

COMPOSITION OF BLUE-WINGED TEAL EGGS IN RELATION TO EGG SIZE, CLUTCH SIZE, AND THE TIMING OF LAYING¹

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Abstract. Blue-winged Teal (*Anas discors*) eggs from 172 nests were analyzed to determine how organic composition was affected by clutch size, laying sequence, nest attempt, laying date, and egg size. On average, eggs weighed 28.1 g and were 46% yolk and 44% albumen. Eggs contained 3.6 g lipid and 3.2 g protein almost equally distributed between yolk and albumen. Yolk increased a disproportionate amount and the proportion of albumen tended to decrease with increased egg mass. Consequently, large eggs contained proportionately more lipid than small eggs. Shell decreased in proportion with increasing egg mass. For most egg traits 60 to 80% of the variation occurred between clutches rather than within clutches. Teal eggs did not vary in composition in relation to clutch size, laying sequence, nest attempt, or the timing of laying on either a seasonal or yearly basis. Eggs in renests weighed 0.8 g less than eggs from the first clutch of the same females; however, this disparity was not reflected in differences in lipid or lean dry mass for the collected eggs of known renesters.

Key words: *Albumen; Anas discors; Blue-winged Teal; clutch size; egg composition; Manitoba; renesting; shell; yolk.*

INTRODUCTION

Although variation in egg size, like most traits, is largely attributable to differences between species, considerable variation is apparent within species. This intraspecific variation in egg size has been partitioned into effects due to laying date (Kendeigh et al. 1956, Coulson 1963), laying sequence (Kendeigh et al. 1956, Coulson 1963, Parsons 1970, Howe 1976), individual female (Coulson 1963, Grant 1982, Ricklefs 1984), and factors acting on laying females such as age, nutrition, and paired status (Richdale 1955, Kendeigh et al. 1956, Coulson 1963, Nisbet 1973, Beckerton and Middleton 1982). Several studies have shown positive relationships between egg size and growth rate and survival of wild hatched young (Parsons 1970; Schifferli 1973; Howe 1976; Nisbet 1973, 1978; Ankney 1980; Beckerton and Middleton 1982). The advantages of large eggs should be particularly great for birds whose chicks must find their own food. This prediction is supported by the observation that precocial birds lay larger, more energy dense eggs than do altricial birds (Nice 1962, King 1973, Ar and Yom-Tov 1978). Countering the selection for large eggs is the selective pressure for laying many eggs. If clutch size in birds with self-feeding young is limited by the availability of nutrients for egg production (Lack 1967, 1968a; Ankney and MacInnes 1978), then the size of eggs should reflect a balance between laying fewer large eggs or many small

eggs. In light of the direct effect that egg provisioning has on survival of precocial chicks and the potential that laying large eggs has for reducing the number of eggs laid, it is surprising that there have been so few studies on intraspecific variation in the eggs of precocial birds. In this paper, I present information on Blue-winged Teal egg size and organic composition in relation to year, laying date, sequence in the laying cycle, nest attempt, and clutch size.

METHODS

Blue-winged Teal eggs ($n = 591$ eggs from 172 nests) were taken from nests of wild free-ranging birds that were breeding in the prairie pot-hole region of southwestern Manitoba. Eggs were collected in 1979 and 1981 to 1983. The eggs collected in 1979 were either one or both of the first two eggs ($n = 25$) laid in a nest or one or both of the last two eggs ($n = 38$) laid in a nest. Eggs were taken before incubation began and were weighed, heated in an 80°C water bath for 25 to 40 min, individually bagged, and then frozen for analyses that were performed the following winter. Water loss from processing and freezer storage averaged 0.1 g. Thawed eggs were separated into albumen, yolk, and shell (with membranes). Shell and yolk were weighed separately and albumen mass was obtained by subtraction from the fresh egg mass. Egg components were freeze dried (1979) or oven dried (1981 to 1983) at 70°C to a constant mass. For the 1979 eggs, the nitrogen content of both yolk and albumen was determined by the Kjeldahl method and protein was calculated using 16% nitrogen in

¹ Received 28 May 1985. Final acceptance 1 July 1986.

