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VARIATION IN SIZE AND COMPOSITION OF HORNED AND PIED-BILLED GREBE EGGS[1]

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Egg composition varies widely among bird species, primarily in relation to hatchling maturity (Sotherland and Rahn 1987). Egg composition also varies within species, with variation attributable to individual females, egg size, laying sequence within the clutch, and food availability (Ricklefs 1984, Alisauskas 1986, Rohwer 1986, Eldridge and Krapu 1988). Recently, Sotherland and Rahn (1987) reviewed interspecific trends in egg composition among 127 species of birds; however, few data were available for class 4 precocial birds (Podicipedidae and Rallidae). In this note I report on egg composition of Horned Grebes (*Podiceps auritus*, hereafter HG) and Pied-billed Grebes (*Podilymbus podiceps*, hereafter PBG).

Fieldwork was conducted on 121 small (0.1–3.0 ha) semipermanent wetlands located approximately 10 km SE of Minnedosa (50°16′N, 99°50′W), Manitoba. Nest searches were conducted every 6 days throughout May and early June of 1988. I revisited laying-stage nests daily and collected up to four freshly laid (e.g., <24 hr) eggs per nest. I distinguished between HG and PBG nests by identifying resident adults.

I determined fresh egg mass (±0.1 g) and linear egg dimensions (length and maximum breadth, ±0.05 mm) on the day of collection. Egg volume (cm^3) was estimated using Hoyt's (1979) equation: $V = 0.000507 \cdot (LB^2)$. Eggs were boiled for 5 min, individually bagged in plastic, and frozen for 4 months. I later determined wet masses of yolk, albumen, and shell (shell membranes were peeled away from the shell and added to the albumen; Alisauskas 1986). On average, eggs lost 8% of their fresh mass during boiling, freezing, and handling; I assumed that this loss was primarily albumen water and added it to the albumen wet mass. Wet components were dried at 80°C for 48–72 hr to determine dry masses. Lipid content of the dried yolk was determined by extraction with petroleum ether in a Soxhlet apparatus (Dobush et al. 1985). I assumed that insoluble yolk residue and dry albumen were primarily protein (Sotherland and Rahn 1987), and that dry shell was primarily mineral (Rohwer 1986). I calculated energy content of eggs by assuming 9.5 kcal/g of lipid and 5.65 kcal/g of protein (Ricklefs 1984).

Statistical tests were conducted using the SAS GLM procedure (SAS Institute 1985). Because of small sample sizes, I used a significance level of $P = 0.10$ to obtain a better compromise between Type I and Type II statistical error.

I collected 19 HG eggs from seven nests and 27 PBG eggs from 10 nests. Fresh egg mass (M) was related to estimated egg volume (V) according to these equations:

$$\text{HG: } M = 1.46 + 0.97(V),\ r^2 = 0.86,\ P < 0.0001,$$
$$\text{PBG: } M = 5.96 + 0.77(V),\ r^2 = 0.52,\ P < 0.0001.$$

The weak relationship for PBG was due to two apparent "outliers"; the regression equation with these two eggs deleted was:

$$\text{PBG: } M = 0.78 + 1.02(V),\ r^2 = 0.95,\ P < 0.0001.$$

In most studies of egg-size variation, fresh egg mass has been highly correlated with estimated egg volume (e.g., $r^2 > 0.95$; Ricklefs 1984, Ankney and Johnson 1985). Grebe eggs may be more variable in shape and (or) density than other birds' eggs, thus making linear egg dimensions less efficient predictors of volume and fresh egg mass.

Wet mass of HG eggs averaged 65% albumen, 26% yolk, and 9% shell. Dry egg mass averaged 26% albumen, 43% yolk, and 31% shell. Total composition consisted of 72% water, 13% protein, 9% mineral, and 6% lipid. Composition of PBG eggs was virtually identical to that of HG (Table 1). Wet mass of PBG eggs averaged 63% albumen, 27% yolk, and 10% shell. Dry composition averaged 26% albumen, 42% yolk, and 32% shell. PBG eggs contained 72% total water, 13% protein, 9% mineral, and 6% lipid. These data are consistent with the limited information on egg composition in other grebes (Sotherland and Rahn 1987).

