

PATTERNS OF VARIATION IN SIZE AND COMPOSITION OF GREATER SCAUP EGGS: ARE THEY RELATED?

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ABSTRACT.—We studied egg size variation of Greater Scaup (*Aythya marila*) nesting on the Yukon-Kuskokwim Delta, Alaska from 1991–1996. Mean egg size was 64.36 ± 0.03 (SE) ml. Egg size did not vary with clutch size or serve as an index of body size. There was less than 2% overlap in total clutch volumes for clutches of different sizes indicating that phenotypic clutch size–egg size trade-offs are not occurring among individuals. At the population level, Greater Scaup have less variation in egg size than other species of waterfowl. The proportion of variation in egg size caused by differences among females was 0.20, caused by differences within females among years was 0.25, and caused by differences within females and years (i.e., clutches) was 0.56. The proportion of egg lipid decreased with increasing egg size while the proportion of egg protein increased with egg size. Thus, Greater Scaup appear to trade-off lipid for protein as egg size increases. The proportion of variation that was due to differences among females in total egg protein was 0.79 and in total egg lipid was 0.49. We conclude that in the absence of a fitness trade-off between clutch size and egg size, selection has reduced among-individual variation in egg size. Received 16 April 1999, accepted 4 August 1999.

Lack (1967) suggested that trade-offs may occur between the number and size of eggs produced by waterfowl species. Rohwer (1988) argued that the same trade-off between number and size of eggs should occur within species as well. The high repeatability of egg size (i.e., volume or weight) generally found in waterfowl suggests that such trade-offs likely occur among rather than within individuals (Lessells et al. 1989, Larsson and Forslund 1992). Thus, the concept of a clutch size–egg size trade-off implies that females laying small clutches of large eggs and females laying large clutches of small eggs have equal fitness. Accordingly, for a trade-off to exist both clutch size and egg size must be positively related to fitness.

Waterfowl laying larger clutches may be more fit because they tend to fledge more young (Lessells 1986, Rockwell et al. 1987, Flint 1993). For example, Rockwell and co-workers (1987) demonstrated that female Lesser Snow Geese (*Chen caerulescens caerulescens*) laying larger clutches recruited more young than females laying smaller clutches. Fitness may also be related to egg size in some species of waterfowl because

young from larger eggs are better able to survive extreme conditions (Ankney 1980, Rhymer 1988, Thomas and Brown 1988). For example, Dawson and Clark (1996) found that Lesser Scaup (*Aythya affinis*) ducklings from large eggs survived better than those from small eggs under natural conditions (but see Williams et al. 1993). The mechanism by which larger eggs yield higher juvenile survival may be related to egg composition (Dawson and Clark 1996). Egg composition, in terms of lipid and protein, typically varies isometrically with egg weight for waterfowl species (Ankney 1980, Hepp et al. 1987, Owen and West 1988, Hill 1995, Slattery and Alisauskas 1995); however, some species show a proportional increase in lipid with increasing egg size (Birkhead 1984, 1985; Alisauskas 1986; Rohwer 1986; Williams 1994). In either case, young hatching from large eggs tend to be larger at hatching and have absolutely larger reserves than young hatching from smaller eggs (Ankney 1980, Slattery and Alisauskas 1995, Erikstad et al. 1998).

Fitness trade-offs are potential mechanisms maintaining heritable variation in both egg size and composition at the population level (Falconer 1989). Egg size has been shown to be, at least partially, under genetic control, and heritable genetic variation has been found in several species of waterfowl (Batt and Prince 1978, Lessells et al. 1989, Larsson and Forslund 1992). Thus, in the absence of fitness trade-offs, mean egg size for a population

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would be expected to respond to directional selection. Therefore, we predict that patterns of egg size variation within and among populations are linked to clutch size–egg size trade-offs. Additionally, if clutch size–egg size trade-offs exist, then the corresponding variation in egg composition can be used to infer the required relationship between egg size and fitness. It follows then, that patterns of variation in egg composition within populations are also influenced by clutch size–egg size trade-offs.

Our goal in this study was to describe egg size variation in Greater Scaup (*Aythya marila*) with regard to female body size and clutch size. Further, we looked for evidence of clutch size–egg size trade-offs among females. We examined variation in egg composition within and among females and in relation to egg size and compared these results to other species.

