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Intraspecific variation in egg composition.—Intraspecific egg composition may vary depending upon the size of the egg (e.g., Ricklefs 1977, 1984; Boersma 1982; Birkhead and Nettleship 1984; Alisauskas 1986; Hepp et al. 1987; Rohwer 1986; Hill 1988; Arnold et al. 1991). Statistical techniques derived from allometry (the study of size and its consequences) customarily are used to examine the relation between egg size and egg composition (Reiss 1989). Typically, the log of egg component mass, such as wet albumen, is regressed on the log of egg mass ($\log[y] = \log[a] + b \log[x]$). The slopes of these functions (b) depict the rate at which the egg component varies with egg size. When the slope of a log-log function is equal to 1.0 (isometry), increases in egg size are accompanied by proportionate increases in the particular egg component; consequently, the percentage of egg component will remain constant across eggs of different sizes. Slopes greater than 1.0 (positive allometry) indicate that the component mass increases disproportionately with increases in egg mass; accordingly, large eggs will contain proportionately more component mass than will small eggs. Conversely, slopes less than 1.0 (negative allometry) demonstrate that components increase proportionately less than egg mass, so that large eggs will consist of relatively smaller amounts of the egg component.

Investigations of the allometric relation between egg components and egg size have yielded some apparent differences between altricial and precocial birds. For example, Ricklefs (1984) found for the altricial European Starling (*Sturnus vulgaris*) that albumen content varied isometrically with egg mass, whereas both yolk and lipid mass displayed negative allometry. Hence, the percentage of albumen remained more or less constant in eggs of different sizes, but the percentage of yolk and lipid decreased with increasing egg size. In contrast, Ankney (1980) demonstrated for the precocial Lesser Snow Goose (*Chen caerulescens*) that both albumen and yolk varied isometrically with egg size. To determine the generality of these findings a comparative analysis, using the published data on egg composition allometry, was conducted. The purpose of the present study was to ascertain whether differences exist between altricial and precocial birds with respect to the allometric variation of egg composition.

Methods.—I compiled data from 31 species in 16 families (a summary of species and sources is available from the author). For each species I noted the slope (b) of the allometric (log-log) functions for wet albumen mass, dry albumen mass, wet yolk mass, dry yolk mass, and lipid mass (y variables) regressed on egg mass (x). The general category of development for the species, altricial or precocial, was also recorded (Nice 1962). Because there is disagreement regarding the developmental classification of pelagic-feeding seabirds, I did not include them in the overall analysis (3 families) and present their data separately. The main

TABLE 1
MEAN ($\pm$ SE) ALLOMETRIC VARIATION^a OF EGG COMPOSITION FOR ALTRICIAL AND PRECOCIAL FAMILIES

Allometric function	Precocial	Altricial	r^b	P^c
Wet albumen	1.04 (0.06) N = 6	1.21 (0.04) N = 5	2.68	0.02
Dry albumen	1.02 (0.05) N = 5	1.16 (0.09) N = 4	1.33	0.23
Wet yolk	0.90 (0.09) N = 7	0.57 (0.09) N = 4	2.64	0.03
Dry yolk	0.90 (0.15) N = 5	0.62 (0.08) N = 4	1.67	0.15
Lipid	0.81 (0.16) N = 4	0.69 (0.10) N = 4	0.64	0.55

^a Slope of log(egg component) regressed on log(egg mass).

^b Independent t -tests.

^c Two-tailed P values.

data set contained information from seven precocial families and six altricial families. Due to the limited number of families, I did not further divide the data set into finer developmental classifications (e.g., semi-precocial, semi-altricial). Seven families (Apterygidae, Phasianidae, Sulidae, Pellecanidae, Corvidae, Sturnidae, Tyrannidae) had data from only one species as the family representative. Analyses were repeated using the species as independent data points and, notably, all of my results were consistent, regardless of whether species or family was the unit of analysis.

