BIOENERGETICS OF EGG PRODUCTION BY FEMALE HOUSE SPARROWS

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ABSTRACT.—To determine the daily and total energy expenditures of breeding female House Sparrows (*Passer domesticus*), we collected 276 females near London, Ontario between April 1981 and May 1983. Protein and fat content of developing follicles, eggs, and oviducts were determined and converted into their energy equivalents. Eight days were required to develop and lay a modal clutch of 4 eggs. Fat energy requirements were not estimable accurately because total body fat did not decline linearly over the egg production period; therefore, energy requirements were estimated as a range. Based on a 4-egg clutch, the maximum daily costs of reproduction, 16.5–17.6 kJ/day, equalled 44–47% of a female's standard metabolic rate. We estimate that daily costs vary less than 10% for other clutch sizes (3 or 5). The total energy demand of reproduction was 66–71 kJ. Protein requirements comprised 59–63% of the total costs and were apportioned among oviduct (5–6%), yolk protein (17–19%), and albumen (36–39%). Fat requirements accounted for the remaining 37–41% of total costs. Based on our estimates of energy needed for reproduction, and on other evidence, we suspect that egg production by House Sparrows is not constrained by energy acquisition. *Received 15 July 1985, accepted 16 October 1985.*

DESPITE much research on breeding strategies of passerines, little is known about the temporal distribution of the energetic costs of reproduction (Walsberg 1983). Without estimates of the temporal distribution of reproductive costs, neither the relationship between energy expenditure and fecundity nor the evolutionary optimization of reproductive effort can be clarified (see Stearns 1976, Drent and Daan 1980).

Research on the daily energy necessary to produce and lay eggs has depended on indirect methods. These include estimates extrapolated from time-activity budgets (Schartz and Zimmerman 1971, Ettinger and King 1980, Mugaas and King 1981, Biedenweg 1983, Finch 1984), estimates based on food utilization studies of caged birds (El-Wailly 1966, Brisbin 1969), and estimates based on the chemical composition or caloric content of egg, the duration of egg production, and the average clutch size (Kendeigh 1973, King 1973, Ricklefs 1974, Schifferli 1976, Bancroft 1985). To our knowledge, no study has estimated the daily energy expenditures of a breeding passerine based on the proximate analysis of developing follicles, eggs, and the oviduct.

The purpose of this study was to determine the total and daily cost of reproduction of a breeding passerine, the House Sparrow (*Passer domesticus*).

STUDY AREA AND METHODS

House Sparrows were collected within a 50-km radius of London, Ontario (43°02′N, 81°09′W). Many sites were used to avoid repeated sampling of the same local population (Lowther 1983). Some birds were collected with mist nets, Potter live traps, and nest-box traps, but most birds were collected by shooting between 0800 and 1200 EST. Birds were collected during March–May 1981, March–June 1982, and January–May 1983.

No collections were made after the first fledgling House Sparrow was seen in a season. This ensured that only individuals engaged in their first clutch of the season were included. This precaution also controlled for female age because females nesting during the first peak in nesting are usually more than 1 yr old (Summers-Smith 1963, Dawson 1972).

Females were placed in the following categories for analysis:

Prereproductive (PRD).—Females collected in late winter–early spring that had no yolky developing follicles (*n* = 113).
Reproductive (RD).—Females with one or more yolky

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TABLE 1. Mean ± 1 SE dry weights (mg) of preovulatory follicles of House Sparrows. Numbers in parentheses are sample sizes.

Day before ovulation	
−4	—[a]
−3	14.5 ± 1.68 (84)
−2	60.4 ± 3.81 (50)
−1	166.0 ± 7.10 (38)
0	252.0 ± 8.78 (13)

[a] Because only 2 females were found with 4 yolky preovulatory follicles (they were collected after noon), we could not estimate accurately Day −4 preovulatory follicle weight. The smallest yolky preovulatory follicle found weighed 1 mg.

TABLE 2. Estimated dry weight (mg) of protein and fat allocated daily to follicles in House Sparrows.

