 3.7	110.6 \pm 2.6
Ash	19.3 \pm 0.5	19.1 \pm 0.6	18.4 \pm 0.8	19.3 \pm 0.8	19.9 \pm 0.6
Body mass	678 \pm 13 ^a	668 \pm 17 ^a	634 \pm 20 ^a	692 \pm 21 ^b	710 \pm 14 ^b
Females					
Fat	21.6 \pm 2.4	20.1 \pm 3.3	21.9 \pm 3.5	21.8 \pm 5.3	25.0 \pm 4.1
Protein	83.9 \pm 1.3	84.3 \pm 1.8	85.4 \pm 1.9	83.5 \pm 2.8	82.7 \pm 2.2
Ash	13.9 \pm 0.3	14.7 \pm 0.4	14.5 \pm 0.4	14.8 \pm 0.6	14.5 \pm 0.5
Body mass	519 \pm 9 ^a	569 \pm 12 ^b	524 \pm 13 ^a	562 \pm 19 ^b	544 \pm 14 ^b

Means followed by different superscripts were significantly different (*t*-tests, $P \leq 0.05$).

Results section. Initial statistical models included all main effects listed above, plus all two-way interactions. Higher-order interactions were usually inestimable or uninterpretable, and were therefore excluded. We determined statistical significance of individual effects based on type III sums of squares (SAS Institute Inc. 1985). We deleted nonsignificant ($P > 0.05$) effects, beginning with the highest P value, until all remaining variables were either significant or included within a significant interaction, provided that the overall model also was significant at $P < 0.05$.

All significance tests were two-tailed at $\alpha = 0.05$. Means and least-squared means are presented $\pm \text{SE}$.

RESULTS

We collected 138 male and 181 female coots during 1987–1991. Sample sizes were >15 for all reproductive categories except early brood-rearing (Table 1). Samples included 55 supplementally-fed coots: predominantly laying females ($n = 16$), incubating males and females ($n = 8$ and 10, respectively), and late brood-rearing males ($n = 10$).

Body size ($\text{PC}_{1\text{sex}}$) affected the mass of all nutrient reserves except female fat reserves ($r^2 = 0.00$, $P = 0.59$); we corrected all other nutrient reserves for body size variation using the following regression equations (Males: Fat = $33.9 + 3.23 \cdot \text{PC}_{1\text{sex}}$, $r^2 = 0.06$, $P = 0.008$; Protein = $108.6 + 2.72 \cdot \text{PC}_{1\text{sex}}$, $r^2 = 0.13$, $P < 0.001$; Ash = $18.5 + 0.43 \cdot \text{PC}_{1\text{sex}}$, $r^2 = 0.08$, $P = 0.003$; Females: Protein = $82.2 + 1.41 \cdot \text{PC}_{1\text{sex}}$, $r^2 = 0.06$, $P = 0.002$;

Ash = $13.86 + 0.43 \cdot \text{PC}_{1\text{sex}}$, $r^2 = 0.12$, $P < 0.001$).

Nutrient reserves did not vary between stages of the breeding cycle, except for a doubling of male fat reserves between early and late brood-rearing (Table 2). Male body mass did not change between early and late brood-rearing, but decreased during incubation. Female body mass increased during laying, declined during incubation, and increased again during early brood-rearing (Table 2). These changes in body mass were unrelated to changes in nutrient reserves; for males, fresh body mass was strongly correlated with changes in ingesta mass ($r = 0.93$, $n = 5$, $P = 0.02$), whereas changes in female body mass were closely associated with ingesta mass and development of reproductive tissue during the laying period. These comparisons illustrate the dangers of using fresh (live) body mass to draw inferences about body condition.