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egg protein (Romanoff and Romanoff 1949). After 1979, eggs were not analyzed for protein because albumen protein content and dry albumen weight were very closely correlated (Pearson correl. Coeff. = 0.99, $P < 0.0001$), as were yolk protein and ash-free lean dry yolk ($r = 0.92$, $P < 0.0001$). References to protein content concern only the 1979 sample of eggs. Lipid was extracted from yolk using a 5:1 mixture of petroleum ether and chloroform in Soxhlet or Randall extractors (Randall 1974). Lipid and protein determinations for the 1979 eggs were done in duplicate and had an average discrepancy between samples of the same egg of 0.9% for albumen protein, 3.0% for yolk protein, and 1.6% for lipid. Ash content of components was obtained by combustion at 500°C in a muffle furnace for 8 hr. Shell thickness (± 0.01 mm) was determined by averaging three measures taken at the mid-length of each egg.

To obtain eggs from known second laying attempts, females caught while laying their first clutch were marked with nasal saddles (Sugden and Poston 1968) and/or back-mounted radio transmitters. Once a marked female's first clutch was complete, the eggs were removed and the female was tracked until she was found at a second nest. None of the six pairs where both the male and female were marked showed a mate shift between nest attempts. Incidental observations of the other pairs gave no indication that females changed mates between nest attempts. After first clutches were taken, all marked females were accompanied by their paired male for at least three weeks, regardless of whether the female eventually laid a replacement clutch. Females that were repeatedly observed and did not lay a replacement clutch were classified as nonrenesters.

Some of the statistics concerning egg mass involve a larger sample of Blue-winged Teal egg size measurements taken (on eggs that were not collected) in the same area during 1978 to 1983. For nests that had begun incubation, the fresh egg mass (M) was estimated from length (L) and breadth (B) in cm by the equation:

$$M = 0.551LB^2.$$

The constant in this equation (Hoyt 1979) was derived from measurements of length, breadth, and fresh mass for Blue-winged Teal eggs from 109 nests. Calculated egg masses deviated by an average of 0.9% from actual mass for a sample of eggs from 57 nests not used to generate the above equation.

In order to partition the variation in egg components I collected 26 complete clutches (273 eggs). These eggs were separated into component parts and dried, but lipid extractions were not performed on most of these

eggs. Of the 591 eggs collected, only 294 (from 145 nests) were analyzed for lipid content. Data from separate years were pooled for most analyses, as mass and composition of collected eggs did not vary by years. Eggs laid by a single female may not be treated as statistically independent. Therefore, the analyses and tables in this paper are based on means of nests, except the analyses designed to partition egg variation between and within nest or laying attempts. I used the SAS statistical package for most of the data analyses (SAS Institute 1982).

Frequent nest checks during laying have never shown more than a single egg appearing in a Blue-winged Teal nest per day. The absence of clutches of more than 13 eggs further suggests that intraspecific parasitism is absent or extremely rare in Blue-winged Teal; so all the eggs in a nest could reliably be assigned to a single female.

RESULTS

EGG COMPOSITION

Fresh Blue-winged Teal eggs weighed 28.1 ± 0.19 g and were 35.6% dry matter (Table 1). Yolk comprised $45.7 \pm 0.3\%$ of the egg mass and $57.4 \pm 0.2\%$ of the dry egg mass. The 1979 eggs had 1.63 ± 0.02 g protein and 1.96 ± 0.04 g ash-free lean dry mass in the yolk and 1.57 ± 0.03 g protein and 1.85 ± 0.03 g ash-free dry mass in the albumen (Table 2). Yolk supplied all of the lipid and 51% of both the total protein and the ash-free lean dry weight of the egg contents.

