

COMPOSITION OF EARED GREBE AND WESTERN GREBE EGGS¹

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Proportional changes of egg composition with intraspecific variation in egg size have been demonstrated for many birds (e.g., Ricklefs 1977, Ricklefs and Montevecchi 1979, Boersma 1982, Warham 1983, Ricklefs 1984, Alisauskas 1986, Rohwer 1986, Meathrel et al. 1987, Hill 1988). These proportional variations can be detected by examining the slope of the linear function when the log of an egg component (Y) is regressed on the log of egg mass (X). Slopes equal to 1.0 (isometry) indicate that the egg component increases at the same rate as egg size. Slopes greater than 1.0 (positive allometry) or less than 1.0 (negative allometry) signify that the egg component increases at a faster rate or a slower rate, respectively, than does egg mass. Evidently, these allometric patterns are influenced by the mode of chick development: By examining the intraspecific variation for egg composition of 31 species from 16 families, Hill (1995) demonstrated that precocial and altricial birds differed in their intraspecific allometry for egg composition. In general, yolk and albumen tended to vary isometrically for precocial birds, whereas for altricial birds albumen showed positive allometry and yolk displayed negative allometry (e.g., Ricklefs and Montevecchi 1979, Ankney 1980, Birkhead and Nettleship 1984, Murphy 1986, Hepp et al. 1987, Muma and Ankney 1987, Owen and West 1988, Martin and Arnold 1991). The Podicipedidae family, however, did not follow the allometric patterns for egg composition typical of precocial birds; in Horned Grebes (*Podiceps auritus*) and Pied-billed Grebes (*Podilymbus podiceps*), the only grebe species studied to date, relative albumen levels increased with egg size while relative yolk levels decreased (Arnold 1989). Insofar as only two species from the Podicipedidae have been studied, it is uncertain whether this pattern is common to all grebes. In this work; we report on the egg composition of two additional grebes, the Eared Grebe (*Podiceps nigricollis*) and the Western Grebe (*Aechmophorus occidentalis*).

METHODS

Fieldwork was conducted in two extensive marsh areas located on Boca Lake and Malheur Lake at the Malheur National Wildlife Refuge in eastern Oregon. Boca Lake supported an Eared Grebe colony, while Malheur Lake contained a mixed-species colony of both Eared and

Western grebes. Consequently, Western Grebe eggs were only collected at the Malheur colony, whereas Eared Grebe eggs were collected at both sites. For each lake, nest searches were conducted every other day during July 1993. Seventy freshly laid (as determined by their blue color) Eared Grebe eggs and 23 Western Grebe eggs were collected from 61 and 23 nests, respectively.

In the field, fresh egg mass (± 0.1 g) was taken with a Pesola spring scale and linear dimensions (length and maximum width, ± 0.1 mm) were measured with vernier calipers. Upon return to the field lab, eggs were boiled for 5 min, individually bagged in plastic, frozen and shipped in dry ice, and then stored in a freezer for three months prior to analysis. Following defrosting, wet masses of yolk, albumen, and shell were recorded. Because we were interested in comparing our results with those of Arnold (1989), we followed his procedures for egg composition analyses. Shell membranes were peeled away from the shell and were added to the wet albumen. Eared Grebe eggs lost 6.14% and Western Grebe eggs lost 6.75% of their fresh mass during boiling, freezing, and handling. It was assumed that this loss was primarily albumen water and, therefore, we added it to the albumen wet mass. Wet components were dried to a constant mass at 90°C to determine dry masses. The lipid content of the dried yolk was ascertained by extraction with petroleum ether in a Soxhlet apparatus for 6 hr (Dobush et al. 1985). The solvent and the extracted lipids were then air-dried, while the beaker containing them was loosely covered, to a constant mass for approximately 48 hr under a fume hood. We assumed that insoluble yolk residue and dry albumen were primarily protein (Sotherland and Rahn 1987, Arnold 1989) and that dry shell was primarily mineral (Rohwer 1986, Arnold 1989). Energy content was calculated by assuming 39.6 kJ/g of lipid and 23.5 kJ/g of protein (Ricklefs 1984). Egg volume (cm^3) was estimated using Hoyt's (1979) equation ($V = 0.000507 [\text{LB}^2]$).

