NUTRIENT CONTENT OF EGGS AND THE ENERGETICS OF CLUTCH FORMATION IN THE BOAT-TAILED GRACKLE

G. THOMAS BANCROFT[1]

Department of Biology, University of South Florida, Tampa, Florida 33620 USA

ABSTRACT.—Shell, yolk, and albumen represent 10.5%, 21.9%, and 67.6%, respectively, of fresh-egg weight of Boat-tailed Grackles (*Quiscalus major*). The proportion of egg composed of dry yolk increases as egg weight increases. The average 8.1-g egg contains 33.6 kJ of which 66.1% is in yolk and 33.9% is in albumen. The average three-egg clutch was estimated to cost 131 kJ for yolk development and albumen deposition. These costs were spread over a 6-day period, with a peak of 28 kJ occurring on the day before egg laying began. At hatching, the yolk sac represents 19% of hatchling wet weight. Only 10% of the energy present in the egg at laying is expended during incubation. Hatchlings have substantial yolk reserves that contain 49% of the hatchlings' energy. *Received 12 May 1983, accepted 9 June 1984.*

EGG size may vary greatly within populations and within clutches. The proportion of egg made up by yolk, albumen, and shell may vary with egg size (Ricklefs 1977a, 1984; Howe 1978; Nisbet 1978; Ricklefs et al. 1978; Ricklefs and Montevecchi 1979) and indicates variation in the energy females commit to clutch completion. The total energetic costs of egg formation include the energy required for ova development, growth of a functioning oviduct, albumen deposition, and shell deposition (King 1973, Ricklefs 1974). Few estimates are available for the energetic costs of clutch completion in altricial birds. The present paper analyzes the pattern of variation in the composition of eggs, energetic costs of clutch completion, and use of energy in the egg during incubation in the Boat-tailed Grackle (*Quiscalus major*).

METHODS

I collected eggs in March and April of 1980 and 1981 in Hillsborough Co., Florida. I collected seven clutches of three eggs on the day the third egg was laid and two single eggs on the morning they were laid. I collected one three-egg clutch when the first egg was pipped. Two eggs had been incubated for 12 days and one egg for 11 days. All eggs were weighed to the nearest 0.001 g and frozen for later analyses. Fresh eggs were separated into shell, egg white, and yolk. Eggs that were about to hatch were separated into embryo, yolk sac, and shell. Components were weighed and dried over concentrated sulfuric acid under a vacuum at room temperature. Dry weight was recorded and water content determined by subtraction. Total lipid content was determined by the chloroform-methanol extraction method of Freeman et al. (1957). Protein level was determined by the colorimetric method of Lowry et al. (1951), using bovine serum albumen as the standard. Ash content was determined by heating samples for 4 h at 500°C. Constants given by Brody (1945) and Kleiber (1961) were used to convert the g organic material into caloric units: 39.6 kJ/g lipid and 23.7 kJ/g protein.

Using Ricklefs's (1974) model, I estimated the costs of clutch formation from dry weight and energy content of yolk and albumen, rate of ovum growth, laying interval, and clutch size. No information was available on costs of oviduct development, costs of shell deposition, or modification of behavior, and they are not included in my estimates. Ricklefs (1976) found that the ova of European Starlings (*Sturnus vulgaris*) develop over a three-day period. I assumed that Boat-tailed Grackles have a similar pattern of ova development and calculated from his model that 58%, 23%, and 17% of the dry weight of each ovum was deposited on successive days of development. Each ovum in the clutch was assumed to begin development on successive days. Grackles typically lay one egg per morning until the clutch is complete (Bancroft 1983); therefore, the albumen for a given egg must be deposited in less than 24 h. Daily energy costs were calculated by multiplying the energy density by the weight of yolk or albumen deposited and assuming the costs of biosynthesis were 75% (see Ricklefs 1974). The cost curves were calculated based on the mean clutch weight of 24.2 g (Bancroft 1984a).

