FIELD METABOLISM AND FOOD CONSUMPTION OF SAVANNAH SPARROWS DURING THE BREEDING SEASON

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Abstract.—I applied the doubly labeled water (DLW) technique to measure rates of water flux and energy expenditure of Savannah Sparrows (*Passerculus sandwichensis*) during two breeding seasons on Kent Island, New Brunswick, Canada. Simultaneous to DLW measurements, I constructed time-activity budgets for territorial males, monitored nest attentiveness for incubating females, and quantified frequency of nest visitation for parents feeding young. To ascertain the relationship between brood size and adult energy expenditure, I measured the energy expenditure of adults feeding 2, 4, and 6 nestlings.

There was little difference in field metabolic rates (FMR) between territorial males [161.0 ± 21.7 (SD) ml CO_2/h] and males that fed 4 nestlings (157.6 ± 19.7 ml CO_2/h). Incubating females expired CO_2 at rates lower than males during the same time period (134.4 ± 7.9 vs. 161.0 ± 21.7 ml CO_2/h) but similar to rates for females feeding 4 young, the normal brood size (134.4 ± 7.9 ml CO_2/h for incubating females vs. 136.5 ± 26.9 ml CO_2/h for females feeding young). Incubating females expended energy at a lower rate than females making 8 or more trips to the nest per hour, the average feeding rate for females late in the nestling period. For males and females together, water influx and efflux rates averaged 17.1 ± 3.2 and 17.2 ± 3.0 ml H_2O/day, suggesting that birds balanced water intake against water losses. Mean daily solar radiation (MDSR; W/m²) also influenced FMR during the nestling period. The equation ml CO_2/h = 172.6 − 0.07 (MDSR) described the relationship.

When brood sizes were manipulated, parents responded by altering their frequency of nest visitation; as frequency increased, so did the FMR of females but not of males. The equation ml CO_2/h = 98.4 + 5.3 (mean visits/h) described the relationship.

Construction of a food budget indicated that, on average, territorial males consumed 21.1 g fresh arthropods per day, while incubating females ingested 17.5 g/day or 210.0 g during the 12-day incubation period. Through the 8-day nestling period, males augmented their foraging by 75%, females by 87%, to feed a brood of 4. *Received 20 March 1986, accepted 6 November 1986.*

The acquisition of food and efficient expenditure of energy are fundamental constraints in the evolution of a species' life-history pattern. Theory emphasizes that short-lived species, such as passerine birds, should have high levels of reproductive effort, with a concomitantly high energy expenditure. The generality of this idea remains uncertain because of the lack of empirical information regarding the energy expended for reproduction for any species (Congdon et al. 1982). First steps toward understanding a species' life-history pattern include knowledge of its activity patterns and consequent energy expenditure during the breeding season (Mugaas and King 1981).

In the past, investigators used time-energy budget analyses to translate a bird's time budget into a field metabolic rate (FMR; Walsberg 1978, Ettinger and King 1980, Mugaas and King 1981). But because time-energy budget studies use energy equivalents based on laboratory studies to convert activity to energy expenditure, they often contain significant uncertainties (Weathers and Nagy 1980, Williams and Nagy 1984a). A more direct, and presumably more reliable, method of appraising the FMR of free-ranging birds is the doubly labeled water (DLW) technique (Lifson and McClintock 1966, Nagy 1980), which estimates CO_2 production by tracking differences in the loss of isotopes of hydrogen (²H or ³H) and oxygen (¹⁸O).

Among breeding passerines, the DLW technique has been applied to the Northern Mockingbird (*Mimus polyglottos*; Utter 1971), Purple Martin (*Progne subis*; Utter and Le Febvre 1973), Common House-Martin (*Delichon urbica*; Hails and Bryant 1979; Bryant and Westerterp 1980, 1983; Westerterp and Bryant 1984), and European Starling (*Sturnus vulgaris*; Ricklefs and Williams 1984). For house-martins, FMR in-

creased as birds spent more time flying but was unaffected by components of the physical environment such as temperature, solar radiation, and wind. Incubating house-martins had reduced power requirements compared with birds rearing young, and there was a positive relationship between FMR and brood mass. Incubating female starlings also had significantly lower power requirements than they had while rearing chicks (Ricklefs and Williams 1984).

I examined water flux and energy expenditure of Savannah Sparrows (*Passerculus sandwichensis*) during the breeding season using the DLW technique and simultaneously monitored the birds' activity, environment, and food abundance. I manipulated brood size late in the nestling period to measure the effect of brood size on energy expenditure by parent birds.

STUDY AREA AND METHODS

The study was conducted at the Bowdoin Scientific Research Station on Kent Island, New Brunswick, Canada ($66°46'W$, $44°35'N$), during the summers of 1981 and 1982. Situated near the mouth of the Bay of Fundy, the island contains a large grassy field (10.7 ha) dominated by *Agrostis stolonifera* and *Festuca rubra* that provides nesting habitat for ca. 100 pairs of Savannah Sparrows.

Fog regularly influences the weather on the island, with an average of 13.0 days of fog in June and 17.8 in July (McCain 1975). Temperatures are generally cool, with an average of $10.5°C$ in June and $13.1°C$ in July. Precipitation averages around 6 cm for each month (Cunningham 1942, McCain 1975).

Savannah Sparrows arrive on Kent Island in April and begin nesting in late May to early June. Females lay an average of 4.02 ± 0.55 eggs (Dixon 1978). Males neither incubate eggs nor feed the female during incubation. Both parents feed the young, but only the female broods them. Brooding time by females decreases from 30–40 min/h for 0–1-day-old nestlings to 7 min/h when nestlings are 8 days old (Bedard and Meunier 1983, Williams unpubl. data). By day 5, sparrow chicks in nests of 4 young thermoregulate, and females reduce their brooding to primarily early morning and late evening (Williams unpubl. data). Broods of 5 chicks sometimes occur, but because parents rarely fledge this number of young, Dixon (1978) concluded that in normal food years adults may be unable to provide adequately for 5 nestlings. Nestlings fledge in 8–9 days.

