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COMPOSITION OF WOOD DUCK EGGS IN RELATION TO EGG SIZE, LAYING SEQUENCE, AND SKIPPED DAYS OF LAYING

ROBERT A. KENNAMER,[1] SARAH K. ALSUM,[2] AND SHEILA V. COLWELL[3]
Savannah River Ecology Laboratory, Drawer E, Aiken, South Carolina 29802, USA

ABSTRACT.—We collected 138 freshly laid Wood Duck (*Aix sponsa*) eggs from 13 nests to determine the effects of egg size, laying sequence, and skipped laying days on egg composition. All components except yolk ash and eggshell, both wet and dry, increased in direct proportion to fresh-egg mass. Egg size increased during the first half of laying and decreased thereafter. The effects of laying sequence were component-specific. Absolute levels of neutral lipids (comprising 65.6% of dry yolk) were near average until about 75% of the clutch was completed and then declined. Mass of albumen components tended to increase sharply with the first few eggs and then decrease as laying progressed. Fat indices (egg lipid/lean dry-egg content) tended to be highest in the first 40% of the clutch. We interpret laying-sequence effects on egg composition as adaptations that enable female Wood Ducks to initiate incubation before clutch completion and still allow for synchronous hatching without compromising the hatching success of first-laid eggs. Hens frequently skipped a laying day between the penultimate and ultimate egg, which tended to increase the mass of the yolk component in last-laid eggs compared with those that were laid the day following the penultimate egg.
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VARIATION IN AVIAN EGG SIZE is largely attributable to differences among species, and contrasting developmental modes dictate primary differences in constituent proportions (Ricklefs 1977, Carey et al. 1980, Sotherland and Rahn 1987). Egg size also varies considerably within species, typically varying more among than within clutches (Ricklefs 1984, Rohwer 1986, Hepp et al. 1987). Intraspecific variation in egg size is related to proximate factors such as laying date (Runde and Barrett 1981, Bancroft 1984), food supply (Horsfall 1984, Pierotti and Bellrose 1986), and age (Ryder 1975, Crawford 1980, Gratto et al. 1983). Such factors however, exercise their influence within the confines of a large heritable component of egg size (Ojanen et al. 1979, Van Noordwijk et al. 1980).

Recent attention has been focused on intraspecific variation in the composition of eggs. As with egg size, egg composition typically varies more among than within clutches (Ricklefs 1984, Bancroft 1985, Alisauskas 1986, Hepp et al. 1987) and has been shown to vary with respect to female quality in Wood Ducks (*Aix sponsa*) as indexed by post-laying body mass (Hepp et al. 1987). Egg composition, however, is not known to vary greatly due to other factors (e.g. clutch size; Rohwer 1986, Arnold et al. 1991; but see Owen and West 1988). Intraclutch variation in egg composition has received less attention (but see Nisbet 1978, Alisauskas and Ankney 1985, Rohwer 1986, Meathrel and Ryder 1987).

Nest attentiveness in precocial waterfowl commonly increases through the laying period with persistent incubation beginning after the clutch has been completed (Caldwell and Cornwell 1975, Cooper 1978, Afton 1980, Kennamer et al. 1990). Despite up to four days of total asynchrony among eggs in experimentally manipulated Lesser Snow Goose (*Chen caerulescens*) clutches, hatching synchrony can still be achieved (Davies and Cooke 1983). Kennamer et al. (1990) documented 100% hatching success in a Wood Duck clutch with up to four days of natural cumulative asynchrony. Apparently, embryos communicate with one another to synchronize their hatching by adjusting developmental rates (Vince 1964, Ockleford and Vince 1985). Reasons for such a complicated incubation strategy in species that hatch synchronously may relate to a combination of egg-viability and nest-predation effects (Arnold et al. 1987, Flint et al. 1994). In any case, egg com-

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[1] E-mail: kennamer@srel.edu

[2] Present address: W1396 Stokdyk Ingelse Road, Oostburg, Wisconsin 53070, USA.

