FIELD METABOLISM OF TREE SWALLOWS DURING THE BREEDING SEASON

JOSEPH B. WILLIAMS

*Department of Physiology, College of Medicine, University of Arizona,
Tucson, Arizona 85724 USA*

ABSTRACT.—I used doubly labeled water to study the field metabolic rate (FMR) of Tree Swallows (*Tachycineta bicolor*) on Kent Island, New Brunswick, Canada, during the breeding season. I tested the hypothesis that aerially foraging species have higher energy requirements than other species.

For incubating female swallows, carbon dioxide production averaged 201.4 ± 15.8 ml CO_2/h. While feeding 5 young, male and female swallows expired CO_2 at a rate of 211.6 ± 23.3 and 231.0 ± 26.4 ml CO_2/h, respectively. During this period males worked at similar levels to females, but the power consumption of females that fed young was significantly higher than incubating females. For both parents together, the mean number of visits to the nest/h was correlated with CO_2 production: ml CO_2/h = 201.6 + 2.49 (visits/h).

On Kent Island, Tree Swallows had a higher FMR than Savannah Sparrows (*Passerculus sandwichensis*), suggesting that aerial-foraging birds have a higher FMR than ground-foraging species. For 7 species of hirundines, energy expenditure was associated positively with body mass; log(kJ/d) = 1.34 + 0.53 log(body mass, g). This relationship differed from one for species which use alternative foraging modes (ground foraging and flycatching, $n = 11$), log(kJ/d) = 0.89 + 0.75 log(body mass, g). Aerial foragers expend from 16–38% more energy/day than do other birds of similar size that spend less time flying. *Received 1 September 1987, accepted 8 June 1988.*

ENERGY requirements during flight are relatively high (Berger and Hart 1974, Pennycuick 1975), and aerial feeding presumably requires more energy than other foraging modes. As a consequence, birds that forage in flight, such as swallows, may exhibit relatively high rates of daily energy expenditure (DEE; Mugaas and King 1981, Kavanau 1987). This hypothesis gains indirect support from time-energy budget (TEB) studies where subtle differences in flight time result in substantial variation in estimates of energy expenditure (Utter and Le Febvre 1973, Bryant and Westerterp 1983).

However, aerial insectivores have wing shapes which may decrease the cost of flight (Hails 1979). An alternative hypothesis is that aerially foraging species expend less energy during flight than other species, and as a consequence, the overall field metabolic rate (FMR) may be equivalent to similar-sized birds which use alternative foraging modes.

I used the doubly labeled water (DLW) method to estimate the FMR of Tree Swallows (*Tachycineta bicolor*) during the breeding seasons of 1981 and 1982. I compared their FMR with published values for Savannah Sparrows (*Passerculus sandwichensis*; Williams 1987) to test the hypothesis that aerial-foraging species have higher energy requirements than ground-foraging species. By an allometric analysis, I tested the idea that, in general, hirundines have a higher FMR than other birds that use alternative foraging modes which require less time in flight.

METHODS

Study area and species.—This 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. The island contains 2 grassy fields (10.7 and 4.0 ha) in which about 100 Tree Swallow nest boxes have been erected. The boxes were painted white with the entrance facing north, away from prevailing winds. The fields, dominated by *Agrostis stolonifera* and *Festuca rubra*, provided nesting habitat for about 100 pairs of Savannah Sparrows (Williams 1987).

The breeding biology of Tree Swallows on Kent Island has been described by Paynter (1954) and that of Savannah Sparrows, by Dixon (1978). Both species are migratory; both lay eggs in early June. Swallows nest in boxes; sparrows construct well-hidden open-cup nests, usually on the ground. The females of both species incubate unassisted by the male. Although male swallows may bring food to their incubating mates (Kuerzi 1941), I did not observe this behavior. Modal clutch size for swallows varied from 5–6 eggs depending on the year (Winn 1949, Paynter 1954);

TABLE 1. CO_2 production, energy use, and water flux rates for incubating female Tree Swallows on Kent Island, New Brunswick, Canada.

Date	Mean mass (g)	ml CO_2/h	kJ/d	Water flux (ml/d)		Ta[a]	FMR/BMR
				In	Out		
1981							
17–18 June	25.3	193.3	114.1	14.0	14.3	11.8	3.4
17–18 June	22.5	191.7	113.2	18.8	18.4	11.8	3.8
7–8 June	22.2	181.6	107.2	17.5	18.3	11.0	3.6
15–16 June	21.8	202.1	119.3	16.4	17.2	9.0	4.1
12–13 June	23.1	201.9	119.2	19.4	19.5	11.0	3.9
19–20 June	24.5	230.1	135.9	13.6	13.9	10.5	4.2
1982							
8–9 June	19.9	206.2	121.7	16.4	15.9	13.5	4.6
7–8 June	20.6	185.4	109.5	13.7	13.8	10.3	4.0
3–4 June	23.2	219.9	129.8	14.7	15.2	9.0	4.2
Mean	22.6	201.4	118.9	16.1	16.3	10.9	4.0
(SD)	(±1.7)	(±15.8)	(±9.3)	(±2.2)	(±2.1)	(±1.4)	(±0.4)

[a] Mean air temperature for experimental period.

