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VARIATION IN SIZE AND COMPOSITION OF BUFFLEHEAD (*BUCEPHALA ALBEOLA*) AND BARROW'S GOLDENEYE (*BUCEPHALA ISLANDICA*) EGGS

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ABSTRACT.—We investigated the relationships between egg nutrient constituents and fresh egg mass in Bufflehead (*Bucephala albeola*) and Barrow's Goldeneye (*B. islandica*). We found consistently positive relationships between egg mass and yolk, albumen, lipid, mineral, and water (absolute amounts); however, the proportions of nutrient components to fresh mass were highly variable in the eggs of both species (allometric relationships). In Bufflehead eggs, all components except mineral exhibited negative allometry with fresh egg mass. In Barrow's Goldeneye eggs, only mineral exhibited negative allometry, whereas yolk, lipid, and water all exhibited positive allometry with fresh egg mass. Overall, larger eggs of both species contained greater absolute amounts of nutrients; therefore, larger eggs were of better quality than smaller eggs. Nutrient content, however, was more highly correlated with mass in Barrow's Goldeneye eggs than in Bufflehead eggs. We propose that this may be due to the source of egg nutrients: because of their smaller body size, Buffleheads typically rely more on exogenous nutrients than Barrow's Goldeneyes. *Received 5 January 2005, accepted 16 December 2005.*

For many bird species, nutrient content is positively correlated with egg size. Consequently, egg size is often used as an indicator of egg and hatchling quality (Birkhead 1984, Sotherland and Rahn 1987, Pelayo and Clark 2002). There are many potential benefits to laying larger, and presumably better quality, eggs, including increased hatchling size (Alisauskas 1986, Dawson and Clark 1996, Anderson and Alisauskas 2001, Pelayo and Clark 2002), increased growth rate of both embryos and hatchlings (Martin 1987, Badzinski et al. 2002), and higher probability of survival after hatching (Dawson and Clark 1996). Such benefits may lead to selective pressure for females to produce larger eggs with greater protein and lipid stores (Lack 1967). However, the selective pressure to produce larger eggs is constrained by a number of factors, including heredity (Martin 1987), the female's metabolic and physiological capabilities (Rohwer 1988, Thomson et al. 1998), and nutrient availability (Alisauskas and Ankney 1992).

The eggs of species with precocial young, such as waterfowl (Anseriformes), have larger yolks than do those of species with altricial young (Ricklefs 1977). Newly hatched Bufflehead (*Bucephala albeola*) and Barrow's Goldeneye (*B. islandica*) ducklings often struggle to exit their nest cavity, and, once out, they follow the female to the nearest body of water, which may be located immediately below the nest or up to 2 km away (Savard et al. 1991, Gauthier 1993, Eadie et al. 2000). Ducklings must rely on stored yolk reserves until they reach the water and begin to feed (Birkhead 1985). Barrow's Goldeneye and Bufflehead ducklings can experience high mortality rates in the 1st week after hatch due to their inexperience in foraging (Savard et al. 1991). Thus, ducklings with large yolk reserves likely survive for longer periods with little or no food than do those with relatively small yolk reserves.

In some species, nutrient content does not depend on egg size, and the benefits of laying larger eggs may not exist. In the European Starling (*Sturnus vulgaris*), for example, larger eggs contained proportionately less yolk and lipid than smaller eggs (Ricklefs 1984), suggesting that in some species, the chicks that hatch from larger eggs may not experi-

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ence the advantages of proportionately larger yolk reserves.

The primary objective of this study was to determine the relationship between size and nutrient composition in the eggs of Bufflehead and Barrow's Goldeneye breeding in British Columbia. The two species nest sympatrically and have a similar diet (Thompson and Ankney 2002), but they exhibit significant differences in body and egg size.

METHODS

Study area.—The study area included approximately 250 km^2 of the Cariboo Parklands in central British Columbia, Canada (52° 07′ N, 122° 27′ W, approximate center point). Montane and boreal wetlands used by breeding Bufflehead and Barrow's Goldeneye were typically too alkaline and/or too shallow to support fish, and had well developed and diverse aquatic invertebrate communities (for a more detailed description of the study area, see Thompson 1996).

Egg collection and preparation.—Bufflehead (n = 21) and Barrow's Goldeneye (n = 40) clutches were collected in 1993 and 1994 in conjunction with a broader study investigating nutritional strategies for reproduction in these species (Thompson 1996). Digital calipers were used to measure egg length and width (breadth) to the nearest 0.1 mm, and a Mettler balance was used to weigh fresh eggs to the nearest 0.1 g. Eggs were then boiled and frozen, pending analysis. Later, the boiled eggs were thawed and separated into their component parts: yolk, albumen (including egg membranes), and shell. Egg components were dried to a constant mass at 80° C and measured to the nearest 0.01 g. Because egg lipid is confined to the yolk, the dried yolk was washed with petroleum ether in a modified Soxhlet apparatus to extract the lipid component (Dobush et al. 1985).

