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### Daily Energy Expenditure by Female Savannah Sparrows Feeding Nestlings

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The adaptive significance of many life-history traits of birds presumably can be understood within the context of patterns of energy allocation (Cody 1966, King 1974). Yet precious few data exist for the energy expenditure of free-living birds during their reproductive period. In particular, little is known about the energy requirements of females while they are feeding their young.

Most extant information on the energetic cost of feeding young has been gathered indirectly by measuring the weight loss of parents as they feed different numbers of young (Hussell 1972) or from studies of caged parents (Brisbin 1969). With the advent of the doubly labeled water (DLW) technique (Lifson et al. 1955, Nagy 1975), reasonable estimates of the daily energy expenditure (DEE) of free-ranging birds now can be obtained (Nagy 1980). In essence, the technique involves isotopic labeling of an animal's body water with oxygen-18 and tritium or deuterium. From the difference between the turnover rates of the two isotopes, the rate of CO<sub>2</sub> production can be measured. When we concurrently compared CO<sub>2</sub> production in Savannah Sparrows (*Passerculus sandwichensis*) using DLW and standard laboratory techniques, we found a mean difference of +6.5% (range -0.2 to +11.0,  $n = 7$ ), suggesting that acceptable estimates of CO<sub>2</sub> can be obtained while these birds are functioning in their normal environment (Williams and Nagy 1984a). Furthermore, Nagy and Costa (1980) have shown that water flux rates estimated with tritiated water vary within  $\pm 10\%$  of actual flux rates in most situations.

Using the DLW method, Utter and LeFebvre (1973) calculated that female Purple Martins (*Progne subis*) with nestlings metabolized an average of 183.6 kJ/day ( $n = 2$ ; mean wt = 47.7 g), which is somewhat higher than that of males during the same time period (142.9 kJ/day;  $n = 2$ ). Males apparently did not feed nestlings as much as did females. Unfortunately, the number and age of the nestlings were not reported. Hails and Bryant (1979) found that female Common House-Martins (*Delichon urbica*, 20 g) feeding young metabolized 75.3 kJ/day, but the DEE of female birds was not correlated with brood mass.

In this study, we used DLW to measure the DEE

of female Savannah Sparrows while they were feeding nestlings. Specifically, we wanted to compare the DEE of females while feeding a normal brood of 3 young with those feeding 2 young, late in the nestling period when energy demands presumably are greatest.

*The study area and birds.*—Our study area lay in the middle and upper littoral zone of a large salt marsh located on the Point Mugu Naval Air Station, Pt. Mugu, California (34°07'N, 119°07'W). The vegetation consisted of, in decreasing order of importance, *Salicornia virginica*, *Frankenia grandifolia*, *Batis maritima*, and *Monanthochloe littoralis*. Large, barren salt pans and shallow tidal channels intermixed with patches of vegetation to form a mosaic of sites used by Savannah Sparrows for foraging and nesting.

The breeding biology of the Savannah Sparrow at Pt. Mugu has been studied extensively by J. B. Williams and will be reported in detail elsewhere. In brief, these small, ground-nesting passerines reside there year-round and commence breeding in early April. Males defend territories (ca. 0.1 ha) and aid in provisioning the young, but only females incubate eggs. Of 83 nests found in 1978 and 1979, 78% contained 3 eggs, 18% held 4 eggs, and only about 4% held 2 eggs. Mean clutch size for these 83 nests was  $3.16 \pm 0.46$  SD. In this study we removed a nestling from broods of 3 to make broods of 2 young several days prior to DLW measurement.

*Field and laboratory methods.*—We first determined the impact that capturing and handling females had on their subsequent behavior and the time required after disturbance for females to resume normal parental activities. To this end, we gave the birds sham injections of distilled H<sub>2</sub>O and restrained them in a cloth bag for 1 h. We then released the female bird and watched from a blind for her return. In most cases, females handled 3-4 h before sunset resumed caring for young within 2-3 h after their release; however, about 20% of the females that we netted abandoned their young. All birds for which we present data in this study resumed feeding their young within 3 h after their release. Each female was color-banded to facilitate recognition.

We captured birds by placing mist nets around their

TABLE 1. CO<sub>2</sub> production and water influx of female Savannah Sparrows.