Savannah Sparrows usually lay 4 eggs. In both species, females brood the young until they are about 5 days old, and in both species males and females jointly provide food for the young (Quinney 1986, Williams 1987). Nestling swallows fledge fully feathered and are able to fly after 19–20 days in the nest, whereas sparrows leave the nest in 8–9 days and acquire the ability to fly 7–10 days later.

First-year female swallows, distinguishable from older females by plumage coloration (Winn 1949), may produce smaller clutches (De Steven 1978) and were excluded from this study.

Laboratory metabolism.—Oxygen consumption ($\dot{V}_{O_2}$) of adult Tree Swallows was measured by means of a closed-circuit manometric system (Williams and Prints 1986). In brief, 4 stainless steel chambers (2,000 ml) were wrapped with 3/8 inch copper tubing through which a mixture of water and methanol was circulated with a refrigerated bath. Temperature, as measured by a 38-gauge thermocouple and a Bailey Thermometer (Model 12), could be controlled to within ±0.1°C. During each trial, expired CO_2 and H_2O vapor were removed using Ascarite and Drierite, thus a decrease in pressure within the chamber was a result of O_2 uptake. As birds consumed O_2, I restored the pressure in the chamber by infusion of O_2 with a calibrated glass syringe. The walls of each chamber were coated with flat black paint to minimize reflected thermal radiation. Birds were equilibrated 1–2 h before experimentation. Experiments were performed during daylight hours (1000–1800) and each trial lasted 60 min. I corrected all $\dot{V}_{O_2}$ values to STPD. Williams and Prints (1986) and Obst et al. (1987) have shown close agreement (5–8% difference) between measurements of $\dot{V}_{O_2}$ as given by this method and $\dot{V}_{O_2}$ as determined with an open-flow system.

Field metabolism.—The field protocol for using DLW

on Tree Swallows followed Williams (1987). Birds were captured late in the afternoon at nest boxes and injected in the pectoral muscle with 0.10 ml tritiated water (1 μ Ci/g body mass) mixed with 97 atom % oxygen-18. After an hour equilibration period (Williams and Nagy 1984), injected individuals were marked with white paint on the tip of the tail, banded with a numbered aluminum band, and released. Laboratory procedures for the distillation of water from blood samples and for the assay of tritium followed Williams (1987). Water samples were analyzed for ^{18}O content by Dr. Ken Nagy at the University of California, Los Angeles. Water influx and efflux were calculated using equations 6 and 5, respectively, of Nagy (1975), and rates of CO_2 production using equation 8. Background levels of isotopes obtained from uninjected conspecifics were subtracted from all values prior to calculations. Validation studies have shown reasonable agreement (±10%) between gravimetric measurement of CO_2 production and CO_2 production as estimated by DLW (Williams and Nagy 1984, Williams 1985).

The factor of 24.6 J/ml CO_2 was used to convert metabolic rates from units of CO_2 to units of energy (Williams and Nagy 1985). To convert O_2 consumption to heat production, I used 20.08 J/ml O_2 (Schmidt-Nielsen 1979).

Nine birds that were feeding nestlings eluded recapture after 24 h and were not re-bled until the following morning. For these individuals, I subtracted CO_2 production during the second night period from their total CO_2 production (see Williams 1987). I assumed an R.Q. of 0.75 and that mean ambient air temperature at night was a reasonable estimate of the thermal environment (Mugaas and King 1981).

All females that were injected while incubating had laid 5 or 6 eggs. To determine when injected females

resumed incubation, I placed a thermocouple in the nest and continuously monitored nest temperature with a Linear strip-chart recorder. Only 1 female (12–13 June 1981; Table 1) failed to return to the box by nightfall (2–3 h after injection). She resumed incubation at daybreak the next morning. All females were recaptured at night in their nest boxes approximately 24–30 h after injection.

For adults tending young, I injected one animal of a pair during the late afternoon.The following day, the visits of both parents were recorded for 6 1-h periods spaced throughout the day. All birds included in this analysis fed chicks, although the variability in visitation frequency was high. Broods of 3 and 7 were constructed by adding or subtracting equal aged young to broods of 5 or 6. During both years, periods of inclement weather at times impeded swallows from feeding young, and some nestlings died. Thus, sample sizes for brood manipulation experiments are low.

I measured air temperature (T_a) and relative humidity (RH) continuously with a Weathermeasure hygrothermograph placed in a standard weather instrument shelter (Stevenson screen). Each instrument was calibrated daily with a Bailey thermometer and a sling psychrometer, respectively. Twice each day, at 0700 h and 1900 h, I recorded fog conditions and precipitation (mm H_2O). Fog was scored as present or absent at each of the observation times. Precipitation was measured with a standard rain gauge and recorded daily. During experimental periods, at 2 h intervals, I measured irradiance (W/m²) with a LiCor 185A pyranometer calibrated against an Eppley pyranometer. Wind speed was measured 1 m above the ground with a hand-held anemometer (Dwyer Model No. 460) which was previously calibrated against a pitot tube in the laboratory.

Data were analyzed by means of a SPSS/PC statistical package (Norusis 1984). Means are presented ±1 SD unless otherwise indicated.

RESULTS

During June and July, the weather on Kent Island is cool and moist, with frequent fog (Cunningham 1942, McCain 1975). Fog covered the island at 1 of the 2 observation periods on 13 and 14 days in June and July of 1981, respectively. Similar values for 1982 were 8 and 12 days. Rain fell on 30 days in 1981 and on 21 days in 1982. Temperatures averaged about 11°C in June and 13°C in July for both years.

