

FACTORS AFFECTING VARIATION IN THE EGG AND DUCKLING COMPONENTS OF WOOD DUCKS

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ABSTRACT.—We collected 3 eggs from each of 35 female Wood Ducks (*Aix sponsa*). Fresh-egg mass averaged 44.2 g and consisted of 53.1% albumen, 36.4% yolk, and 9.6% shell. Albumen and yolk contained 86.2% and 44.9% water, respectively. Lipids comprised 65.1% of the dry yolk. All egg components except dry albumen increased in direct proportion to fresh-egg mass. Variation among females explained 52–80% of the total variation in mass and composition of eggs. Body mass of hens during early incubation was correlated with estimates of pre-egg-laying lipid reserves ($r_s = 0.66$); therefore, body mass was a good measure of female quality. Body mass of females was independent of age and structural size, and was positively related to mean egg mass, egg composition, energy content of eggs (kJ/g), and clutch mass, but not to clutch size or time of nesting. Female body mass explained more variation in albumen components than in yolk or shell components. These results support Drobney's (1980) hypothesis that prebreeding condition of female Wood Ducks is important because it allows hens to accumulate exogenous protein for egg synthesis. The data do not support predictions based on optimal egg size theory.

The body mass of ducklings averaged 23.7 g ($n = 43$); there were no intersexual differences in mass or composition. Ducklings contained 65.9% water and 32.5% lipids (dry mass). Components of ducklings increased in direct proportion to fresh-egg mass, but egg mass was a poor predictor of duckling lipid content. *Received 8 October 1986, accepted 2 February 1987.*

INTEREST in how females partition energy for reproduction has been stimulated partly by the positive relationship between egg size and fitness parameters of newly hatched birds, i.e. size (Schifferli 1973, Moss et al. 1981), survival (Parsons 1970, Lundberg and Väisänen 1979, Ankney 1980), and growth rate (O'Connor 1975, Williams 1980). In general, egg size varies within and between populations, with most variation (50–98%) attributable to differences among females (Ojanen et al. 1981, Grant 1982, Ricklefs 1984). There is a large heritable component to egg size (Ojanen et al. 1979, Van Noordwijk et al. 1980), but proximate factors like age (Ryder 1975, Crawford 1980, Gratto et al. 1983), laying date (Runde and Barrett 1981, Birkhead and Nettleship 1982, Bancroft 1984), and food supply (Horsfall 1984, Pierotti and Bellrose 1986) also affect egg size. Variation in egg size also may occur within clutches (Howe 1976), but this variation usually is much less than variation among females (Ricklefs 1984, Alisauskas 1986, Redmond 1986).

Interspecific variation in egg composition depends largely on the precocity of the species (Ricklefs 1977, Carey et al. 1980). Yolk size, for

example, increases in direct proportion to egg size in precocial (Vangilder 1981) and semiprecocial species (Alisauskas 1986), but yolk size increases less than proportionately to egg size in some altricial birds like European Starlings (*Sturnus vulgaris*; Ricklefs 1984) and Brown-headed Cowbirds (*Molothrus ater*; Ankney and Johnson 1985). The relationship between composition of eggs and precocity is fairly well established (see Carey et al. 1980), but few studies have examined intraspecific variation in egg composition that is due to proximate factors such as age, body mass, and laying date of the female. Moreover, few studies have linked egg size and composition to the size and composition of the neonate.

In this study of Wood Ducks (*Aix sponsa*), we investigated within- and among-female variation in the size and composition of eggs. Female Wood Ducks use endogenous fat reserves to meet 88% of the lipid and energy requirements of egg synthesis, but most egg protein demands are satisfied with exogenous nutrients (Drobney 1980). Because of the dependence on lipid reserves during egg laying, a female's "decision" to reproduce may depend on reaching a

threshold level of fat reserves that may be similar among females (see Alisauskas and Ankney 1985). Therefore, we predicted for Wood Ducks that egg lipids would vary less among females than would egg proteins. We tested effects of egg mass, laying date, and body mass and age of females on variation in egg composition, and examined the effect of egg mass on structural size, body mass, and lipid reserves of day-old ducklings. Finally, we evaluated our findings in light of predictions based on optimal egg size theory (Smith and Fretwell 1974, Brockelman 1975).