Statistical analyses.—High rates of intraspecific brood parasitism, particularly for Barrow's Goldeneye, precluded reliable discrimination between eggs of the host and parasite; therefore, within-clutch analyses of variation in egg size and composition were not conducted. For each variable, we inspected a scatter plot to identify eggs that were significantly larger or smaller than average (outliers). Using Principle Component Analyses (PCA), outliers were identified as points on the scatter plot that lay distinctly apart from all others (McGarigal et al. 2000). Outliers exert undue pull on the direction of the component axes, strongly affecting the ecological efficacy of the ordination (McGarigal et al. 2000). A few eggs that deviated noticeably from the norm were removed from the data set. Final sample sizes for Bufflehead and Barrow's Goldeneye (after eliminating outliers) were 123 and 226 eggs, respectively.

Preliminary analysis indicated that the residuals were normally distributed and the data did not exhibit any nonlinear trends. We used linear regression to determine the relationship between absolute amounts of individual egg components (dependent variables: dry yolk, dry albumen, lipid, mineral, and water) and fresh egg mass (independent variable). We examined proportional nutrient content by $\log_{10} - \log_{10}$ (hereafter log-log) regressions of egg components versus fresh egg mass (Alisauskas 1986). A regression slope of unity (b = 1.0) signifies that a component makes up a constant fraction of the total egg mass. Slopes significantly <1 or >1 imply that components make up a decreasing or increasing fraction of the total egg as egg mass increases. For each species, we tested both absolute and proportional variation in egg composition. We used analysis of covariance (ANCOVA) to test whether there was differential partitioning of egg nutrients between the two species. Means and slopes are reported ± SE, and significance was set at $P = 0.05$. All analyses were conducted using MINITAB (Minitab, Inc. 2003).

RESULTS

Dimensions and composition of Bufflehead and Barrow's Goldeneye eggs are presented in Table 1. Fresh mass of Bufflehead eggs consisted of 42% wet yolk, 40% wet albumen, and 9% mineral. Overall, water composed approximately 52% of fresh egg mass. Similarly, the composition of Barrow's Goldeneye eggs averaged 40% wet yolk, 45% wet albumen, and 9% mineral. Water composed approximately 57% of fresh egg mass.

There was a consistently positive relationship between fresh egg mass and absolute amounts of dry yolk, dry albumen, lipid, mineral, and water in the eggs of both species (Table 2). In Bufflehead eggs, all components

TABLE 1. Dimensions (mm) and composition (g) of Bufflehead (n = 123) and Barrow's Goldeneye (n = 226) eggs collected in central British Columbia, 1993–1994.

	Bufflehead		Barrow's Goldeneye	
Variable	Mean ± SE	CV[a] (%)	Mean ± SE	CV[a] (%)
Length	50.20 ± 0.15	3.33	61.69 ± 0.13	3.06
Breadth	36.22 ± 0.07	2.13	43.76 ± 0.06	2.10
Fresh egg mass	36.68 ± 0.19	5.89	66.41 ± 0.22	5.04
Mineral	3.36 ± 0.03	9.82	6.24 ± 0.02	6.09
Wet albumen	14.71 ± 0.22	16.93	30.17 ± 0.23	11.60
Dry albumen	2.66 ± 0.02	9.77	4.94 ± 0.02	7.09
Wet yolk	15.46 ± 0.23	16.24	26.00 ± 0.27	15.65
Dry yolk	7.60 ± 0.06	8.55	13.31 ± 0.06	6.99
Yolk lipid	5.14 ± 0.04	8.95	8.94 ± 0.04	7.27
Yolk protein	2.45 ± 0.02	8.57	4.31 ± 0.02	7.19
Water	19.91 ± 0.14	7.89	37.92 ± 0.21	8.47

[a] Coefficient of variation.

except mineral exhibited negative allometry with egg mass (Table 3). The log-log regression slope for mineral did not differ from unity (b = 0.96 ± 0.11), indicating that mineral mass made up a constant proportion of total egg mass. In Barrow's Goldeneye, yolk, lipid, and water all exhibited positive allometry, whereas mineral exhibited negative allometry and albumen exhibited isometry with egg mass (Table 3). Results of the ANCOVA indicated that the nutrients of Bufflehead and Barrow's Goldeneye eggs are partitioned in different ways; the slopes of the regression lines for each nutrient differed (all $P < 0.001$) between species.