NUTRIENT RESERVES OF PRELAYING COOTS

Among prelaying females, fat reserves varied among years (9.9 g higher in 1991) and declined by 0.6 g per day (Table 3). Yearling (SY) females had smaller protein and ash reserves than did adult (ASY) females. Protein and ash reserves also varied among years, being smaller in 1988 than in 1987 and 1991 (Table 3). Protein also declined by 0.5 g per day among ASY females, but did not vary by date among SY females. To determine if prelaying females exhibited a nutrient-reserve threshold for onset of

TABLE 3. Nutrient reserves of prelaying and laying (includes RFG and end-of-laying) female American Coots in relation to year (1987, 1988, 1991), collection date (15 April = 0), age (SY vs. ASY), supplemental feeding (FED vs. CTRL), and nutrient commitment to clutch formation (R-Nutrient; assessed for layers only, see Methods). Only significant effects are presented.

Dependent variable	Model			Intercept	Independent variable ^a	<i>b</i>	<i>F</i>	<i>P</i>
	<i>F</i>	<i>P</i>	<i>R</i> ²					
Prelayers								
Fat	6.20	0.004	0.17	30.50	Year (1991)	9.90	6.11	0.02
					Date	-0.58	8.59	0.005
Protein	4.87	0.002	0.25	95.15	Year (1988)	-5.96	6.97	0.01
					Date	-0.53	11.63	0.001
					Age (SY)	-12.36	6.29	0.02
					Date · Age (SY)	0.48	4.81	0.03
Ash	6.48	0.003	0.18	14.67	Year (1988)	-1.41	12.16	0.001
					Age (SY)	-1.02	7.00	0.01
Layers								
Fat	20.76	0.001	0.56	57.69	R-Fat	1.36	20.25	0.001
					Date	-1.12	16.98	0.001
					Food (FED)	14.18	11.56	0.001
					Year (1987, 1988)	-5.41	0.98	0.33
					Year · R-Fat (1987, 1988)	-1.13	15.25	0.001
Protein	11.76	0.001	0.21	86.70	Food (FED)	4.34	6.31	0.01
					Year (1988)	-6.57	18.36	0.001
Ash	5.21	0.007	0.11	13.09	Age (SY)	-1.04	6.45	0.01
					Year (1988)	-1.08	6.92	0.01

^a For class variables, the category in parentheses represents the group for which the parameter estimate (*b*) applies; e.g., in 1991, females had 9.90 g more fat than in 1987 and 1988 combined (years were combined if LSD tests indicated that 2 of the 3 years did not differ).

RFG, we excluded late-RFG females plus any pre-RFG females collected before 30 April, the earliest observed date of RFG (Table 1). Females that had initiated RFG had larger nutrient reserves than did pre-RFG females, although only the protein relationship was significant (Fig. 1).

Nutrient reserves of prelaying males were unaffected by year, date, or age.

NUTRIENT RESERVES OF LAYING COOTS

During 1991, females accumulated body fat during laying (Fig. 2). This was not an artifact of supplemental feeding, because the same relationship was observed when fed birds were deleted from the analysis (1991 CTRLs: $FAT = 23.9 + 0.58 \cdot R-FAT$; $F_{1,20} = 5.65$, $P = 0.03$). Protein and ash reserves were unaffected by investment in clutch formation (Fig. 2). Fat reserves declined by 1.12 g per day (Table 3), but protein and ash reserves did not vary with collection date. Supplementally-fed females averaged 14.2 g more body fat and 4.3 g more protein than did unsupplemented females. Adult females had 1.0 g more body ash than did SY females (Table 3), but fat and protein reserves did not vary between age

classes. All three reserves were smaller in 1988 than in 1991, and 1987 samples were usually intermediate (Table 3).