Laboratory metabolism.—The resting metabolic rate (RMR) of post-absorptive Tree Swallows during the day averaged 79.3 ± 12.6 ml O_2/h (Fig. 1; $n = 12$; mean mass = 21.6 ± 1.9 g). Reducing RMR by 25% (Aschoff and Pohl 1970, Calder and King 1974) yields an estimate for
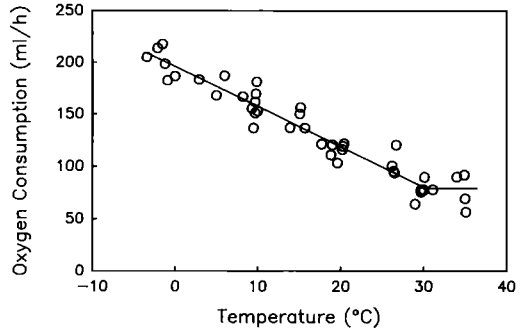

Fig. 1. Laboratory metabolism of Tree Swallows on Kent Island, New Brunswick.

the nighttime basal metabolism (BMR) of 59.5 ml O_2/h, or 1.19 kJ/h.

Below 30°C, $\dot{V}_{O_2}$ increased as T_a declined: ml O_2/h = 195.5 − 3.77 (T_a, °C) ($n = 40$, $r^2 = 0.93$, $P < 0.0001$). At a metabolic rate of zero, this equation extrapolates to 53.5°C suggesting that heat transfer from swallows in metabolism chambers is not constant below their lower critical temperature (T_{lc}). The heat transfer coefficient, calculated as the slope of the regression line for metabolism below the T_{lc}, was 3.5 J/g·h^{-1}·°C^{-1}.

Field metabolism.—For incubating females, CO_2 production averaged 201.4 ± 15.8 ml CO_2/h or 118.9 kJ/d (Table 1). Carbon dioxide production was unrelated to T_a, wind, or solar irradiance. The ratio of FMR to BMR averaged 4.0.

Body mass of females declined from the incubation period (mean mass = 22.6 ± 1.7, $n = 9$) to the nestling period (mean mass = 19.3 ± 1.4, $n = 18$; $t = 5.23$, $P < 0.01$). While feeding 5 young, male and female swallows expired CO_2 at an average rate of 211.6 and 231.0 ml CO_2/h, respectively (Table 2). Expired CO_2 translated into 124.9 kJ/d for males and 136.4 kJ/d for females. During this period, males worked at similar levels to females ($t = 1.4$, $P = 0.18$), but power consumption of females feeding young was significantly higher than that of incubating females ($t = 3.0$, $P < 0.01$).

Combining all data, males expired CO_2 at a rate of 213.6 ± 22.1 ml CO_2/h ($n = 7$) and females at a rate of 229.7 ± 28.9 ml CO_2/h ($n = 18$), values which are statistically indistinguishable ($t = 1.33$, $P > 0.10$).

For males and females together, the mean number of visits/hour correlated with CO_2 production (Fig. 2): ml CO_2/h = 201.6 + 2.49 (visit/

TABLE 2.   Rates of CO_2 production, energy use, and water flux for Tree Swallows feeding young on Kent Island, New Brunswick (1981 and 1982).

Date	Mean body mass (g)	Nestling age (d)	ml CO_2/h	kJ[a]/d	Water flux (ml/d) Influx	Efflux	FMR/ BMR
Brood size = 3							
Males							
7–8 July 1982	21.2	4	200.0	118.1	20.3	20.8	4.2
Females							
3–4 July 1982	16.6	14	195.9	115.7	22.3	21.7	5.2
26–27 July 1982	21.5	14	286.0	168.9	26.5	26.4	5.9
1–3 July 1982	19.7	15	202.4	119.5	15.3	16.2	4.6
19–21 July 1982	17.1	15	190.9	112.7	14.1	14.5	5.0
25–26 July 1982	19.0	15	228.0	134.6	20.0	20.0	5.3
Mean	18.8	12.8	217.2	128.3	19.8	19.9	5.0
(SD)	(±2.0)		(±36.1)	(±21.3)	(±4.6)	(±4.2)	(±0.6)
Brood size = 5							
Males							
24–26 June 1981	20.3	2	209.7	123.8	10.6	11.2	4.6
23–24 June 1981	20.2	3	216.9	128.1	20.8	20.9	4.8
25–26 June 1982	22.5	6	230.4	136.0	19.5	19.6	4.5
29 June to 1 July 1981	18.9	13	172.7	102.0	15.1	15.3	4.1
1–3 July 1982	18.1	14	228.3	134.8	20.8	20.9	5.6
Mean	20.0	7.6	211.6	124.9	17.4	17.6	4.7
(SD)	(±1.7)	(±5.6)	(±23.3)	(±13.8)	(±4.4)	(±4.2)	(±0.6)
Females							
3–4 July 1981	20.0	2	195.8	115.6	12.4	13.1	4.3
24–26 June 1981	20.3	3	214.9	126.9	13.6	14.1	4.7
25–26 June 1981	19.2	4	258.8	152.8	21.1	21.3	6.0
18–19 June 1981	22.3	5	217.2	128.2	24.9	24.9	4.3
23–24 June 1981	19.5	5	260.9	154.0	27.0	26.6	5.9
10–12 July 1981	18.4	7	236.5	139.6	16.3	16.4	5.7
24–25 June 1981	19.6	11	220.1	129.9	18.6	18.7	5.0
24–25 June 1981	17.7	12	275.2	162.5	17.1	16.8	6.9
5–7 July 1982	19.0	15	198.0	116.9	18.2	18.2	4.6
30 June to 1 July 1982	18.7	15	217.7	128.5	20.4	20.5	5.2
30 June to 1 July 1982	19.0	15	246.2	145.4	20.8	20.9	5.6
Mean	19.4	8.5	231.0	136.4	19.1	19.2	5.3
(SD)	(±1.2)	(±5.1)	(±26.4)	(±15.6)	(±4.4)	(±4.2)	(±0.8)
Brood size = 7							
Males							
3–5 July 1982	18.1	14	236.9	139.9	16.4	16.5	5.8
Females							
23–24 June 1982	20.1	4	253.9	149.9	30.7	30.3	5.6
21–22 June 1982	20.4	7	235.8	139.2	21.0	21.5	5.1
Mean	20.3	5.5	244.9	144.6	25.9	25.9	5.4
(SD)	(±0.2)	(±2.1)	(±12.8)	(±7.6)	(±6.9)	(±6.2)	(±0.4)

