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EGG VOLUME AS A PREDICTOR OF HATCHLING WEIGHT IN THE BROWN-HEADED COWBIRD

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Variations in dimensions or weights of eggs of certain bird species have been correlated with age of female, date, clutch size (e.g. Nice 1937:112–120, Romanoff and Romanoff 1949:61–87; see also Coulson 1963), and more recently with annual environmental conditions (Jenkins et al. 1967:111) and sequence of laying in the clutch (Kendeigh et al. 1956, Murton et al. 1974, Howe 1976, Nolan 1978). Among conceivable explanations for such trends, the most probable appear to be differences in absolute and relative quantities of energy-yielding and other constituents packaged in the egg (see Berg and Bearse 1957). These differences, in turn, should affect size and viability of the embryo and/or hatchling; and at least some of them, therefore, are presumably the products of selection (Howe 1976).

We considered it important to learn how, if at all, egg size is related to hatchling size in a passerine and investigated that question in the Brown-headed Cowbird (*Molothrus ater*). We selected the cowbird for this purpose because data on the size of eggs of brood parasites (Wickler 1968:193–194, Friedmann 1963:21–22) and the size of their young at hatching (Southern 1964) are of interest in themselves. The results demonstrate that a cowbird egg's length and breadth can be used to predict the weight and probably the overall body size of the nestling produced. Since recent evidence (see below) suggests that correlations comparable to the one presented herein can be expected rather widely among birds, our methods may have general utility in field studies.

METHODS

On the advice of Frank W. Preston (pers. comm.) that volume is "the best single specification of size" of eggs, we selected volume as the parameter to be measured. Considerations of convenience reinforced this decision: volume can be calculated from an egg's length and breadth, which are easily found. Weight, on the other hand, is hard to obtain in the field and is subject to the added disadvantage that it changes throughout incubation.

The frequently used formula for volume, length × breadth^2 × 0.524 (e.g. Romanoff and Romanoff 1949:108), assumes that the egg is an ellipsoid of revolution, an assumption not always justified (Preston 1974). We therefore found true volumes of cowbird eggs that we collected (1970–1976) on and near a study area (described in Thompson and Nolan 1973) outside Bloomington, Indiana, and on the basis of these values calculated a coefficient to replace the 0.524 in the conventional formula. An egg's actual volume was obtained from 3 weights, those (1) of the egg, (2) of a sealed container filled with distilled water, and (3) of the same container filled with distilled water and the egg.

Weight 1 was subtracted from weight 3 and the difference subtracted from weight 2, yielding the weight and volume of water the egg had displaced (for other details, see Nolan 1978). The mean volume of 45 eggs was 2.890 ml ± (= standard deviation) 0.319 ml; extremes were 3.78 ml and 2.34 ml (compare Wetherbee and Wetherbee 1961). The mean value of the coefficients derived from the 45 volumes was 0.515 ± 0.014; extremes were 0.548 and 0.491.

To investigate the relation between egg volume and hatchling weight we used 41 cowbird eggs collected from the same location and over the same period as the sample just described. These we incubated (at 37°C, 60% relative humidity) until they hatched. Volumes (ml) were calculated as equal to length × breadth^2 × 0.515. The sample was not randomly selected: eggs in nests of certain hosts that we were studying ordinarily were left uncollected, and we made special efforts to include a few unusually large and unusually small cowbird eggs. However, distributions of volumes and hatchling weights did not deviate from normal ($P = > 0.2$, Kolmogorov-Smirnov test). Considering the time interval and the area over which eggs were collected, it is unlikely that any female contributed more than one egg to the sample.

Young were weighed within 10 h (usually within a few minutes) of hatching. (Hatching was at all times of day and night; compare the contrary finding by Wetherbee and Wetherbee 1961:156.) Weights were rounded to 1 cg; for several reasons greater precision was unattainable. Post-hatching weight loss varies with time spent in the incubator, and neonates may defecate even though they have not eaten (Wetherbee and Wetherbee 1961). Further, frequency and times of egg turnings varied and incubator temperature and humidity fluctuated slightly (see Rol'nik 1970:307–308, 314–315, 327, 333), all of which could have affected hatchling weight.

The foregoing procedures can be simplified by investigators who are not interested in egg volumes and who want only to predict hatchling weight from easily measured egg parameters. Obviously, any significant statistical relationship between egg volume and hatchling weight will also exist between hatchling weight and the product of egg length × breadth^2, and no constant need be considered.

RESULTS

The weights of young plotted against the volumes of the eggs that produced them (Fig. 1), reveal a close positive linear relationship. The regression equation is $Y = -0.05 + 0.78X$. Because egg volumes were calculated from a formula and hatchling weights were subject to the slight experimental error mentioned, we make no probability statement about the regression. The results of a correlation analysis are $r = 0.96$, $df = 39$, $P = <0.01$.

Mean calculated egg volume was 3.009 ml ± 0.333 ml and mean hatchling weight 2.289 g ± 0.271 g (compare Wetherbee and Wetherbee 1961). Extremes of volume were 3.905 ml and 2.411 ml. The largest egg measured 24.2 × 17.7 mm and produced a young bird weighing 3.11 g; the smallest egg, 20.0 × 15.3 mm, produced a young weighing 1.75 g. The mean length of the 41 eggs was 21.49 mm ± 1.10 mm, the mean width 16.46 mm ± 0.61 mm. Although both length alone and breadth alone correlated significantly with hatchling weight, neither correlation was as close as that of volume (length, $r = 0.75$; breadth, $r = 0.89$).