METHODS

In January–April 1986 we randomly collected 3 unincubated eggs from the clutches of 35 female Wood Ducks that used nest boxes at the Savannah River Plant (SRP) in Aiken and Barnwell counties, South Carolina. We substituted three hard-boiled chicken eggs at the time Wood Duck eggs were removed from nests so hens would not compensate for the eggs that were taken. Clutch size, therefore, should not have been affected by our manipulation. Length and breadth of all eggs in the clutch were measured to the nearest 0.1 mm with vernier calipers. Eggs collected from nests were weighed to the nearest 0.001 g on a Mettler balance and refrigerated in plastic bags for 0–7 days (\bar{x} = 3 days). After storage, eggs were heated in water at 90°C for 10–15 min to harden contents and ease the separation of shell, albumen, and yolk. Wet masses of components were recorded to the nearest 0.001 g and oven dried to a constant mass at 60–65°C. Water content was the difference between wet and dry masses of the components. Lipids were removed from dried yolks using petroleum ether in a Soxhlet apparatus (Dobush et al. 1985). Lipid content was the difference in mass of the dried sample before and after extraction. We refer to the mass of the dried yolk sample after lipid extraction as the lean dry mass (LDM). Total energy of eggs was calculated using energy equivalents of 33.82 kJ/g for dry yolk and 21.85 kJ/g for dry albumen (Drobney 1980).

We also collected 43 eggs from 19 females. These eggs were in various stages of incubation and were hatched in an incubator at 37.5°C and 88% relative humidity. Egg lengths and breadths were measured before incubation, and ducklings were hatched in separate compartments to determine the relationship between egg size and the size and composition of the neonate. Hatchlings were allowed to dry (<24 h) and then were sexed, killed, weighed (nearest 0.01 g), and placed in plastic bags before freezing. After they were thawed and reweighed, total body length was measured with a ruler (nearest 1 mm), and the tarsus, exposed culmen, and wing lengths were measured

with vernier calipers (nearest 0.1 mm) (see Baldwin et al. 1931). Ducklings were oven dried to constant mass at 70–75°C, and water, lipid, and lean dry mass were determined as for egg yolks.

Female Wood Ducks were weighed with a Pesola spring scale to the nearest 5 g before the thirteenth day of incubation (\bar{x} = 5 days); tarsus and wing length also were measured for some hens. Nest initiation dates and the occurrence of nest parasitism were monitored by checking nest boxes each week. More than one egg laid per day indicated a parasitized or “dump” nest in which more than one female was depositing eggs. In our sample of 35 nests, 4 nests were dump nests. Eggs from dump nests were included only in summaries of egg composition (Table 1) and the allometric analyses of egg mass to component mass (Table 2). Dump nests were deleted in other analyses that related egg size or egg composition to characteristics of individual females. Clutch size was determined for 28 of 31 normal (i.e. nonparasitized) nests. The modal value was 13 eggs (n = 9) and ranged from 11 to 16.

Nesting activity of Wood Ducks in nest boxes has been monitored at the SRP since 1979. Each year most hens that nested in boxes were captured and banded with U.S. Fish and Wildlife Service leg bands. In addition, many of the ducklings that hatched in nest boxes were individually web-tagged. Return of web-tagged females to nest boxes in subsequent breeding seasons provided a sample of known-age females. Our sample of female Wood Ducks included 8 individuals of known age; 10 females that nested and were banded in previous years but were not web-tagged initially, so exact age was not known; and 10 females neither banded nor web-tagged. Hepp et al. (1987), using 8 yr of capture-recapture data, showed that female Wood Ducks are highly philopatric to previous nest locations. Therefore, we assumed unmarked hens (no leg band or web tag) were first-time breeders that hatched either from natural cavities or from nest boxes but were not web-tagged, and not older hens that simply changed nest sites. We separated females into three age categories to test for age-specific variation in the size and composition of eggs: (1) first-time breeders, including females that were web-tagged as ducklings in 1985 (1-yr-olds) and all unmarked females that were assumed to be breeding for the first time; (2) second-time breeders, including females that were web-tagged as ducklings in 1984 (2-yr-olds) and females caught as unmarked hens in 1985 during their first assumed breeding attempt in nest boxes; and (3) females that nested in three or more breeding seasons.