Shell mass for eggs from 72 nests was 2.24 ± 0.03 g before ashing and 2.04 ± 0.2 g after ashing. This difference largely reflects the mass of shell membrane, but also includes the small component of glycoprotein that comprises the organic matrix of the shell (Romanoff and Romanoff 1949, Sturkie and Mueller 1976). Egg shells were obtained from a sample of 18 eggs (from 18 nests) taken at the beginning of hatching and hatched in jars in an incubator. The ashed mass of these shells, which were obtained from eggs of similar size to the collected fresh eggs, was 1.87 ± 0.03 g. This indicated a highly significant loss of shell minerals during development (t -test, $t = 6.31$, $n = 90$, $P < 0.0001$). Shell thickness (without shell membranes) for 60 hatched eggs was 0.19 ± 0.002 mm, whereas thickness of 36 shells of unincubated eggs averaged 0.23 ± 0.002 mm (0.27 ± 0.003 mm with shell membranes included).

VARIANCE BETWEEN FEMALES

One-way analysis of variance (ANOVA) on 78 completed Blue-winged Teal clutches where I weighed all the eggs ($n = 833$) showed that

TABLE 1. Mass of fresh Blue-winged Teal egg components.

Component	Wet mass			Dry mass		
	$\bar{x} \pm 1 \text{ SE}$	%	n^a	$\bar{x} \pm 1 \text{ SE}$	%	n^a
Total egg	28.1 \pm 0.2	—	172	10.0 \pm 0.1	—	172
Yolk	12.9 \pm 0.1	45.7	172	5.7 \pm 0.04	57.4	172
Albumen	12.4 \pm 0.1	44.3	155	2.0 \pm 0.02	20.1	172
Shell	2.8 \pm 0.05	10.0	155	2.2 \pm 0.02	22.3	172

^a Sample sizes represent number of nests. Eggs from the same nest were averaged to provide one observation from that nest. Wet shell weight was not recorded for the single egg in 17 nests, so some samples have only 155 observations.

69% of the variation in egg mass was variation between clutches (Table 3). Similarly, the within and between clutch variations in egg composition were partitioned by ANOVA on the eggs from 26 completed Blue-winged Teal clutches. As with egg mass, most of the variation in composition was attributable to differences between clutches and not to intra-clutch variation (Table 3). ANOVAs done with partial clutches, but more total eggs, partitioned the variance in roughly the same fashion, although the within-clutch component, which was based on as few as two or three eggs per nest, was usually 3 to 5% lower than an analysis of the same variable that only used data from full clutches.

COMPOSITION IN RELATION TO EGG MASS

I regressed log component mass against the logarithm of egg mass to see if the proportionate composition of Blue-winged Teal eggs changed with egg size (Tables 4 and 5). If the slope of such a regression could not be distinguished from a slope of 1.0, then the proportion of the dependent variable (egg component) did not change over the observed range of egg sizes. With increasing egg size, the proportion of yolk and albumen changed slightly and these changes were reflected in the changing organic composition of teal eggs. The proportion of dry yolk increased and the proportion of dry albumen decreased (Table 4). The lipid fraction of teal eggs increased slightly with increasing egg size. This increase in the lipid fraction of large eggs was caused by increased yolk, since the proportion of lipid did not change with yolk size ($F = 3.76$, $P > 0.05$, $n = 145$). The proportions of wet albumen and wet yolk showed a tendency to change as egg size

increased, but neither regression slope differed significantly from a slope of 1.0 (Table 4). As expected, dry egg mass was closely related to wet egg mass, as was the total water component (Table 4). Log-log regressions with dry egg mass as the independent variable showed the same patterns of increased yolk and lipid and decreased albumen and lean mass with increasing dry mass (Table 5).

Shell thickness was not significantly related to egg mass (Pearson correl. $r^2 = 0.01$, $P > 0.05$). This would suggest that shell represents a surface that relates to egg volume; so I expected the slope of the log dry shell mass vs. log egg mass regression to be 0.67. This value was just within the lower margin of the 95% confidence intervals of the regression slope (Table 4).

The analysis of 26 complete clutches (8 to 12 eggs per nest) made it possible to see if intraclutch variation in egg composition paralleled interclutch variation. Analysis of covariance (ANCOVA) that used the proportion of dry albumen or dry yolk as the dependent variable, egg mass as the covariate, and nest as the class effect showed that the F -ratios for the interaction of nest and egg mass were highly significant ($P < 0.001$, $n = 26$ nests and 273 eggs). This indicates that females differ in the way they allocate yolk and albumen to different sized eggs in their clutch. Simple regressions of log component vs. log egg mass done for each of the 26 clutches where all eggs were analyzed showed the same female effect. There was a great deal of variability between slopes for individual clutches, and several clutches had slopes that did not differ significantly from zero. However, the averages of the slopes of the 26 log-log regressions of dry yolk vs. egg

TABLE 2. Organic composition of fresh Blue-winged Teal eggs.