Clutch initiation dates were negatively correlated with fat ($r = -0.27$, $n = 66$, $P = 0.03$) and protein reserves ($r = -0.24$, $P = 0.05$), whereas mean egg volume was positively correlated with these two variables (fat: $r = 0.40$, $n = 47$, $P = 0.003$; protein: $r = 0.43$, $P = 0.003$). For 53 females that were collected ± 4 days from clutch completion (i.e., end-of-layers, or layers with ≤ 4 developing follicles for which final clutch size could be predicted), fat and protein reserves were positively correlated with clutch size ($r = 0.35$, $P = 0.01$). To determine which of these correlations were most likely to be causal, we performed multivariate analyses that incorporated all reserve estimates, plus year, age, and laying date as potential covariates. Initiation date was affected by age ($F_{1,63} = 6.09$, $P = 0.02$) and fat reserve ($F_{1,63} = 5.09$, $P = 0.03$) (Model: $INIT = 138.4 + 3.1(SY) - 0.06 \cdot FAT$; $F_{2,63} = 5.81$, $P < 0.001$, $R^2 = 0.16$), but clutch size varied only with year ($F_{2,49} = 7.45$, $P < 0.001$) and initiation date ($F_{1,49} = 6.38$, $P = 0.01$). Although not significant ($P =$

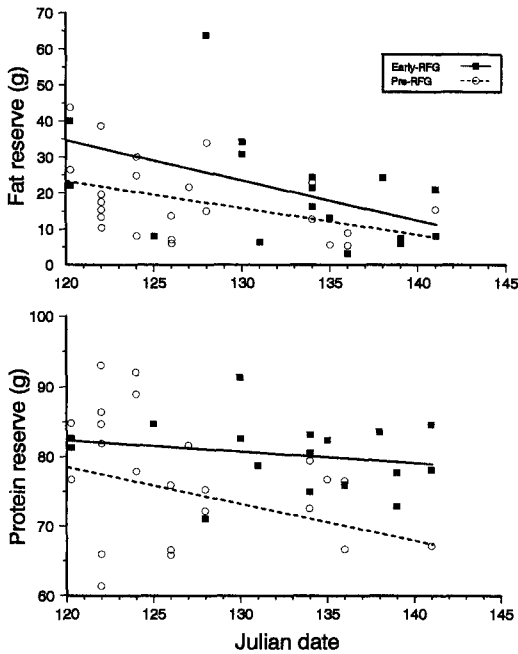


FIGURE 1. Fat and protein reserves of pre-RFG (0 developing follicles) and early-RFG American Coots (1–2 developing follicles) in relation to collection date. Regression slopes did not differ between groups, but early-RFG females averaged 7.6 g more fat ($F_{1,37} = 3.31$, $P = 0.08$) and 6.1 g more protein ($F_{1,37} = 6.10$, $P = 0.02$) than did pre-RFG females (ANCOVA analysis controlling for date; see Table 3).

0.15), clutch size was most strongly related to protein reserve. Egg volume was affected only by protein reserve.

Among 27 late-laying females (i.e., ≤ 4 developing follicles, ≥ 4 eggs already laid), there were no relationships between number of developing follicles and nutrient reserves ($P \geq 0.16$). Likewise, for 20 females that had just completed their clutches and had from 0 to 5 atretic follicles, number of atretic follicles was unrelated to variation in nutrient reserves at the end of laying ($P \geq 0.30$).

Laying-stage males that had access to supplemental food had 39.0 g larger fat reserves ($F_{1,24} = 14.50$, $P < 0.001$) than did unsupplemented males; supplemental feeding effects were also suggestive for protein reserves (effect size = 9.8 g, $P = 0.07$). Adult males had 19.0 g more total protein ($F_{1,24} = 21.21$, $P < 0.001$) than did yearlings. Protein and ash reserves were also larger in 1987 than in 1988 ($P = 0.03$).

NUTRIENT RESERVES OF INCUBATING AND BROOD-REARING COOTS

Because of small sample sizes, we combined data from males and females to analyze nutrient dynamics of incubating and brood-rearing coots. Males had larger reserves than did females, but there were no significant interactions between sex and other predictor variables. Supplementally-fed coots had larger fat and protein reserves during both incubation and brood-rearing (Table 4). Fat reserves increased by 1.5 g per day throughout incubation (Fig. 3), and increased by a further 0.7 g per day between early and late brood-rearing (Table 4). Year effects were often significant, with most reserves being smaller in 1988 than in 1990 or 1991 (Table 4).