	Day						
	−4	−3	−2	−1	0	+1	+2
Protein	6	19	43	35			
		6	19	43	35		
			6	19	43	35	
				6	19	43	35
Total weight	6	25	68	103	97	78	35
Fat	8	27	63	50			
		8	27	63	50		
			8	27	63	50	
				8	27	63	50
Total weight	8	35	98	148	140	113	50

developing follicles or an oviducal egg, or both (*n* = 126).

Early incubation (EI).—Females that had laid the last egg of their clutch on the day before they were collected (*n* = 37).

Collected females were tagged individually and the ovary, oviduct, and, if present, oviducal egg of each were removed and stored in 10% formalin until analyzed. In 1983, fresh weights of the ovary, oviduct, and, if present, oviducal egg of each female were recorded to the nearest 0.01 g. Next, after the digestive tract had been stripped of all contents, the carcass was weighed to the nearest 0.1 g. The entire carcass was then oven-dried at 90°C to a constant weight (Kerr et al. 1982) and weighed to the nearest 0.01 g.

Clutch size was determined by counting the number of pre- and postovulatory follicles per ovary, but only on Days +1 to +4 could clutch size be assessed accurately (see Schifferli 1976). Day 0 is the first day a yolk is ovulated. After each female was placed into a category, and if possible, the clutch size determined, the ovaries, pre- and postovulatory follicles, oviduct, and oviducal eggs were removed from formalin, oven-dried at 90°C to a constant weight, and weighed to the nearest 0.001 g.

In 1982, 125 nest boxes (15 × 13 × 10 cm) were located at 6 collection sites (between 10 and 30 boxes/site) to obtain clutch size data and from which to collect eggs for determination of egg composition. Nest boxes were visited every 1–3 days until the first egg appeared. As eggs were laid, they were removed and replaced with dummy eggs to encourage the female to continue laying. Each egg was weighed to the nearest 0.01 g, placed in an airtight plastic container, and refrigerated until further analyses (Ricklefs 1984).

Later, eggs were boiled and separated into shell, albumen, and yolk. These components were oven-dried at 75°C to a constant weight and weighed to the nearest 0.001 g. We attempted to extract neutral fats from the yolks using petroleum ether in a Goldfisch extractor. Because the resulting coefficients of variation exceeded 25%, we opted not to use our estimates of yolk protein or yolk fat. Instead, we used Schifferli's (1976) estimate of the percentage of fat in a dry House Sparrow yolk (59%) to estimate the amount of protein and fat in the yolks we collected.

We tested for annual differences in the body sizes of House Sparrows by comparing the femur lengths of PRD females. Femur length was chosen as an index of body size rather than body weight because the latter can fluctuate rapidly over several days, e.g. during premigratory hyperphagia (Odum et al. 1964). By using femur length, we avoided any potentially misleading short-term fluctuations in body weight. However, it was also necessary to select a predictor of nutrient reserves. Femur length correlated positively with fresh body weight ($r^2 = 0.23$, df = 101, $P < 0.001$). Thus, because no annual differences in femur length were detected ($F = 0.12$, df = 100, $P > 0.50$), all three years' data were pooled.

RESULTS

Daily nest visits during egg-laying revealed that the House Sparrows normally laid an egg each day for 3–6 days. We constructed an energy budget for the modal clutch size at our site, 4 eggs. Because 4 days are required for a follicle to attain maturity from the quiescent stage (Schifferli 1980), 8 days are needed to produce and lay 4 eggs (Day −4 to Day +4).

Because eggs are laid daily, the difference in weight between any two consecutively developing follicles represents the growth of the

TABLE 3. Mean ± 1 SE dry weights (mg) of House Sparrow albumens by egg sequence. Sample sizes in parentheses.

Egg sequence number	
1	194.5 ± 8.1 (11)
2	215.0 ± 8.4 (12)
3	222.5 ± 5.9 (12)
4	215.6 ± 7.6 (16)

TABLE 4. Actual and estimated mean dry oviduct weights of female House Sparrows during the reproductive period.