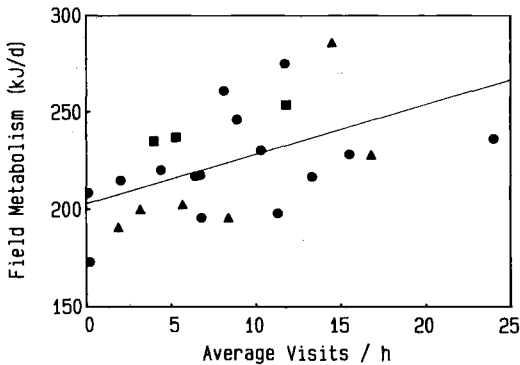[a] 24.6 J of heat/ml CO_2 (Williams and Nagy 1985).

Fig. 2. Field metabolism as a function of the average visits/h of Tree Swallows on Kent Island, New Brunswick. Squares represent birds feeding 3 nestlings; circles, birds feeding 5 nestlings; triangles, birds feeding 7 nestlings.

h) ($n = 25$, $r^2 = 0.21$, $P < 0.02$). Nest visitation was unrelated to nestling age for either sex (males $r^2 = 0.04$, $P > 0.5$, females $r^2 = 0.02$, $P > 0.6$). Males averaged 7.4 visits/h (SD = 5.0, $n = 7$), and females, 9.1 visits/h (SD = 5.6, $n = 18$).

Water influx and efflux.—In general, water influx equaled efflux indicating that birds balanced water intake against water losses (Tables 1 and 2). For incubating females, water influx averaged 16.1 ± 2.2 ml H_2O/d (Table 1), and increased to 20.1 ± 5.0 ml H_2O/d during the chick rearing period (Table 2). Water influx correlated with CO_2 production for birds with nestlings (Fig. 3). Water influx (ml/d) = $-1.71 + 0.09$ (ml CO_2/h) ($n = 25$, $r^2 = 0.30$, $P < 0.001$). Solar irradiance positively influenced water influx, ml H_2O/d = $14.3 + 0.02$ (W/m²) (Fig. 4; $n = 25$, $r^2 = 0.29$, $P < 0.001$).

DISCUSSION

Aschoff and Pohl (1970) predicted a BMR of 1.24 kJ/h for a 21.6 g passerine in its night phase. This is within 4% of the value that I have estimated for Tree Swallows. Savannah Sparrows on Kent Island had a resting metabolic rate of 86.0 ± 8.8 ml O_2/h or 1.73 kJ/h (Williams unpubl.; $n = 13$, mean mass = 18.9 ± 1.3). Because Tree Swallows were slightly heavier than Savannah Sparrows ($t = 5.5$, $P < 0.001$), I calculated mass independent measurements of metabolism by dividing $\dot{V}_{O_2}$ by mass$^{0.67}$ (Heusner 1985). In the TNZ, swallows had a lower metabolic rate than sparrows (swallows = 10.1
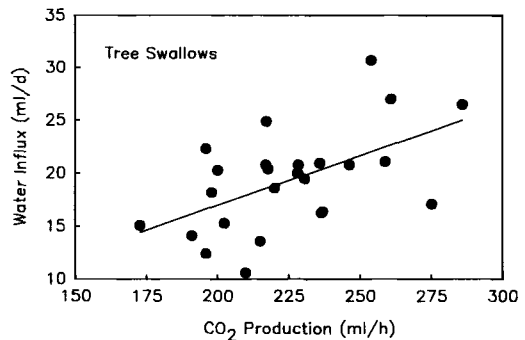

Fig. 3. Water influx as a function of CO_2 production for Tree Swallows with nestlings on Kent Island, New Brunswick.