I mist-netted birds late in the afternoon (1600–1800 AST) and injected them in the pectoral muscle with 0.10 ml tritiated water mixed with 95 atom % oxygen-18 using a laboratory-calibrated glass syringe (Williams and Nagy 1984a, 1985b; Williams and Prints

1986). After a 1-h period to allow equilibration of isotopes, I took a 60-μl blood sample from the brachial vein, weighed and color-banded the bird, placed a small amount of white paint on the outer tail features to facilitate rapid identification, and then released the bird. Males were determined by the presence of a cloacal protuberance (Wolfson 1952).

Blood samples were microdistilled to obain pure water (Wood et al. 1975), then assayed in 10-μl aliquants for tritium activity with a Beckman LS-2800 liquid scintillation counter using a toluene-Triton X 100-PPO scintillation cocktail (see Nagy 1983). The ^{18}O contents of water samples were measured in triplicate by Dr. Ken Nagy at the Laboratory of Biomedical and Environmental Sciences, University of California, Los Angeles. Water influx and efflux were calculated using Eqs. 6 and 5, respectively, of Nagy (1975), and rates of CO_2 production were calculated using his Eq. 8. Background levels of isotopes obtained from uninjected birds were subtracted from all values before calculations.

Estimates of CO_2 ($\dot{V}_{CO_2}$) production obtained by the DLW technique have been compared with direct measures of CO_2 production for seven species of birds ranging in mass from 16 to 380 g. Results showed mean errors varied between -4.9 and 6.5% (Williams 1985, Williams and Prints 1986). For Savannah Sparrows, Williams and Nagy (1984b) reported that, on average, DLW values were +6.5% higher than those obtained gravimetrically; errors for individual comparisons varied from -0.2 to $+11.0\%$ ($n = 7$).

To convert metabolic rates from units of CO_2 to units of energy and to calculate metabolic water production and feeding rates, I employed the conversion factors of 24.6 J of heat/ml CO_2 and 0.60 μl of metabolic water/ml CO_2 derived by Williams and Nagy (1985a). These values were based on a diet containing 62% protein (dry matter), 15% fat, 15% carbohydrate, and 8% ash. They assumed that 75% of ingested energy was metabolizable and that assimilated food contained the same proportions of protein, fat, and carbohydrates as did the diet. This conversion factor is within 5% of that determined empirically by Nagy (1983) for an insectivorous lizard.

Twelve birds eluded recapture after 24 h and were not bled a second time until the following morning. For these individuals I calculated their nighttime metabolism during their second night period from equations for the standard metabolic rate (SMR; *sensu* Kendeigh et al. 1977) of Savannah Sparrows (Williams and Hansell 1981) and converted units of kJ to units of CO_2 production with the relationship 26.8 J/ml CO_2. I assumed that birds were postabsorptive during the night and had an RQ of 0.75 (Ricklefs and Williams 1984). I subtracted this level of CO_2 production from their total CO_2 production, bringing to parity this group of birds and other birds that were recaptured after approximately 24 h.

Insect abundance was assessed during both years

TABLE 1. Frequencies (by percent) of various activities for territorial male Savannah Sparrows on Kent Island, New Brunswick.

Date	Perch	Walk	Fly	Preen	Sing	Aggres-sion	Other	n (s)	ml CO_2/h	kJ/day
1981										
2 June[a]	58.5	38.3	1.3	1.3	0.5	0.0	0.04	3,780	—	—
2 June[a]	17.3	79.1	1.8	0.0	0.0	0.0	0.04	2,780	—	—
3 June	31.4	59.4	3.9	4.7	0.1	0.5	0.01	10,810	171.3	101.1
3 June	29.0	56.6	3.5	5.8	4.5	0.5	0.02	11,900	204.9	121.0
5 June[a]	59.7	15.6	2.5	3.6	18.4	0.1	0.03	18,920	—	—
8 June	50.3	29.3	1.8	2.3	15.7	0.5	0.01	14,950	135.0	79.7
Mean	41.0	46.4	2.5	3.0	6.5	0.3	0.03		170.4	100.6
1982										
23 May	16.4	77.6	1.2	3.8	0.3	0.6	0.01	9,530	149.6	88.3
25 May	34.1	60.5	1.1	3.7	0.1	0.4	0.10	8,060	196.2	115.8
28 May	45.3	46.9	3.1	3.8	0.2	0.8	0.01	14,680	142.2	84.0
3 June	66.9	15.0	1.3	8.2	8.6	0.0	0.00	12,850	138.6	81.8
Mean	40.7	50.0	1.7	4.9	2.3	0.5	0.03		156.7	92.5

[a] Time budgets for uninjected birds included for comparison.

by means of sweep-net sampling and sticky traps (Southwood 1966). Trends were similar for both techniques, and only results from the sweep-net sampling are reported here. From a 2-ha grid composed of 25-m² quadrats, I selected randomly five quadrats each week and collected insects in each of these areas using 40 sweeps of an insect net per quadrat. After killing and drying the insects at 80°C, I weighed them to the nearest 0.01 g using a Mettler balance (model 4400).

Time-activity budgets for injected males during the prenesting and incubation periods were constructed following the methods of Williams and Batzli (1979). At a signal emitted every 10 s from an electronic metronome, I recorded the activity of the bird as perch, walk, fly, preen, sing, aggression, or other. Birds perching on vegetation showed no movement other than head turning. As birds foraged they walked or hopped along the ground picking up arthropods. Aggressive behavior usually included rapid, flying chases of intruders and sometimes included physical combat. The "other" category included such activities as manipulation of food items, courting a female, and copulation. I began timing injected birds at sunrise and searched for them on their territory for 6 1-h periods spaced evenly throughout the day. Males sometimes foraged away from their territory; thus, sample sizes for activity budgets varied.

To determine that females had resumed incubating their eggs after injection of isotopes, I monitored attentiveness (minutes spent warming the eggs per hour). This was accomplished by positioning a 36-gauge thermocouple in the rim of the nest and following changes in temperature by means of a potentiometric strip-chart recorder (Linear Corp.) located 30 m from the nest. Davis et al. (1984) showed close agreement between attentiveness calculated from chart recordings and visual observation.

To determine whether birds cared for their young normally after being held captive for 1 h, I monitored the pattern of nest visitation of control birds and compared it with that of injected birds. From a blind 30 m from each nest during 6 1-h periods throughout the day, I recorded the number of trips both sexes made to the nest.