RESULTS AND DISCUSSION

Wet mass of Western Grebe eggs averaged 59% albumen, 29% yolk, and 11% shell, whereas dry egg mass averaged 25% albumen, 43% yolk, and 32% shell (Table 1). Total composition of Western Grebe eggs consisted of 73% water, 12% protein, 9% mineral, and 6% lipid. Egg volume of Western Grebe eggs averaged 44.3 ± 1.4 SE.

Eared Grebe egg masses did not differ between the two lakes ($t(68) = 0.22$, $P > 0.05$) nor did egg composition (Multivariate Analysis of Variance: $F(7, 62) = 0.94$, $P > 0.05$). Consequently, we combined data from the two lakes for analyses. Wet mass of Eared

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TABLE 1. Dimensions (mm), volumes (cm³), composition (g), and energy content (kJ) of 70 Eared Grebe and 23 Western Grebe eggs ($\bar{x} \pm SD$).

	Eared Grebes	Western Grebes
Length	44.60 \pm 1.89	58.13 \pm 2.89
Width	30.20 \pm 0.76	38.69 \pm 2.48
Original mass	22.80 \pm 1.67	48.38 \pm 4.05
Egg, wet	21.40 \pm 1.67	45.10 \pm 3.63
Egg, dry	5.86 \pm 0.46	12.88 \pm 1.04
Egg, water	16.95 \pm 1.33	35.50 \pm 3.29
Shell, wet	2.34 \pm 0.24	5.30 \pm 0.70
Shell, dry	1.81 \pm 0.17	4.14 \pm 0.56
Albumen, wet	13.13 \pm 1.79	28.24 \pm 3.31
Albumen, dry	1.54 \pm 0.18	3.17 \pm 0.45
Yolk, wet	6.76 \pm 0.97	13.99 \pm 1.13
Yolk, dry	2.50 \pm 0.26	5.57 \pm 0.58
Yolk, fat	1.38 \pm 0.21	3.07 \pm 0.41
Yolk, lean	1.12 \pm 0.27	2.49 \pm 0.48
Total protein	2.66 \pm 0.35	5.66 \pm 0.72
Total energy	117.4 \pm 9.74	254.9 \pm 17.36

Grebe eggs averaged 59% albumen, 30% yolk, and 11% shell, whereas dry mass averaged 26% albumen, 43% yolk, and 31% shell (Table 1). Total composition consisted of 77% water, 11% protein, 7% mineral, and 5% lipid. Egg volume of Eared Grebe eggs averaged 20.7 \pm 0.19 SE.

To examine proportional changes in egg composition with egg size, the \log_{10} of egg component masses (y variables) were regressed on the \log_{10} of fresh egg mass (x variable: Table 2). Wet and dry shell remained proportionally constant with egg mass in Western Grebes. In Eared Grebes, wet shell varied isometrically but relative dry shell decreased. For both species, wet albumen showed positive allometry with egg mass. Wet yolk was weakly correlated with egg mass in the Eared Grebe ($r^2 = 0.11$, $df = 69$, $P < 0.05$) and only approached significance in the Western Grebe ($r^2 = 0.16$, $df = 22$, $P = 0.059$). Lipid levels were not significantly related to egg mass in either species. Dry albumen, dry yolk, yolk lean, and total protein increased propor-