DISCUSSION

The percentages of wet yolk in Bufflehead (42%) and Barrow's Goldeneye eggs (40%) were similar to those reported by Lack (1967) for other waterfowl, such as Common Goldeneye (*Bucephala clangula*; 44%) and Muscovy Duck (*Cairina moschata*; 40%), but were greater than those reported for Greater Snow Goose (*Anser caerulescens atlanticus*; 36%) and Mute Swan (*Cygnus olor*; 34%). In Bufflehead and Barrow's Goldeneye, yolk, albumen, lipid, mineral, and water (absolute amounts) all exhibited a positive relationship with egg size. Log-log regression analysis of component masses versus fresh egg mass indicated interspecific differences. In Bufflehead eggs, all components except mineral exhibited negative allometry with egg mass. In Barrow's Goldeneye eggs, only mineral exhibited negative allometry, whereas yolk, lipid, and water exhibited positive allometry with egg mass. Thus, on average, large Bufflehead eggs do not contain proportionately more nutrients than small eggs, whereas large Barrow's Goldeneye eggs do contain more nutrients than small eggs. The results for Bufflehead are

TABLE 2. Summary of linear regression analyses (egg components versus fresh egg mass; absolute amounts; all $P < 0.001$) for Bufflehead (n = 123) and Barrow's Goldeneye (n = 226) eggs collected in central British Columbia, 1993–1994.

	Bufflehead			Barrow's Goldeneye		
Component	b (SE)[a]	Intercept	r^2	b (SE)[a]	Intercept	r^2
Mineral	0.09 (0.01)	−0.04	0.37	0.06 (0.01)	2.45	0.26
Dry albumen	0.04 (0.01)	0.95	0.15	0.07 (0.00)	−0.01	0.51
Dry yolk	0.15 (0.02)	1.76	0.28	0.23 (0.01)	−1.93	0.69
Yolk lipid	0.11 (0.02)	1.12	0.27	0.16 (0.01)	−1.71	0.67
Yolk protein	0.04 (0.01)	0.83	0.21	0.07 (0.01)	−0.23	0.53
Water	0.32 (0.06)	8.03	0.20	0.67 (0.05)	−6.55	0.49

[a] Slope of regression ± SE.

TABLE 3. Summary of allometric regression analyses (egg components versus fresh egg mass; all $P < 0.001$) for Bufflehead ($n = 123$) and Barrow's Goldeneye ($n = 226$) eggs collected in central British Columbia, 1993–1994.

Component	Bufflehead			Barrow's Goldeneye		
	b (SE)[a]	Intercept	r^2	b (SE)[a]	Intercept	r^2
Mineral	0.96 (0.11)	−0.98	0.35	0.60 (0.06)	−0.29	0.26
Dry albumen	0.61 (0.13)	−0.54	0.14	1.00 (0.06)	−1.13	0.52
Dry yolk	0.81 (0.12)	−0.38	0.27	1.12 (0.05)	−0.92	0.68
Yolk lipid	0.80 (0.12)	−0.54	0.25	1.16 (0.05)	−1.16	0.67
Yolk protein	0.68 (0.01)	−0.67	0.20	1.03 (0.05)	−1.25	0.54
Water	0.58 (0.11)	0.39	0.18	1.16 (0.08)	−0.54	0.45

[a] Slope of regression ± SE; a regression slope of unity ($b = 1.0$) signifies that a component makes up a constant fraction of the total egg mass. Slopes significantly <1 or >1 indicate that components make up a decreasing or increasing fraction of the total egg as egg mass increases.

similar to those of Jager et al. (2000), who found that larger Eurasian Oystercatcher (*Haematopus ostralegus*) eggs contained more lean dry matter and lipid (absolute amounts) than smaller eggs, but the proportion of both constituents decreased with egg size.

In several bird species, hatchlings from large eggs have a higher probability of survival to fledging than do hatchlings from small eggs (Payne 1978). Bufflehead and Barrow's Goldeneye hatchlings were not measured or monitored in this study, therefore it is not known whether large eggs of these species do indeed produce larger ducklings. However, larger Ruddy Duck (*Oxyura jamaicensis*) eggs produced larger, more mature ducklings that were provisioned with greater energy reserves and exhibited greater survival rates than ducklings from smaller eggs (Pelayo and Clark 2002).

Overall, larger eggs in both species contained more nutrients, although nutrient content of Barrow's Goldeneye eggs was more highly correlated with egg mass than it was in Bufflehead eggs (Table 2). This suggests that nutrients in Bufflehead and Barrow's Goldeneye eggs are partitioned differently. A possible mechanism for this difference is the source of egg nutrients: because Buffleheads have a smaller body size, they rely more on exogenous nutrients, whereas the larger Barrow's Goldeneyes can rely more on endogenous nutrients (Thompson 1996, Hobson et al. 2005). This may explain the higher CVs for the constituents of Bufflehead eggs, as they are less able to buffer the effects of variable food supplies by drawing on endogenous reserves.

Our results show that larger eggs of Buffleheads and Barrow's Goldeneyes contain more nutrients than smaller eggs, which may increase the survival of their hatchlings during the 1st crucial week of life. This is especially important given that Buffleheads and Barrow's Goldeneyes nest in boreal and montane regions where food typically is less available than in, for example, the prairie wetlands of North America, used by many temperate nesting ducks (Thompson 1996, Thompson and Ankney 2002). Further studies should be conducted on these species to examine variation in egg composition within and between clutches and to determine whether hatchlings from larger eggs are larger and have lower mortality than those from smaller eggs.

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