METHODS

This study was conducted along the lower Kashunuk River drainage (61° 20' N, 165° 35' W) on the outer coastal fringe of the Yukon Delta National Wildlife Refuge, Alaska. This study was conducted under appropriate Federal (PRT-692350), state (93-69), and refuge special use collection permits. The study area consists of relatively flat sedge meadows and numerous ponds (Flint and Grand 1996a, Grand et al. 1997). Nest searches were conducted from mid-May through mid-July (see Flint and Grand 1996a). When nests were discovered, the number of eggs, nest location, and date were recorded. Eggs were individually numbered and candled to determine the stage of embryonic development (Flint and Grand 1996a). Nests were revisited at 7 day intervals and the number of eggs and stage of development of embryos were recorded. Maximum lengths and breadths of all eggs were measured to the nearest 0.1 mm. Clutch size was defined as the number of eggs known to have been laid into a nest for nests found during egg laying and as the number of eggs in the nest at time of discovery for nests found during incubation.

In 1994–1996 a sample of hens was captured on the nest at hatching using bow traps (Flint and Grand 1996b). Hens were weighed to the nearest 10 grams and culmen and total tarsus lengths were measured to the nearest 0.1 mm. Females were marked with aluminum U.S. Fish and Wildlife Service tarsal bands.

In 1996, we collected a sample of 30 complete clutches at 4 days of incubation in conjunction with a separate study of renesting ecology. These eggs were weighed, measured (length and breadth) with calipers, and we measured the external volume by submerging the egg and measuring the displacement of water to the nearest 0.5 ml. Variables in the relationship between volume and linear measures were estimated us-

ing analysis of covariance with volume as the dependent variable, females as a factor, and length \times breadth² as the single covariate (Hoyt 1979, Flint and Sedinger 1992, Flint and Grand 1996b). We included the interaction between females and length \times breadth² to compare the slope of this relationship among females. The fitted relationship was used to predict egg volume from linear measures for eggs where volume was not measured directly (i.e., eggs measured in the field).

In 1993, a sample of nests was visited every other day after 7 eggs had been laid to determine the date of clutch completion. We collected a sample of 88 eggs from 11 clutches as soon as laying was complete. These eggs were boiled for 15 min and frozen. Each egg was later thawed and weighed whole. Because entire clutches were collected at the end of laying and some incubation occurred during laying, vascularization or embryonic development was noted as being present during dissection. The egg was separated into shell, albumen, and yolk and these components were dried to a constant weight at approximately 80° C. Fat was extracted from the yolk using petroleum ether (Dobush et al. 1985) in a Soxhlet apparatus. Total yolk protein was estimated as whole yolk dry weight minus yolk fat. We assumed that dried albumen weight was composed entirely of protein (Montevicchi et al. 1983) and estimated total egg protein as total yolk protein plus albumen dry weight.

We examined variation in egg size with clutch size using a nested ANOVA with clutches nested within clutch sizes. We used the mean square error among clutches with clutch sizes as the denominator in the *F*-test of clutch size effects. Total clutch volume was calculated as the sum of the individual egg volumes within a clutch for the sample of nests that survived to incubation. We used the sum of the log transformed measurements of culmen and tarsus as an index of structural size and examined variation in mean egg size in relation to this index for the sample of nests from which we captured females using linear regression. The proportion of variation in egg size caused by differences within clutches, within females among years, and among females (i.e., repeatability) were calculated using a nested ANOVA and modifying the methods of Lessells and Boag (1987) for a nested design (Sokal and Rohlf 1981).

We examined variation in both total egg lipid and protein (separately) using ANCOVA with female (i.e., clutch) and egg development as factors and egg size as a covariate. We also included an interaction between female and egg size. To examine allometric relationships of egg components we used \log_{10} - \log_{10} regression of egg components against egg weight; isometry was concluded if the slope of these relationships was not different from 1. Repeatability of egg components was estimated using a nested design with eggs nested within females. All analyses were conducted using SAS version 6.12 (SAS Institute 1990).