	Oviduct weight	
	Actual	Estimated[a]
PRD	0.006	—
Day		
−4	—	0.064
−3	0.120	—
−2	0.186	—
−1	0.276	—
0	—	0.333
+1	0.399	—
+2	0.333	—
+3	0.297	—
+4	—	0.120
EI	0.100	—

[a] Derived from regression of actual weights. Day −4 weight determined using oviduct weights from PRD, Days −3, −2, and −1; Day 0 weight determined using oviduct weights from Days −3, −2, −1, and +1; and Day +4 weight determined using oviduct weights from Days +1, +2, and +3 and EI. See Methods for definition of PRD and EI.

larger follicle over 24 h (Ricklefs 1974). The average weights of Day −4 to Day 0 follicles are given in Table 1. The average protein or fat allocated per follicle per day was determined by subtracting the weights of two consecutively developing follicles and multiplying that weight by the average percentage of protein or fat per yolk. Daily protein and fat allocations, per follicle, were summed according to the day of development (Table 2).

Although albumen weight did not vary with egg sequence (1-way ANOVA, $F = 1.66$, $n = 51$, $P > 0.05$), for the sake of accuracy we used the average dry weight of albumen according to egg sequence (Table 3). These weights represent daily protein allocated to albumen.

Oviducal protein (Table 4) was estimated from females of known clutch size 4, and from females with unknown clutch sizes before Day +1. On days when no oviduct weights were measured, we estimated oviduct weight from linear regression equations derived from average oviduct weights spanning the day in question (see Table 4). The oviduct probably does not enlarge as quickly as the difference between the PRD and Day −4 weight suggests, but no other means of determining Day −4 oviduct weight could be devised. Oviduct weight declined after Day +1.

As determined elsewhere (Krementz 1984), not all of the nutrients necessary for egg development were derived from endogenous reserves. Therefore, conversion efficiencies for endogenous vs. exogenous nutrients had to be estimated. We used the 77% conversion efficiency for both exogenous protein and fat into reproductive material (Brody 1945; see Alisauskas and Ankney 1985 for a rationale for using Brody's estimate). We know of no published estimates of the costs of converting endogenous reserves into reproductive material. Astheimer and Grau (1985), however, used a value

of 75%. Although a conversion efficiency of 100% is thermodynamically impossible, we believe the actual conversion efficiency is significantly higher than 77%. We therefore used a 100% conversion efficiency and point out that these estimates are liberal.

The following equation was used to correct for exogenous vs. endogenous nutrient reserve use:

$$C = E\,[R/Pr + (1 - R)/Pd],$$

where C = cost to the female (kJ) in producing 1 g of egg nutrient, E = energy equivalent of egg nutrient (kJ/g), R = proportion of egg nutrients supplied by female reserves, $(1 - R)$ = proportion of egg nutrients supplied directly by the diet, Pr = efficiency for converting nutrient reserves to egg nutrients (1.00), and PD = efficiency for converting dietary nutrients to egg nutrients (0.77) (Alisauskas and Ankney 1985).

Knowing that 1 g of stored protein is equal to 23.86 kJ (Kleiber 1961) and that for of every 1 g of reproductive protein, 0.15 g comes from endogenous reserves (Krementz 1984), then to produce 1 g of egg protein, a female would expend 23.86 (0.15 + 0.85/0.77) = 29.9 kJ.

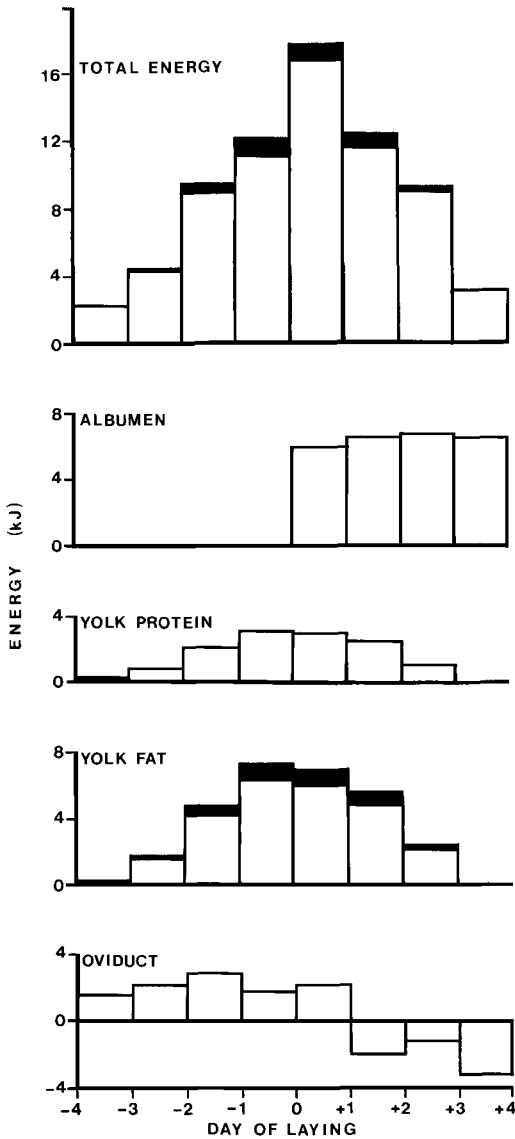Although total body fat declined with in-