Artificial broods of 2 and 6 nestlings were constructed by adding or subtracting 2 nestlings of the same age to nests with 4 young. This was done at sunrise the day of observation. Savannah Sparrows on Kent Island do not raise 6 young to fledging (pers. obs.). But in 7 of 9 nests, parents sustained this number during my 14–15-h trials. In 2 nests that contained 6 young, a nestling died sometime during the latter part of the trial.

Temperature and relative humidity were measured with a Weathermeasure hygrothermograph, wind with a hand-held anemometer (Dwyer Model No. 460), and solar radiation with a Li Cor-185A pyranometer. Temperature and relative humidity were measured continuously; wind and solar radiation were recorded every other hour throughout the day.

Data were analyzed using a SPSS/PC statistical package (Norusis 1984). Means are presented ±1 SD.

RESULTS

Insect abundance increased as the breeding season progressed both in 1981 and in 1982. In 1981 the mean dry mass of insect samples ranged from a low of 38.7 ± 37.6 mg (5 samples, 40 sweeps each) on 6 June to a high of

TABLE 2. CO_2 production and water flux rates for territorial male Savannah Sparrows on Kent Island, New Brunswick.

Date	Mean mass (g)	$\bar{T}a$[a]	Hours[b]		ml CO_2/h	kJ/day	Water flux (ml/day)		FMR	
			Active	Sleep			In	Out	BMR[c]	SMR[d]
1981										
2–4 June	22.7	9.4	18.70	15.14	171.3	101.1	12.4	13.1	3.0	1.3
3–5 June	20.9	10.0	19.87	15.17	151.1	89.2	13.0	14.3	2.9	1.2
4–6 June	20.4	10.3	19.50	15.06	204.9	121.0	12.6	13.3	4.0	1.7
7–9 June	20.3	11.8	18.43	14.93	135.0	79.7	12.9	13.2	2.7	1.2
9–10 June	22.1	12.3	15.00	7.49	155.6	91.9	16.8	17.3	2.8	1.3
10–11 June	21.1	9.4	16.45	7.48	152.0	89.7	18.8	19.1	2.9	1.2
20–21 June	20.7	12.5	20.45	7.39	177.2	104.6	16.7	16.4	3.4	1.6
1982										
22–23 May	21.5	8.5	14.77	7.84	149.6	88.3	16.0	15.7	2.8	1.1
25–26 May	21.9	8.5	19.08	7.85	196.2	115.8	20.4	20.0	3.6	1.4
25–27 May	21.1	8.0	20.72	15.66	171.1	101.0	15.7	15.9	3.2	1.3
27–28 May	21.1	8.5	19.98	7.69	142.2	84.0	15.4	15.5	2.7	1.1
2–3 June	21.0	11.0	16.62	7.57	138.6	81.8	11.4	11.1	2.6	1.1
15–16 June	20.7	9.8	22.63	7.37	148.6	87.7	20.2	20.0	2.9	1.2
Mean					161.0	95.1	15.6	15.8	3.0	1.3

[a] Mean air temperature during measurement period.

[b] I assumed birds were active 30 min before sunrise and asleep 30 min after sunset. Sunrise and sunset were determined from the American Ephemeris and Nautical Almanac (1980).

[c] BMR calculated as 1.48 $kJ \cdot g^{-1} \cdot day^{-1}$ (Williams and Hansell 1981).

[d] SMR calculated from the equation $kJ \cdot g^{-1} \cdot day^{-1} = 4.5 - 0.1$ (temperature, °C).

275.8 mg on 24 July. In 1982 insect samples ranged from 7.0 ± 7.0 mg on 5 June to 581.8 ± 32.2 mg on 22 July.

During 1981 all males for which I constructed time-activity budgets were paired with a female that was incubating. In 1982 observations were made earlier in the season, and only one male had a nest with eggs within its territory; others were in the nest-building stage of breeding. All 10 males for which I constructed time budgets actively defended a territory.

While maintaining their territory, males spent most of their time perching on vegetation or walking on the ground in search of arthropods (Table 1). The energetically more ex-

pensive activities of flying and aggression occupied less than 5% of their time. In a multiple regression analysis, activity variables were unrelated to CO_2 production.

Male Savannah Sparrows on territories expired CO_2 at an average rate of 161.0 ± 21.7 ml CO_2/h ($n = 7$) and metabolized energy at a rate of 95.1 ± 12.8 kJ/day (Table 2). Average water influx and efflux were 15.6 ± 3.0 ml/day and 15.8 ± 2.8 ml/day, respectively. In a multiple regression analysis with ml CO_2/h as the dependent variable and global radiation (W/m²), mean air temperature, mean wind speed (m/s), and mean body mass as independent variables, only radiation and wind speed together affect-

TABLE 3. CO_2 production and water flux rates for incubating female Savannah Sparrows on Kent Island, New Brunswick.

Date	Mean mass (g)	$\bar{T}a$[a]	Hours[a]		ml CO_2/h	kJ/day	Water flux (ml/day)		FMR[a]	
			Active	Sleep			In	Out	BMR	SMR
11–12 July 1981	21.1	11.0	21.10	7.63	125.3	74.0	17.9	17.6	2.37	1.03
15–16 July 1982	21.4	8.5	18.49	7.67	138.9	82.0	17.9	17.7	2.59	1.05
3–5 June 1982	18.7	9.0	21.48	14.11	138.9	82.0	10.6	10.8	2.96	1.22
Mean					134.4	79.3	15.5	15.4	2.64	1.10

[a] See Table 2 for explanations of symbols and calculations.

ed $\dot{V}_{CO_2}$. The equation ml $CO_2/h = 174.5 + 18.8$ (wind speed) $-$ 0.11 (radiation) described the relationship ($F = 4.3$, $r^2 = 0.49$, $P = 0.05$). Individual comparisons revealed only a weak trend of radiation negatively influencing CO_2 production ($F = 3.4$, $r^2 = 0.25$, $P = 0.09$).

Female sparrows were very sensitive to disturbance during the incubation period. Of the 10 females injected, only 3 returned to incubate their eggs. For these three, $\dot{V}_{CO_2}$ averaged 134.4 $\pm$ 7.9 ml CO_2/h (Table 3), a lower value than for territorial males (t-test, variances unequal, $t = 3.54$, $P < 0.05$), but not for females feeding 4 nestlings (136.5 $\pm$ 26.9 ml CO_2/h) ($t = 0.13$, $P > 0.6$; Table 4). Incubating females metabolized energy at a rate of 79.3 $\pm$ 4.7 kJ/day. Water influx and efflux equaled 15.5 $\pm$ 4.2 ml/day and 15.4 $\pm$ 4.0 ml/day, respectively.