---

[1] Present address: Research Department, National Audubon Society, Indian Mound Trail, Tavernier, Florida 33070 USA.

The Auk 102: 43–48. January 1985

TABLE 1. Weights (g) and composition (% of wet or dry weight or energy content) of Boat-tailed Grackle eggs in central Florida.

	n	Mean	SE	Minimum	Maximum
Total weight	23	7.72	0.13	6.59	8.90
Shell weight	23	0.81	0.02	0.61	0.97
Yolk weight	23	1.69	0.06	1.18	2.45
Albumen weight	23	5.22	0.09	4.48	6.02
Yolk					
Water (% wet weight)	23	60.5	0.9	55.0	71.1
Lipid (% dry weight)	22	56.3	0.6	51.3	61.9
Protein (% dry weight)	23	38.5	0.4	35.6	41.7
Ash (% dry weight)	20	2.6	0.2	1.4	4.7
Total energy (kJ)	22	20.70	0.6	15.69	27.43
Albumen					
Water (% wet weight)	23	90.7	0.1	89.3	91.9
Protein (% dry weight)	19	91.8	0.9	82.5	97.2
Ash (% dry weight)	19	5.7	0.2	3.7	7.1
Total energy (kJ)	19	10.62	0.20	8.98	11.87
Shell					
Water (% wet weight)	23	34.5	1.0	27.7	48.5
Yolk/albumen (dry)	23	1.37	0.03	0.99	1.62
Whole egg					
Water (% wet weight)	23	78.4	0.1	77.4	79.4
Energy (kJ/egg)	18	31.54	0.91	25.86	39.14
Energy (kJ/g wet weight)	18	4.06	0.05	3.69	4.40

RESULTS

Composition of eggs.—Table 1 presents the wet weight, dry weight, and composition of 23 Boat-tailed Grackle eggs that were collected within 2 days of laying. The percentage of water in the yolk varies (CV = 6.8%) more than that of the albumen (CV = 0.7%). Of the dry weight of egg contents, lipids represented 32.4% (SE = 0.1, $n = 22$). In composition, grackle eggs closely resemble those of other altricial birds (Ricklefs 1977b, Carey et al. 1980).

Between-clutch variation accounted for more than 55% of the variation in weight of egg components (Table 2). Significant variation with sequence of laying occurred only for yolk wet weight. Within-clutch variation in yolk wet weight accounted for 35.3% of the total variation, whereas for yolk dry weight within-clutch variation was only 12.6% of the total variation.

Because eggs showed strong within-clutch resemblances, I calculated correlation coefficients and regression equations based on clutch means. Fresh-egg weight was significantly correlated ($P < 0.05$) with water content ($r = 0.999$), wet and dry weights of yolk ($r = 0.829$, $r = 0.957$) and albumen ($r = 0.947$, $r = 0.751$), and dry weight of shell ($r = 0.912$), but not shell wet weight ($r = 0.600$, $P = 0.09$). Figure 1 shows the relationship between dry weight of yolk and fresh-egg weight. The slope of the functional regression (see Ricker 1973) was significantly greater than 1 ($t = 3.19$, $P < 0.05$). Energy content (EC) of the eggs showed a similar relationship to fresh-egg weight [$EC = 1.832\ wt^{1.391}$, $n = 9$, coefficient of determination (R^2) = 0.901, $P < 0.01$], but the slope for this equation was not quite significantly greater than 1 ($t = 2.36$, $P = 0.051$).