Animal number	Mean mass (g)	% BW <sup>a</sup>	Water influx (ml·kg <sup>-1</sup> ·day <sup>-1</sup> )	CO <sub>2</sub> production (ml·kg <sup>-1</sup> ·h <sup>-1</sup> )	T (h) <sup>b</sup>
328	16.70	64.1	706	7.14	23.83
231	17.55	67.3	661	7.44	22.42
345	17.75	64.8	991	5.80	27.17
8,347	17.48	65.5	647	6.24	23.50
347	15.11	64.8	741	8.76	24.00
129	16.48	64.3	556	6.41	24.08
104	16.38	65.5	814	7.44	26.57
172	17.85	66.3	855	7.02	25.13
225	17.42	62.3	723	8.07	22.67
360	17.00	67.2	774	6.18	25.87
Mean ± SD	16.97 ± 0.83	65.21 ± 1.50	766 ± 15 <sup>c</sup>	7.05 ± 0.92	24.52 ± 1.61

<sup>a</sup> % body water, determined by oxygen-18 dilution space, equals g H<sub>2</sub>O/g wet body mass × 100.

<sup>b</sup> Time from release until recapture.

necks, and injected them intramuscularly with 100  $\mu$ l of tritiated water (1  $\mu$ c/g of body mass) mixed with oxygen-18 enriched water (H<sub>2</sub><sup>18</sup>O, 95 atom %) by means of a glass syringe. After restraining them for 1 h, a period previously determined in the laboratory to allow complete equilibration of isotopes (Williams and Nagy 1984a), we collected 100  $\mu$ l of blood from a brachial vein. Beginning 1 h after their release, we watched their nests from a blind. We studied only one bird at a time, so that it could be given complete attention during the measurement period. For birds that resumed feeding their young, we recaptured the female about 24 h after her release, bled and weighed her a second time, and released her. Blood samples were stored in flame-sealed heparinized capillary tubes at 4°C pending analysis.

In the laboratory each blood sample was micro-distilled to obtain pure water (Wood et al. 1975), then assayed for tritium activity and for oxygen-18 content as reported earlier (Williams and Nagy 1984b). The volume of CO<sub>2</sub> expired was converted to kJ of energy metabolized by assuming an RQ of 0.85, 24.0 J/ml CO<sub>2</sub> produced, and 20 J/ml O<sub>2</sub> consumed. These factors are intermediate between those for insectiv-

orous animals and those for herbivorous and granivorous animals (Williams and Nagy 1984b). Rates of water influx were calculated from tritium results using Eq. 4 of Nagy and Costa (1980), and rates of CO<sub>2</sub> production were calculated using Eq. 2 of Nagy (1980).

Hourly weather records including air temperature, wind speed (m/s), and total radiation (W/m<sup>2</sup>) were obtained from the Pt. Mugu weather station, located approximately 1 km from our study area.

*Water influx.*—Total body water volume, determined by oxygen-18 dilution space, equaled 65.8% of body mass (Table 1). Rates of water influx averaged 766 ml·kg<sup>-1</sup>·day<sup>-1</sup> for female sparrows, which is not significantly different ( $t = 1.17$ ,  $P > 0.2$ ) from the mean value of 858 ml·kg<sup>-1</sup>·day<sup>-1</sup> reported for 6 territorial male Savannah Sparrows (Williams and Nagy 1984b). There was no significant difference in water intake between females feeding 2 ( $719 \pm 166$  ml·kg<sup>-1</sup>·day<sup>-1</sup>,  $n = 5$ ) or 3 ( $792 \pm 56$  ml·kg<sup>-1</sup>·day<sup>-1</sup>,  $n = 4$ ) nestlings ( $t = 1.15$ ,  $P > 0.2$ ), nor any significant relationship between water intake and mean daily air temperature ( $r^2 = 0.11$ ,  $t_{\text{slope}} = 1.12$ ,  $P > 0.2$ ), wind ( $r^2 = 0.06$ ,  $t_{\text{slope}} = -0.77$ ,  $P > 0.4$ ), or total solar radiation ( $r^2 = 0.26$ ,  $t_{\text{slope}} = 1.77$ ,  $P > 0.05$ ). Pulmocuta-

TABLE 2. Summary of mean rates of CO<sub>2</sub> production for female birds feeding young.