Component	Composition (dry mass \pm 1 SE)			
	Lipid ($n = 145$) ^a	Protein ($n = 36$) ^a	Ash-free lean ($n = 61$) ^a	Ash ($n = 40$) ^a
Yolk	3.60 \pm 0.03	1.63 \pm 0.02	1.92 \pm 0.03	0.11 \pm 0.003
Albumen	—	1.57 \pm 0.03	1.88 \pm 0.03	0.11 \pm 0.003
Shell	—	—	—	2.04 \pm 0.021 ^b

^a n = number of nests. Eggs from the same nest were averaged into one observation.

^b $n = 72$.

TABLE 3. Analysis of variance for size and composition of eggs between nests of Blue-winged Teal ($n = 26$ nests, 273 eggs).

	<i>F</i>	<i>P</i>	<i>r</i> ²	SD ^a
Mass ^b	21.5	<0.0001	0.69	1.13
Egg (%)				
Yolk	15.86	<0.0001	0.62	3.00
Albumen	5.31	<0.0001	0.67	3.16
Shell	6.64	<0.0001	0.40	2.51
Water	2.52	<0.0001	0.47	1.14
Dry egg (%)				
Yolk	32.17	<0.0001	0.77	1.31
Albumen	40.42	<0.0001	0.81	1.01
Shell	11.87	<0.0001	0.55	0.90
Lipid ^c	7.49	<0.0001	0.88	1.11
Lean ^c	9.05	<0.0001	0.90	0.85

^a Within clutch SD.

^b Based on 78 full clutches (833 eggs), few of these egg were collected.

^c Sample size = 145 nests, 294 eggs.

mass and dry albumen vs. egg mass were very close to a slope of 1.0, which indicates no change in proportionality. This suggests that over the narrow range of intra-clutch egg mass variation the relationship of component to egg size follows approximately the same pattern as shown by the full range of Blue-winged Teal egg sizes.

EGG COMPOSITION AND CLUTCH SIZE

Eggs were collected from 88 nests of known final clutch size. To discover whether clutch size affected average egg composition or the way organic composition related to clutch size, I ran ANCOVAs using clutch size as a class variable with values of 9, 10, 11, and 12 eggs and egg mass as the covariate. Clutch size influenced neither the slopes nor the intercepts of the log relations of yolk mass, albumen mass, shell mass, lipid, and lean yolk regressed against

log egg mass. This revealed that clutch size does not influence the composition of teal eggs.

EGG COMPOSITION AND THE TIME OF LAYING

Nested ANOVA with eggs nested by clutch showed that fresh egg mass differed a small amount between the years of 1978 and 1983 ($F = 6.34$, $P < 0.0001$, $n = 4597$ eggs in 494 nests). The year effect explained less than 0.1% of the variation in egg weight, and the largest difference in egg masses between years was 0.2 g. A similar analysis using the much smaller sample of collected eggs did not show significant differences in egg mass between years. Similarly, tests for between year differences in the mass or proportions of albumen, yolk, total lean, and lipid found no significant differences ($P > 0.05$ for all nested ANOVAs).

The laying chronology of Blue-winged Teal varies considerably from year to year depending upon spring weather (unpublished data). To standardize laying chronologies, I ranked laying dates relative to that year's median nest initiation date for the 30-day peak of nesting. I used the 30-day peak because nest searching effort after this peak was not constant for all years. If the laying date was not known exactly, it was estimated as the midpoint of the possible laying dates. The average egg mass for 529 Blue-winged Teal nests regressed against nest initiation date showed no systematic change in egg mass with laying date ($F = 0.1$, $P > 0.05$). Fresh mass of the collected eggs also failed to show a change through the course of the nesting season ($F = 1.8$, $P > 0.05$, $n = 172$). Likewise, the mass of albumen, yolk, and shell did not vary according to laying date. The proportion of lipid in dry yolk was the only egg component that showed a significant re-

TABLE 4. Regressions of log egg component mass against log egg mass.