Temporal sequence of energy expenditure.—Energy-expenditure curves were calculated only for costs of ova development and albumen deposition (Fig. 2). The daily energy expenditure for ova development was highest on the day of first ovulation (Fig. 2). At this point all three ova were developing. Daily energy expenditure for egg development began as 17 kJ on the first day of ova development and reached a maximum (28 kJ) on the last day before laying began. Energy requirements decreased during laying because fewer eggs were developing. To produce the average clutch (24.2 g) a female needed 131 kJ over a six-day period. Half of all three-egg clutches weighed between 22.8 g and 25.5 g (Bancroft 1984a). Thus, energy expendi-

TABLE 2. The percentage of total variance in component weight attributable to differences within and between clutches of Boat-tailed Grackles.[a]

Component	Weight	Percent between clutch	Percent within clutch		
			Sequence[b]	Other[c]	F[d]
Wet yolk	1.68	64.7	22.7	12.6	10.36**
Wet albumen	5.16	57.0	8.6	34.5	2.85*
Water	6.00	68.5	11.3	20.1	5.95**
Dry yolk	0.65	87.3	4.5	8.1	16.92**
Dry albumen	0.48	66.4	9.5	24.1	4.73**

[a] Based on a two-way analysis of variance.

[b] Percentage of variance factored out by sequence of laying.

[c] Percentage of variance represented by error component.

[d] F = model mean square divided by error mean square; * $P < 0.05$; ** $P < 0.01$.

ture for half the population would have been between 123 and 139 kJ. The average clutch of two eggs weighed 16.3 g and needed 89 kJ to produce. Half of all two-egg clutches ranged from 15.1 to 17.3 g and required 82–94 kJ to produce.

From the equation of Kendeigh et al. (1977), I estimated a basal metabolic rate (BMR) of 89 kJ/day for female Boat-tailed Grackles. Energy requirements for laying were approximately 19% of BMR three days before laying, 31% of BMR on the day before the first egg was laid, and 16% of BMR on the day albumen for the last egg was synthesized (Fig. 2).

Energy content of hatchlings.—Just prior to hatching, yolk sacs in three eggs averaged 19% of wet and 45% of dry egg contents. The three eggs contained 28.4 kJ, compared to an estimated energy content of 31.7 kJ when laid. The remaining yolk contained 49% (14.0 kJ) of the energy. Of the energy estimated to be present in the yolk at laying (20.6 kJ), 68% was still present in the yolk sac just before hatching.

For Boat-tailed Grackles the lipid index of eggs (lipid weight/lipid-free dry weight of egg contents) averaged 0.482 (SE = 0.011, n = 22). The lipid index of two eggs that had been incubated 12 days averaged 0.362 with and 0.164 without the yolk sac. These two eggs were estimated to have lipid indices of 0.499 at laying.

DISCUSSION

Eggs of Boat-tailed Grackles averaged 8.1 g (n = 1,094) and ranged from 5.5 to 11.2 g (Bancroft 1984a). More than 80% of the variation in egg weight was attributable to between-clutch variation in weight. Egg weight varied significantly with laying sequence. Last-laid eggs in clutches of two and three were significantly lighter than earlier eggs. Although yolk wet weights of third eggs were less than those of the first two, dry weights showed no significant differences with laying sequence. This suggests that the average difference of 0.32 g (n = 161; Bancroft 1984a) between the weights of the first and last eggs in three-egg clutches results from differences in water content. The correlation between fresh-egg weight and organic content, and the significant between-clutch variation in wet and dry weight of components, clearly show that between-clutch variation is partly a result of differences in organic content. Organic content of eggs of Common Terns (*Sterna hirundo*, Nisbet 1978) and Common Grackles (*Quiscalus quiscula*, Howe 1978) did vary significantly with laying sequence as well as between clutches.

In Boat-tailed Grackles, yolk dry weight increased in direct proportion to fresh-egg weight. A similar pattern occurs in Common Grackles (Howe 1978); mean yolk content/clutch was directly correlated with mean dry weight, but albumen weight showed no significant correlation with egg dry weight. In the Starling, yolk size decreased in proportion to fresh-egg weight (Ricklefs 1977a, 1984). In the Northern Gannet (*Sula bassanus*), yolk size is independent of fresh-egg weight, whereas albumen size is directly correlated (Ricklefs and Montevecchi 1979). In the Common Tern and the Laughing Gull (*Larus atricilla*) the proportion of the egg composed of yolk decreased and albumen increased with an increase in egg weight (Nisbet 1978, Ricklefs et al. 1978).