[3] Present address: National Park Service, Southeast Support Office, 100 Alabama Street Southwest, Atlanta, Georgia 30303, USA.

position relative to laying sequence may be important in allowing eggs of precocial species to hatch synchronously. For example, if eggs deposited early in the laying cycle contained proportionately more lipid than last-laid eggs, then developing embryos in first-laid eggs could be incubated over a longer time, thereby allowing sufficient time for completion of incubation in last-laid eggs. Such an adaptation could allow females to lay larger clutches without compromising hatching success or provisioning of neonates.

In precocial species, resources allocated to eggs are used for both embryogenesis and residual energy in hatchlings. Neonate size and energy reserves at hatching are important to the survival of young waterfowl in the first few days after they leave the nest (Kear 1965, Thomas and Brown 1988). In a study of Wood Ducks, however, Hepp et al. (1987) found that egg mass was a relatively good predictor of neonate mass but was a poor predictor of neonate lipid content. The lack of a strong relationship between egg mass and neonate lipid content suggests that lipid metabolism varies among developing embryos and/or that cumulative energy expenditures up to the time of hatching vary among clutch mates.

The Wood Duck is a precocial species in which residual energy reserves at the time of hatching may be critical to duckling survival. Because female Wood Ducks may nest more than 3 km from the nearest water (Bellrose and Holm 1994), day-old ducklings sometimes must travel substantial distances overland sustained only by their lipid reserves at hatching. Wood Ducks lay large clutches of large eggs with high energy density (Drobney 1980). The energetic cost of producing a Wood Duck egg is about 500 kJ (Drobney 1980), and endogenous fat reserves play an important role in enabling females to meet these large energy requirements during reproduction. In contrast, protein requirements for egg production in Wood Ducks are satisfied through daily foraging during the laying cycle (Drobney 1980). Because within-clutch variation in egg composition may result from changes in female provisioning as laying progresses, it is clearly necessary to consider egg composition of complete clutches with known laying sequences. Furthermore, Wood Ducks (Bellrose and Holm 1994), like other species (e.g. Blue Goose, Cooch 1958; American Coot [*Fulica americana*], Arnold 1990) sometimes skip days of egg laying during clutch formation, which may also alter egg composition within clutches. In this study, we determined the effects of egg size, laying sequence, and skipped days of laying on egg composition in Wood Ducks.

METHODS

The study took place on an 87-ha abandoned reactor cooling impoundment (Pond B) on the Department of Energy's Savannah River Site in west-central South Carolina (33°06′N, 81°18′W). A complete description of the study area is given by Whicker et al. (1990). Freshly laid Wood Duck eggs ($n = 138$) were collected daily from 13 nests (all nests on the impoundment) during March to June of 1991 and 1992 (Colwell et al. 1996). Eggs removed from nest boxes were replaced with hard-boiled chicken eggs to discourage females from abandoning nests or compensating for eggs that were collected. Clutch size, therefore, should not have been affected by our manipulations. Intraspecific nest parasitism is common in Wood Ducks and is most reliably identified by the addition of more than one egg per day to a nest (Bellrose 1980). No clutches increased at a rate greater than one egg per day. Furthermore, nest boxes had been located at this impoundment only since 1990, and studies have shown that increasing intraspecific nest parasitism in Wood Ducks is associated with growing population densities and with limited suitable nest sites (Bellrose and Holm 1994, Kennamer unpubl. data).

Length and maximum breadth of eggs were measured with digital calipers (± 0.01 mm), and mass of fresh eggs was recorded on a Mettler balance (± 0.01 g). On the day of collection, eggs were heated in water to harden contents and allow separation of shell (including membranes), albumen, and yolk; wet masses of these separated components were recorded (± 0.01 g). Any difference between fresh-egg mass and the sum of its separated components (assumed to have resulted from changes in water content of albumen during heating in the water bath) were added or subtracted from the wet albumen mass. Egg components were oven-dried at 70°C to constant mass (± 0.01 g).