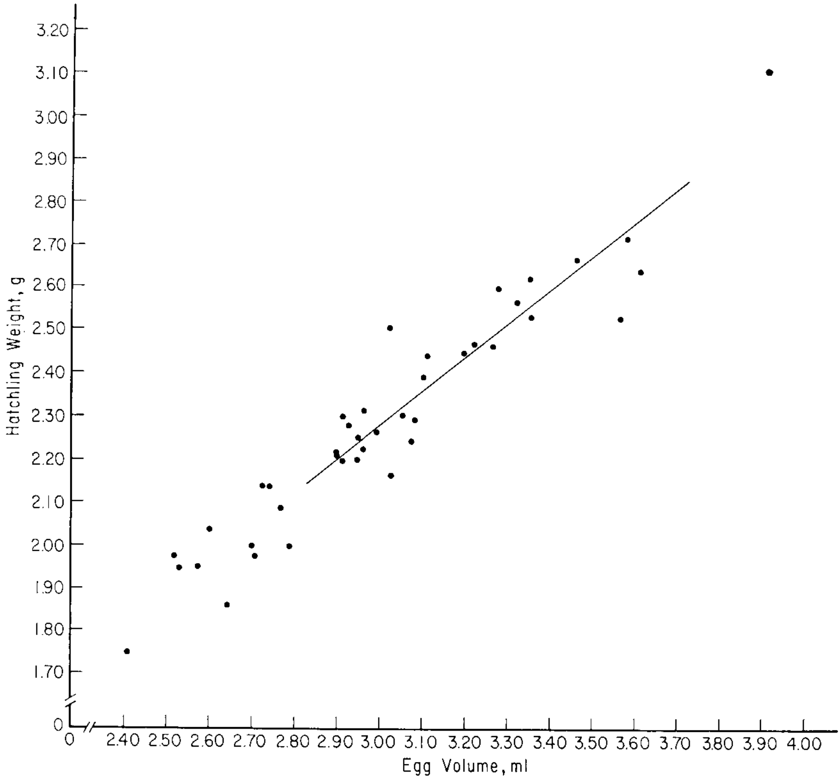

FIG. 1. Regression of weight of newly hatched Brown-headed Cowbirds on calculated volume (see text) of eggs that produced them. The regression equation is $Y = -0.05 + 0.78X$.

Wetherbee (1961:419–421), in a review of neonatal condition of many North American bird species, calculated neonatal weights as percentages of egg volumes and found that in most species the value is about 75%. The cowbirds in his sample, at 81%, represented an extreme; and Wetherbee considered their deviation a possible adaptation for brood parasitism. The means of our data (first sentence of the preceding paragraph) yield a figure of 76%, which is below many of Wetherbee's percentages for non-parasitic passerines.

DISCUSSION

Discovery of a linear correlation between volume of egg and weight of hatchling in the cowbird might be of narrow interest if that relationship were a specialization associated with parasitic reproduction, but this possibility is remote. In chickens (*Gallus gallus*; Halbersleben and Mussehl 1922, Skoglund et al. 1952, Godfrey et al. 1953) and possibly in Red Grouse (*Lagopus lagopus scoticus*; Jenkins et al. 1967:111) larger eggs produce larger chicks. More recently, positive egg size-hatchling size relationships have been reported in 4 other bird species, 2 of them passerines and 1 an icterid: the Herring Gull (*Larus argentatus*; Parsons 1970), the Wood Pigeon (*Columba palumbus*; Murton et al. 1974), the Great Tit (*Parus major*; Schifferli 1973), and the Common Grackle (*Quiscalus quiscula*; Howe 1976). Most interestingly, Schifferli (1973) found that weights of Great Tit eggs could be estimated from the formula 0.527 × length × breadth^2 and that the regression coefficient of hatchling weight on egg weight is 0.725. Assuming that cowbird and tit eggs are about the same shape, the striking similarities of Schifferli's formula for weight and his regression coefficient to our formula for volume and our regression coefficient strongly suggest that our data do not reflect a specialization for brood parasitism.

Most investigators named above considered whether egg size and/or hatchling weight affected viability and/or rate of development. In general, advantages for heavier eggs and young were indicated (but see Davis 1975 on the Herring Gull and Skoglund et al. 1952, Godfrey et al. 1953 on chickens).

Reasons for the greater weight of young Great Tits produced from large eggs were thought by Schifferli (1973) to be either larger overall body size or the possession of greater reserves of yolk (see Parsons 1970, Howe 1976), or both these factors. Our inspection of newly hatched cowbirds revealed that bodies, wings, and heads of the heaviest individuals were considerably larger than those of the lightest. Heavy young looked bigger in all respects.

All studies referred to in this section, except those of the Herring Gull, focused on weights of eggs and related these to weights of young. (Schifferli calculated at least some egg weights from their measurements.) We reiterate our view that most workers will find it impractical to obtain egg weights directly, and we conclude by emphasizing the utility of our methods. Especially when data on hatchling size are required on a large scale, the convenient procedure would appear to be to work out a regression equation and then simply to measure eggs.

SUMMARY

Known volumes and measurements of eggs of the Brown-headed Cowbird (*Molothrus ater*) collected near Bloomington, Indiana, revealed that the formula length × breadth^2 × 0.515 produces a good estimate of the volume of these eggs. Volumes of a second sample of cowbird eggs were calculated from measurements, the eggs incubated, and young were weighed shortly after hatching. Calculated egg volumes and hatchling weights were positively and linearly correlated ($n = 41$; $r = 0.96$); the regression coefficient of hatchling weight on egg volume was 0.78. The significance of the results and the methods is discussed.

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