The yolk/albumen ratio averaged 1.37 for Boat-tailed and 0.95 for Common grackles (Howe 1978). The mean dry weight of albumen

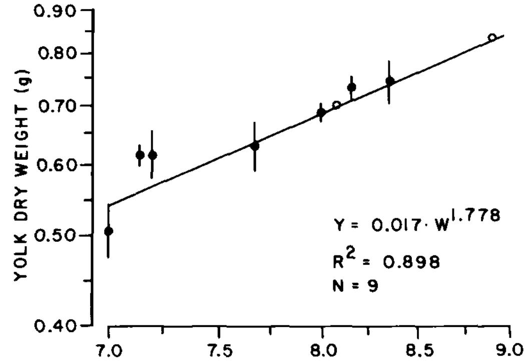

Fig. 1. Dry-yolk weight relative to fresh-egg weight of Boat-tailed Grackles in central Florida. Closed circles represent mean yolk and egg weight within 7 three-egg clutches. Vertical lines show one standard deviation on either side of mean. Open circles are for two single eggs.

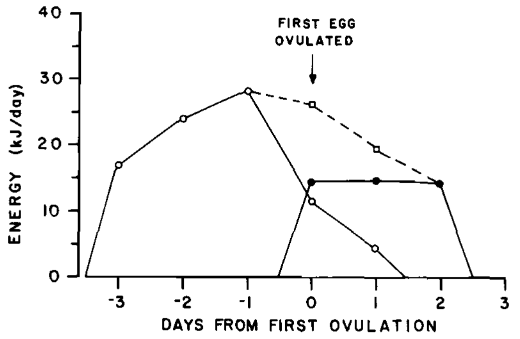

Fig. 2. Calculated mean daily energetic costs of yolk and albumen production in the Boat-tailed Grackle for a clutch of three eggs. Open circles represent daily costs of yolk production, closed circles represent daily costs of albumen production, and squares represent daily costs of yolk and albumen production combined.

for Boat-tailed and Common grackles was essentially equal. Thus, the difference in yolk/albumen ratio reflects the increased yolk size of Boat-tailed Grackles. Female Boat-tailed and Common grackles are similar in size, but Boat-tailed Grackle eggs average 1.2 g heavier (Howe 1978, Bancroft 1984a). Female nestlings of both species grow at close to the same rate and attain about the same weights at fledging, whereas male Boat-tailed Grackles fledge at 30–40 g heavier than Common Grackle males in about the same amount of time (Howe 1976, 1978, 1979; Bancroft 1983, 1984b).

The difference in yolk size between these two grackles may reflect a trade-off between number and size of eggs. Boat-tailed Grackles in Florida lay either two or three eggs, and the female raises the nestlings by herself (Bancroft 1983). Monogamous Common Grackles typically lay four or five eggs (Howe 1976, 1978), and the male helps care for nestlings (Howe 1979). Early in the nestling period Boat-tailed Grackle females must divide their time between brooding young and foraging. The young may need a larger yolk reserve for this period. In Common Grackles the male will provide some food during this period.

For Boat-tailed Grackles the total energetic cost of development while in the egg is relatively low. Eggs at hatching contained only 3.3 kJ (10.4%) less than when they were laid. Vleck et al. (1980) derived an equation for altricial birds that predicts the energy (E) used during incubation as a function of fresh-egg weight ($E = 0.59\ wt_{egg}^{0.78}$). This equation predicted that Boat-tailed Grackles should have expended 12.4 kJ of energy during incubation. Apparently, development is more costly in Red-winged Blackbirds (*Agelaius phoeniceus*) because blackbird hatchlings contained only 49% of the energy in freshly laid eggs (Fiala and Congdon 1983). The relatively low amount of energy used during incubation of grackle eggs was correlated with the large yolk sac remaining at hatching. The yolk sac of grackles represented 19% of hatchling weight. For 31 altricial species the yolk sac averaged 8% of wet weight at hatching (Romanoff 1944, Schmekel 1960, Vleck et al. 1980). For grackles the yolk sac contains sufficient nutrients and energy to sustain growth and maintenance through the day of hatching and into the next day (Bancroft 1983). Young usually are fed during this period, and the yolk reserve may last longer.