We used the Statistical Analysis System (SAS) to complete statistical summaries and analyses (SAS Inst. 1985). Linear regression and analysis of variance were performed with the general linear model (GLM) procedure. The VARCOMP procedure was used to partition variation of egg components into within- and among-female parts (Lessells and Boag 1987). Using

TABLE 1. Dimension (mm) and composition (g) of Wood Duck eggs ($n = 105$). Values are means, standard deviations (SD), and coefficients of variation (CV).

Variable	Mean	SD	CV (%)
Egg mass	44.18	3.53	8.0
Length	51.33	2.04	4.0
Breadth	39.35	1.07	2.7
Yolk			
Wet	16.11	1.64	10.2
Dry	8.87	0.90	10.1
Water	7.23	0.78	10.7
Lipid (g)	5.78	0.60	10.3
Lean dry mass	3.09	0.34	11.0
Lipid (%)	65.14	1.47	2.3
Albumen			
Wet	23.43	1.95	8.3
Dry	3.23	0.30	9.4
Water	20.20	1.71	8.5
Shell			
Wet	4.23	0.41	9.6
Dry	3.81	0.37	9.6
Total energy (kJ)	370.80	33.37	9.0
kJ/g	8.37	0.29	3.6

the PRINCOMP procedure, we completed a principal component analysis (PCA) of the correlation matrix to help describe the relationship among the mass and composition of eggs and the characteristics of female Wood Ducks.

RESULTS

Dimensions, mass, and composition of eggs.—Fresh-egg mass averaged 44.2 g and consisted

of 53.1% albumen, 36.4% yolk, and 9.6% shell, while dry mass of eggs was comprised of 55.7% yolk, 24.0% shell, and 20.3% albumen (Table 1). Length (L), breadth (B), and fresh mass (M) of eggs collected for this study were used to develop an equation that estimates fresh-egg mass from external measurements:

$$M = 0.993 + 0.00054(LB^2)$$

[$F(1,103) = 3,832, P < 0.0001, R^2 = 0.97$]. Because L and B were measured for every egg in the clutch, we estimated the mean egg mass and clutch mass of every nest.

Relationship of egg components to egg mass.—We investigated the allometry of egg composition by regression of the logarithm of each component's mass on the logarithm of fresh-egg mass. The slope of the regression estimates the exponent, b , of the relationship $Y = aX^b$. Values of b not significantly different ($P > 0.05$) from 1.0 indicate that the mass of egg components increases in direct proportion to fresh-egg mass. Results of log-log regression analyses indicated that all components increased in direct proportion to fresh-egg mass except the dry albumen component (Table 2).

Sources of variation in egg size and egg composition.—Most variation in the mass (71%) and composition of eggs (52–80%) was due to variation among females (Table 3). Among-female variation was greatest for the shell and albumen components and accounted for more than half the variation in yolk composition.

Age class and body mass of incubating fe-

TABLE 2. Summary of log-log regressions of egg components (Y) on fresh-egg mass (X) ($n = 105$).^a

	a	b	s_b	95% CI	R^2
Yolk					
Wet	-0.60	1.10	0.069	0.96-1.24	0.71
Dry	-0.89	1.11	0.068	0.98-1.25	0.72
Water	-0.93	1.09	0.081	0.93-1.25	0.64
Lipid (g)	-1.09	1.12	0.071	0.98-1.26	0.71
Lean dry mass	-1.32	1.10	0.089	0.92-1.28	0.60
Albumen					
Wet	-0.18	0.94	0.045	0.85-1.03	0.81
Dry	-0.77	0.78	0.086	0.61-0.95	0.44
Water	-0.29	0.97	0.045	0.88-1.06	0.82
Shell					
Wet	-0.76	0.84	0.088	0.67-1.02	0.47
Dry	-0.82	0.85	0.087	0.68-1.02	0.48
Total energy	0.23	1.04	0.046	0.95-1.13	0.84

^a a is the intercept and b the slope in the regression equation $Y = aX^b$; s_b is the standard error of b ; CI is the 95% confidence interval of the slope; R^2 is the coefficient of determination.

TABLE 3. Variation in the mass and composition of eggs among Wood Duck hens ($n = 87$ eggs from 29 females).

Variable	Among-female variance component (%) ^a	R ² ^b
Fresh-egg mass	71.0	0.35**
Yolk		
Wet	53.0	0.18*
Dry	52.3	0.21*
Water	56.4	NS
Lipid (%)	68.9	NS
Lipid (g)	52.0	0.19*
Lean dry mass	55.9	0.20*
Albumen		
Wet	78.2	0.36**
Dry	74.5	0.31**
Water	78.1	0.34**
Shell		
Wet	73.1	0.25*
Dry	79.7	0.18*
kj/egg	55.0	0.29**

^a $P < 0.0001$ for all variables.