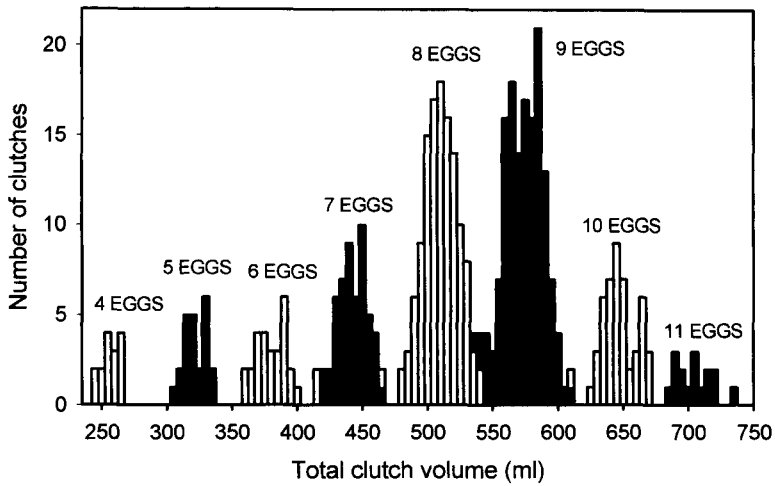


FIG. 1. Total clutch volume for Greater Scaup clutches of different sizes from the Yukon-Kuskokwim Delta 1991–1996. Clutch volumes were rounded to the nearest 5 ml. Overall only 3 of 235 (1.3%) clutch volumes (i.e., two 9 egg clutches and one 10 egg clutch) occurred within the volume distribution of another clutch size. Other stacked bars represent tied values resulting from rounding of total clutch volumes where actual estimates of total clutch volume did not overlap. For example, a 7 egg clutch with a volume of 467 ml is stacked with an 8 egg clutch of 468 ml because rounding is required to develop the distributions.

RESULTS

We measured length, breadth, weight, and volume of 271 eggs. The equation:

$$\text{Volume} = 31.84 + 0.2729 \times \text{length} \times \text{breadth}^2, \quad (1)$$

described the relationship between displacement (ml) and linear egg measurements (cm) ($r^2 = 0.44$, $F_{1,269} = 209.10$, $P < 0.001$). To compare variation in predicted egg volumes with variation in measured volumes we calculated the repeatability of measured egg volumes (33.4%) and found it similar to the repeatability of estimated egg volumes (36.4%).

We measured a total of 3937 eggs in the field. Mean egg length was 6.352 ± 0.003 (SE) cm and egg breadth was 4.328 ± 0.002 cm. Mean estimated egg size was 64.36 ± 0.03 ml (CV = 0.03). We had no data on variation in egg size with laying sequence, but the average range of egg size within clutches was 3.3 ml.

Egg size did not vary with clutch size ($F_{12,470} = 0.74$, $P > 0.05$). For the analyses of the relationship between egg size and body size we used 93 observations of individual females captured on nests. Average egg size per clutch was not related to our index of body size ($F_{1,90} = 0.35$, $P > 0.05$). Overall only 3

of 235 (1.3%) clutch volumes (i.e., two 9-egg clutches and one 10-egg clutch) occurred within the volume distribution of another clutch size (Fig. 1).

For estimates of repeatability of egg size we captured 20 females 41 times (only 1 female was captured 3 times). The proportion of variation in egg size attributed to differences among females (i.e., repeatability) was 0.20, proportion of variation attributed to differences within females among years was 0.25, and proportion of variation attributed to differences within females and years (i.e., clutches) was 0.56. Using a standard approach of calculating the mean egg size per clutch and treating clutches as individual observations within females (e.g., Flint and Grand 1996b) yields a repeatability of mean egg size of 0.36.

Total egg protein varied with egg size ($F_{1,64} = 67.96$, $P < 0.001$), but not among females ($F_{9,64} = 1.55$, $P > 0.05$). The relationship between egg protein and size also did not vary among females (i.e., no interaction, $F_{9,64} = 1.59$, $P > 0.05$). Total egg protein was not significantly influenced by early embryonic development ($F_{1,64} = 3.23$, $P > 0.05$). Similarly, total egg lipid varied with egg size ($F_{1,64} = 65.80$, $P < 0.001$), but not among females ($F_{9,64} = 1.98$, $P = 0.055$). However, the rela-

TABLE 1. Allometric relationships between total egg lipid, protein and water in relation to egg weight.

Allometric relationship	r^2	Slope	LCL ^a	UCL ^a	t^b	P
Weight and egg lipid ^c	0.62	0.85	0.71	0.99	2.09	0.04
Weight and egg protein ^c	0.84	1.11	1.01	1.21	2.16	0.03
Weight and egg water	0.95	1.01	0.96	1.06	0.52	>0.05

^a Upper and lower 95% confidence limits for slope.

^b Test of null hypothesis that slope = 1.0.

^c Egg lipid and protein are in dry weight.

tionship between total egg lipid and egg size varied among females (i.e., interaction; $F_{9,64} = 2.04$, $P = 0.049$). Total egg lipid was not influenced by early embryonic development ($F_{1,64} = 0.17$, $P > 0.05$).