There may be a selective advantage in having larger yolk reserves at hatching. Yolk reserves provide nutrients necessary for growth during the first few days of the nestling period, when the female must divide her time between brooding and foraging. Hatchling weight was significantly correlated with fresh-egg weight (Bancroft 1984a), and future studies may show that larger eggs with proportionately more yolk provide hatchlings with greater yolk reserves. However, survival of third-hatched young through day 6 of the nestling period was not related to egg weight (Bancroft 1984a). Egg size influences growth rates of young in several species (Schifferli 1973, O'Connor 1975, Howe 1976), possibly including Boat-tailed Grackles. Grackles that attain asymptotic weights more quickly often will fledge earlier, and this may increase their chances of survival (Bancroft 1983, 1984b).

Female Great-tailed (*Quiscalus mexicanus*), Common, and Boat-tailed grackles have similar body weights and egg sizes (Selander and Giller 1961, Howe 1978, Bancroft 1984a). Because Great-tailed and Common grackles have larger clutch sizes, they expend more energy on clutch completion than do Boat-tailed Grackles. Peak daily energy requirements for egg formation of Boat-tailed Grackles was 31% of BMR, which was less than the 45% of the average BMR estimated for passerines (Ricklefs 1974). As a percentage of body weight, clutch weights of Boat-tailed Grackles also average less than some small passerines (King 1973, Ricklefs 1974, Rahn et al. 1975). This suggests that for Boat-tailed Grackles the relative energetic investment in a clutch is substantially below that of many passerines. Boat-tailed Grackles begin nesting in March (Bancroft 1983). Eggs laid during March are smaller (Bancroft 1984a) and presumably have proportionately less yolk than those laid later. Although Boat-tailed Grackles have a relatively low energetic commitment to egg production compared to other species (King 1973, Ricklefs 1974, Rahn et al. 1975), the smaller eggs during March suggest that grackles begin nesting before they can accumulate sufficient nutrients and energy to lay the largest egg possible.

ACKNOWLEDGMENTS

Glen E. Woolfenden provided the intellectual environment to undertake this study and the advice necessary to complete it. Field work was supported by grants from the Frank M. Chapman Memorial Fund of the American Museum of Natural History and from the Ding Darling Foundation. John M. Lawrence taught me the techniques for nutrient analysis and allowed me to use the equipment in his lab. Discussions with William Bros, Wayne Hoffman, John M. Lawrence, and Earl D. McCoy improved various aspects of this study. John M. Lawrence and Glen E. Woolfenden read and improved an early draft of the manuscript. Finally, I thank my wife, Ann, who provided help with field and laboratory work, and most of all provided invaluable encouragement and support throughout this project.

LITERATURE CITED

BANCROFT, G. T. 1983. Reproductive tactics of the sexually dimorphic Boat-tailed Grackle. Unpublished Ph.D. dissertation, Tampa, Univ. South Florida.

———. 1984a. Patterns of variation in size of Boat-tailed Grackle eggs. Ibis 126: 496–509.

———. 1984b. Growth and sexual dimorphism of the Boat-tailed Grackle. Condor 86: 423–432.

BRODY, S. 1945. Bioenergetics and growth. New York, Hafner.

CAREY, C., H. RAHN, & P. PARISI. 1980. Calories, water, lipid, and yolk in avian eggs. Condor 82: 335–343.

FIALA, K. L., & J. D. CONGDON. 1983. Energetic consequences of sexual dimorphism in nestling Red-winged Blackbirds. Ecology 64: 642–647.