Attentiveness averaged 29.4 $\pm$ 10.2, 34.6 $\pm$ 9.1, and 29.7 $\pm$ 8.1 min/h for the three incubating females during daylight hours. These values are similar to the normal incubation pattern of uninjected females on Kent Island (Williams unpubl. data).

Regardless of brood size, females tended to visit the nest more frequently than males did (both sexes uninjected; Fig. 1). For male-female comparisons at each brood size, analysis of covariance showed intercepts but not slopes to be significantly different ($P < 0.01$ in all cases). Both males ($F_{slope} = 2.25$, NS; $F_{intercept} = 15.48$, $P < 0.001$) and females ($F_{slope} = 3.93$, $P < 0.05$; $F_{intercept} = 7.73$, $P < 0.02$) differed in the number of visits they made to the nest, and pairwise comparisons revealed parents with 2 chicks made fewer trips to the nest than did those with 4 or 6 young.

Roughly 20% of the birds injected abandoned their nestlings. Of the remaining birds, experimental males fed nestlings at the same rate as did control males ($n = 10$) (ANCOVA $F_{slope} = 1.73$, $P > 0.20$; $F_{intercept} = 0.74$, $P > 0.50$), but the nest visitation of injected females ($F_{slope} = 1.61$, $P > 0.20$; $F_{intercept} = 8.05$, $P < 0.05$) differed from control females ($n = 10$, comparison not shown). Exclusion of one low datum for a female with nestlings 7 days old rendered the difference not statistically significant ($F_{slope} = 0.62$, $P > 0.50$; $F_{intercept} = 0.68$, $P > 0.50$). Furthermore, mass gain per nestling did not differ for nestlings fed by injected parents (1.71 $\pm$ 0.73 g, $n = 10$) compared with those fed by uninjected parents (1.64 $\pm$ 0.69 g, $n = 10$)
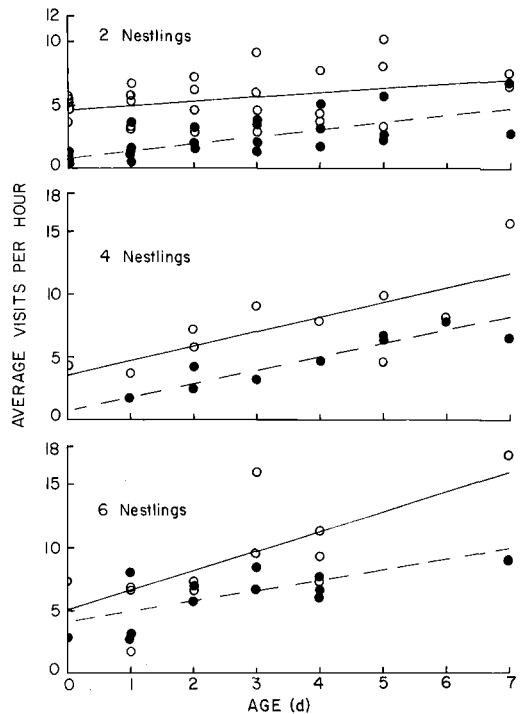

Fig. 1. Average frequency of nest visitation for uninjected male and female Savannah Sparrows. Each point represents the mean of 6 h of observation spaced evenly throughout the day. Open circles represent females, closed circles represent males. Lines indicate overall trends.

($t = 0.22$, $P = 0.83$). All data points for the feeding rates of injected birds fell within 95% prediction limits (Sokal and Rohlf 1981), which yielded upper and lower bounds for the feeding rate at each nestling age for uninjected males and females. I conclude that most experimental birds fed chicks at rates similar to control birds. At least one bird may have altered its feeding rate in response to captivity, as was also shown by Hails and Bryant (1979), so behavior should be closely monitored in studies of this kind.

When a bird abandoned its nest, I continued to record the nest visitation of the other parent and compared the single parents' feeding rates with rates predicted by regression equations for uninjected individuals (control) in intact pairs (Table 5). In general, birds doubled their mean visits per hour in the absence of their mates, even with 6 young in the nest.

Among birds tending 4 nestlings, males respired CO_2 at a rate of 157.6 $\pm$ 19.7 ml CO_2/h

TABLE 4. Rates of CO_2 production, energy use, and water flux for adult Savannah Sparrows feeding young of various ages on Kent Island, New Brunswick, during the 1981 and 1982 breeding seasons.