Fig. 1. Daily energy budget of female House Sparrows over the reproductive period. The total energy budget is the sum of the subcomponent budgets: albumen, yolk protein, yolk fat, and oviduct. The shaded portions of the total energy and yolk fat budgets represent the difference between complete use of exogenous fat reserves (high estimate) and partial use of endogenous fat reserves (low estimate) in the production of eggs. The negative energy budget of the oviduct on Days +1 to +4 represents catabolism of oviduct protein. See text for details.

creased commitment of fat to developing follicles, the decline was not linear (Krementz 1984). Thus, it is difficult to determine how much fat for the clutch came from endogenous

vs. exogenous sources. Presumably, some but not all fat for reproduction came from exogenous reserves and most of the endogenous fat used for eggs was stored briefly, i.e. 1–3 days (Schifferli 1976, Krementz 1984). Our inability to determine accurately the source of fat for egg production led us to estimate a range of energy budgets. The low energy budget of yolk fat was estimated by assuming that 70% of the fat for egg production came from endogenous reserves (Krementz 1984). A 70% decline in endogenous fat assumes a constant linear decline of fat during egg production. One gram of fat equals 37.67 kJ/g (Ricklefs 1974). To produce 1 g of egg fat, a female would expend $37.67(0.7/1 + 0.3/0.77) = 41.05$ kJ. The high energy budget of yolk fat was estimated by assuming that no fat for egg production came from endogenous reserves. Under this assumption a female would expend $37.67(1/0.77) = 48.92$ kJ to produce 1 g of egg fat.

The total energy budget indicated that a maximum demand occurred on Day 0 (Fig. 1). The energy cost of yolk protein increased quickly until Day −1, when it plateaued, and then declined between Days +1 and +2 (Fig. 1). The energy cost of yolk fat resembled that of yolk protein except that the energy cost of fat always exceeded the cost of protein by at least 90%. The energy cost for albumen protein was relatively high and exceeded energy costs of fat on Days +1 through +3. The influence of resorbed oviduct protein was noticeable on Days +1 through +3, without which the total energy budget would have been more sigmoid.

An average RD female in 1983 weighed 29.5 ± 0.37 g. We estimated an average RD female expended 37.2 kJ/day, using Aschoff and Pohl's (1970) equation for daily standard metabolic rate (SMR) for passerines. Maximum daily costs of egg production occurred on Day 0 at 16.5–17.6 kJ/day. The maximum energy expended on the daily reproductive costs was 44–47% of SMR of a laying female. The maximum daily reproductive costs of different-size clutches, 3 or 5, would not vary greatly (<10%).

Summing the daily energy budgets yielded the total energy required, 65.8–70.6 kJ, to produce an average clutch of 4 eggs. Protein accounted for 58.8–63.1% of the total energy while fat contributed 36.9–41.1%. Reproductive protein was subdivided into oviduct (5.4–5.8%), yolk protein (17.4–18.7%), and albumen (36.0–38.6%) components.

This energy budget does not include the energy necessary to acquire, convert, and assimilate calcium into eggshell, and therefore the budget is conservative.