FREEMAN, N. K., F. T. LINDGREN, Y. C. NG, & A. V. NICHOLS. 1957. Serum lipids analysis by chromotography and infrared spectrophotometry. J. Biol. Chem. 227: 449–464.

HOWE, H. F. 1976. Egg size, hatching asynchrony, sex, and brood reduction in the Common Grackle. Ecology 57: 1195–1207.

———. 1978. Initial investment, clutch size, and brood reduction in the Common Grackle (*Quiscalus quiscula* L.). Ecology 59: 1109–1122.

———. 1979. Evolutionary aspects of parental care in the Common Grackle *Quiscalus quiscula* L. Evolution 33: 41–51.

KENDEIGH, S. C., V. R. DOLNIK, & V. M. GAVRILOV. 1977. Avian energetics. Pp. 127–204 *in* Granivorous birds in ecosystems (J. Pinowski and S. C. Kendeigh, Eds.). Cambridge, England, Cambridge Univ. Press.

KING, J. R. 1973. Energetics of reproduction in birds. Pp. 78–120 *in* Breeding biology of birds (D. S. Farner, Ed.). Washington, D.C., Natl. Acad. Sci.

KLEIBER, M. 1961. The fire of life. New York, Wiley.

LOWRY, O., N. J. ROSEBROUGH, A. L. FARR, & R. J. RANDAL. 1951. Protein measurement with Folin phenol reagent. J. Biol. Chem. 193: 265–275.

NISBET, I. C. T. 1978. Dependence of fledging success on egg-size, parental performance and egg-composition among Common and Roseate Terns, *Sterna hirundo* and *S. dougallii*. Ibis 120: 207–215.

O'CONNOR, R. J. 1975. Initial size and subsequent growth in passerine nestlings. Bird-Banding 46: 329–340.

RAHN, H., C. V. PAGANELLI, & A. AR. 1975. Relation of avian egg weight to body weight. Auk 92: 750–765.

RICKER, W. E. 1973. Linear regressions in fishery research. J. Fish. Res. Board Can. 30: 409–434.

RICKLEFS, R. E. 1974. Energetics of reproduction in birds. Pp. 152-297 *in* Avian energetics (R. A. Paynter, Jr., Ed.). Publ. Nuttall Ornithol. Club No. 15.

———. 1976. The chemical composition of the ovary, oviduct, and follicles of the Starling (*Sturnus vulgaris*). Auk 93: 184-187.

———. 1977a. Variation in size and quality of the Starling egg. Auk 94: 167-168.

———. 1977b. Composition of eggs of several bird species. Auk 94: 350-356.

———. 1984. Variation in the size and composition of eggs of the European Starling. Condor 86: 1-6.

———, D. C. HAHN, & W. A. MONTEVECCHI. 1978. The relationship between egg size and chick size in the Laughing Gull and Japanese Quail. Auk 95: 228-237.

———, & W. A. MONTEVECCHI. 1979. Size, organic composition and energy content of North American Gannet *Morus bassanus* eggs. Comp. Biochem. Physiol. 64A: 161-165.

ROMANOFF, A. L. 1944. Avian spare yolk and its assimilation. Auk 61: 235-241.

SCHIFFERLI, L. 1973. The effect of egg weight on the subsequent growth of nestling Great Tits *Parus major*. Ibis 115: 549-558.

SCHMEKEL, L. 1960. Daten über das Gewicht des Vogeldottersackes vom Schlupftag bis zum Schwinden. Rev. Suisse Zool. 68: 103-110.

SELANDER, R. K., & D. R. GILLER. 1961. Analysis of sympatry of Great-tailed and Boat-tailed grackles. Condor 63: 29-86.

VLECK, C. M., D. VLECK, & D. HOYT. 1980. Patterns of metabolism and growth in avian embryos. Amer. Zool. 20: 405-416.