± 1.7 ml O_2/(mass$^{0.67} \cdot$h); sparrows = 12.1 ± 1.3 ml O_2/(mass$^{0.67} \cdot$h); $t = 3.3$, $P < 0.01$), but below the TNZ, they consumed O_2 at a higher rate than sparrows (ANCOVA, $t_{slopes} = 5.3$, $P < 0.01$). For swallows, ml O_2/(mass$^{0.67} \cdot$h) = $25.9 - 0.51$ (T_a, °C) ($n = 40$, $r^2 = 0.91$, $P < 0.001$); for sparrows, ml O_2/(mass$^{0.67} \cdot$h) = $19.6 - 0.26$ (T_a, °C) ($n = 25$, $r^2 = 0.64$, $P < 0.001$). At an air temperature of 11.5°C, the mean air temperature during DLW measurements, mass independent laboratory metabolism for swallows was 20.1 ml O_2/(mass$^{0.67} \cdot$h) and for sparrows was 16.7 ml O_2/(mass$^{0.67} \cdot$h), a 16.9% difference. The plumage thickness of swallows may be less than that of sparrows, which results in greater heat loss.

During incubation, female Tree Swallows expend less energy than when they feed young. Common House-Martins (*Delichon urbica*), Bank Swallows (*Riparia riparia*), and European Starlings (*Sturnus vulgaris*) show the same diminution in FMR during incubation, and also nest
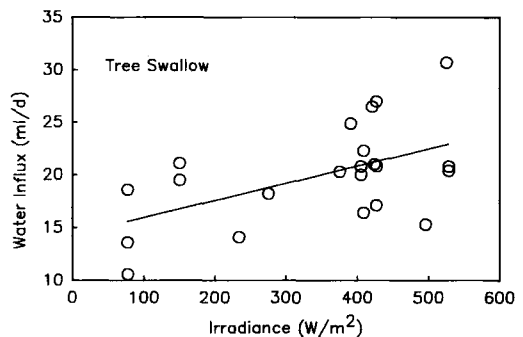

Fig. 4. Water influx as a function of irradiance for Tree Swallows with nestlings on Kent Island, New Brunswick.
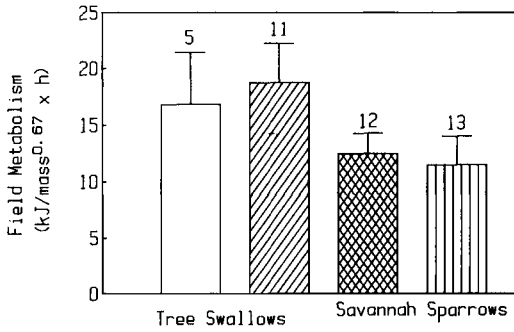
Fig. 5. Mass independent field metabolism for Tree Swallows and Savannah Sparrows while feeding young. The open bar represents male swallows, bar with diagonal lines represents female swallows, bar with cross-hatching represents male sparrows, and bar with vertical lines represents female sparrows. Lines above bars indicate 95% confidence intervals; numbers above bars, sample size.
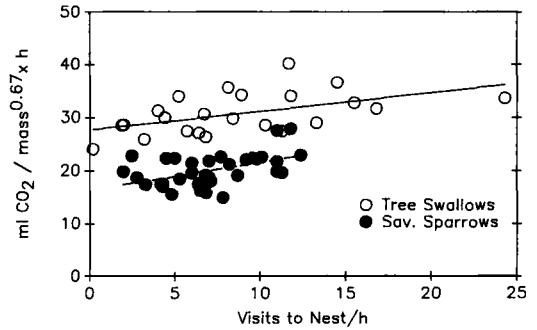

Fig. 6. Mass independent field metabolism as a function of nest visitation rate for Tree Swallows and Savannah Sparrows. Elevations but not slopes are statistically different. For swallows, ml CO_2 $mass^{0.67}$ × h = 27.7 + 0.34 (visits/h) (r^2 = 0.26, P = 0.003); for sparrows, ml CO_2 $mass^{0.67}$ × h = 16.4 + 0.52 (visits/h) (r^2 = 0.24, P < 0.001).

in cavities or boxes (Westerterp and Bryant 1984); Ricklefs and Williams 1984). Savannah Sparrows on Kent Island build an open-cup nest and only the female incubates. The FMR of sparrow females was equivalent during the incubation and early nestling periods (Williams 1987).

Female Tree Swallows weigh less during the nestling period than during the incubation period (see also Westerterp and Bryant 1984, Ricklefs and Williams 1984, Williams 1987). Mass loss may reflect physiological stress from increased activity while adults feed their young (Hussell 1972). However, knowledge of the time when weight declines is critical in interpreting this pattern (Freed 1981). Female swallows lose mass during the incubation period (Williams unpubl.). Changes in body mass during incubation in hirundines mostly reflect changes in lipid reserves (Jones 1987) and suggest that the incubation period may be energetically stressful for female Tree Swallows on Kent Island.

Female sparrows (18.3 g) weigh slightly less than male (20.0 g) or female (19.4 g) swallows during the nestling period (ANCOVA, F = 5.2, P < 0.005). While provisioning 5 young, mass independent values of field metabolism (MIFMR) (Heusner 1985) for Tree Swallows exceeded values for Savannah Sparrows that tended 4 young (Fig. 5; ANCOVA, F = 31.1, P < 0.001). The MIFMR of male swallows was higher than in male sparrows by 25.6%, and the MIFMR of female swallows was higher than female sparrows by 38.8%. I attribute a portion of these

differences to the increased thermoregulatory costs of swallows. However, swallows spend a substantial proportion of their day flying, and heat produced as a by-product of this activity may substitute for the heat required for thermoregulation (Tucker 1968, Palandino and King 1984). Consequently the difference in thermoregulatory costs between swallows and sparrows is reduced. Thus, the increased flight time of swallows is, to a large extent, responsible for their higher FMR.