^b Summarizes results of regression analyses to test effects of the body mass of female Wood Ducks on the mass and composition of eggs. Values used in the analyses were within-clutch means ($n = 24$). * = $P < 0.05$, ** = $P < 0.01$, NS = not significant.

males were not correlated (Spearman's coefficient, $r_s = 0.14$, $P < 0.50$). Analysis of covariance (ANCOVA) using body mass as the covariate further tested the effects of female age on the mass and components of eggs and showed no effect ($P > 0.05$) for every component tested. Instead, body mass alone explained 18–36% of variation in egg mass and egg composition (Table 3). This was clearer for albumen components than for yolk components. Heavy females laid significantly heavier eggs with larger yolk, albumen, and shell components and also produced clutches of greater mass, but not of larger number, than light females (Fig. 1). Body mass of incubating females was not correlated with tarsus length ($r_s = 0.38$, $df = 9$, $P > 0.05$) or wing length ($r_s = 0.16$, $df = 5$, $P > 0.05$). Clutch

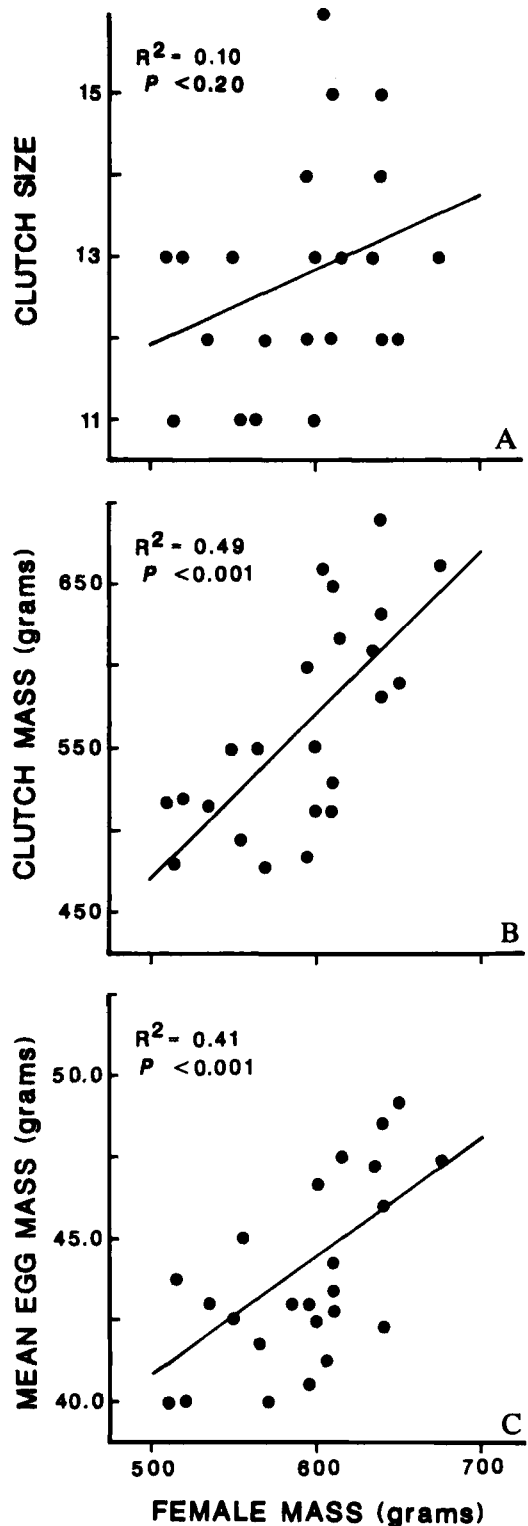


Fig. 1. Relationship of (A) clutch size, (B) clutch mass, and (C) mean egg mass to the body mass of female Wood Ducks. The regression equations describing the relationships are: clutch size, $Y = 7.25 + 0.0093X$; clutch mass, $Y = -33.79 + 1.006X$; and mean egg mass, $Y = 20.23 + 0.0397X$.

TABLE 4. Summary of principal component analysis of the correlation matrix of egg mass, egg composition, and characteristics of female Wood Ducks ($n = 22$ females).

