

VARIATION IN WEIGHT AND COMPOSITION OF BROWN-HEADED COWBIRD EGGS

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Female Brown-headed Cowbirds (*Molothrus ater*; hereafter called "cowbirds") lay more eggs per breeding season than do females of any other passerine that has been studied (Scott and Ankney 1980). They lay an average of 40 eggs in eight weeks in southern Ontario, and do so without using endogenous nutrient reserves (Ankney and Scott 1980). It is unknown, however, if this high rate of egg production is concomitant with a reduction in egg size and/or quality, and an increased variation in egg weight and composition. Thus, we undertook this research to: (1) determine the variation in weight and composition of cowbird eggs, (2) compare this variation with data from other altricial birds, particularly European Starlings (*Sturnus vulgaris*; Ricklefs 1977a, b, 1984), and (3) determine seasonal patterns in egg weight. Also, because we obtained 16 eggs from one female, we were able to compare variation in egg weight and composition within and among females.

METHODS

We obtained fresh cowbird eggs, near London, Ontario, using the technique described by Dufty (1983): females were caught in Potter traps and were placed in small cages that were suspended 8 cm above a 2.5-cm layer of sawdust and had 1.25-cm mesh wire bottoms; the following morning, eggs were collected, weighed to the nearest 0.01 g, placed in air-tight glass vials, and refrigerated until subsequent analysis. We trapped between 17:00-20:30 on 33 days between 6 May and 6 July 1983. Caged birds were not given food, but all had been feeding on millet in the trap before their removal. Birds were released before 08:30, most before 07:30.

We measured the length and breadth of each egg to the nearest 0.1 mm, with vernier calipers. Eggs then were lightly boiled for 5-10 min to ease separation of yolk from albumen. The yolk, albumen, and shell were dried to constant weight at 80°C (Kerr et al. 1982). Lipids were ex-

tracted from each yolk with petroleum ether (B.P. 30-60°C) in a Goldfisch apparatus for 6 h.

For comparative purposes, we used the energy equivalents given by Ricklefs (1977b): 9.5 kcal/g lipid and 5.65 kcal/g non-lipid dry weight.

RESULTS AND DISCUSSION

We obtained 40 eggs from 17 female cowbirds; one female, DA3, laid 16 eggs, two females each laid three eggs, four females each laid two eggs, and 10 females laid one egg each. We present the results of analyses of (a) all eggs, (b) the eggs from DA3, and (c) the eggs from the "other females." Several lines of evidence suggest that our data from DA3 were not seriously biased by the amount of time that she spent in captivity. First, we obtained seven eggs from her on mornings after she had spent two (or more) consecutive nights in captivity (\bar{x} egg weight = 2.84 g) and nine eggs on mornings when she had not spent two consecutive nights in captivity (\bar{x} egg weight = 2.95 g); these means do not differ significantly ($t = 0.84$, $P > 0.4$). Second, she laid nine eggs during the 12 days that we trapped between 2-15 June; that laying rate (0.75 eggs/day) is similar to that (0.73) reported by Scott and Ankney (1980) for a large sample of shot birds. Finally, the proportional composition of her eggs was virtually identical to those obtained from the other females and her eggs had a slightly higher caloric density (Table 1).

Fresh egg weight (W), in grams, was related to egg length (L) and breadth (B), in centimeters, by these equations:

$$\text{All eggs} - W = 0.111 + 0.526 \text{ LB}^2,$$

$$r^2 = 0.97, \quad P < 0.001;$$

$$\text{DA3} - W = -0.013 + 0.548 \text{ LB}^2,$$

$$r^2 = 0.99, \quad P < 0.001;$$

$$\text{Other females} - W = 0.199 + 0.512 \text{ LB}^2,$$

$$r^2 = 0.95, \quad P < 0.001.$$

The coefficients of determination (r^2) suggest that the relationship between egg weight and LB^2 is no more variable in a sample of eggs from different females than in a sample of eggs from a single female. The slope of the equation for all eggs was similar to that (0.530) reported by Ricklefs (1984) for starling eggs. The slope for the sample of eggs from different females was similar to that (0.515) reported by Nolan and Thompson (1978) for an equation relating cowbird egg-volume to LB^2 .

The proportional composition of cowbird eggs (calculated from \bar{x} values in Table 1) closely resembled that of starling eggs (Ricklefs 1977b: Table 1; 1984: Table 2), and was typical of that of other altricial species. For example, the percent lipid in the average cowbird egg (4.7%) was within the range (4-7%) calculated by Ricklefs (1977b) for three other altricial species. Similarly, the caloric density

TABLE 1. Means and variation of egg components (g) from one female cowbird compared to those from several different cowbirds.