The difference in FMR between sparrows and swallows is not directly attributable to the fact that swallows fed an additional nestling. MIFMR was higher for swallows than for sparrows per nest visit (Fig. 6; ANCOVA, t_{slope} = 1.82, NS, $t_{elevation}$ = 325.3, P < 0.001). Moreover, when sparrows fed 6 nestlings, their FMR was lower than for swallows that fed 5 (Williams 1987).

Hirundines may, in general, have a higher FMR than other birds. I have plotted FMR (kJ/d) as a function of body mass for 7 species of aerially foraging birds during the nestling period (Fig. 7). With the exception of Cliff Swallows (Withers 1977), all the data refer to DLW measurements of FMR. Log(kJ/d) = 1.34 + 0.53 log(body mass, g) describes the relationship (r^2 = 0.78, P < 0.01). For comparison, I plotted the FMR of 11 species of birds that are either ground-foraging insectivores, flycatchers, or picivores also during the nestling period (Fig. 7). Six of these studies used the DLW method. I combined flycatchers and ground foragers because the foraging routine of flycatchers often entails no more
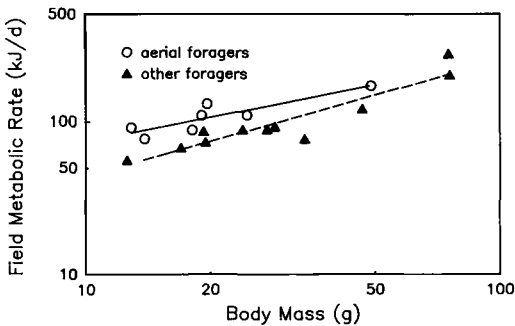
Fig. 7. Field metabolism as a function of body mass for hirundines (open circles) and other birds of similar size (closed triangles). Lines are statistically different. (See Appendix for species and sources.)

flight time than the routine of ground-foraging species (Ettinger and King 1980). The line which describes these data, $\log(kJ/d) = 0.89 + 0.75 \log(\text{body mass, g})$ ($r^2 = 0.87$, $P < 0.001$), lies below the line for aerial foragers (ANCOVA, $t_{\text{slope}} = 1.1$, NS, $t_{\text{elevation}} = 9.9$, $P < 0.001$). Thus, aerial foragers expend from 16 to 38% more energy than similar-sized species that employ alternative foraging modes. Walsberg (1983) found a statistically insignificant (10%) difference between the DEE of aerial foragers (hummingbirds and swallows) and that of other birds. Powers and Nagy (unpubl.) found a FMR of 32 kJ/d for Anna's Hummingbirds (*Calypte anna*), a value intermediate between predictions of the 2 equations. These birds were not feeding young. When Tree Swallows fed their chicks more frequently, their CO_2 production increased. Swallows often spend more time flying when insects are abundant (Bryant and Westerterp 1983). Feeding frequency also was related positively to FMR in Common House-Martins (Bryant and Westerterp 1983) and Savannah Sparrows (Williams 1987). The number of visits each parent Tree Swallow made to the nest was unrelated to nestling age (see also Lombardo 1987).

Drent and Daan (1980) speculated that an energetic plateau exists approximately equal to 4.0 times BMR for optimal reproductive performance. Above this level, birds accrue serious physiological consequences. When raising young, Savannah Sparrows and other small passerines work at levels near 3.0 times BMR (Williams 1987). In contrast, FMR/BMR ratios for Tree Swallows during the nestling period exceeded the hypothetical limit, apparently without immediate adverse consequences. These ra-

tios are among the highest thus far reported, which may indicate that Kent Island is energetically stressful for swallows. It would be interesting to know if the survival rate of Tree Swallows on Kent Island was lower than for swallows from other populations.

The influence of weather on the FMR of birds varies. Favorable weather conditions, such as warm, calm days, were associated with higher levels of energy expenditure in Common House-Martins (Bryant and Westerterp 1983). Fair weather also was correlated positively with a larger number of flying insects. Thus, house-martins spent more time foraging. However, foul weather such as strong winds caused a significant increase in the FMR of Black-legged Kittiwakes (*Rissa tridactyla*; Gabrielsen et al. 1987). For Tree Swallows, I found no relationship between FMR and weather. Water influx was positively related with irradiance, which suggests that the foraging success of swallows was higher on clear days, when insects were presumably more abundant.

LITERATURE CITED

ASCHOFF, J., & H. POHL 1970. Rhythmic variations in energy metabolism. Fed. Proc. 29: 1541–1552.
BAKKEN, G. S. 1980. The use of standard operative temperature in the study of thermal energetics of birds. Physiol. Zool. 53: 108–119.
BERGER, M., & J. S. HART. 1974. Physiology and energetics of flight. Pp. 260–415 *in* Avian biology, vol. 4 (D. S. Farner and J. R. King, Eds.). New York, Academic Press.
BRYANT, D. M. 1979. Reproductive costs in the house martin (*Delichon urbica*). J. Animal Ecol. 48: 655–676.
———, C. J. HAILS, & P. TATNER. 1984. Reproductive energetics of two tropical bird species. Auk 101: 25–37.

————, & K. R. WESTERTERP. 1983. Short-term variability in energy turnover by breeding House Martins *Delichon urbica*: a study using doubly-labeled water. J. Anim. Ecology 52: 525–543.