	Principal components		
	I	II	III
Egg mass	0.34	-0.12	0.14
Yolk			
Wet	0.33	-0.23	-0.15
Dry	0.35	-0.16	-0.13
Lipid (g)	0.34	-0.23	-0.04
Lean dry mass	0.33	-0.03	-0.25
Albumen			
Wet	0.32	-0.09	0.24
Dry	0.26	-0.01	0.44
Shell			
Wet	0.30	0.30	-0.14
Dry	0.29	0.28	-0.20
Clutch size	-0.03	0.53	0.42
Time of nesting	-0.16	-0.43	0.09
Female age	0.03	0.39	-0.49
Female body mass	0.24	0.23	0.37
Percentage of total variance	55.7	14.8	9.6
Cumulative percentage	55.7	70.5	80.1

mass ($r_s = -0.60$, $P < 0.01$) and clutch size ($r_s = -0.46$, $P < 0.02$) were correlated inversely with time of nesting, but mean egg mass and female age were not. Body mass of females during incubation was not related significantly to time of nesting [$F(1,21) = 3.53$, $P < 0.10$, $R^2 = 0.14$].

Principal components analysis resulted in three principal components that accounted for 80% of the variance in the data (Table 4). The first principal component explained 55.7% of the variation and again illustrated the positive association between body mass and the mass and composition of eggs. The second component (14.8%) reflected the negative relationship between time of nesting and the other female variables (clutch size, female age, and body mass), with negative values for yolk components and positive values for wet and dry shell. The third component (9.6%) described the inverse relationship between female age and the variables clutch size, body mass, and albumen.

Relationship of egg mass to the size and composition of day-old Wood Ducks.—There were no intersexual differences ($P > 0.05$) in the mass or composition of ducklings, so data were combined (Table 5). Wet mass of ducklings (23.7 g)

TABLE 5. Mean values of body mass (g), composition (g), and dimensions (mm) of day-old Wood Ducks ($n = 43$).

	Mean	SD	CV (%)
Wet body mass	23.67	2.25	9.5
Dry body mass	8.06	0.70	8.7
Water	15.61	1.73	11.1
Lipid (g)	2.62	0.38	14.7
Lipid (%)	32.47	2.98	9.2
Lean dry mass	5.44	0.45	8.2
Tarsus	18.20	0.78	4.3
Culmen	15.26	0.63	4.1
Wing length	15.47	0.70	4.5
Total length	145.75	5.34	3.7

consisted of 65.9% water. Lipids comprised 32.5% of duckling dry mass, which indicated that about 50% of egg lipids are metabolized during incubation.

Duckling components increased in direct proportion to fresh-egg mass, although most relationships were weak (Table 6). The lipid content of ducklings was related more strongly to the wet and dry mass of ducklings than to fresh-egg mass.

DISCUSSION

Egg and duckling composition.—Composition of Wood Duck eggs was similar to the egg composition of other species of Anatidae, as well as other groups of precocial birds (Carey et al. 1980; Vangilder 1981; Birkhead 1984, 1985). Eggs of precocial species generally contain larger percentages of yolk and smaller percentages of albumen than eggs of nonprecocial species (Ricklefs 1977, Ricklefs et al. 1978). In the altricial Boat-tailed Grackle (*Quiscalus major*; Bancroft 1985) and Eastern Kingbird (*Tyrannus tyrannus*; Murphy 1986), the yolk/albumen (dry) ratio was 1.37 and 1.32, respectively, compared with 2.47 for Wood Ducks. Yolk contains more energy than albumen, so eggs of precocial species have more energy per unit mass than altricial species. Wood Duck eggs averaged 8.37 kJ/g compared with an average of 4.77 kJ/g for several altricial species (Carey et al. 1980).