DISCUSSION

TIMING OF BREEDING

During early to mid-May, female coots with large fat and protein reserves were more likely to have initiated RFG than were females with small reserves. Furthermore, among coots that had begun laying, clutch initiation dates were negatively correlated with fat reserves. Both of these observations are consistent with the hypothesis of a seasonally declining nutrient-reserve threshold that affects onset of breeding (e.g., Reynolds 1972, Alisauskas and Ankney 1994b, Esler and Grand 1994). However, Ruddy Ducks (*Oxyura jamaicensis*; Alisauskas and Ankney 1994b), Northern Pintails (*Anas acuta*; Esler and Grand 1994), and presumably Mute Swans (*Cygnus olor*; Reynolds 1972) all used nutrient reserves during clutch formation, whereas coots did not. Thus, our findings are somewhat paradoxical: coots with larger fat and/or protein reserves began nesting earlier, but they did not use these reserves to help produce eggs or to meet energetic costs of incubation. Interestingly, the correlation between clutch initiation dates and fat reserves remained just as strong if we included or excluded pre-layers, layers, or end-of-layers. Among Northern Pintails, females with larger fat reserves began laying earlier and also used those reserves at a faster rate, so that by the end of laying there was no difference in fat reserves between early and late nesters (Esler and Grand 1994). This pattern of nutrient-reserve usage is precisely what one might predict if the correlation between fat reserves and timing of breeding were