Component	<i>n</i> ^a	Intercept	Slope \pm 1 SE	<i>r</i> ²	95% Confidence intervals
Albumen					
Wet mass	155	-0.29	0.95 \pm 0.10	0.36	0.71-1.20
Dry mass	172	-0.72	0.70 \pm 0.05	0.51	0.58-0.83
Water	155	-0.34	0.93 \pm 0.12	0.29	0.65-1.21
Yolk					
Wet mass	172	-0.44	1.07 \pm 0.09	0.46	0.85-1.29
Dry mass	172	-0.92	1.15 \pm 0.06	0.67	1.01-1.30
Water	172	-0.59	0.99 \pm 0.15	0.22	0.63-1.35
Dry lean	145	-1.36	1.13 \pm 0.08	0.59	0.95-1.32
Whole egg					
Water	172	-0.15	0.97 \pm 0.02	0.95	0.93-1.01
Lipid	145	-0.19	1.22 \pm 0.08	0.63	1.03-1.41
Dry lean	145	-0.91	1.04 \pm 0.05	0.77	0.93-1.15
Dry shell	172	-0.74	0.75 \pm 0.04	0.73	0.67-0.84
Dry egg	172	-0.53	1.05 \pm 0.03	0.88	0.98-1.12

^a n = nests. Eggs from the same nest were averaged to one observation. See Table 1 for explanation of variation in sample sizes.

TABLE 5. Regressions of log egg component mass against log dry egg mass.

Component	<i>n</i> ^a	Intercept	Slope ± 1 SE	<i>r</i> ²	95% Confidence intervals
Albumen dry	172	-0.55	0.85 ± 0.08	0.38	0.66-1.05
Shell dry	172	-0.47	0.82 ± 0.05	0.60	0.70-0.94
Yolk dry	172	-0.38	1.14 ± 0.04	0.83	1.04-1.23
Lean yolk	145	-0.81	1.09 ± 0.06	0.70	0.95-1.23
Total lean	145	-0.34	0.94 ± 0.04	0.81	0.85-1.03
Lipid	145	-0.62	1.20 ± 0.05	0.78	1.08-1.33

^a *n* = nests. Eggs from the same nest were averaged to one observation.

relationship with day of laying ($F = 21.72$, $P < 0.0001$, $r^2 = 0.11$, $n = 145$). The regression slope of -0.00054 indicated that the lipid in dry yolk decreased from 67.8% to 64.6% over the 61 day range of the collected eggs. This change in the percent of fat in yolk did not result in a significant decrease in lipid content as the nesting season progressed ($F = 1.8$, $P > 0.05$, $n = 145$), presumably because of a non-significant trend for yolk mass to increase through the season.

EGG SIZE AND COMPOSITION IN RELATION TO LAYING SEQUENCE WITHIN AND BETWEEN CLUTCHES

To examine the potential effect that within-clutch laying sequence has on egg size or composition, I collected eggs in 1979 that were either one or both of the first two, or one or both of the last two eggs of a clutch. These data were analyzed using an ANOVA model where eggs from the same clutch were nested within laying sequence (first or last laid eggs). First and last laid eggs did not differ in mass for yolk, albumen, shell, or total egg (F values all with $P > 0.05$, $n = 25$ first and 38 last eggs). I tested for differences in lipid and protein levels with laying sequence by using an ANOVA model where eggs from the same clutch were nested by sequence and replicate measures were nested by egg. Neither the mass of lipid, yolk protein, nor albumen protein differed by sequence; furthermore, only a small fraction of the variation in these traits was due to differences in duplicate analyses of the same egg.