Date	Mean body mass (g)	Nest-ling age (days)	Mean Ta (°C)		Hours		ml CO_2/h	kJ/day[b]	Water flux (ml/day)	
			Day	Night	Active[a]	Sleep			In	Out
Brood size = 2										
Males										
24–25 June 1982	21.5	6	11.5	10.5	18.97	6.37	146.0	86.2	20.6	21.4
8–9 July 1982	19.7	6	13.0	12.0	18.47	7.57	145.8	86.1	19.6	19.3
Mean	20.6	6	12.3	11.3	18.72	6.97	145.9	86.2	20.1	20.4
Females										
17–18 June 1982	19.5	5	10.5	10.0	17.93	7.39	163.8	96.7	20.4	19.9
2–3 July 1982	18.5	6	11.5	10.5	18.62	7.47	130.8	77.2	15.7	16.4
7–9 July 1982	20.0	6	13.0	12.0	23.38	15.40	130.0	76.8	11.8	12.5
9–10 July 1982	18.8	6	14.5	12.0	18.92	7.48	115.8	68.4	14.4	14.7
Mean	19.2	5.8	12.4	11.1	19.71	9.44	135.1	79.8	15.6	15.9
Brood size = 4										
Males										
17–18 June 1981	19.0	2	13.5	10.0	18.57	7.35	133.4	78.8	15.7	15.6
6–7 July 1981	20.2	3	14.5	11.5	18.73	7.43	131.5	77.6	17.9	17.9
11–12 June 1982	21.4	4	9.0	9.0	16.58	7.42	177.4	104.7	15.0	15.7
14–16 July 1981	20.4	4	15.5	12.5	23.56	15.56	168.7	99.6	13.4	13.4
17–19 July 1981	18.7	5	12.5	12.8	21.58	15.76	160.8	94.9	17.4	17.7
12–14 July 1981	20.6	6	12.5	11.5	23.44	15.56	162.9	96.2	18.7	19.0
9–10 June 1981	20.1	8	7.0	4.5	15.00	7.49	140.0	82.7	18.9	18.4
8–9 July 1981	21.8	8	14.0	15.5	16.53	7.47	174.2	102.8	17.7	17.1
15–16 June 1982	19.4	8	10.5	9.0	22.63	7.37	165.9	97.9	19.6	19.6
23–24 July 1981	19.3	8[c]	15.8	13.0	18.72	7.80	127.2	75.1	17.6	16.9
16–18 July 1981	20.0	9[c]	14.5	12.3	25.76	15.76	186.6	110.2	13.4	13.6
7–8 July 1982	19.6	9[c]	13.0	12.0	19.80	7.56	163.1	96.3	20.7	20.3
Mean	20.0	6.2	12.7	11.1	20.08	10.20	157.6	93.1	17.2	17.1
Females										
15–17 July 1981	18.6	1	13.5	12.5	22.60	15.56	110.0	65.5	11.3	11.7
9–10 July 1981	19.9	2	19.0	13.5	17.95	7.61	143.1	84.5	18.4	18.3
6–7 July 1981	19.1	3	14.5	11.5	18.92	7.48	122.4	72.3	22.4	22.4
15–16 July 1981	19.2	4	15.5	13.5	18.99	7.65	199.7	117.9	23.0	23.3
17–19 July 1981	17.6	5	12.5	12.8	22.74	15.76	130.4	77.0	14.1	14.5
8–9 July 1981	20.0	6	14.0	15.5	16.97	7.51	147.8	87.3	18.6	18.3
12–14 July 1981	17.7	6	12.5	11.5	23.08	15.56	149.7	88.4	17.1	17.5
16–18 July 1981	16.5	6	14.5	12.3	22.64	15.76	97.5	57.6	9.9	10.2
24–25 July 1981	17.3	6	14.0	12.5	16.02	8.80	151.2	89.3	15.5	15.7
12–13 June 1981	19.2	7	8.0	8.0	15.68	7.43	125.8	74.3	16.7	16.9
7–8 July 1981	17.4	8	14.3	14.0	19.00	7.64	106.8	63.1	13.5	13.4
10–11 June 1982	18.8	8	10.5	9.5	18.67	7.49	161.5	95.3	15.9	16.6
22–23 July 1981	17.1	8[c]	17.0	13.0	15.95	7.80	128.3	75.7	16.2	16.4
Mean	18.3	5.4	13.8	12.3	19.17	10.16	136.5	80.6	16.4	16.6
Brood size = 6										
Males										
7–8 July 1982	19.6	4	13.0	12.0	19.80	7.56	134.1	79.2	20.7	20.3
27–28 June 1982	20.8	5	14.0	10.5	18.83	7.43	137.9	81.4	17.1	16.8
9–10 July 1982	20.0	6	14.5	12.0	17.93	7.63	162.2	95.8	20.7	20.2
15–16 June 1982	19.4	6	10.5	9.0	16.40	7.41	165.9	97.9	19.6	19.6
Mean	20.0	5.3	13.0	10.9	18.24	7.51	150.0	88.6	19.5	19.2

TABLE 4. Continued.

Date	Mean body mass (g)	Nest-ling age (days)	Mean Ta (°C)		Hours		ml CO_2/h	kJ/day	Water flux (ml/day)	
			Day	Night	Active	Sleep			In	Out
Females										
17–18 June 1982	18.2	5	10.5	10.0	20.15	7.38	195.2	115.3	20.3	20.3
18–19 June 1982	19.2	5	10.0	9.0	21.42	7.38	142.9	84.4	20.2	20.0
19–21 July 1982	16.7	6	14.0	13.0	26.27	15.76	139.9	82.6	12.1	12.7
27–29 July 1982	15.2	7	13.5	12.5	27.40	16.26	142.0	83.8	14.4	14.6
25–26 June 1982	17.7	7	11.5	10.0	18.10	7.41	153.8	90.8	19.6	19.5
Mean	17.4	6.0	11.9	10.9	22.67	10.84	154.8	91.4	17.3	17.4

[a] I assumed birds were active 30 min before sunrise and until 30 min after sunset.

[b] Units of CO_2 converted to units of energy using 24.6 J heat/ml CO_2 (Williams and Nagy 1985a).

[c] Nestlings fledged during experiment.

and females at 136.5 ± 26.9 ml CO_2/h, values that differed statistically (*t*-test, $t = 2.2$, $P < 0.04$; Table 4). These figures translate into 93.0 kJ/day and 80.6 kJ/day, respectively. The statistical difference between the $\dot{V}_{CO_2}$ of males and females was not attributable to age differences of the nestlings they were feeding (for males, mean age of nestlings = 6.2 ± 2.5 days; for females, mean age of nestlings = 5.4 ± 2.3 days; $t = 0.82$, $P = 0.42$), but was attributable, at least in part, to the larger size of males (mean body mass of males = 20.2 ± 1.0 g; mean body mass of females = 18.4 ± 1.1 g; $t = 3.68$, $P < 0.002$). With the data for males and females combined, $\dot{V}_{CO_2}$ was unrelated to nestling age, brood mass, brood mass gain, or mass gain per nestling, but $\dot{V}_{CO_2}$ was related to brood size (see below). Separate comparisons of $\dot{V}_{CO_2}$ for males and females for these same variables revealed no significant trends.