For many birds species, the primary source of variation in egg size and composition is among females (Ricklefs 1984, Alisauskas 1986, Rohwer 1986). I tested for female effects on egg size and composition using one-way ANOVAs. This analysis was restricted to nests for which at least two eggs were collected (five HG and seven PBG nests, 17 and 24 eggs, respectively). Female effects accounted for substantial variation in egg volume and fresh egg mass for each species. Much of the variation in egg composition also occurred among females (Table 2). Total water was highly consistent within clutches; 69% and 93% of the variation in water content of HG and PBG eggs, respectively, was among females (Table 2). Because water content is the primary determinant of egg mass, a large component of among-female variation in egg mass does not reflect nutrient quality (see also Ricklefs 1984). Substantial variation in wet and dry shell masses occurred among PBG fe-

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TABLE 1. Dimensions (mm), volumes (cm^3), composition (g), and energy content (kcal) of 19 Horned and 27 Pied-billed grebe eggs ($\bar{x}$ ± 1 SD).

	Horned Grebes	Pied-billed Grebes
Length	43.70 ± 1.55	44.29 ± 1.22
Breadth	30.13 ± 0.55	30.12 ± 0.79
Volume	20.12 ± 2.10	20.39 ± 2.59
Egg, wet	20.98 ± 1.11	21.56 ± 1.39
Egg, dry	5.82 ± 0.41	6.13 ± 0.34
Egg, water	15.17 ± 0.86	15.42 ± 1.21
Shell, wet	1.90 ± 0.17	2.07 ± 0.11
Shell, dry	1.81 ± 0.16	1.98 ± 0.09
Albumen, wet	13.63 ± 1.07	13.74 ± 1.21
Albumen, dry	1.52 ± 0.17	1.57 ± 0.15
Yolk, wet	5.46 ± 0.65	5.75 ± 0.53
Yolk, dry	2.49 ± 0.31	2.58 ± 0.21
Yolk, fat	1.32 ± 0.19	1.42 ± 0.12
Yolk, lean	1.16 ± 0.14	1.16 ± 0.11
Total protein	2.69 ± 0.20	2.73 ± 0.21
Total energy	27.77 ± 2.40	28.92 ± 2.01

males, but not among HG females (Table 2). For yolk components, however, substantial variation was attributable to females for HG, but not for PBG. Because of the high consistency of dry yolk components within HG females, total energy content was also highly consistent within females. Within PBG females, however, energy content of eggs was not statistically consistent (Table 2). Because these analyses were not based on complete clutches, coefficients of determination may be slightly biased (see below).

In several studies, significant variation in egg size and composition was attributable to laying sequence within the clutch (Ricklefs 1984, Alisauskas 1986, Forbes and Ankney 1988; but see Rohwer 1986). I tested for effects of laying sequence on egg size and composition in HG and PBG using simple linear regression, assuming a linear trend of the response variable with egg sequence (visual inspection of scatter plots revealed no curvilinear trends). For HG, egg size and composition were independent of laying sequence ($P \geq 0.19$ for all comparisons). Among PBG, three component masses declined with laying sequence: yolk wet mass (Y = 6.49 − 0.13[seq], $r^2 = 0.13$, $P = 0.06$), yolk dry mass (Y = 2.91 − 0.06[seq], $r^2 = 0.17$, $P = 0.03$), and yolk lipid (Y = 1.64 − 0.04[seq], $r^2 = 0.24$, $P = 0.01$). Forbes and Ankney (1988) found that first-laid eggs in PBG clutches averaged 8% lighter than subsequent eggs. Unfortunately, I obtained no first-laid eggs in this study, so any observed effects reflect changes occurring in eggs 2–9. Although egg size remained constant after the first-laid egg in PBG clutches (Forbes and Ankney 1988, this study), egg quality (as indicated by yolk components) declined with laying sequence.

To further examine proportional changes in egg composition with egg size, I conducted log-log regressions of egg component masses on fresh egg mass (e.g., Ricklefs 1984). Proportions of shell were essentially constant with egg mass in HG, but not in PBG (Table 3). I did not measure eggshell thickness, but the poor correlation between egg mass and shell mass in PBG suggests that shells were highly variable in thickness. Water content remained proportionately constant with egg mass in HG, but in PBG large eggs contained proportionately more water. Yolk components did not increase proportionately with egg mass in HG or PBG, and hence energy content was poorly correlated with egg size in both species (HG: $r^2 = 0.20$; PBG: $r^2 = 0.30$). However, dry albumen and total protein increased proportionately with egg mass in both species.