I assessed changes in egg size or composition between clutches of the same female by comparing the eggs from the first nest of the season with eggs from known reneest attempts during the same season. Such comparisons employed a two way ANOVA where nest attempt and female were fixed and random effects, respectively. The mass of first nest eggs (28.5 ± 0.3 g) was significantly different than the mass of reneest eggs (27.7 ± 0.2 g) for a sample of 572 eggs from 36 females ($F = 9.94$ for attempt, $P < 0.01$). The interaction of female and nest attempt for the same ANOVA was very highly significant ($F = 5.83$, $P < 0.0001$). This two-

way ANOVA partitioned egg size variation into a large female component (51.6%), a 35.2% component within clutches, a trivial 0.4% component to nest attempt, and a 12.8% component attributable to the interaction between attempt and female. The collected eggs included 190 from the first nest or the reneest of 34 females. This smaller sample of eggs did not exhibit a significant difference in mass between the first ($\bar{x} = 27.7$ g) and reneest ($\bar{x} = 27.6$ g) eggs (F attempt = 1.6, $P > 0.05$). Similar two-way ANOVAs that examined the total dry mass or the mass or percent of yolk, albumen, lipid, or lean egg components fail to reveal significant differences between first and reneest eggs. In all analyses there were significant interactions between attempt and female.

Twenty-seven Blue-winged Teal females whose eggs were taken immediately after clutch completion were known to defer further egg laying for the season. The eggs of these non-reneesters weighed 28.2 ± 0.3 g, which was slightly less than the 28.5 ± 0.3 g eggs in the first nests of females that did reneest (Nested ANOVA, F attempt = 9.62, $P < 0.002$, $n = 607$ eggs in 66 nests). However, this slight difference in egg mass between non-reneest eggs and eggs from the first nest of reneesting females did not show up in the smaller sample of eggs collected for proximate analysis (Nested ANOVA $F = 1.87$, $P > 0.05$, $n = 167$ eggs in 48 nests). Likewise, the composition of these two groups of eggs did not differ to a significant extent.

For 32 reneesting females where I had three or more egg masses per clutch I did pairwise comparisons of the intraclutch egg size variability between first and reneest clutches. For 5 females the reneest clutch was more variable than the first egg set, 3 females were the opposite, and the remaining 24 females did not show a significant F_{\max} test (Sokal and Rohlf 1981). A Wilcoxon signed ranks test (Sokal and Rohlf 1981) using data from the same 32 pairs of nests did not show any differences in variability between first-nest and reneest eggs ($T_s = 228$, $P > 0.05$). Intraclutch egg size variance was not correlated with clutch size, average egg size per clutch, or nest initiation date.

DISCUSSION

Blue-winged Teal egg composition was quite similar to that of other waterfowl species. The proportion of yolk (46%) in teal eggs was similar to the proportions reported by Lack (1968b) for several other *Anas* species, but was considerably higher than the 35% yolk that Ricklefs (1977) found in eggs from captive Mallards (*Anas platyrhynchos*). Organic composition of the yolk of Blue-winged Teal eggs differs slightly from that of domestic ducks of Mallard ancestry (Romanoff and Romanoff 1949). Yolk protein values were 27.9% and 32.1%, whereas lipid values were 61.4% and 63.8% of the dry yolk for Blue-winged Teal and domestic ducks, respectively. Albumen composition of teal eggs was similar to albumen for most other birds (Romanoff and Romanoff 1949, Ricklefs 1977).

Intraspecific variation in Blue-winged Teal eggs primarily reflects differences between clutches. In most aspects of size and proportionate composition the clutch effect accounted for 60 to 80% of the total variance. Such partitioning of variance was consistent with other studies of egg composition for both precocial and altricial species (Manning 1978, Ojanen et al. 1978, Ricklefs and Montevecchi 1979, Grant 1982, Ricklefs 1984). In Blue-winged Teal this clutch effect was primarily due to the similarity of eggs laid by the same female, because those females that laid two clutches produced similar eggs for both nests. Egg measurements for the same female taken over two or more years shows the same consistency in both Velvet Scoters (*Melanitta fusca*) and Black-legged Kittiwakes (*Rissa tridactyla*) (Koskimies 1957, Coulson 1963).