Because Savannah Sparrow nestlings reach their maximum energy requirement around the age of 5–6 days (Williams and Prints 1986), I restricted my comparisons of FMR of adult birds rearing different brood sizes to those caring for nestlings 6–9 days old. Whole animal FMR (ml CO_2/h) was unaffected by brood size (2: $n = 5$, 4: $n = 15$, 6: $n = 5$; $F = 1.1$, $P = 0.36$). Males weigh more than females and also respire CO_2 at a higher rate. I assessed the effect of brood size on FMR of adults independent of mass by analysis of covariance with $\dot{V}_{CO_2}$ as the dependent variable, brood size as the independent variable, and mean body mass as the covariate. This procedure revealed a significant effect of brood size on $\dot{V}_{CO_2}$ ($F = 5.3$, $P = 0.01$). Second, I evaluated the logarithm of both $\dot{V}_{CO_2}$ and mean

body mass (MBM) and performed a least-squares regression for these two transformed variables, which resulted in the equation ln $\dot{V}_{CO_2}$ = ln 2.66 + 0.79 ln MBM ($r^2 = 0.14$, $F = 6.3$, $P = 0.02$). Next, I divided measures of $\dot{V}_{CO_2}$ by $mass^{0.79}$, generating a mass-independent measure of metabolism (see Heusner 1985). Analysis of variance of these data indicated that $\dot{V}_{CO_2}/mass^{0.79}$ varied with brood size (Fig. 2; $F = 4.2$, $P < 0.03$), and a Student-Newman-Keuls multiple-comparison test showed that the metabolic rate of birds feeding two nestlings differed from those feeding six. If adults feeding 5-day-old nestlings were added to the analysis, mass-independent metabolism was affected only weakly by brood size ($F = 2.9$, $P = 0.07$).

The $\dot{V}_{CO_2}$ of all females combined, irrespective of brood size, increased as their frequency

TABLE 5. Nest visitation by single-parent birds.

Date (1982)	Sex	No. of nest-lings	Age of nest-lings	Visits/h[a]	Predicted visits/h[b]	Actual/predicted[c]
20 July	M	2	6	9.4	4.3	2.2
21 July	M	2	7	9.5	4.8	2.0
28 July	F	2	5	13.5	6.4	2.1
28 June	F	2	7	11.3	7.1	1.6
26 July	F	3	5	23.3	7.3	3.2
28 July	F	3	7	24.5	8.6	2.8
19 June	F	6	5	23.0	12.7	1.8
21 June	M	6	6	18.0	8.8	2.0

[a] Mean visits/h for each day.

[b] Values obtained from regression equations relating nest visitation and nestling age for uninjected birds (Fig. 1).

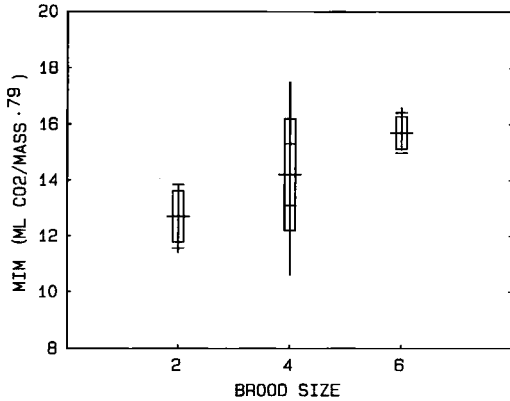[c] Calculated as [(actual visits/h) ÷ (predicted visits/h)].

Fig. 2. Mass-independent metabolism (MIM) vs. brood size in Savannah Sparrows. Boxes represent 1 SD, upper and lower horizontal lines equal 95% confidence intervals, middle horizontal lines represent means, and vertical lines represent ranges.
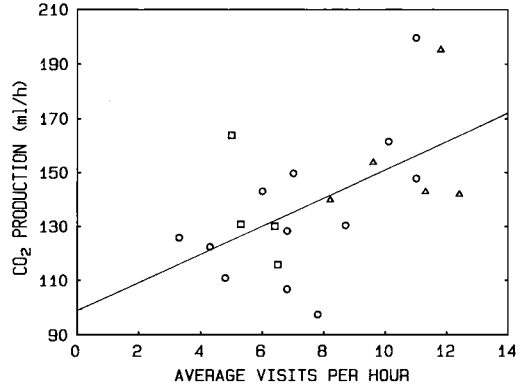

Fig. 3. Relationship between whole animal metabolism (ml CO_2/h) and nest visitation (visits/h) for female Savannah Sparrows feeding 2, 4, and 6 young. Squares represent birds with 2 young; circles, birds with 4 young; and triangles, birds with 6 young.

of nest visits increased (Fig. 3). The equation ml CO_2/h = 98.4 + 5.3 (mean visits/h) described the relationship ($n = 21$, $r^2 = 0.31$, $F = 8.4$, $P < 0.01$). In contrast, males expired CO_2 at a rate that varied independently from their feeding trips per hour ($n = 14$, $r^2 = 0.05$, $F = 0.74$, $P = 0.41$), even though they made visits more frequently late in the nestling period (Fig. 1).

I tested for dependence of $\dot{V}_{CO_2}$ on environmental variables with a backward multiple-regression procedure. The independent variables were mean temperature during the experimental interval, mean wind speed (m/s) at a height of 1 m, and mean daily solar radiation (MDSR; W/m²). The dependent variable was $\dot{V}_{CO_2}$. MDSR was calculated by adding the measurement of solar radiation taken every other hour and dividing by the number of measurements per day. Only MDSR affected $\dot{V}_{CO_2}$ (Fig. 4). The equation ml CO_2/h = 172.6 − 0.07 [MDSR (W/m²)] described the relationship ($n = 32$, $r^2 = 0.23$, $F = 9.5$, $P = 0.004$). To eliminate birds providing for nestlings in different brood sizes as a confounding variable, I restricted this analysis to birds tending 4 young. Again only MDSR affected $\dot{V}_{CO_2}$, with the equation ml CO_2/h = 179.9 − 0.09 [MDSR (W/m²)] describing the relationship ($n = 17$, $r^2 = 0.36$, $F = 9.36$, $P = 0.007$).

Water influx and efflux amounted to 17.1 ± 3.2 and 17.2 ± 3.0 ml H_2O/day ($n = 40$), supporting the notion that, in general, birds balanced water intake against water losses during the nestling period (Table 4).

Water flux varied independently of brood size (ANOVA; influx, $F = 0.79$, $P = 0.46$; efflux, $F = 0.70$, $P = 0.50$) and did not differ between the sexes (t-tests; influx, $t = 1.65$, $P = 0.11$; efflux, $t = 1.38$, $P = 0.18$).