All components of Wood Duck eggs except dry albumen increased in direct proportion ($b = 1.0$) to fresh-egg mass. In general, mass of components correlated well with egg mass. Isometric increases of egg components with fresh-egg mass also have been reported for other pre-

TABLE 6. Log-log regression of the components of day-old Wood Ducks (Y) on the independent variables (X) fresh-egg mass, wet mass of duckling, and dry mass of duckling ($n = 43$).^a

	a	b	s_b	95% CI	R^2
Fresh-egg mass					
Wet mass	-0.26	1.01	0.16	0.68-1.33	0.49
Dry mass	-0.77	1.03	0.13	0.77-1.30	0.60
Water	-0.42	0.99	0.21	0.57-1.42	0.35
Lipid (g)	-1.15	0.96	0.31	0.33-1.59	0.19
Lean dry mass	-0.99	1.06	0.11	0.83-1.29	0.68
Wet mass of duckling					
Dry mass	-0.11	0.74	0.08	0.57-0.90	0.66
Water	-0.37	1.14	0.04	1.05-1.23	0.94
Lipid (g)	-0.82	0.90	0.19	0.52-1.28	0.35
Lean dry mass	-0.17	0.66	0.09	0.48-0.84	0.57
Dry mass of duckling					
Lipid (g)	-0.80	1.34	0.15	1.04-1.65	0.65
Lean dry mass	-0.02	0.83	0.07	0.69-0.98	0.76

^a a is the intercept and b the slope in the regression equation $Y = aX^b$; s_b is the standard error of b ; CI is the 95% confidence interval of the slope, b ; R^2 is the coefficient of determination.

social species such as Snow Geese (*Chen caerulescens*; Ankney 1980), Japanese Quail (*Coturnix japonica*; Ricklefs et al. 1978), and Mallards (*Anas platyrhynchos*; Vangilder 1981, Birkhead 1985). The relationship between egg mass and egg components differs in nonprecocial species. In many altricial species, for example, yolk mass decreases proportionately and albumen mass increases proportionately with increasing fresh-egg mass (Ricklefs 1984, Ankney and Johnson 1985, Murphy 1986). However, Bancroft (1985) reported that dry mass of yolk and energy content of eggs increased in direct proportion to fresh-egg mass in Boat-tailed Grackles. Egg mass accurately predicts size of yolk in some altricial species (Bancroft 1985, Murphy 1986) but not in others (Ricklefs 1984). In a semiprecocial species, the American Coot (*Fulica americana*), yolk mass but not mass of the albumen increased in direct proportion to egg mass (Alisauskas 1986). There is obviously much interspecific variation in allometry of egg composition, and some of this variation can be attributed to the developmental mode of young (altricial vs. precocial). Variation within developmental groups also occurs, however, which suggests that there are species-specific patterns of egg composition and perhaps facultative adjustment of egg composition.

Relationships between egg composition and the size and composition of the neonate are not well known. Components of day-old Wood Ducks increased in direct proportion to the

fresh-egg mass predicted from egg measurements. Relationships of water and lipid content of the neonate and egg mass, however, were weak. A stronger relationship existed between lipids and the wet and dry mass of the neonate. Semiprecocial chicks of American Coots differ from Wood Duck ducklings in that there is a proportionately greater increase in dry mass and LDM of coot chicks in relation to egg mass (Alisauskas 1986). Other components of coot chicks increased in direct proportion to egg mass. Compared with coots (see Alisauskas 1986), the lipid index (g lipid/LDM) of day-old Wood Ducks is higher (0.48 vs. 0.30) and the water index (g water/LDM) is lower (2.87 vs. 4.34), illustrating the greater functional maturity (see Ricklefs et al. 1980) and larger fat reserves of Wood Ducks at hatching. The rather poor relationship between egg mass and lipid content of neonates ($R^2 = 0.30$ and 0.19 , respectively) is common to both American Coots and Wood Ducks, and is important for understanding the relationship between egg size and neonate quality. The stronger correlation between egg lipids and fresh-egg mass ($r = 0.84$) than between lipids of the neonate and neonate mass ($r = 0.59$) supports data on coots (Alisauskas 1986) and suggests the rate of lipid metabolism varies among individuals. Hence, egg mass of Wood Ducks is a relatively good predictor of neonate mass but a poor predictor of lipid content of the neonate.