Variable	Egg source								
	All birds (n = 40)			DA3 (n = 16)			Other females (n = 24)		
	\bar{x}	(Range)	C.V.	\bar{x}	(Range)	C.V.	\bar{x}	(Range)	C.V.
Egg weight	3.17	(2.53-3.82)	12.6%	2.90	(2.53-3.40)	9.0%	3.35	(2.56-3.82)	11.3%
Wet yolk	0.581	(0.452-0.705)	10.0%	0.552	(0.452-0.705)	10.9%	0.599	(0.516-0.680)	8.4%
Dry yolk	0.244	(0.173-0.290)	11.1%	0.231	(0.173-0.280)	11.7%	0.252	(0.215-0.290)	9.1%
Wet albumen	2.279	(1.712-2.905)	14.3%	2.054	(1.712-2.528)	10.2%	2.430	(1.803-2.905)	12.4%
Dry albumen	0.232	(0.180-0.313)	15.5%	0.212	(0.182-0.276)	12.3%	0.245	(0.180-0.313)	14.7%
Wet shell	0.310	(0.243-0.391)	13.5%	0.294	(0.235-0.343)	11.6%	0.321	(0.252-0.40)	14.5%
Dry shell	0.206	(0.143-0.266)	14.6%	0.205	(0.158-0.251)	12.7%	0.207	(0.143-0.266)	15.9%
Dry egg	0.680	(0.521-0.819)	11.3%	0.643	(0.521-0.786)	10.4%	0.704	(0.564-0.819)	10.7%
Yolk lipid	0.149	(0.117-0.183)	12.8%	0.142	(0.117-0.182)	12.7%	0.154	(0.127-0.183)	11.7%
Water	2.491	(1.970-3.067)	13.3%	2.258	(1.970-2.626)	9.1%	2.642	(1.974-3.067)	11.7%
Energy*	1.120	(0.990-1.220)	11.1%	1.150	(0.990-1.220)	11.4%	1.110	(1.06-1.220)	10.6%

* Kcal/g fresh weight excluding shell.

TABLE 2. Allometric regressions of egg components on egg weight in cowbirds.

Variable	Statistics*		
	<i>a</i>	<i>b</i> (95% confidence limits)	<i>r</i> ²
All birds (<i>n</i> = 40)			
Shell			
Wet	-0.918	0.662 (0.386-0.939)	0.38
Dry	-1.060	0.742 (0.436-1.048)	0.39
Yolk			
Wet	-0.501	0.528 (0.330-0.726)	0.43
Dry	-0.922	0.616 (0.404-0.828)	0.48
Lipid	-1.136	0.618 (0.363-0.873)	0.39
Albumen			
Wet	-0.198	1.110 (1.028-1.192)	0.95
Dry	-1.203	1.120 (0.968-1.272)	0.86
Whole egg			
Dry	-0.578	0.820 (0.684-0.956)	0.81
Water	-0.130	1.050 (1.015-1.086)	0.99
Kcal	0.100	0.825 (0.692-0.958)	0.81
DA#3 (<i>n</i> = 16)			
Shell			
Wet	-1.105	1.114 (0.671-1.557)	0.68
Dry	-1.251	1.211 (0.710-1.712)	0.66
Yolk			
Wet	-0.616	0.771 (0.240-1.302)	0.41
Dry	-1.064	0.919 (0.348-1.490)	0.46
Lipid	-1.253	0.875 (0.252-1.499)	0.39
Albumen			
Wet	-0.199	1.106 (0.958-1.254)	0.95
Dry	-1.262	1.254 (0.984-1.524)	0.88
Whole egg			
Dry	-0.659	1.012 (0.667-1.357)	0.74
Water	-0.108	0.999 (0.905-1.093)	0.97
Kcal	-0.001	1.045 (0.672-1.418)	0.72
Other birds (<i>n</i> = 24)			
Shell			
Wet	-1.029	0.846 (0.437-1.255)	0.46
Dry	-1.210	0.998 (0.565-1.432)	0.51
Yolk			
Wet	-0.431	0.396 (0.131-0.661)	0.30
Dry	-0.850	0.479 (0.200-0.758)	0.37
Lipid	-1.106	0.557 (0.182-0.932)	0.30
Albumen			
Wet	-0.175	1.067 (0.933-1.201)	0.93
Dry	-1.198	1.118 (0.866-1.370)	0.79
Whole egg			
Dry	-0.600	0.854 (0.686-1.022)	0.84
Water	-0.124	1.041 (0.995-1.085)	0.99
Kcal	0.137	0.754 (0.587-0.921)	0.80