Neutral lipids were removed from approximately 1-g samples of dried yolk in a Soxtec extraction apparatus using petroleum ether as a solvent. Previous studies have indicated that petroleum ether removes less non-lipid material than other solvents and removes primarily neutral lipids (Dobush et al. 1985). We used an extraction time of 3 h followed by 1 h of rinsing. All weighing of pre- and post-extracted dry samples was done in a humidity-controlled ($<$ 0.05%) sealable plexiglass glove-box. Lipid content

TABLE 1. Dimensions, estimated energy content, and composition of Wood Duck eggs (n = 138) from Pond B, Savannah River Site, 1991 to 1992. CV is coefficient of variation.

Variable	$\bar{x} \pm$ SD	CV (%)
Fresh-egg mass (g)	40.51 ± 2.61	6.4
Length (mm)[a]	50.05 ± 1.74	3.5
Breadth (mm)[a]	38.24 ± 0.90	2.4
Total energy (kJ)	332.49 ± 27.80	8.4
Energy density (kJ/g)	8.21 ± 0.38	4.6
Yolk		
Wet mass (g)	14.16 ± 1.44	10.2
Dry mass (g)	7.99 ± 0.82	10.2
Water (g)	6.17 ± 0.66	10.7
Lipid (g)	5.23 ± 0.53	10.2
AFLDM (g)[b]	2.48 ± 0.30	12.1
Ash (g)	0.27 ± 0.05	19.8
Lipid (% dry yolk)	65.55 ± 1.89	2.9
Albumen		
Wet mass (g)	22.19 ± 1.70	7.7
Dry mass (g)	2.86 ± 0.29	10.2
Water (g)	19.33 ± 1.48	7.6
Shell		
Wet mass (g)	4.16 ± 0.32	7.6
Dry mass (g)	3.47 ± 0.23	6.6

[a] Length and breadth measurements from 132 of 138 total eggs.

[b] Ash-free lean dry mass.

TABLE 2. Summary of log-log regressions of egg components on fresh-egg mass for 138 Wood Duck eggs from Pond B, Savannah River Site, 1991 to 1992.

Component	Intercept	Slope (SE)	95% CI	R^2
Total energy	0.17	1.08 (0.060)	0.96–1.20	0.71
Yolk				
Wet mass	−0.71	1.16 (0.091)	0.98–1.34	0.55
Dry mass	−0.94	1.15 (0.093)	0.97–1.33	0.53
Water	−1.10	1.17 (0.097)	0.98–1.36	0.52
Lipid	−1.07	1.11 (0.093)	0.93–1.29	0.51
AFLDM[a]	−1.48	1.16 (0.127)	0.91–1.41	0.38
Ash	−3.42	1.77 (0.193)	1.39–2.15	0.38
Albumen				
Wet mass	−0.18	0.95 (0.058)	0.84–1.06	0.67
Dry mass	−0.81	0.78 (0.114)	0.56–1.00	0.26
Water	−0.29	0.98 (0.055)	0.87–1.09	0.70
Shell				
Wet mass	−0.54	0.72 (0.081)	0.56–0.88	0.37
Dry mass	−0.58	0.70 (0.067)	0.57–0.83	0.44

[a] Ash-free lean dry mass.

of each sample was estimated as the difference in mass of the dried sample before and after extraction. Proportions of lipid in the extracted dry yolk samples were used to determine lipid content of the entire dry yolk for each egg. Duplicate extractions were completed for 13 eggs, and the coefficients of variation of lipid proportions in those samples averaged 0.48% (range 0.007 to 1.84%). In addition, blanks (i.e. empty extraction thimbles) and standards made from the homogenized dried yolks of six chicken eggs were extracted along with each run of the Soxtec apparatus in a different column each time. The sample of 11 standards had a coefficient of variation of 1.59%, and the mass of the blanks before versus after extraction was not significantly different (paired $t = -1.86$, $n = 11$, $P = 0.09$).