Water influx and efflux paralleled $\dot{V}_{CO_2}$ for females. The correspondence between influx and $\dot{V}_{CO_2}$ was described by the equation ml H_2O/h = 0.11 + 0.004 (ml CO_2/h) ($n = 22$, $r^2 = 0.46$, $F = 16.9$, $P < 0.001$). The relationship between efflux and $\dot{V}_{CO_2}$ was described by the equation ml H_2O/h = 0.14 + 0.004 (ml CO_2/h) ($n = 22$, $r^2 = 0.48$, $F = 18.3$, $P < 0.001$). Water flux for males was unrelated to $\dot{V}_{CO_2}$. Additionally, for males and females together water flux was unrelated to nestling age, the number of visits to the nest per hour, or environmental variables.

DISCUSSION

Early in the breeding period, male Savannah Sparrows either perched or walked on the ground more than 80% of the time (Table 1). This pattern conforms to time-activity budgets for other ground-foraging passerines (Hubbard 1978).

Even though the amount of time males spent perching, walking, and singing varied considerably, there was no relationship between the time spent in each category and FMR. This

could mean these activities have similar metabolic costs. In the Loggerhead Shrike (*Lanius ludovicianus*) the energetic cost of alert perching, preening, eating, and hopping varied by only 13% (Weathers et al. 1984). Moreover, for Savannah Sparrows, complete activity budgets were difficult to obtain because of the time they spent off their territories. While away from their territories, birds foraged most of the time and perched very little (pers. obs.); when they returned they often perched on vegetation, presumably monitoring their territories for intruders. Because of the relatively small differences in activity costs and the uncertainties in the activity schedule for this species, it is not surprising that activity variables did not correlate with FMR.

Territorial male sparrows expended 95.1 kJ of energy per day, which is close to the calculated value of 90 kJ/day for similar-size male White-crowned Sparrows (*Zonotrichia leucophrys*; Hubbard 1978), but higher than the value of 58.2 kJ/day found for aerial-feeding territorial male house-martins (body mass = 17.8 g; Bryant and Westerterp 1980). The allometric equation of Walsberg (1983), based on 42 studies using widely different methodologies, predicts an FMR of 82.2 kJ/day for adult sparrows. Nagy (MS) recently analyzed data for FMR from 24 studies on passerines using DLW; his equation yielded a value of 87.5 kJ/day.

The idea that birds expend less energy during incubation than at other times of the reproductive cycle (Walsberg and King 1978) received support from a number of time-energy budget studies (Walsberg 1977, Ettinger and King 1980, Mugaas and King 1981) and from at least one study employing doubly labeled water (Ricklefs and Williams 1984). The data presented here indicates that the power requirements of female Savannah Sparrows during incubation are generally lower than their male partners, but females also weigh less than males and thus have a lower overall energy expenditure by virtue of their smaller body size. The FMR of incubating females was not significantly different from females feeding 4 young, the normal brood size on Kent Island. Because of my small sample size for FMR of incubating females, the reliability of this result is low. But several lines of evidence suggest that the daily energy expenditure of an incubating sparrow may not be substantially lower than at other
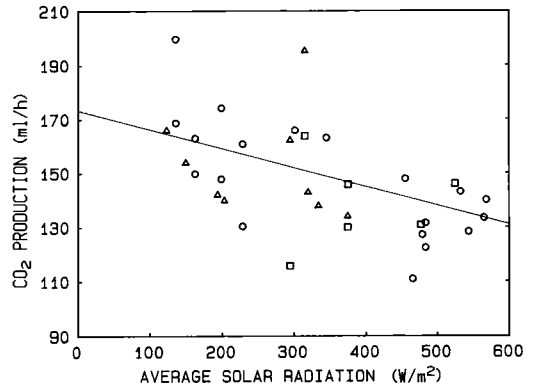

Fig. 4. Relationship between CO_2 production (ml CO_2/h) and average daily radiation. Squares represent birds with 2 young; circles, birds with 4 young; and triangles, birds with 6 young.

times during the reproductive period, as has been suggested for other species (Walsberg 1985). Incubating female sparrows are not fed by their male partners, and therefore must leave their nest to forage 2–5 times per hour (Davis et al. 1984, pers. obs.). This level of activity is similar to a female with nestlings, at least for the first few days of the nestling period (Fig. 1). Of females tending nestlings, those that made 8 or more trips to the nest per hour had a significantly higher FMR than did incubating birds. Each time the incubating female returns to the nest, she must rewarm the eggs and nest, which requires added heat production (Biebach 1986).

In Savannah Sparrows in Baja, California (Williams and Dwinnel unpubl. data), incubating females (*n* = 16) expended energy at rates statistically indistinguishable from those feeding 3 young (*n* = 7) (130.4 vs. 119.6 ml CO_2/h, respectively). These data suggest that the FMR of incubating sparrows may not differ much from those tending young nestlings. Late in the nestling period, however, the energy demands of the brood require the female to markedly increase her feeding trips, which results in an elevated FMR.

While tending 4 chicks, Savannah Sparrows on Kent Island expended energy at a higher rate than sparrows in southern California (Table 6). The difference is small, however, considering that sparrows on Kent Island live in a harsher environment and on average raise one more nestling. Energy expenditures of Kent Is-

TABLE 6. Comparison of the FMR of passerine birds while rearing young.

Species	n	Sex	Body mass (g)	Brood size	kJ/day[a]	FMR/ BMR[b]	Source
Purple Martin	2	F	47.7	?	193.5	3.3	Utter and Le Febvre 1973
Purple Martin	2	M	50.3	?	147.6	2.7	Utter and Le Febvre 1973
Common House-Martin	16	F	17.8	?	78.3	3.0	Hails and Bryant 1979
Common House-Martin	10	M	17.8	?	72.2	2.8	Hails and Bryant 1979
Common House-Martin	56	M & F	17.8	?	85.9	3.3	Bryant and Westerterp 1980
Common House-Martin	55	M & F	18.2	1–7[c]	88.0	3.6	Bryant and Westerterp 1983
European Starling	7	F	74.0	3–7	301.0	4.0	Ricklefs and Williams 1984
European Starling	4	M	77.0	3–7	252.8	3.2	Ricklefs and Williams 1984
Savannah Sparrow	10	F	17.0	1–3	67.7	2.7	Williams and Nagy 1985b
Savannah Sparrow	12	F	18.4	4	80.6	3.0	This study
Savannah Sparrow	9	M	20.2	4	93.0	3.1	This study

[a] Units of CO_2 converted to units of kJ with the conversion factor 24.6 J/ml CO_2 (Williams and Prints 1986).
[b] Where I calculated BMR, I used the Aschoff and Pohl equation, night phase (Aschoff and Pohl 1970).
[c] Most broods apparently contained 4 nestlings.

land sparrows are comparable to those of similar-size house-martins even though the latter is an aerial-foraging species.