For many birds, the mass of a fresh egg has been a good predictor of its nutrient and energy content (Ankney 1980, Ankney and Johnson 1985, Alisauskas 1986, Rohwer 1986; but see Ricklefs 1984). Furthermore, fresh egg mass has been positively correlated with measures of offspring quality such as nutrient composition of hatchlings, growth rates, fasting endurance, and ther-

TABLE 2. Analysis of variance in size and composition of eggs among clutches of Horned and Pied-billed grebes (n = 5 nests, 17 eggs, n = 7 nests, 24 eggs, respectively).

	Horned Grebes			Pied-billed Grebes		
	F	r^2	P	F	r^2	P
Length	13.90	0.82	0.0002	1.97	0.41	0.13
Breadth	0.82	0.21	0.54	5.02	0.64	0.004
Volume	2.51	0.46	0.10	2.75	0.49	0.05
Egg, wet	3.92	0.57	0.03	34.98	0.93	0.0001
Egg, dry	6.16	0.67	0.006	4.12	0.59	0.01
Egg, water	6.46	0.68	0.005	35.09	0.93	0.0001
Shell, wet	1.88	0.38	0.18	6.50	0.70	0.001
Shell, dry	3.25	0.52	0.05	18.59	0.87	0.0001
Albumen, wet	14.78	0.83	0.0001	9.71	0.77	0.0001
Albumen, dry	4.34	0.59	0.02	3.46	0.55	0.02
Yolk, wet	20.58	0.87	0.0001	2.07	0.42	0.11
Yolk, dry	152.43	0.98	0.0001	0.57	0.17	0.75
Yolk, fat	28.14	0.90	0.0001	0.51	0.15	0.79
Yolk, lean	37.35	0.93	0.0001	0.82	0.22	0.57
Total protein	4.84	0.62	0.01	3.92	0.58	0.01
Total energy	16.11	0.84	0.0001	1.75	0.38	0.17

TABLE 3. Regressions of $\log_e$(egg component mass) against $\log_e$(fresh egg mass) for 19 Horned Grebe and 27 Pied-billed Grebe eggs.[a]

Component	Horned Grebes				Pied-billed Grebes			
	a	b	b:(90% CI)	r^2	a	b	b:(90% CI)	r^2
Egg, dry	−1.13	0.95	0.57–1.33	0.51	0.23	0.51	0.27–0.75	0.36
Egg, water	−0.38	1.01	0.85–1.17	0.89	−0.92	1.19	1.09–1.29	0.96
Shell, wet	−2.95	1.18	0.73–1.63	0.56	0.08	0.21	−0.06–0.48	0.07
Shell, dry	−3.04	1.19	0.72–1.66	0.53	−0.04	0.24	0.02–0.46	0.07
Albumen, wet	−1.08	1.21	0.83–1.59	0.65	−1.18	1.24	1.05–1.43	0.84
Albumen, dry	−4.30	1.55	0.87–2.23	0.48	−2.42	0.93	0.54–1.32	0.39
Yolk, wet	0.40	0.43	−0.54–1.40	0.03	−0.35	0.68	0.25–1.11	0.23
Yolk, dry	−0.40	0.43	−0.60–1.46	0.03	−0.43	0.45	0.01–0.89	0.11
Yolk, fat	−0.99	0.41	−0.76–1.53	0.02	−1.07	0.46	0.02–0.90	0.11
Yolk, lean	−1.18	0.44	−0.55–1.43	0.03	−1.20	0.44	−0.06–0.94	0.08
Total protein	−2.17	1.04	0.61–1.48	0.51	−1.25	0.73	0.42–1.04	0.40
Total energy[b]	1.05	0.75	0.12–1.38	0.20	1.49	0.61	0.30–0.92	0.30

[a] $\log_e$(component mass) = a + b($\log_e$[egg mass]).
[b] kcal.

moregulatory abilities (Schifferli 1973, Ankney 1980, Alisauskas 1986, Rhymer 1988). For HG and PBG, however, fresh egg mass was poorly correlated with lipid and energy content, and only moderately correlated with protein content, suggesting that few benefits are likely to accrue to large-egg hatchlings in these two species.

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