Variation of egg mass and composition.—Most

variation (52–80%) in egg mass and egg components was due to variation among female Wood Ducks. Other investigators have reported similar values of among-female variation for egg size and composition (Bancroft 1984, Ricklefs 1984, Redmond 1986), and some have suggested that there is a large heritable component to the shape and mass of eggs (Van Noordwijk et al. 1980, Grant 1982). Variation among female Wood Ducks accounted for more of the variability in albumen (i.e. protein) components (74–78%) than in lipid components (52–69%), thus confirming our prediction that egg proteins would vary more among females than egg lipids. Both coots (Alisauskas and Ankney 1985) and Wood Ducks (Drobney 1980) use lipid reserves to meet nearly all the lipid and energy requirements of clutch development but use primarily exogenous sources of protein for synthesis of egg protein. If female Wood Ducks delay egg laying until they attain a threshold level of lipid reserves (see Alisauskas and Ankney 1985), then variation among females should explain less variability in egg lipids than in protein components of eggs. Because coots are territorial, Alisauskas (1986) suggested that higher among-female variation in protein components of eggs was related to variation in territory quality. Wood Ducks are not territorial, so greater variation of protein components among females probably reflects differences in the ability of individuals to obtain exogenous protein. Drobney (1980) showed that female Wood Ducks satisfy protein requirements of egg development by consuming large amounts of invertebrate food. He suggested that use of lipid reserves during laying allows hens to forage almost exclusively on invertebrate prey, thus meeting the protein demands of reproduction. The level of a female's prelaying lipid reserves, therefore, may affect the ability to deposit egg protein.

Body mass of female Wood Ducks in early incubation was independent of age and structural size (i.e. tarsus and wing length) and was significantly related to mean egg mass, energy content of eggs (kJ/g), egg components, and clutch mass but not to clutch size. Because heavy hens allocated more total energy to development of clutches, we suggest that body mass in early incubation is a good index to the physiological condition or "quality" of the prebreeding female. Using predicted values of clutch

mass together with the amount of yolk and yolk lipids in an average Wood Duck egg, we estimated the lipid content of clutches. Because lipid reserves of female Wood Ducks provide about 88% of the lipid and energy requirements of an average clutch (Drobney 1980), the lipid content of clutches should be a relatively good estimate of female lipid reserves before egg laying. Estimates of pre-egg-laying lipid reserves were correlated positively ($r_s = 0.66$, $P < 0.001$) with body mass in early incubation, supporting the use of body mass as an index to female quality.

Some studies have revealed positive relationships between the body mass or size of females and the mass or volume of eggs (Väisänen et al. 1972, Redmond 1986), but others show no relationship (Batt and Prince 1978). This is one of the first studies we are aware of that actually relates female body mass to the composition of eggs (see Murphy 1986). Body mass of female Wood Ducks explained more variation in albumen components than in yolk or shell components. Apparently, heavy females, because of larger lipid reserves, are more effective in gathering exogenous protein, which explains the stronger relationship between hen mass and the albumen components. PCA also showed the strong association between female body mass and the mass and composition of eggs, and it suggested that, to a much lesser degree, time of nesting and female age may interact with body mass and clutch size to influence egg mass and composition. We support Drobney's (1980) contention that a female's prebreeding condition is extremely important because it enables her to accumulate exogenous protein for development of eggs. Exogenous protein is important for egg synthesis and helps to maintain endogenous protein reserves, thereby increasing the probability of renesting or producing another brood. Therefore, females may delay the production of eggs until lipid reserves are adequate. We note that if trade-offs exist between the benefits of attaining lipid reserves and the costs of delaying the time of nesting, then females may produce eggs when lipid reserves are below the threshold (or the threshold value may change) because costs of nesting later in the season may more than offset any benefits derived from further increasing lipid reserves. For example, late-nesting females may have lower probabilities of renesting (Krapu 1981) or

raising a second brood (Fredrickson and Hansen 1983), and young hatched later in the season may have lower survival rates than young hatched from early nests (see Perrins 1980).

Optimality theory predicts an inverse relationship between clutch size and the size of the egg or neonate (Smith and Fretwell 1974, Brockelman 1975). These models assume that the amount of energy an organism can devote to reproduction is limited; therefore, energy added to eggs or offspring will have a negative effect on clutch size. Implicit in this idea is that larger offspring will survive and reproduce better than small offspring. These models assume that egg or neonate size has been optimized by natural selection. If egg size has been optimized, then there should be little variation in egg size among females, and females that have more energy for reproduction should produce larger clutches but not larger eggs. The relationship between egg size and clutch size for Wood Ducks was not significant ($r_s = -0.12$, $P > 0.50$). Furthermore, heavy females with large prelaying lipid reserves did not increase clutch size but produced significantly larger eggs. The slight positive relationship between body mass and clutch size suggests that adjustment in clutch size may occur, but it occurs secondarily to adjustment in egg size. Hence, these results do not support predictions based on optimal egg size theory.

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