Lean-dry residues from the extracted dry yolk samples were ashed in a muffle furnace at 500°C for 8 h. Masses of samples before and after ashing were obtained (± 0.1 mg). Twelve blanks (i.e. empty crucibles), treated exactly as the crucibles that contained samples, did not differ in mass before and after placement in the muffle furnace (paired $t = -2.02$, $P = 0.07$). Proportions of ash in the combusted lean-dry yolk samples were used to determine ash content of the entire yolk, and yolk ash-free lean dry mass (AFLDM) was determined by difference in lean dry yolk and yolk ash. Energy content of eggs was estimated based on Drobney's (1980) analysis of Wood Duck eggs (yolk, 33.82 kJ/g dry mass; albumen, 21.85 kJ/g dry mass).

Statistical analyses.—Data summaries and statistical analyses were completed using the SAS (1989). We used linear regression to investigate log-log relationships between egg components and fresh-egg mass. To investigate the effect of laying sequence on various egg components, we standardized egg sequence (because clutch sizes varied) by expressing the position of eggs within clutches as proportions of their respective clutch sizes. The sequence of the first two to three eggs was unknown for four clutches; data from these eggs were not included in analyses of sequence effects. We used linear and second-order polynomial regressions to describe the relationships between relative fresh-egg mass and relative component masses versus laying sequence. We expressed fresh-egg mass and component masses as deviations from within-clutch means to control for variation among nests. In most cases, second-order polynomial equations provided the best fit to the data. We used Kruskal-Wallis tests to compare composition of the last two eggs in nests where females skipped versus did not skip a day of laying between these eggs. Results were considered significant at $P \leq 0.05$ for all tests.

RESULTS

Composition and allometry of eggs.—Dimensions, organic composition, and estimated energy content of Wood Duck eggs are presented in Table 1. Allometry of egg composition was

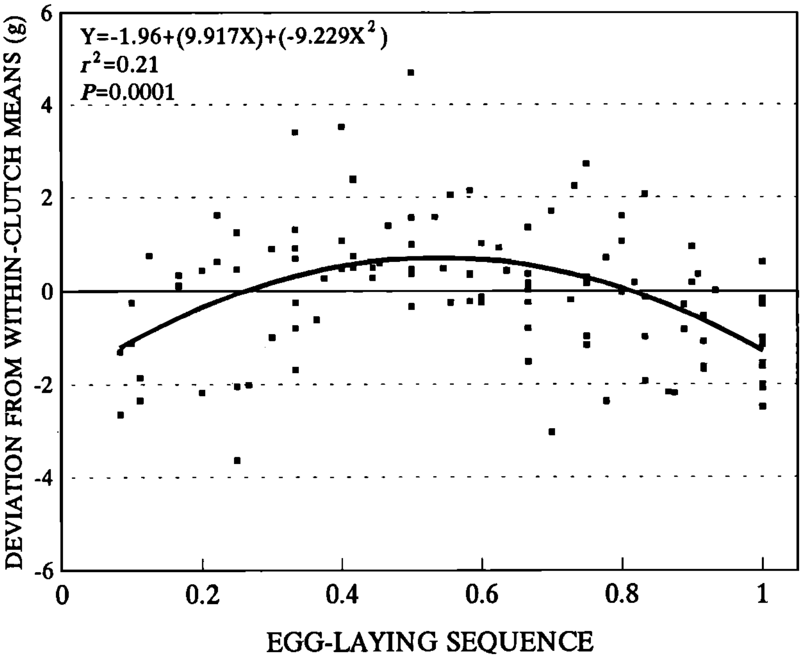

FIG. 1. Relation between egg mass (deviations from within-clutch means) and laying sequence (standardized for different clutch sizes) for 11 first clutches of Wood Ducks from the Savannah River Site, 1991 to 1992.

investigated by regressing the common logarithm of each component's mass on the common logarithm of fresh-egg mass. Regression slopes not significantly different from 1.0 indicate that egg component masses increase in direct proportion to fresh-egg mass. Results of log-log regressions indicated that the slope was >1.0 for the relation between yolk ash and fresh-egg mass (Table 2). Conversely, slopes of the relationships between eggshell (wet and dry) and fresh-egg mass were <1.0 (Table 2). All other egg components increased in direct proportion with egg mass.