* *a* and *b* are the intercept and slope in the equation $\log Y = a + b \log X$; confidence intervals calculated as $b \pm t_{(n-2)} S_b$, where S_b = the standard error of *b*; *r*² is the coefficient of determination.

of cowbird eggs (1.12 kcal/g fresh weight excluding shell) was virtually the same as the mean (1.14 kcal/g) reported by Carey et al. (1980: Table 2) for 23 altricial species.

The eggs from DA3 weighed, on average, 13% less than those from other females (Table 1). Nearly all (85%) of this difference was due to differences in water content. The dry yolk, albumen, and shell of DA3's eggs averaged 8%, 13%, and 1% lighter in weight, respectively, than those components of eggs from other females. Surprisingly, the eggs and most egg components of DA3 were about as

variable in weight as those of eggs of other female cowbirds (C.V.s in Table 1), but her yolks and yolk lipids were more variable. This is in marked contrast with Ricklefs' (1984) finding that, for starlings, most variation in egg composition was *between* rather than *within* females. We obtained four series of eggs, i.e., eggs obtained on consecutive days, from DA3 and the egg weights (in g) were: Series 1—3.32, 2.87; Series 2—2.67, 2.71, 2.72, 2.68; Series 3—3.40, 3.32, 2.83; Series 4—3.04, 2.73. Clearly, egg weights varied considerably between and within clutches from the same female cowbird. This suggests that much variation in egg weight in cowbirds is environmentally induced. Cowbird eggs and egg components may be more variable in weight than those of other passerines, as the C.V.s (Table 1) are considerably higher for them than they are for those reported by Ricklefs (1977a) for starling eggs.

To determine the relation between fresh egg weight and egg components, we regressed the logarithms of component weights on the logarithms of fresh egg weights (after Ricklefs 1984); a slope (*b*) that has confidence intervals that do not include 1.0 shows that the component becomes a greater, or lesser, proportion of the egg with increased egg weight. Table 2 shows that, for all eggs, the slopes, and coefficients of determination (*r*²), for the various egg components were similar to those for starling eggs (Ricklefs 1984: Table 4), with one exception. Yolk and lipid weights were more highly correlated with egg weight in cowbirds (*r*² = 0.43, 0.39 for yolk and lipid weights, respectively) than they were in starlings (*r*² = 0.22, 0.14).

The variation of egg components with egg weight followed several patterns in a sample of eggs from one female vs. a sample of eggs from other females (Table 2, Fig. 1). Albumen and water varied similarly in both samples, and both components varied in direct proportion to egg weight. The high coefficients of determination show that egg weight is an excellent predictor of the weights of these components, regardless if the eggs are from one, or more than one, female. Shell weight also varied directly with egg weight in both samples (Table 2) but for a given egg weight, the shells of DA3's eggs on average, weighed more (Fig. 1). The patterns of variation in yolk and yolk lipid weights differed between the samples as the slopes were higher, particularly for yolk weight, in the one-female sample. This suggests that yolk weight varies more directly with egg weight in eggs from one female than within the overall population. This pattern may be an artifact, however, because (1) the eggs laid by DA3 did not span the entire weight range of those laid by other females, and it is in the heavier eggs that dry yolk weight appears to not increase with increased egg weight (Fig. 1), and (2) one egg laid by DA3 contained a disproportionately small yolk (Fig. 1) and, thus, increased the slope of yolk weight on egg weight. When we regressed dry yolk weight (*Y*) on egg weight (*X*) for eggs of other females, that were within the range of eggs laid by DA3 (2.5–3.4 g), the resulting equation

$$\log Y = -0.953 + 0.700 \log X,$$

$$df = 10, \quad r^2 = 0.53, \quad P < 0.01,$$

was similar to that describing the same relation in the eggs of DA3, when the data were analysed without including those for the small-yolked egg:

$$\log Y = -0.996 + 0.787 \log X,$$

$$df = 13, \quad r^2 = 0.54, \quad P < 0.01.$$

Data are needed from eggs of a female cowbird that lays eggs heavier than average to evaluate if egg yolks vary more predictably with egg weight *within*, rather than *between*, females. Regardless, it appears that Ricklefs' (1984) caution that egg weight is a poor measure of egg "quality" in starlings is less applicable to cowbird eggs; kcals/egg are highly correlated with egg weight in cowbirds (Table 2, Fig. 1).