Sample sizes differed across the component variables because some measurements (e.g., dry masses and lipid mass) were not taken in the original studies. To test for differences between altricial and precocial families, t -tests were conducted on the allometric functions for the various egg components. Isometry was determined by t -tests comparing the data for precocial or altricial families to a population mean of 1.00; significant differences indicated either positive (>1) or negative allometry (<1), depending upon the particular mean value. Standard deviates (z -scores), within each developmental category, were calculated by using the mean and standard deviation corresponding to that group. These standard deviates were examined to determine the degree of departure from the group average for families within each of the two developmental categories.

Results and discussion.—The allometric functions for two egg components differed significantly between precocial and altricial families (Table 1): wet albumen b was significantly larger for altricial species whereas wet yolk b was significantly larger for precocial species. The mean slope for altricial families indicates positive allometry for wet albumen ($t = 5.27$, $df = 4$, $P < 0.01$), so that increases in egg size for these birds would be associated with disproportionate increases in albumen. In contrast, wet yolk ($t = -4.79$, $df = 3$, $P < 0.05$) and dry yolk ($t = -4.62$, $df = 3$, $P < 0.05$) display negative allometry for altricial birds. In addition, there was a trend for lipid to display negative allometry for altricial birds ($t = -3.11$, $df = 3$, $P = 0.053$). Yolk mass (wet and dry), albumen mass (wet and dry), and lipid mass increased isometrically with egg size in precocial species. Data from the five pelagic-feeding species (Table 2) show positive allometry for albumen and negative allometry for yolk, thus reflecting a pattern more similar to altricial species.

TABLE 2
ALLOMETRIC VARIATION^a OF EGG COMPONENTS FOR PELAGIC-FEEDING BIRDS

Family	Species	Wet albumen	Dry albumen	Wet yolk	Dry yolk	Reference
Hydrobatidae	<i>Oceanodroma furcata</i>	1.65	—	0.05	—	Boersma, 1981
	<i>O. leucorhoa</i>	0.72	0.44	0.65	0.52	Montevocchi et al., 1983
Procellariidae	<i>Puffinus griseus</i>	1.35	—	0.46	—	Warham, 1983
	<i>P. tenuirostris</i>	1.20	—	0.67	—	Meathrel et al., 1993
Diomedidae	<i>Diomedea immutabilis</i>	1.27	—	0.58	—	Warham, 1983

^a Slope of log(egg component) regressed on log(egg mass).

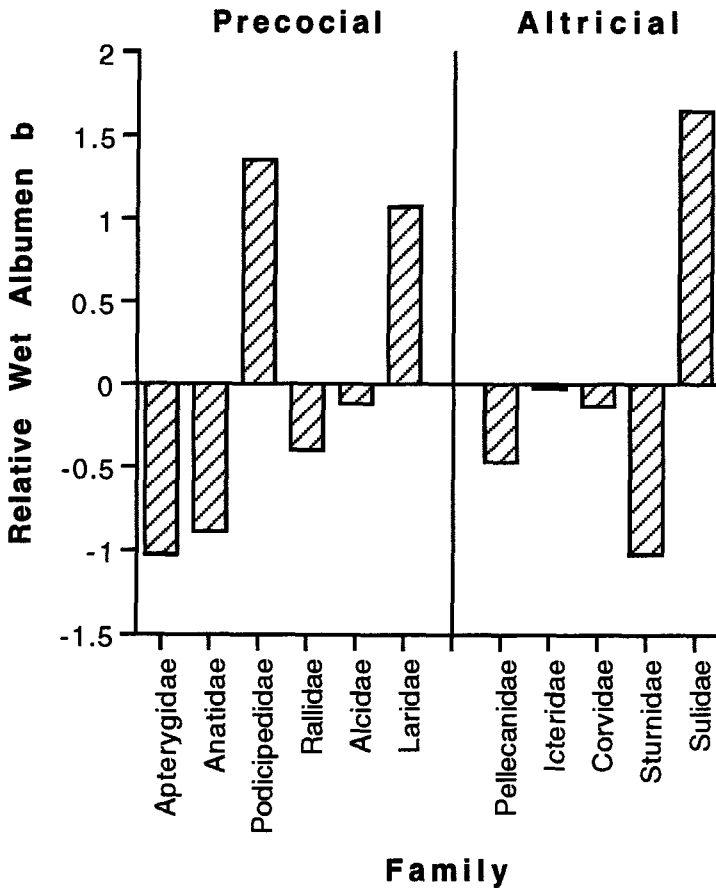


FIG. 1. Relative wet albumen *b* (z-scores) for precocial and for altricial families.