Egg composition in relation to laying sequence.—To investigate possible relationships between egg composition and laying sequence, deviations in component mass from within-clutch means were plotted against standardized egg sequence for 11 first clutches (Figs. 1–3). For fresh-egg mass, eggs that were heavier than average tended to occur in the middle of the laying sequence, and eggs that were lighter than average tended to be laid at the beginning and end of the sequence (Fig. 1). For dry yolk and lipids, masses tended to remain near average values throughout most of the sequence, but began to decline after about 70 to 75% of the clutch had been laid (Figs. 2 and 3, respectively). Yolk AFLDM and yolk ash mass tended to be below average early in the laying sequence and then increase to levels that remained near average (Fig. 3). Dry albumen content was markedly below average both early and late in the laying sequence, and above average in the middle of the laying sequence (Fig. 2). Dry eggshell mass tended to remain near average until 75 to 80% of the clutch had been laid (Fig. 2).

Timing and consequences of skipped laying days.—Nine of 13 (69.2%) nests had at least one skipped day during the laying cycle. Four of these nests (44.4%) had more than one skipped day during laying. Considering only nests in which at least one skipped day of laying occurred, 83 laying days occurred when skips could have taken place. In these same nests, the observed frequency of skipped laying days was 12 (14.5%). Skipped days were seldom observed during early (eggs 1 through 3) laying (22.2% of 18 possible days) or mid-laying (7.1% of 56 possible days), but occurred frequently between the last two eggs of a clutch (44.4% of 9 possible days. The distributions of observed

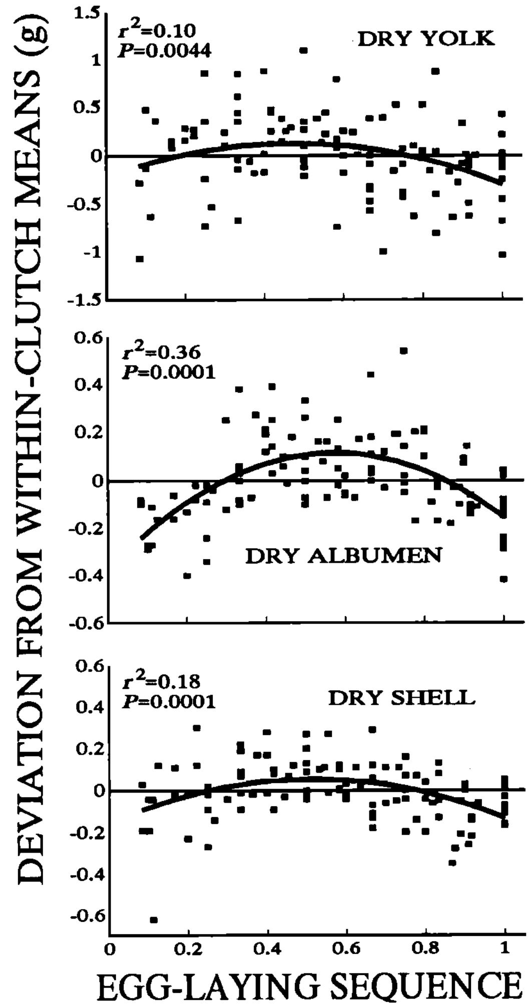

FIG. 2. Relations between yolk-, albumen-, and shell-component dry masses (deviations from within-clutch means) and laying sequence (standardized for different clutch sizes) for 11 first clutches of Wood Ducks from the Savannah River Site, 1991 to 1992.