DISCUSSION

Our estimates of the daily and total energy requirements of egg production for the House Sparrow are similar to the estimates of the energy required for egg production in other passerines (King 1973, Ricklefs 1974).

The energy budget of the oviduct produced the most unexpected finding. The negative energy budget during Days +1 to +3 (Fig. 1) suggests that the oviduct is a storage organ for protein. In poultry, the oviduct produces albumen proteins from just before the first ovulation until just after the final ovulation of that clutch; at no time before the final ovulation does the oviduct weight decline (Romanoff and Romanoff 1949, Solomon 1983). The gradual weight loss noted in the oviduct of the House Sparrow after the first ovulation suggests either that albumen production in the oviduct does not keep pace with needs or that the oviduct acts in more of a storage capacity than it does in poultry. If the former were true, then albumen weight should have declined with sequence of laying, which did not occur. To store proteins in the oviduct makes more sense than storing protein in the flight muscles, as suggested by Jones and Ward (1976), because the flight muscles are among the muscles that a bird can least afford to catabolize (see Marsh 1984).

The energy budgets for yolk protein, yolk fat, and albumen are similar to those predicted by King (1973) and Ricklefs (1974). Furthermore, the maximum cost of ovogenesis that we calculated for House Sparrows, 44–47% of SMR of a laying female, lies at the lower end of the range predicted by King (1973) for altricial passerines, 45–58% of BMR. We believe using these two estimates comparatively is legitimate because the only difference between SMR and BMR is that SMR estimates are based on animals that are not necessarily within their thermoneutral zone (Kendeigh 1973: 19). Clearly, ovogenesis for the House Sparrow is less demanding than the energetic demands of ovogenesis in Anseriformes, 156–239% of BMR (King 1973). Regardless, 44–47% of daily SMR of a laying female could be sufficiently high to limit clutch size. That the production of eggs

by passerines is a "strenuous" and potentially limiting function has been suggested frequently (Jones and Ward 1976, Schifferli 1976, Stobo and McLaren 1975, Greenlaw 1978, Murphy 1978, Järvinen and Väisänen 1984). We would be naive to construct a hypothesis regarding passerine reproductive strategies based only on the comparison of passerine and anseriform energy demands. This is especially true when we know that some tropical passerines incorporate effective tactics for reducing the costs of egg production, e.g. laying an egg every other day (see Ricklefs 1974).

To further assess the energy demands of ovogenesis for House Sparrows, consider the daily energy budgets of egg-laying vs. incubating female House Sparrows. Schifferli (1976) and Kendeigh (1973) both estimated the average daily costs of egg production for female House Sparrows. Schifferli (1976) based his estimate on the energy content of the nutrients in an average House Sparrow clutch (4.2 eggs at his study site), the energy required to enlarge the oviduct, and the energy required to transport the additional weight of the developing follicles, oviducal egg, and oviduct. Schifferli (1976) calculated a daily energy demand for laying females of 13.4 kJ·bird^{-1}·day^{-1}. Kendeigh (1973) based his estimate on an average clutch size of 4.7, an average egg weight of 2.78 g, a rapid egg formation period of 7.7 days, and a conversion efficiency of exogenous nutrients into egg products of 77%. He calculated the daily energy requirements of egg production to be 10.9 kJ·bird^{-1}·day^{-1}. We estimated that the average energy demand during the 8-day period was 8.2–8.8 kJ·bird^{-1}·day^{-1}. Schifferli (1976) also estimated the average amount of energy needed by an adult to collect and transport the food consumed by a brood of 4 nestlings as 32.2 kJ·bird^{-1}·day^{-1}. Thus, the daily energetic demand of egg production in House Sparrows is only 26–42% of the energy demand of nestling care. We conclude that the production and laying of eggs by House Sparrows is not expensive. Therefore, we suggest that the clutch size of House Sparrows is not constrained by the acquisition of energy for eggs.

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100 Years Ago in The Auk

From "Notes and News" (1886, Auk 3: 288):

"The A. O. U. Code and Check-List was published March 20. It forms a volume of 400 pages, and is sold at a price so low as barely to meet the cost of publication. The Committee having the work in hand are at last through with what proved a very auduous [sic] task, which they spared no pains to thoroughly perform."