Species	Adult mass (g)	Age of young (days)	Brood size	ml CO <sub>2</sub> ·g <sup>-1</sup> ·h <sup>-1</sup>	<i>n</i>	Source
Pacific Swallow	14.1	8-15	1-5	9.93 ± 3.00 <sup>a</sup>	2	Bryant et al. 1984
Savannah Sparrow	17.3	4-8	2	7.06 ± 1.33	4	This study
Savannah Sparrow	17.3	5-7	3	7.18 ± 0.79	4	This study
House Martin	20.0	?	?	7.45 ± 1.58	16	Hails and Bryant 1979
Blue-throated Bee-eaters <sup>b</sup>	33.8	10-25	1-2	3.60 ± 0.48	6	Bryant et al. 1984
Mockingbird	46.9	?	?	6.23	1	Utter 1971
Purple Martin	47.7	?	?	6.87 ± 0.30	2	Utter and LeFebvre 1973
European Starling	74.1	8-12	2-7	6.89 ± 0.96	7	Ricklefs and Williams 1984

<sup>a</sup> Values ± 1 SD.

<sup>b</sup> Individuals were not sexed.

TABLE 3. Daily energy expenditure (DEE) of female Savannah Sparrows determined by doubly labeled water.

Animal number	Mean air temperature (°C) <sup>a</sup>	Number of nestlings	Age of nestlings (days)	DEE (kJ/day)	DEE/BMR	DEE/EE <sup>b</sup>
328	10.4	1	5-6	67.7	2.74	1.00
231	17.2	2	6-7	74.1	2.85	1.25
345	14.3	2	7-8	58.4	2.22	0.90
8,347	11.5	2	4-5	61.9	2.39	0.90
347	13.9	2	5-6	75.1	3.36	1.34
129	12.2	2	2-3	60.0	2.46	0.94
104	19.6	3	5-6	69.1	2.85	1.34
172	15.6	3	5-6	71.1	2.69	1.13
225	14.4	3	6-7	79.8	3.09	1.25
360	14.9	3	5-6	59.6	2.37	0.97
Mean ± SD	14.4 ± 2.7		5.5 ± 1.3	67.7 ± 7.5	2.70 ± 0.35	1.10 ± 0.18

<sup>a</sup> Temperature taken from hourly weather records at Pt. Mugu weather station.

<sup>b</sup> EE is existence energy as defined by Kendeigh (1949).

neous water loss in captive Savannah Sparrows living at 10°C averaged 175.2 ml H<sub>2</sub>O·kg<sup>-1</sup>·day<sup>-1</sup> (Williams and Hansell 1981), which is only 23% of the total lost on the average by females in this study. Thus, water lost via urine and feces may account for most of the total water loss in the field. Captive Savannah Sparrows drank water offered *ad libitum* at rates ranging between 113 and 750 ml·kg<sup>-1</sup>·day<sup>-1</sup>, depending on salinity of the drinking water, while feeding on a mixture of birdseed and chick starter (Cade and Bartholomew 1959, Poulson and Bartholomew 1962). Minimum drinking-water requirements for weight maintenance ranged between 350 and 702 ml·kg<sup>-1</sup>·day<sup>-1</sup>, depending on salinity. Our measurements of total water influx (Table 1), which include drinking as well as performed and metabolically produced water in the food (mixed diet of insects and plant matter), are intermediate between *ad libitum* and minimum drinking rates.

**CO<sub>2</sub> production.**—During the nestling period, rates of CO<sub>2</sub> production by females varied between 5.80 and 8.76 ml·g<sup>-1</sup>·h<sup>-1</sup>, with a mean of 7.05 ml·g<sup>-1</sup>·h<sup>-1</sup> (Table 1). These rates are similar to those of territorial male Savannah Sparrows (7.28 ml·g<sup>-1</sup>·h<sup>-1</sup>, Williams and Nagy 1984b;  $t = 0.41$ ,  $P > 0.6$ ), but higher than those of the slightly larger Phainopepla (*Phainopepla nitens*, 22.7 g) confined to an outdoor aviary (6.15 ml·g<sup>-1</sup>·h<sup>-1</sup>,  $n = 6$ ,  $t = 2.15$ ,  $P < 0.05$ , Weathers and Nagy 1980). No significant relationship existed between CO<sub>2</sub> production and air temperature ( $r^2 = 0.03$ ,  $t_{\text{slope}} = 0.54$ ,  $P > 0.5$ ), wind ( $r^2 = 0.08$ ,  $t_{\text{slope}} = -0.95$ ,  $P > 0.3$ ), or total solar radiation ( $r^2 = 0.001$ ,  $t_{\text{slope}} = 0.002$ ,  $P > 0.9$ ).