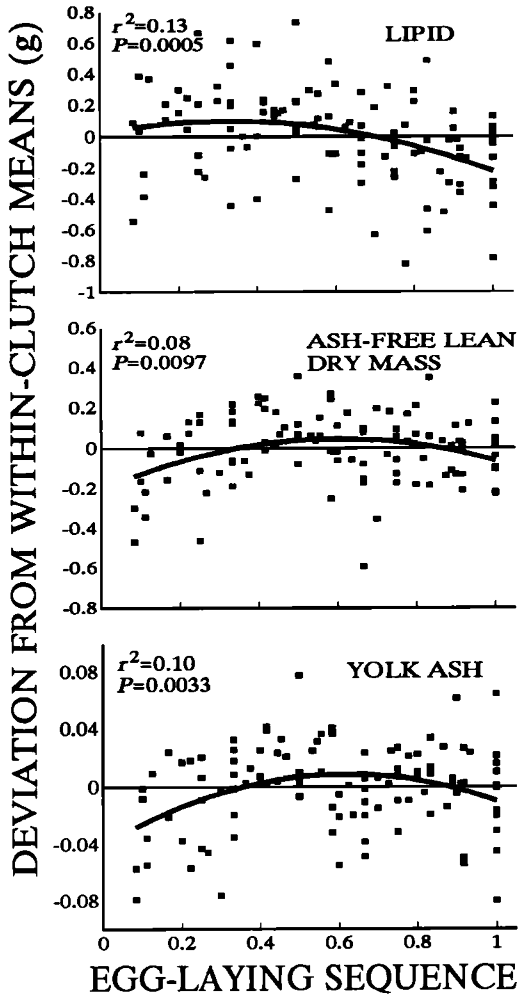

FIG. 3. Relations between dry-yolk component masses (deviations from within-clutch means) and laying sequence (standardized for different clutch sizes) for 11 first clutches of Wood Ducks from the Savannah River Site, 1991 to 1992.

and expected skipped days in the laying sequence were significantly different (χ^2 = 6.45, df = 2, $P < 0.05$).

To determine if skipping a day of laying influenced egg quality, we compared component masses between penultimate and last-laid eggs of females that skipped a day before the last egg (n = 4) and those that did not (n = 9). The differences approached significance for wet and dry yolk, yolk AFLDM, and lipid (Table 3). Wet yolk mass, for example, increased by a median of 0.76 g from the penultimate to the last egg for females that skipped a day before laying the last egg. In contrast, a decline in wet yolk mass continued from the penultimate to the last egg for females that did not skip a day (Table 3).

DISCUSSION

The composition of Wood Duck eggs was similar to that reported by Hepp et al. (1987) at this same general location in 1986. Our results indicated that larger eggs have proportionately less shell material than smaller eggs. Eggshell provides both a protective enclosure for the

TABLE 3. Differences in component masses (g) between penultimate and last eggs from nests in which female Wood Ducks skipped a day between laying the last two eggs versus those that did not. Test statistics and P-values based on two-tailed Kruskal-Wallis test.

Component	Median difference with skip	Median difference without skip	χ^2	P
Fresh-egg mass	−0.755	0.600	0.857	0.35
Yolk				
Wet mass	−0.755	0.120	3.429	0.06
Dry mass	−0.470	0.080	3.438	0.06
Water	−0.195	0.130	2.381	0.12
Lipid	−0.375	0.026	2.881	0.09
AFLDM[a]	−0.105	0.013	3.429	0.06
Ash	−0.009	0.008	0.095	0.76
Albumen				
Wet mass	0.055	0.420	0.214	0.64
Dry mass	0.055	0.030	0.000	1.00
Water	0.010	0.270	0.095	0.76
Shell				
Wet mass	−0.025	−0.020	0.024	0.88
Dry mass	−0.095	−0.070	0.485	0.49

[a] Ash-free lean dry mass.