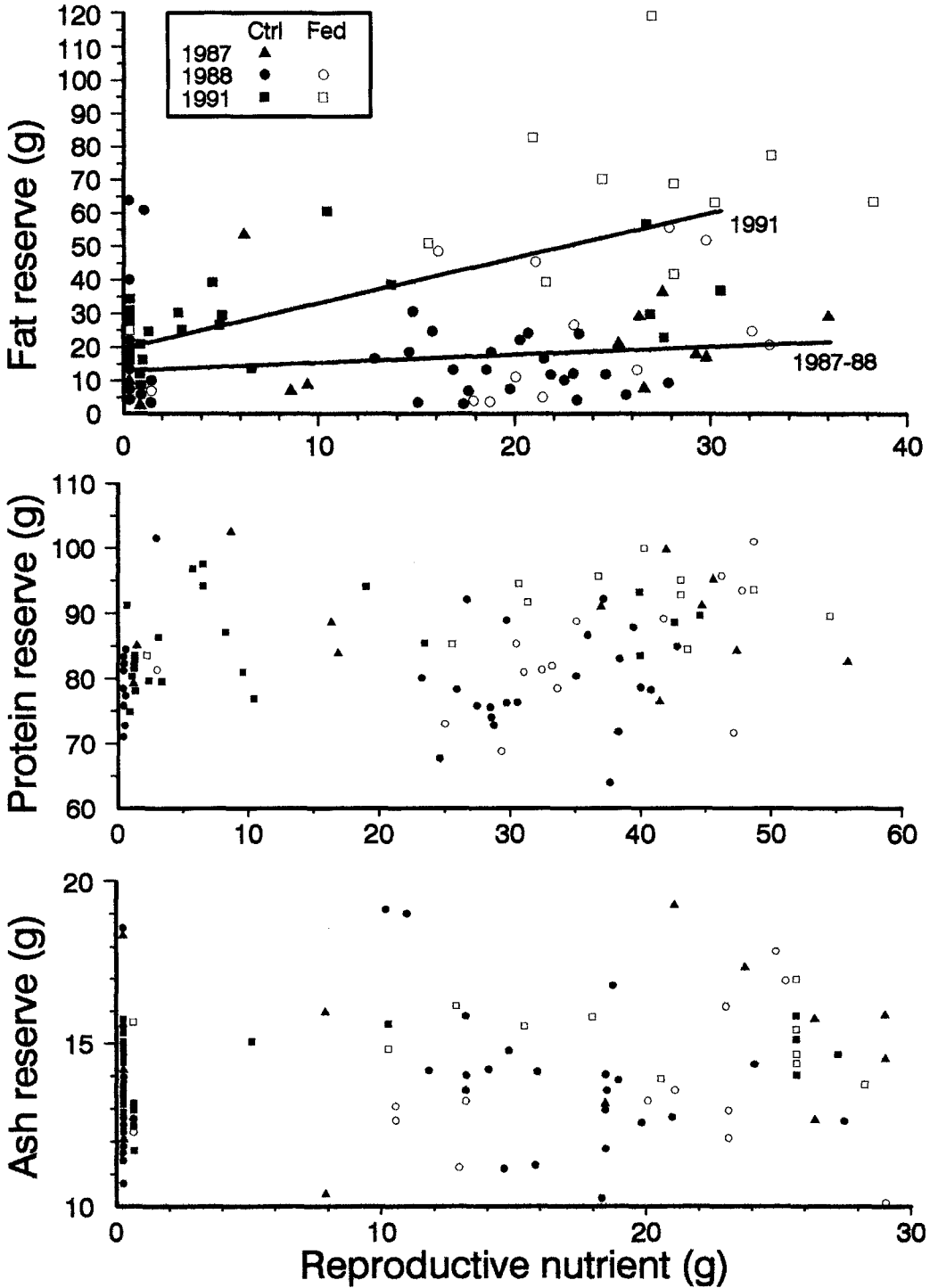


FIGURE 2. Nutrient reserves of RFG, laying, and end-of-laying American Coots in relation to nutrient investment in egg formation. Reproductive nutrients represent fat in the top, protein in the middle, and ash in the bottom graph. For fat reserves, the relationship was nonsignificant in 1987–1988 and positive in 1991. Regression lines include unsupplemented birds only and have been standardized to a mean collection date of 19 May (see Table 3). Relationships were nonsignificant for protein and ash reserves.

TABLE 4. Factors affecting nutrient reserves of male and female American Coots during incubation and brood-rearing. Data from males and females were combined for analysis. Sex effects were significant for all models ($P = 0.05$ to 0.001) and are indicated by separate intercepts for males and females. Other conventions as in Table 3.

Dependent variable	Model			Intercepts		Independent variable	<i>b</i>	<i>F</i>	<i>P</i>
	<i>F</i>	<i>P</i>	<i>R</i> ²	Male	Female				
Incubation									
Fat	4.74	0.004	0.35	20.83	7.33	Days Incubated	1.46	11.63	0.002
						Food (FED)	17.62	7.25	0.01
						Year (1991)	25.08	5.34	0.03
Protein	45.00	0.001	0.78	110.27	80.86	Food (FED)	5.57	5.06	0.03
						Year (1991)	9.16	5.20	0.03
Brood-rearing									
Fat	12.66	0.001	0.36	18.16	4.91	Food (FED)	21.18	13.61	0.001
						Date ^a	0.72	12.34	0.001
Protein	52.31	0.001	0.70	105.15	78.52	Food (FED)	5.49	3.90	0.05
						Year (1990)	9.01	12.06	0.001
Ash	31.72	0.001	0.48	18.51	13.90	Year (1990)	1.53	5.19	0.03

^a Day 0 = June 21.

causal. However, the absence of nutrient-reserve usage by laying coots suggests that this pattern is not necessarily causal. The question therefore remains: "Why do fat coots initiate nesting earlier, given that they do not use stored fat during egg formation or incubation?"

Early-nesting coots might use nutrient reserves as a hedge against food shortages that occur unpredictably during laying or incubation. By this hypothesis, nesting females should require more nutrients than non-nesting females, and the risk of food shortage should decline seasonally. Late-spring snowstorms might cause such unpredictable food shortages. Fredrickson (1969) documented mass starvation of prelaying coots when a blizzard swept

through Iowa in late March. In prairie Canada, we have twice witnessed severe snowstorms when coots were beginning to nest (8 May 1983, SE Saskatchewan; 10 May 1984, SW Manitoba). Although we did not observe any suspected food shortages or catastrophic events during 1987–1991, it is difficult to address hypotheses related to "bad year effects" with anything less than 10–20 years of data (Boyce and Perrins 1987).