Drent and Daan (1980) postulated that an energetic plateau approximately equal to 4 × BMR exists for optimal reproductive performance above which birds accrue serious physiological consequences. The data in Table 6 suggest that, in general, smaller passerines work at levels nearer 3.0 × BMR. Some birds can raise more young than they normally do (Charnov and Krebs 1974, Ricklefs 1977), implying that they do not work at their maximum sustainable level. Single-parent Savannah Sparrows feeding young had much higher feeding rates than did members of intact pairs (Table 5) indicating that, when paired, sparrows did not work at maximum levels, even when feeding 6 young.

To understand energy allocation one must determine the proportion of FMR attributable to basal and thermoregulatory demands (i.e. maintenance metabolism). Maintenance metabolism is difficult to measure for free-ranging animals. As an approximation for Savannah Sparrows I applied Williams and Hansell's (1981) equation. Calculated in this way, maintenance metabolism subsumes 73% of FMR for males ($n = 12$) and 76% for females ($n = 13$). For Black-billed Magpies (*Pica pica*) Mugaas and King (1981) reported that females allocated 55% of their total energy expenditure to maintenance during the nestling period but males devoted only 41%. These results emphasize the importance of understanding the thermostatic coupling of breeding birds with their microen-

vironment as a prerequisite to understanding the allocation of energy to more elective expenditures such as reproduction. Moreover, the negative correlation between energy expenditure and higher levels of solar radiation indicates that birds may be able to alter substantially their thermostatic demands by foraging in microsites where they are exposed to direct sunlight.

The FMR of Savannah Sparrow females increased as their frequency of nest visitation increased. Early in the nestling period female activity, as indexed by the frequency of nest visits, was low, and brooding, which may be energetically inexpensive, occupied much of the day (20–30 min/h) and all night. I suggest that early in the nestling period the time spent brooding by female Savannah Sparrows and the relatively low food demand of the chicks results in a reduced FMR. When nestlings are older and endothermic (days 5–6), the female decreases her brooding time and increases her activity to meet the nestlings' increased energy demands, resulting in an elevated FMR. For house-martins feeding frequency also was related positively to FMR (Bryant and Westerterp 1983).

In contrast, male FMR varied independently of nest visitation even though the latter increased as chicks aged. When nestlings are young, males actively engage in territorial defense and advertisement. Later in the nestling period they sing less, probably defend their territory less, and reapportion their time by making more feeding trips required to provi-

sion their young. Similarly, male White-crowned Sparrows sang and perched less as the nestling period progressed and foraged more (Hubbard 1978).

Sparrows had an elevated FMR when feeding a brood of 6 nestlings. Hails and Bryant (1979) reported that the FMR of male house-martins varied exponentially with brood mass (proportional to brood mass to the 0.66 power), but the FMR of females remained constant when they were challenged with feeding larger brood masses. This disparity may have a partial resolution because, unlike male sparrows, male house-martins brood small chicks, and therefore the relationship presented by Hails and Bryant may be partly attributable to a reduction in energy expenditure when males were brooding, as I have suggested for female sparrows. Because these authors did not segregate their data according to brood size or nestling age, further comparisons are unwarranted.

A striking feature of the FMR of sparrows feeding young was the variability in the data, even for birds feeding the same number of young within a narrow range of nestling ages (6–9 days). Variation may occur in part because of variability within the DLW technique (Ricklefs and Williams 1984), but I suspect a large component of the variability is attributable to biological variation. Factors such as body mass, condition of the bird, weather, experience of the bird, and differential allocation of effort between the sexes may contribute to the total variation, so that relatively large sample sizes may be required when addressing questions of energy allocation in birds with the DLW technique.

During the breeding season a territorial male requires 95.1 kJ/day of metabolizable energy (Fig. 5). Assuming an assimilation efficiency of 75% (Ricklefs 1974), the male must ingest 126.8 kJ of energy per day. At a food energy content of 23.2 kJ/g dry mass for insects (Golley 1961, Williams and Nagy 1985a), the male must consume 5.5 g of dry food per day. If the water content of insects is 73.9% (Williams and Prints unpubl. data), food consumption for territorial males must be 21.1 g of fresh arthropods per day.

Similar calculations for an incubating female indicate a consumption of 17.5 g of fresh arthropods per day to supply 79.3 kJ/day. If the
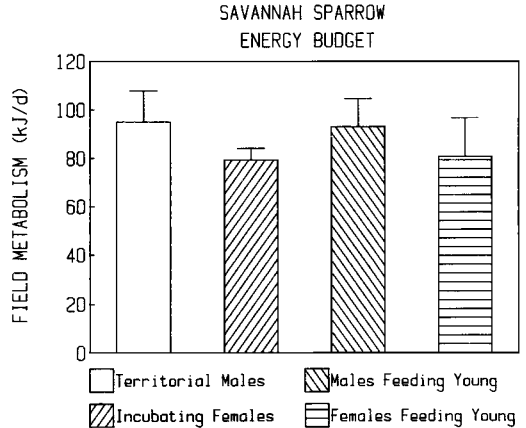

Fig. 5. Summary graph of the energy expenditure of Savannah Sparrows during the breeding season. Lines above bars represent 95% confidence intervals.

incubation period lasts 12 days (Dixon 1978), a female requires 210 g of arthropods during this time.

Using laboratory metabolism data, Williams and Prints (MS) calculated that a brood of 4 Savannah Sparrow nestlings on Kent Island metabolized 898.3 kJ of energy during the 8-day nestling period. Because this estimate does not include thermoregulatory costs, it may underestimate the total metabolized energy by as much as 25% (Williams and Prints 1986). Under this assumption, the total metabolized energy is 1,122.9 kJ. With an assimilation efficiency of 75% for nestlings (Kale 1965), the parents must supply them with 1,497.2 kJ. Parents therefore must find an added 248.2 g of fresh arthropods because males need 165 g of food for self-support for 8 days and females require 142.2 g. If each parent supplies 50% of the nestlings' food requirements, then males, on average, must augment their foraging by 75% (289.1 ÷ 165) and females by 87% to meet this requirement.

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