egg contents and essential minerals for the developing embryo (Romanoff and Romanoff 1949). Eggshells of Blue-winged Teal (*Anas discors*), for example, were thinner in hatched eggs than in fresh eggs (Rohwer 1986). The proportional reduction in shell material of larger Wood Duck eggs suggest at least two explanations. First, females may be limited in their acquisition of sufficient dietary minerals or by the rate of mobilization of body mineral reserves. In North America, however, most small-bodied waterfowl do not rely on mineral reserves for clutch development (Drobney 1980, Ankney and Alisauskas 1991; but see Alisauskas and Ankney 1994). Drobney (1980) observed increased carcass ash in Wood Ducks during laying and concluded that exogenous minerals were incorporated into medullary bone for use in shell calcium. Therefore, we believe that Wood Ducks are not limited in their ability to provide minerals for forming eggs. Alternatively, secretion of shell material may be relatively fixed, regardless of final egg size, by the amount of time that ova spend in the oviduct during shell formation. The period of albumen deposition and shell secretion is only about 24 h in Wood Ducks (Drobney 1980).

Egg size and composition in relation to egg-laying sequence.—Our finding that egg size initially increased with the laying sequence and then declined with the remaining eggs has been noted in several non-waterfowl species (e.g. European Starling [*Sturnus vulgaris*], Greig-Smith et al. 1987; American Coot, Arnold 1991). Among precocial waterfowl, however, this pattern has been reported only in large-bodied species (Canada Goose [*Branta canadensis*], Leblanc 1987; Barnacle Goose [*B. leucopsis*], Owen and West 1988; Black Brant [*B. bernicla nigricans*], Flint and Sedinger 1992; Common Eider [*Somateria mollissima*], Robertson and Cooke 1993). These species generally nest at high latitudes and acquire most of the nutrients and energy necessary for clutch development before arrival on breeding grounds (Ankney and MacInnes 1978, Raveling 1979). In contrast, Wood Ducks are relatively small-bodied and acquire some of the nutrients for clutch formation during the laying period (Drobney 1980).

Studies of Lesser Snow Geese (Williams et al. 1993) and Common Eiders (Robertson and Cooke 1993) have shown that eggs in the middle of the laying sequence have the highest hatching success, in part because last-laid eggs have a higher probability of being abandoned at hatching. Moreover, in both of these studies first-laid eggs suffered from higher levels of pre-incubation abandonment and predation. Such results, when combined with intraclutch egg-size patterns such as we found, offer support for the adaptive hypothesis that nutrient allocation within clutches should vary according to survival and/or fitness potential. However, other possible explanations exist. Flint and Sedinger (1992) proposed that egg-size variation with laying sequence in Black Brant is an adaptation to synchronize hatching. Flint et al. (1994) later predicted that intraclutch patterns in egg composition also may be adaptations for synchronizing waterfowl clutches at hatching. If embryonic development is relatively faster in small eggs, as Flint et al. (1994) suggested, then laying of small last eggs may be important in allowing clutches to hatch synchronously. Perhaps more importantly, at the time of hatching, embryos in small first-laid eggs may require less energy for maintenance than those in large eggs while waiting for the last-laid eggs to complete incubation. First-laid