CALDER, W. A., & J. R. KING. 1974. Thermal and caloric relations of birds. Pp. 259–413 *in* Avian biology, vol. 4 (D. S. Farner and J. R. King, Eds.). New York, Academic Press.

CAMPBELL, G. 1977. An introduction to environmental physics. New York, Springer-Verlag.

CUNNINGHAM, R. 1942. Meteorology. Bull. Bowdoin Sci. Sta. 6: 10–13.

DE STEVEN, D. 1978. The influence of age on the breeding biology of the Tree Swallow (*Iridoprocne bicolor*). Ibis 120: 516–523.

DIXON, C. L. 1978. Breeding biology of the Savannah Sparrow on Kent Island. Auk 95: 235–246.

DRENT, R. H., & S. DAAN. 1980. The prudent parent: energetic adjustments in avian breeding. Ardea 68: 225–252.

ETTINGER, A. O., & J. R. KING. 1980. Time and energy budgets of the Willow Flycatcher (*Empidonax traillii*) during the breeding season. Auk 97: 533–546.

FREED, L. A. 1981. Loss of mass in breeding wrens: stress or adaptation? Ecology 62: 1179–1186.

GABRIELSEN, G. W., F. MEH LUM, & K. A. NAGY. 1987. Daily energy expenditure and energy utilization of free-ranging Black-legged Kittiwakes. Condor 89: 126–132.

HAILS, C. J. 1979. A comparison of flight energetics in hirundines and other birds. Comp. Biochem. Physiol. 63A: 581–585.

————, & D. M. BRYANT. 1979. Reproductive energetics of a free-living bird. J. Anim. Ecol. 48: 471–482.

HEUSNER, A. A. 1985. Body size and energy metabolism. Ann. Rev. Nutr. 5: 267–293.

HUBBARD, J. D. 1978. Breeding biology and reproductive energetics of mt. White-crowned Sparrows in Colorado. Ph.D. dissertation, Univ. Boulder, Colorado.

HUSSELL, D. T. 1972. Factors affecting clutch size in arctic passerines. Ecol. Monogr. 42: 317–364.

JONES, G. 1987. Time and energy constraints during incubation in free-living swallows (*Hirundo rustica*): an experimental study using precision electronic balances. J. Anim. Ecol. 56: 229–245.

KAVANAU, J. L. 1987. Lovebirds, Cockatiels, Budgerigars: behavior and evolution. Los Angeles, California, Science Software Systems, Inc.

KENDEIGH, S. C., V. R. DOL'NIK, & V. M. DAVRILOV. 1977. Granivorous birds in ecosystems. Pp. 127–204 *in* Avian energetics (J. Pinowski and S. C. Kendeigh, Eds.). New York, Cambridge Univ. Press.

KUERZI, R. 1941. Life history studies of the Tree Swallow. Proc. Linn. Soc. New York 52–53: 1–52.

LASIEWSKI, R. C., W. WEATHERS, & M. H. BERNSTEIN.

1967. Physiological responses of the Giant Hummingbird (*Patagonia gigas*). Comp. Biochem. Physiol. 21: 405–414.

LIFSON, N., & R. MCCLINTOCK. 1966. Theory of use of the turnover rates of body water for measuring energy and material balance. J. Theoret. Biol. 12: 46–74.

LOMBARDO, M. P. 1987. Attendants at Tree Swallow nests. II. The exploratory-dispersal hypothesis. Condor 89: 138–149.

MCCAIN, J. W. 1975. A vegetational survey of the vascular plants of the Kent Island group, Grand Manan, New Brunswick. Rhodora 77: 196–209.

MUGAAS, J. N., & J. R. KING. 1981. The annual variation in daily energy expenditure of the Black-billed Magpie: a study of thermal and behavioral energetics. Stud. Avian Biol. 5: 1–78.

NAGY, K. A. 1975. Water and energy budgets of free-living animals: measurement using isotopically labeled water. Pp. 227–245 *in* Environmental physiology of desert organisms (N. F. Hadley, Ed.). Stroudsberg, Pennsylvania, Gowden, Hutchinson and Ross.

NORBERG, R. 1981. Temporary weight decrease in breeding birds may result in more fledged young. Am. Nat. 118: 838–850.

NORUSIS, M. J. 1984. SPSS/PC for the IBM PC/XT. Chicago, SPSS Inc.

NUR, N. 1984. The consequences of brood size for breeding Blue Tits. I. Adult survival, weight change and the cost of reproduction. J. Anim. Ecol. 53: 479–496.

OBST, B. S., K. A. NAGY, & R. E. RICKLEFS. 1987. Energy utilization by Wilson's Storm Petrel (*Oceanites oceanicus*). Physiol. Zool. 60: 200–210.

PALANDINO, F. V., & J. R. KING. 1984. Thermoregulation and oxygen consumption during terrestrial locomotion by White-crowned Sparrows *Zonotrichia leucophrys gambelii*. Physiol. Zool. 57: 226–236.

PAYNTER, R. A. 1954. Interrelations between clutch-size, brood-size, pre-fledgling survival, and weight in Kent Island Tree Swallows. Bird-banding 25: 35–148.

PENNYCUICK, C. J. 1975. Mechanics of flight. Pp. 1–75 *in* Avian biology, vol. 5 (D. S. Farner and J. R. King, Eds.). New York, Academic Press.