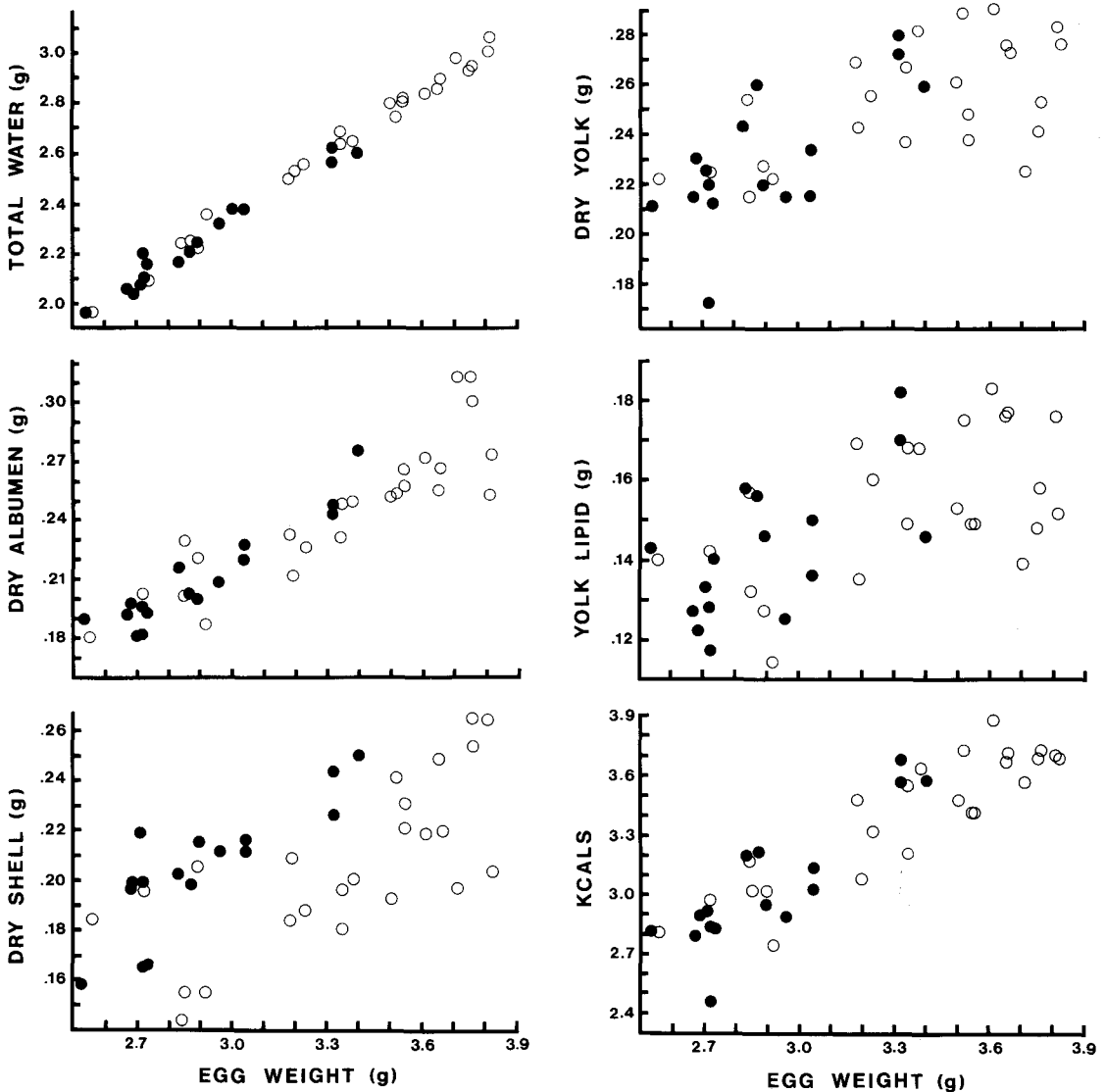


FIGURE 1. Variation in egg components with egg weight for Brown-headed Cowbirds. Closed symbols are for eggs from DA3, open symbols for eggs of other females (see text).