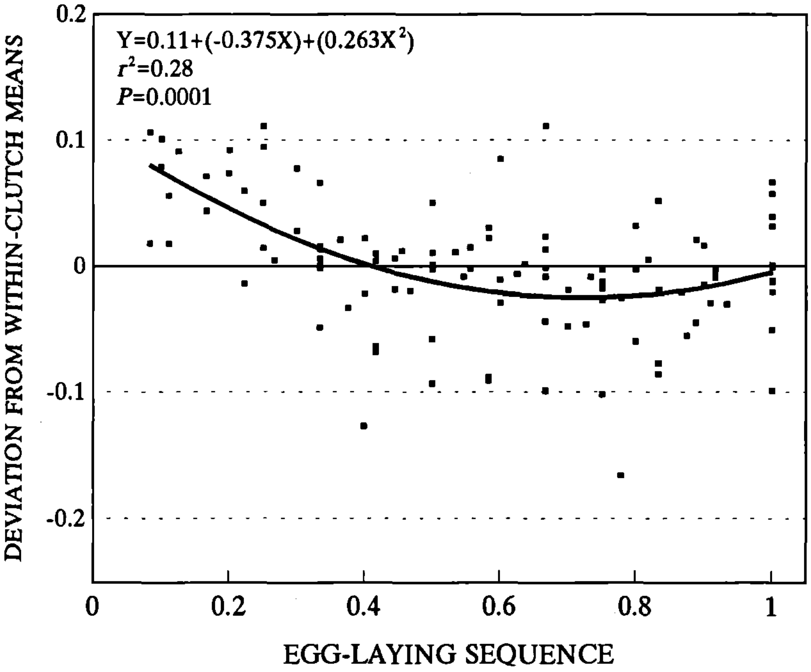

FIG. 4. Relation between lipid indices (lipid mass/lean-dry egg-content mass; deviations from within-clutch means) and laying sequence (standardized for different clutch sizes) for 11 first clutches of Wood Ducks from the Savannah River Site, 1991 to 1992.

Wood Duck eggs are proportionately better provisioned with lipids than are other eggs in the clutch (Fig. 4), containing about 2.5 kJ more energy per gram of lean dry-egg contents than the largest eggs in the clutch. Our results support the notion that intraclutch variation in egg composition may allow developing embryos in early eggs to delay hatching until incubation is completed for last-laid eggs.

The variation in egg size and nutrient allocation with laying sequence that we observed can be viewed as an adaptation for synchronized hatching only if the value of all eggs in the clutch is relatively equal. There are obvious limitations to the amount of asynchrony that can be compensated for (Davies and Cooke 1983, Kennamer et al. 1990), which results in the reduced success in last-laid eggs that is sometimes observed. Hepp et al. (1989), however, found that the body mass of Wood Duck hatchlings that left with the female was positively related to recruitment into the breeding population in only one of six years. Therefore, we believe that the necessity of creating various-sized offspring within clutches to facilitate hatching synchrony may outweigh the potential disadvantages conveyed to hatchlings based on their initial size.

Finally, the incubation/hatching-synchronization strategy described above may allow for relatively large clutch sizes that are typical of waterfowl. In contrast to many nonprecocial species in which the most productive clutch size is not the largest, clutch size in waterfowl generally is not limited by the provisioning abilities of parents. The evolution of such elaborate incubation and egg-composition patterns is likely to have occurred under conditions of relatively low predation pressure (which is not necessarily operating now) and low levels of food limitation compared with such pressures exerted on many smaller altricial species. Clutch size in waterfowl ultimately may be limited by the duration that unincubated eggs can remain viable during laying (Arnold et al. 1987). We suggest that intraclutch variations in egg size and composition in waterfowl are adaptations that permit females to initiate incubation while continuing to lay eggs. Furthermore, these adaptations persist because they result in a minimal loss of offspring that may result from failed hatching and poorly provisioned neonates. Future research should focus on experimental studies that determine the hatchability of first- and last-laid eggs, and that determine yolk reserves in hatchlings from such manipulated eggs.

Egg composition in relation to skipped laying days.—We found that Wood Ducks often skip a day of laying between the penultimate and last egg of the clutch. The increased mass of yolk components following skipped days at the end of laying suggests that the discrepancies were actually nonlaying days rather than occasions when females deposited eggs elsewhere or other females parasitized the nests. Bellrose and Holm (1994) noted that female Wood Ducks laying small clutches missed significantly more days of laying than females laying large clutches, and they suggested that the nutritional status of females was a contributing factor.

To our knowledge, our study is the first to describe the composition of eggs in relation to skipped laying days. Although differences in composition between the last two eggs in skipping versus non-skipping females were only marginally significant, the trends we observed may have important implications in the debate over clutch-size determination in waterfowl. Clearly, the relationship between skipped laying days and egg composition warrants further investigation.

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