Alternatively, large fat reserves may have been correlated with early nesting because of some additional unmeasured factor that had a causal influence on each variable. This unmeasured factor might be vaguely defined as "individual quality" (Verhulst et al. 1995); for example, higher quality birds might be more efficient foragers, which would allow them to accumulate larger fat and protein reserves and to channel more exogenous energy into earlier reproduction. However, this would not necessarily imply that large reserves allowed coots to begin nesting earlier.

CLUTCH FORMATION

Female coots did not use nutrient reserves during clutch formation; in fact, laying females accumulated fat reserves during 1991. Likewise, nutrient reserves had no influence on variation in numbers of developing and atretic follicles among late-layers and end-of-layers, respectively. This suggests that laying females obtained all of their nutrient requirements from their daily diets. Maximum daily energy re-

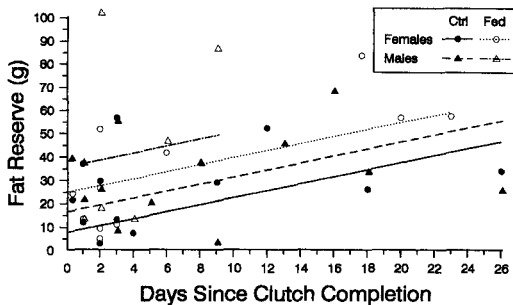


FIGURE 3. Changes in fat reserves of male and female American Coots during incubation. The plotted regression lines illustrate significant increases in fat reserves throughout incubation, as well as significant differences between supplemented and unsupplemented males and females (Table 4).

quirements do not increase with clutch size in coots because clutch size (usually 8–12) is almost always greater than the period of rapid follicle growth (ca. 4–6 days). Daily nutrient requirements therefore reach a plateau, equal to the nutrient content in one egg, so that additional eggs lengthen the period of maximum energy commitment, but do not increase the maximum daily energy requirement (see Alisauskas and Ankney 1994a: Figs. 4–5). Thus, nutrient availability cannot limit clutch size in coots unless food availability in the environment declines to a point where laying females can no longer obtain their daily nutrient requirements during a single day of foraging. Because individual females can produce eggs over extended periods (i.e., up to 57 days in renests; Arnold 1990: Appendix 4), it should be clear that environmental food availability does not limit clutch size in coots. Thus, Alisauskas and Ankney's (1985: 141) suggestion that "the size of a female [coot's] fat reserves influences whether she will nest and her clutch size, as demonstrated in Snow Geese" was not supported by our analyses.

Alisauskas and Ankney (1985) studied coots in a different location (Delta Marsh) and year (1981), and it is certainly possible that their results and conclusions are valid within the context of their study. Nevertheless, ecologists usually search for generalities, so it would be discomfiting to sweep aside all studies of nutrient dynamics that were conducted in a single study area during a single year and conclude that the results and conclusions cannot be generalized to other populations of that species. Nutrient dynamics of laying female Mallards (*Anas platyrhynchos*) have been determined for five different study areas in three different years (Krapu 1981, Young 1993 [4 study areas in 2 years]), and although regressions of fat reserves on reproductive fat did not yield identical regression slopes, all five data sets showed that female Mallards used substantial amounts of fat during clutch formation. Similarly, we examined nutrient dynamics in coots during three different years and laying females did not use reserves during any of these years. During 1991 our data even suggested that coots were storing reserves during clutch formation. We suspect that this somewhat unexpected result in 1991 may be spurious given our small sample of unsupple-

mented females ($n = 33$, with only 7 late-layers), and we further suspect that Alisauskas and Ankney's (1985) result also may be spurious ($n = 19$). Most recent studies of nutrient dynamics of laying females have utilized samples of at least 100 birds (e.g., Ankney and Alisauskas 1991a, Alisauskas and Ankney 1994b, Esler and Grand 1994; this study), and simulation models support the need for samples of this magnitude in order to obtain accurate estimates of regression slopes (T. W. Arnold, unpubl. data).