To see if egg weight varied over the breeding season, we regressed egg weight (Y) on egg date (X) (1 May = 1, 6 July = 67) for the eggs from DA3,

$$Y = 2.74 + 0.0048X, r^2 = 0.07, P > 0.05,$$

and for the eggs from the other females,

$$Y = 3.05 + 0.0104X, r^2 = 0.26, P = 0.01.$$

We can suggest two explanations for why the two samples were different: (1) egg weight generally increases over the breeding season, but those of DA3 were exceptions; (2) by chance, we caught "light egg" females early in the season and not thereafter (see Fig. 2). Regardless, these data do suggest that the high rate of egg production by female cowbirds (Scott and Ankney 1980) is not maintained at the expense of egg weight.

CONCLUSIONS

The composition of cowbird eggs is typical of that of eggs of other altricial species (Carey et al. 1980) and is virtually identical to that of starlings (Ricklefs 1977a, b). Female

cowbirds, on average, do not sacrifice egg quality to maintain their high rate of egg production. Contrary to the assumption that a female cowbird lays eggs of similar size (e.g., Walkinshaw 1949, Elliott 1977), however, the weight of eggs laid by an individual female varied greatly. Remarkably, much of the variation in egg weight and weight of egg components shown by the population as a whole is also found within the eggs of an individual female. Possibly that is also true of other species, but we know of no data for eggs from more than one clutch from an individual female. If the rate of egg production by female cowbirds is determined by availability of host nests (see Ankney and Scott 1980), then it may not be surprising that a female lays eggs that vary considerably in weight. Ankney and Scott (1980) showed that female cowbirds rely exclusively on exogenous nutrients for egg production and a female's ability to obtain them might vary considerably from day to day. Particularly when a female is aware of several nests suitable for parasitizing, however, it probably would not be adaptive for her to skip one or two days in order to produce a bigger egg. It would be interesting, although

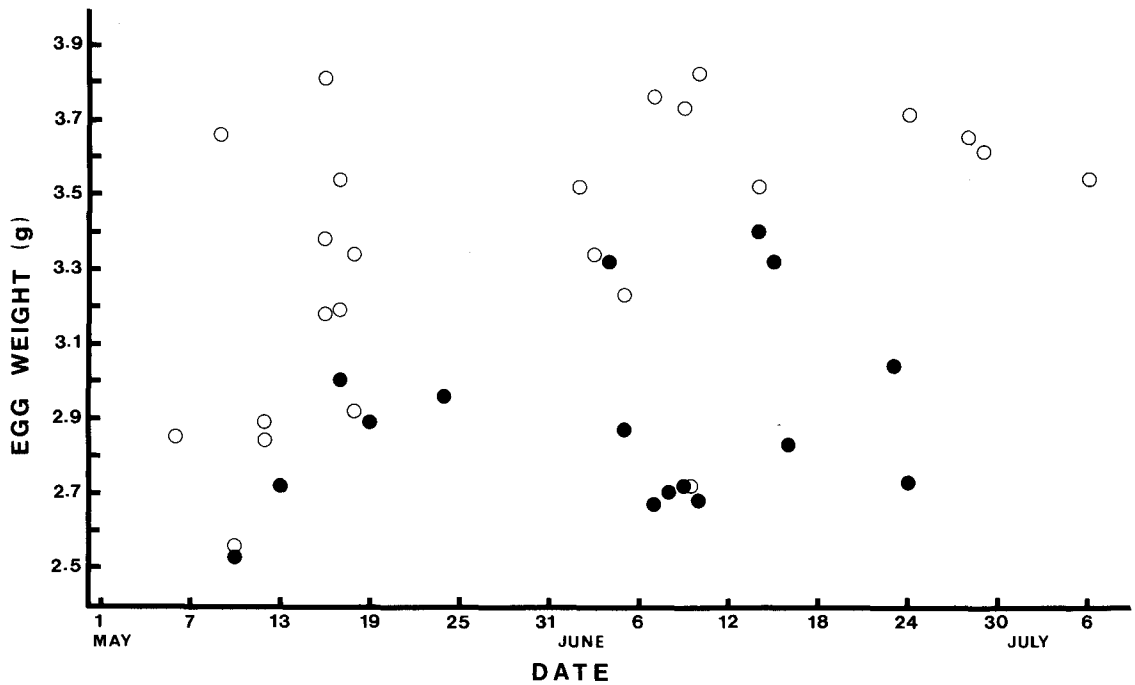


FIGURE 2. Variation in egg weight with date for Brown-headed Cowbirds (symbols as in Fig. 1).

difficult, to determine how much genetic control there is over egg weight in cowbirds.

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