The first two teal eggs in a nest did not differ significantly from the last two eggs laid in a nest. For Snow Geese (*Chen caerulescens*) the last egg laid was generally the smallest (Ankney and Bisset 1976), as it was for Canada Geese (*Branta canadensis*), where egg size declined slightly from the second egg onward (Cooper 1978). Blue-winged Teal eggs from 36 second nests of the season were slightly lighter than eggs in first nests, but this difference was not detected in the smaller sample of collected eggs. Hawaiian Geese (*Nesochen sandvicensis*) show a small decrease in egg size in their second clutch (Kear and Berger 1980), whereas both Canada Geese and captive Mallards lay slightly larger eggs in renests (Cooper 1978, Batt and Prince 1979). Blue-winged Teal eggs laid late in the nesting season were not smaller than early laid eggs, even though many of the late clutches were repeat layings for females that had lost their first clutch. Egg mass increased slightly with later nesting in White-

winged Scoters (Koskimies 1957), remained constant in wild Mallards (Hill 1984), and decreased in Canada Geese and Tufted Ducks (*Aythya fuligula*) (Cooper 1978, Hill 1984). Sequential and seasonal differences in egg size were small changes in all waterfowl. This is not surprising, as the large sequential changes in egg size in many altricial species (especially larids and raptors) help to create the asymmetry in nestling sizes necessary for efficient brood reduction. Brood reduction is an unlikely adaptation for waterfowl, because the young feed themselves and duckling survival and fledging weights are independent of brood size (Rohwer 1985).

Blue-winged Teal were consistent with other waterfowl in showing considerable variation in egg mass between females. Ankney and Bisset (1976) suggested that Snow Geese show exceptional egg size variation because of the disruptive selection of seasonal variation in arctic weather. However, Manning (1978) suggests that the large range of variation in Snow Goose egg sizes that Ankney and Bisset (1976) observed was simply a reflection of a large sample size. The 11% coefficient of variation (CV) of Snow Goose egg mass was not much greater than the 9% CV of egg mass in prairie nesting Blue-winged Teal and Canada Geese (Cooper 1978). According to Lack's (1967) hypothesis, the allocation of egg nutrients directly affects clutch size and should cause selection for an optimum egg size. Thus, the large intraspecific variation in egg size of Blue-winged Teal and other waterfowl was somewhat surprising.

As in other precocial species, fresh egg mass appears to be a reliable predictor of dry egg weight and nutrient composition (Ricklefs 1977, Ankney 1980). Blue-winged Teal eggs, like American Coot (*Fulica americana*) and Mute Swan (*Cygnus olor*) eggs, show a proportional increase in dry yolk (Birkhead 1984, Alisauskas 1986). For the teal and swan eggs this meant a proportional increase in lipid with egg size. This suggests that teal ducklings hatching from large eggs could survive considerably longer than ducklings hatching from small eggs. Large Mallard and Snow Goose eggs produce large young that endure longer periods of starvation than young hatching from small eggs (Krapu 1979, Ankney 1980).

The large variation between Blue-winged Teal females in the way egg composition related to egg size was in striking contrast to European Starlings and American Coots. In starlings and coots the ANCOVAs of composition to egg mass with individual nests as the covariate failed to show a significant interaction term (Ricklefs 1984, Alisauskas 1986). This indicates that starling females all

responded the same way in allocating nutrients to different sized eggs, as do coots; teal females do not show such consistency. This contrast between starlings, coots and teal may reflect parental roles, since the first two species feed their young, but teal do not.

This work demonstrates that Blue-winged Teal eggs show considerable variation in egg size and composition. Most of the variation was due to differences between females. Factors such as year, nesting attempt, clutch size, laying date, and sequence within the clutch had little or no effect on teal egg mass or organic composition. These results were consistent with most other studies of egg size and composition in waterfowl.

ACKNOWLEDGMENTS

I thank Charles Robbins for allowing me to do the protein analyses in his laboratory. Special thanks are due to my wife, Sheila, for her help in all phases of the study. Joe Ball, Harold Prince, William Montevecchi, Robert Ricklefs, and Charles Robbins provided many valuable suggestions for the manuscript. I am grateful for the research support provided by the North American Wildlife Foundation through the Delta Waterfowl Research Station and for the support of the Department of Zoology, Washington State University and the Department of Biology, University of Pennsylvania.

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