Standard deviates of the allometric functions for wet albumen and for wet yolk indicate that the Podicipedidae family tends not to follow predicted patterns for precocial species (Figs. 1 and 2). Although grebes are classified as precocial 4 (Nice 1962), the intraspecific variation of their egg components was more similar to the pattern characteristic of altricial families and pelagic-feeding birds. For example, albumen increased at a greater rate than egg size (wet albumen $b = 1.23$; dry albumen $b = 1.24$) whereas the proportion of yolk decreased with increases in egg size (wet yolk $b = 0.43$; dry yolk $b = 0.44$). Indeed, for each of these egg component functions, the Podicipedidae had the largest standard deviates among all the precocial families. Among altricial families for wet albumen (Fig. 1), the Sulidae had the largest standard deviate, in this case indicating that the slope of their allometric function for wet albumen ($b = 1.36$) was greater than typical for altricial species. The Icteridae had the largest standard deviate for wet yolk allometry (Fig. 2) in that they demonstrated a more isometric pattern than typical for altricial species (wet yolk $b = 0.81$).

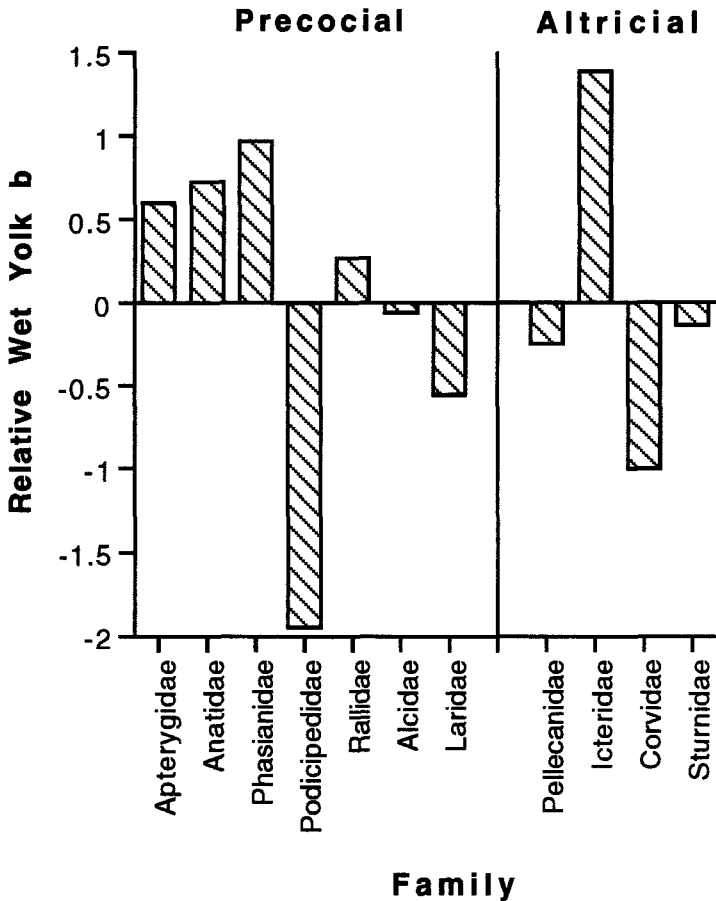


FIG. 2. Relative wet yolk b (z-scores) for precocial and for altricial families.

It remains to be determined whether these allometric patterns correspond to unique adaptations between altricial and precocial birds. Because variation in egg composition within species can affect the developmental characteristics of chicks (e.g., Hill 1993, Sotherland et al. 1990), it is possible that altricial chicks from different-sized eggs might show contrasting developmental patterns. For precocial chicks, however, because egg composition varies isometrically no such size effects would generally be expected. It is suggested that researchers examine the potential impact of these allometric patterns for the ontogeny of chicks from different developmental modes.

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