QUINNEY, T. E. 1986. Male and female parental care in Tree Swallows. Wilson Bull. 98: 147–150.

REYER, H., & K. WESTERTERP. 1985. Parental energy expenditure: a proximate cause of helper recruitment in the Pied Kingfisher (*Ceryle rudis*). Behav. Ecol. Sociobiol. 17: 363–369.

RICKLEFS, R. E. 1974. Energetics of reproduction in birds. Pp. 152–292 *in* Avian energetics (R. A. Paynter Jr., Ed.). Nuttall Ornithol. Club Publ. 15.

————, & J. B. WILLIAMS. 1984. Daily energy expenditure and water-turnover rate of adult European

JOSEPH B. WILLIAMS [Auk, Vol. 105]

Starlings (*Sturnus vulgaris*) during the nesting cycle. Auk 101: 707–715.

ROSENBERG, N., B. BLAD, & S. VERMA. 1983. Pp. 1–495 *in* Microclimate. New York, John Wiley and Sons.

SCHMIDT-NIELSEN, K. 1979. Animal physiology. New York, Cambridge Univ. Press.

TUCKER, V. A. 1968. Respiratory exchange and evaporative water loss in the flying Budgerigar. J. Exp. Biol. 48: 67–87.

UTTER, J. M. 1971. Daily energy expenditure of free-living Purple Martins (*Progne subis*) with a comparison of two northern populations of mockingbirds (*Minus polyglottus*). Ph.D. dissertation. New Brunswick, New Jersey, Rutgers Univ.

———, & E. A. LE FEBVRE. 1973. Daily energy expenditure of Purple Martins (*Progne subis*) during the breeding season: estimates using $D_2{}^{18}O$ and time budget methods. Ecology 54: 597–604.

WALSBERG, G. E. 1977. Ecology and energetics of contrasting social systems in *Phainopepla nitens* (Aves: Ptilogonatidae). Univ. Calif. Berkeley Publ. Zool. 108: 1–63.

———. 1978. Brood size and the use of time and energy by the Phainopepla. Ecology 59: 147–153.

———. 1983. Avian ecological energetics. Avian Biol. 8: 161–220.

WESTERTERP, K. R., & D. M. BRYANT. 1984. Energetics of free-existence in swallows and martins (*hirundinidae*) during breeding: a comparative study using double labeled water. Oecologia 62: 376–381.

WILLIAMS, J. B. 1985. Validation of the doubly-labeled water technique for measuring energy metabolism in starlings and sparrows. Comp. Biochem. Physiol. 80A: 349–353.

———. 1987. Field metabolism and food consumption of Savannah Sparrows during the breeding season. Auk 104: 277–289.

———, & H. HANSELL. 1981. Bioenergetics of captive Belding's Savannah Sparrows (*Passerculus sandwichensis beldingi*). Comp. Biochem. Physiol. 69A: 783–787.

———, & K. A. NAGY. 1984. Validation of the doubly-labeled water technique for measuring energy metabolism in Savannah Sparrows. Physiol. Zool. 57: 325–328.

———, & ———. 1985. Water flux and energetics of nesting Savannah Sparrows in the field. Physiol. Zool. 58: 515–525.

———, & A. PRINTS. 1986. Energetics of growth in nestling Savannah Sparrows: a comparison of double-labeled water and laboratory estimates. Condor 88: 74–83.

WINN, H. 1949. Nestling mortality rate of the Tree Swallow. Bowdoin Sci. Sta. Bull. 11: 19–20.

WITHERS, P. C. 1977. Energetic aspects of reproduction by the Cliff Swallow. Auk 94: 718–725.

APPENDIX. Species and sources for aerial and other foragers (see Fig. 7).

For hirundines (open circles), species and sources are: Sand Martin (*Riparia riparia*), 12.9 g, Westerterp and Bryant 1984; Pacific Swallow (*Hirundo tahitica*), 13.9 g, Bryant et al. 1984; House Martin, 18.1 g, Hails and Bryant 1979; European Swallow (*Hirundi rustica*), 19.1 g, Westerterp and Bryant 1984; Tree Swallow, 19.7 g, this study; Cliff Swallow (*Petrochelidon pyrrhonota*), 24.6 g, Withers 1977; Purple Martin, 49.0 g, Utter and Le Febvre 1983.

For other birds (closed triangles), species and sources are: Willow Flycatcher (*Epidonax traillii*), 12.6 g, Ettinger and King 1980; Savannah Sparrow, 17.0 g, Williams and Nagy 1985; Savannah Sparrow, 19.3 g, Williams 1987; Yellow-eyed Junco (*Junco phaeonotus*), 19.5 g, Wes Weathers, pers. com.; Phainopepla (*Phainopepla nitens*), 24.0 g, Walsberg 1978; Western Bluebird (*Sialia mexicanius*), 27.5 g, P. J. Mock, pers. com.; White-crowned Sparrow (*Zonotrichia leucophrys*), 28.7 g, Hubbard 1978; Blue-throated Bee Eater (*Merops viridis*), 33.9 g, Bryant et al. 1984; Mockingbird (*Mimus polyglottos*), 46.7 g, Utter 1971; Starling, 75.5 g, Ricklefs and Williams 1985; Pied Kingfisher (*Ceryle rudis*), 76.0 g, Reyer and Westerterp 1985.