The proportion of lipid in an egg declined with increasing egg weight, whereas the proportion of protein increased with increasing egg weight (Table 1). Among-female differences explained most of the variation in total egg protein; whereas within-female (i.e., within clutch) differences explained most of the variation in egg lipid components (Table 2). Even with the variation in egg composition within and among females, total clutch volume still predicted most of the variation in total protein ($r^2 = 0.86$, $F_{1,8} = 48.71$, $P < 0.001$) and lipid ($r^2 = 0.93$, $F_{1,8} = 100.05$, $P < 0.001$) investment in a clutch.

DISCUSSION

Egg size.—The relationship between length \times width² and measured volumes fit poorly ($r^2 = 0.44$) for Greater Scaup. For other species of waterfowl these relationships have shown a high r^2 (>90%; Flint and Sedinger 1992, Flint and Grand 1996b, Slattery and Alisaus-

kas 1995). We believe this relatively poor fit is the result of the low coefficient of variation in egg size (i.e., lack of variation in the y-axis). Additionally, we likely detected variation in slope among females because we sampled entire clutches and thus had relatively large samples within females. Other studies have failed to find variation in slope of predictive relationships between egg measures and egg size among females but only sampled a few eggs from each clutch (Flint and Sedinger 1992, Flint and Grand 1996b). We found little difference between estimates of repeatability of predicted volumes and measured volumes. The comparability of these two results indicates that error associated with predicting egg volumes is random within and among females.

We found less variation in egg size at the population level than has been reported for other species of waterfowl. The coefficient of variation of average egg size for Greater Scaup (3%) was substantially less than for Northern Pintails (*Anas acuta*, 11%; Flint and Grand 1996b), Blue-winged Teal (*Anas discors*, 9%; Rohwer 1986), Canada Geese (*Branta canadensis*, 7–9%; Cooper 1978, Leblanc 1989), Black Brant (*Branta bernicla nigricans*, 8%; Flint and Sedinger 1992), or Lesser Snow Geese (8%; Cooke et al. 1995). Thus, it appears selection has reduced the variation in egg size at the population level compared to other species.

The repeatability of egg size that we measured among females is substantially lower than reported for other waterfowl (Batt and Prince 1978, Duncan 1987, Lessells et al. 1989, Flint and Sedinger 1992, Flint and Grand 1996b). When we partitioned variance using a nested ANOVA design, including variation within clutches, we found the among female component of the variance was even lower. Using an approach similar to ours,

TABLE 2. Average egg components dry weight and proportion of variation due to differences among females.

Variable	\bar{x}	SE	Among female variance component (%)
Albumen (g)	4.97	0.046	87.9
Shell (g)	5.23	0.032	73.2
Yolk (g)	14.84	0.109	52.4
Total egg lipid (g)	9.97	0.069	48.8
Total egg protein (g)	9.89	0.077	79.1
Lipid per ml	0.15	0.001	36.2
Protein per ml	0.15	0.001	79.9
Density (g/ml)	0.91	0.003	67.9

Leblanc (1989) reported that the proportions of variation among female Canada Geese, within females—among years, and within clutches were 0.62, 0.05, and 0.33, respectively. Thus, the patterns of egg size variation within and among female Greater Scaup are substantially different than those reported for other waterfowl. The average range of egg sizes within clutches was similar to the range of egg sizes reported for other waterfowl (Leblanc 1987, Owen and West 1988, Flint and Sedinger 1992, Robertson and Cooke 1993, Cooke et al. 1995). Thus, the low repeatability we report is not the result of relatively high variation within females (i.e., clutches), but is strongly influenced by the lack of variation in egg size among females. Relative to other waterfowl species, it appears selection has resulted in reduced egg size variation among female Greater Scaup and maintained variation within clutches that may be related to sequence (Flint and Sedinger 1992, Cooke et al. 1995).

Mean egg size did not vary with clutch size in this study. This is consistent with findings for other waterfowl (Duncan 1987, Rohwer 1988, Rohwer and Eisenhauer 1989, Flint and Sedinger 1992, Flint and Grand 1996b). Therefore, we did not detect a trade-off between clutch size and egg size predicted under the nutrient limitation hypothesis and a simple model of nutrient allocation to eggs (Flint et al. 1996). Additionally, mean egg size was not related to body size and the alternative allocation model described by Flint and coworkers (1996) cannot explain the failure to detect a negative relationship between clutch size and egg size. Finally, the lack of significant overlap in total clutch volumes for clutches of different size, indicated phenotypic trade-offs between clutch size and egg size among females with equal investments in their clutches did not occur (Flint and Sedinger 1992, Flint and Grand 1996b). Thus, we find no evidence of phenotypic clutch size—egg size trade-offs among individuals for Greater Scaup.