T-test comparisons revealed that female Savannah Sparrows produced CO<sub>2</sub> at mass-specific rates comparable to the much larger female Purple Martins and European Starlings (*Sturnus vulgaris*) while feeding young, as well as similar-sized house-martins (Table 2). However, Savannah Sparrows had significantly lower metabolic rates than tropical Pacific Swallows (*Hirundo tahitica*;  $t = 2.85$ ,  $P < 0.05$ ) and higher than the Blue-throated Bee-eater (*Merops viri-*

*dis*;  $t = 36.11$ ,  $P < 0.001$ ). We found no significant relationship ( $P$ 's  $> 0.05$ ) between either CO<sub>2</sub> production and body mass or foraging mode (i.e. aerial vs. ground foragers) for this data set.

**Daily energy expenditure.**—The DEE of female Savannah Sparrows feeding young varied from 58.43 to 79.79 kJ/day (Table 3). The basal metabolic rate (BMR) of Savannah Sparrows (i.e. the metabolism of postabsorptive birds, at night, in their zone of thermoneutrality) is 1.48 kJ·g<sup>-1</sup>·day<sup>-1</sup> (Williams and Hansell 1981). We calculated that DEE/BMR ratios ranged from 2.22 to 3.36, with a mean of 2.70 ± 0.35 ( $n = 10$ ). Combining data for males and females during the brood-rearing period, Bryant et al. (1984) reported mean DEE/BMR ratios of from 3.6 to 4.3 for aerial-feeding hirundines in temperate environments and 5.1 for the tropical Pacific Swallow. These values appear to be higher than those reported for ground-foraging birds such as the Northern Mockingbird (*Mimus polyglottos*, 2.7-3.0, Utter 1971) or the Savannah Sparrow (this study). These data suggest that aerially foraging species expend relatively more energy while raising their young than do comparably sized ground-foraging species. Our measurements of DEE in female Savannah Sparrows (67.7 kJ/day; Table 3) are closer to the predicted value of 73 kJ/day for a nonaerial forager weighing 17.3 g than to the predicted value of 80 kJ/day for a 17.3-g bird that forages in flight (predictions from Eqs. 9 and 10, respectively, of Walsberg 1983).

Some investigators (e.g. Kendeigh et al. 1977) have proposed that the energy cost of free existence can be extrapolated from data on existence energy (EE), which is the rate at which energy is used by caged birds maintaining constant weight (±1-2%) over a period of a few days (Kendeigh 1949). To test this proposal with Savannah Sparrows, we calculated DEE/EE ratios. Existence energy was determined employing the equation of Williams and Hansell (1981), kJ·g<sup>-1</sup>·day<sup>-1</sup> = 5.1 - 0.1 (°C). These ratios ranged from 0.90 to 1.34, with a mean of 1.10 ± 0.18 (Table

3). Thus, sparrow females raising a normal brood of young used energy around 11% above existence levels. There was no difference between females raising broods of 2 and 3 ( $t = 0.83$ ,  $P > 0.4$ ).

**Conclusions.**—The mean  $\text{CO}_2$  production for female Savannah Sparrows feeding mostly older neonates equalled  $7.05 \text{ ml CO}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ ; those feeding broods of 2 were not significantly different from those with broods of 3, the normal clutch size for the population. Energy metabolism was not correlated with weather variables. Assuming  $24 \text{ J/ml CO}_2$ , we calculated a mean DEE of  $67.7 \pm 7.5 \text{ kJ/day}$ . DEE-to-BMR ratios showed that female Savannah Sparrows feeding neonates worked somewhere between 2.2 and 3.4 above basal levels, which is only about 11% above caged existence levels.

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