INCUBATION AND BROOD-REARING

Coots accumulated body fat during incubation. This pattern is in marked contrast to waterfowl, which lose body mass, fat, and/or protein reserves during incubation (reviewed by Afton and Paulus 1992). This difference between coots and ducks is probably related to differences in parental care. In coots, both males and females incubate, and each member of the pair therefore has ample time to forage (Ryan and Dinsmore 1979). However, only the female incubates in most species of waterfowl, so the amount of time available for foraging is greatly curtailed. Thus, incubating female waterfowl are unable to maintain a positive energy budget (Afton and Paulus 1992). Mass gain during incubation is fairly common among other bird taxa, but it is usually associated with biparental incubation or with incubation feeding (Moreno 1989).

Male coots reached a seasonal minima of 21 g body fat during early brood-rearing. Time-budget observations of breeding coots suggest that parental work-loads peak at about 10–14 days after the first egg hatches (Ryan and Dinsmore 1979), and brood-manipulation experiments also indicated a parental-care bottleneck occurring at this time (T. W. Arnold, unpubl. data). Although low fat reserves of male coots during early brood-rearing might indicate nutritional stress, it also could indicate an adaptive reduction in body mass to optimize parental work-loads (Moreno 1989). In any event, this reduction was relatively brief; by late brood-rearing, male fat reserves had more than doubled to their seasonal maxima of 45 g. This increase may have represented pre-migratory hyperphagia, because a large fraction of the Minnedosa coot population participates in molt migrations before initiating

their flightless wing molt (C. D. Ankney and T. W. Arnold, unpubl. data).

EFFECTS OF SUPPLEMENTAL FOOD

We obtained adequate samples of supplementally-fed coots during three periods: laying, incubation, and late brood-rearing. During all three periods, and for both sexes, supplementally-fed birds had 14–21 g larger fat reserves and 4–6 g larger protein reserves than did unsupplemented birds. Taken alone, this evidence might suggest that coots lacking access to supplemental food were nutrient limited; however, we reject this hypothesis based on our observations that supplementally-fed coots did not utilize these additional reserves during egg formation, incubation, or brood-rearing. For example, if supplementally-fed females had channeled their additional 14.2 g of fat reserves into egg formation, they could have laid about 5 additional eggs (14.2 g fat reserve \div 2.7 g fat per egg = 5.3 additional eggs) and presumably begun nesting 5 days sooner. Although supplemental food did affect clutch size and laying date, clutches were only 1 egg larger and 1.5 days earlier (Arnold 1994a). The most pronounced effect of supplemental food on nutrient-reserve dynamics was that supplemented coots completed laying and incubation with much larger reserves (especially fat). Hence, breeding coots responded to additional food primarily by improving their own body condition, and only slightly by increasing their investment in reproduction.

Our data indicate that nutrient dynamics of breeding coots are not part of some simple endogenous rhythm (Moreno 1989). Although such endogenous factors are likely important (e.g., premigratory hyperphagia), they can clearly be modified by exogenous factors such as supplemental food. It is not so obvious, however, whether the larger fat reserves of supplementally-fed coots represent an "adaptive" response; i.e., is fatter necessarily fitter? Clearly, nutrient-storage strategies of coots did not evolve in the presence of ad libitum corn, just as human nutrient-storage strategies did not evolve in the presence of fried food and candy bars. Nevertheless, most of the other effects of supplemental feeding that we observed had positive or presumed positive fitness consequences, including earlier nest initiation, larger clutch size, and higher offspring survival (Ar-

nold 1994a, unpubl. data). Thus, it seems reasonable to presume that changes in body composition associated with supplemental feeding had positive effects on fitness in coots. Unfortunately, philopatry is very low in American Coots (Crawford 1978, Lyon 1993, Arnold 1994b), so testing this hypothesis using adult return rates will be difficult.

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