tionately with egg mass in both species. Total energy, however, showed negative allometry with egg mass, so that large eggs contained proportionately less total energy than did small eggs from these two grebes. These patterns correspond with Arnold's (1989) findings for Pied-billed and Horned Grebes and indicate that the Podicipedidae are likely to be unique among precocial families for the apportionment of egg composition as a function of egg size. Given the importance of egg composition to thermoregulation, developmental maturity, withstanding food deprivation, and hatchling growth it is possible that the ontogeny and survivorship of grebe chicks differs according to egg size (e.g., Walker and Grau 1963, Schifferli 1973, Ankney 1980, Duncan 1988, Rhymer 1988, Hill 1993); however, the pattern for grebes may contrast with that found for other precocial birds whose energy levels vary isometrically with egg size. Consequently, we are presently examining the possible impact of egg size to chick development in Eared and Western Grebes.

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TABLE 2. Regressions of \log_{10} (egg component mass) against \log_{10} (fresh egg mass) for 70 Eared Grebe and 23 Western Grebe eggs.

Components	Eared Grebes				Western Grebes			
	a	b	b:(95% CI)*	r ²	a	b	b:(95% CI)	r ²
Egg, dry	-0.42	0.88	0.73-1.03	0.66	-0.19	0.77	0.51-1.03	0.62
Egg, water	-0.18	1.04	0.99-1.09	0.96	-0.28	1.08	0.99-1.17	0.96
Shell, wet	-0.60	0.71	0.41-1.01	0.25	-0.99	1.01	0.43-1.59	0.36
Shell, dry	-0.72	0.72	0.46-0.98	0.32	-0.77	0.82	0.43-1.52	0.21
Albumen, wet	-0.69	1.33	1.01-1.65	0.52	-0.75	1.31	1.09-1.53	0.86
Albumen, dry	-1.11	0.96	0.64-1.28	0.34	-0.66	0.68	0.07-1.31	0.19
Yolk, wet	-0.09	0.67	0.21-1.13	0.11	0.49	0.39	-0.01-0.79	0.16
Yolk, dry	-0.85	0.92	0.66-1.18	0.41	-0.68	0.84	0.42-1.26	0.42
Yolk, fat	-0.28	0.31	-0.19-0.81	0.02	0.11	0.22	-0.55-0.99	0.02
Yolk, lean	-2.15	1.61	0.91-2.31	0.23	-2.24	1.56	0.86-2.26	0.49
Total protein	-1.27	1.24	0.94-1.54	0.50	-1.04	1.06	0.60-1.52	0.51
Total energy	0.95	0.83	0.64-0.99	0.51	1.30	0.66	0.46-0.86	0.66

* 95% confidence interval of b.

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VIGILANCE IN THE TUFTED TITMOUSE VARIES INDEPENDENTLY WITH AIR TEMPERATURE AND CONSPECIFIC GROUP SIZE¹

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Key words: Vigilance; group size; air temperature; Tufted Titmouse; *Parus bicolor*.

Vigilance in free-living animals has been studied intensively both theoretically and empirically (see Elgar 1989, Lima 1989, McNamara and Houston 1992). When vigilant for predators, an individual must reduce other activities, such as foraging. Therefore, extent of vigilance has been considered the result of a compromise between gathering sufficient food and avoiding predators (Lendrem 1983, 1984; Kaitala et al. 1989). When presented with a choice, birds prefer to forage

near protective cover (Grubb and Greenwald 1982, Lima 1987). Also, as vigilance can provide benefits simultaneously to several individuals foraging together, many studies have concentrated on the relationship between vigilance and group size of conspecific or heterospecific groups (Caraco 1979a, Elgar 1989, Lindstrom 1989, Cimprich and Grubb 1994). Theoretical models of vigilance as a function of group size consider evolutionarily stable levels of vigilance to be affected by such environmental parameters as rates of foraging and predator attacks, and by the internal state of a forager (McNamara and Houston 1992). Although food intake rate and degree of hunger have been considered important determinants of vigilance, the effects of weather conditions, which have been shown to affect birds' foraging behavior (Grubb 1975, 1978; Mayer et

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