Ankney and Bissett (1976) proposed that egg size variation in a population was maintained by annual variation in environmental conditions that caused annual variation in optimal egg size. While not explicitly stated, the concept of a clutch size—egg size trade-off is inherent in this hypothesis. In their example,

Ankney and Bissett (1976) state that the advantage to females laying small eggs is that they can produce more eggs from finite reserves than females laying large eggs. We found considerably less egg size variation at the population level than has been reported for other species. Correspondingly, we also found no evidence of a clutch size—egg size trade-off whereas studies of other species have shown some evidence of a trade-off among individuals with equal investments in their clutches (Ankney and Bissett 1976, Flint and Sedinger 1992, Flint and Grand 1996b). Further, repeatability sets the upper limit to heritability (Falconer 1989); thus, the low repeatability we measured implies little genetic variability for egg size in our study population. Traits influenced by selection are expected to approach fixation and therefore have low heritabilities (Falconer 1989). We suggest for Greater Scaup that clutch size—egg size trade-offs do not occur and selection has reduced variability in egg size.

Egg composition.—Because female waterfowl commonly begin incubation before egg laying is complete (Flint et al. 1994), and we did not collect eggs until egg laying was terminated, some eggs had slight embryonic development at the time of collection. The presence of egg development was not related to either total egg lipid or protein after controlling for variation among females, egg volume, and an interaction between females and egg volume. Thus, we do not believe that the early development observed in some of our collected eggs influenced our results.

The relationship between egg lipid and egg size for Greater Scaup varied among females. This is similar to what Rohwer (1986) found for Blue-winged Teal. Birkhead (1985) reported greater variation in egg composition among females than within clutches for Mallards (*Anas platyrhynchos*). Further, Alisauskas (1986) found that egg lipid was highly variable among female American Coots (*Fulica americana*) and varied within clutches in relation to egg sequence. Hepp and coworkers (1987) found that about half of the variation in egg lipid in Wood Ducks (*Aix sponsa*) was due to differences within females, similar to our results. Varying egg composition may allow females to slightly adjust the total investment in the clutch without altering clutch size

or egg size (Owen and West 1988). The consistent finding that egg lipid varied within females suggests that there may be some adaptive partitioning of resources within clutches, perhaps related to egg laying sequence. However, even with the variation in egg composition described above, total clutch volume explained more than 85% of the variation in total lipid and protein investment in a clutch. Thus, contrary to the results of Flint and Grand (1996b) for Northern Pintails, clutch size is a good predictor of nutrient investment in Greater Scaup clutches.

Heavier eggs had proportionally more protein and less lipid than lighter eggs. Thus, it appears that Greater Scaup trade off lipid for protein as egg weight increases. These results differ from studies of waterfowl that show a proportional increase in lipid with egg size (Birkhead 1984, 1985; Alisauskas 1986; Rohwer 1986; Williams 1994), and differ from studies of other precocial species where egg protein and lipid both increase proportionately with egg weight (Ankney 1980, Hepp et al. 1987, Owen and West 1988, Hill 1995, Slattery and Alisauskas 1995). Ankney and Bissett (1976) argued that because egg yolk, and hence egg lipid, increased with egg size, young hatching from larger eggs survived better because they had absolutely larger lipid reserves. However, young from larger eggs tend to be larger at hatch (Ankney 1980, Slattery and Alisauskas 1995, Erikstad et al. 1998) and thus will also have absolutely higher energy requirements (Rhymer 1988). For Greater Scaup, the proportion of egg lipid decreased with increasing egg size. Therefore, we would not expect large egg size to confer a survival advantage to offspring in our study population.

Given our conclusion that clutch size–egg size trade-offs do not occur, and egg size has been optimized by selection for our population, we would expect no relationship between egg size and fitness for our study population. The proportional decline in egg lipid with increasing egg size fits this prediction. Therefore, we conclude that clutch size–egg size trade-offs likely influence both egg size variation and patterns of egg composition within species. If this hypothesis is correct, we would predict that species showing evidence of phenotypic trade-offs between clutch size and egg

size (e.g., Northern Pintails; Flint and Grand 1996b) would also have patterns of variation in egg composition consistent with the expectation that offspring from larger eggs have a survival advantage.

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