

DAILY ENERGY EXPENDITURE BY NESTLING HOUSE WRENS¹

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Daily energy expenditure, or field metabolic rate (FMR), of dependent chicks is important to birds since parent birds must apply all the energy which chicks use. Measurements of daily chick energy expenditure, added to the daily energy devoted to growth, is a measure of the metabolizable energy parents must supply for each chick daily. We report here on FMR of free-living House Wren (*Troglodytes aedon*) nestlings age 11–14 days, measured with doubly labeled water (DLW). Our measurements complement a study of adult House Wren FMR, in which we experimentally increased brood size to measure reproductive costs (Dykstra and Karasov, in press).

Field work was conducted in 1989 and 1990 at the Leopold Memorial Reserve, along the Wisconsin River in Sauk County, Wisconsin. The Reserve is about 570 ha, of which about two-thirds is flood-plain forest and marsh land, and one-third is upland oak-hickory-pine forest and old-field.

We studied chicks in five nests in House Wren nest boxes placed along field edges in the Reserve. Two clutches were manipulated by adding extra eggs or chicks; these two and one more nest had the male parent trapped and removed, to further increase the ratio of chicks/parent. The fourth and fifth nests were unmanipulated. Final brood sizes were 5, 5, 6, and 6. Wrens at the Leopold Reserve (and elsewhere) typically raise broods of 6–7 chicks (Dykstra and Karasov, in press), and both male and female feed the young. Details of the experimental conditions are described in our study of adult House Wrens (Dykstra and Karasov, in press).

We measured FMR in 17 chicks age 11–14 days; at this age chicks have nearly reached their fledging mass and are no longer brooded by the adults. The nestling period in House Wrens lasts 14–16 days, and hatch day was defined as day one.

We used a Hamilton glass syringe to inject chicks intramuscularly with 60 μ l of doubly labeled water containing 95% ¹⁸O and 1 mCi ³H per ml. Chicks were weighed (± 0.01 g) and some were held with siblings in paper sacks for 1 hr (Moreno et al. 1988, Karasov et al. 1992); others were replaced in the nests immediately. We collected the initial blood sample of about 100 μ l from the brachial vein. Chicks were replaced in their nests, and were removed, weighed, and blood-

sampled again 23.6 to 27.6 hr later. Blood samples were collected in two 75 μ l heparinized capillary tubes, temporarily sealed with clay, and flame-sealed in the laboratory in the evening.

Blood samples were micro-distilled by the methods of Nagy (1983a; Wood et al. 1975). The water samples were pipetted with micropipettes (Drummond "gold-label"). Two 5 μ l or 2 μ l replicates for each sample were analyzed for ³H activity by liquid scintillation. Three 7 μ l replicates of each sample were measured for ¹⁸O content by proton activation by Dr. K. Nagy's laboratory at the University of California at Los Angeles.

CO₂ production and water influx and efflux were calculated using Nagy's (1983a) equations (1, 2, and 3, respectively). Data from birds for whom the initial blood sample was omitted were analyzed by the single-sample DLW technique (Webster and Weathers 1989). Body water content was estimated based on the percent body water measured by desiccation in two 14-day-old chicks (mean = 69.4 \pm 1.7 [SEM]); adult water content in five males was 67.0 \pm 0.6; *t*-test for difference between adults and chicks; *P* = 0.376). Rates of CO₂ production were converted to kJ/d using the relationship 25.7 J/ml CO₂ for an insectivorous food (Nagy 1983b). One potential source of error in the DLW method is the incorporation of isotopes into chick tissue; however, this was not likely a problem in the current study because chicks lost mass.

Daily maximum and minimum air temperatures and precipitation are recorded at the Bradley Study Center on the Leopold Memorial Reserve. These data were used in our analysis. Because most injections and recaptures were done at midday, the maximum temperatures for the injection day and the recapture day of a given experiment were averaged to estimate mean maximum temperature for our analysis.

Mean mass of the 11–14 day old chicks was 9.6 \pm 0.2 g (Table 1, *n* = 17), with mass loss over a 1-day period averaging 0.5 \pm 0.1 g (5%). Mean FMR of wren nestlings was 28.0 \pm 1.6 kJ bird⁻¹ day⁻¹ (Table 1), which was very similar to that predicted by Weathers' (1992) allometric equation for peak nestling FMR, 29.7 kJ/day. Nestling FMR was nearly one-half the mean FMR of an adult (60.8 kJ/day, Dykstra and Karasov, in press) and 1.6 \times the 15-day-old chick standard metabolic rate (17.0 kJ/day, Kendigh 1939). Nestling water influx averaged 4.9 \pm 0.2 ml/day (or 51% of body mass; Table 1; *n* = 16).

Mean maximum temperature averaged 23.6 \pm 0.5°C, with a range of 21.5–25.5°C, while minimum overnight temperature averaged 14.2 \pm 0.6°C, with a range of 10–17°C (*n* = 4, Table 1).

Chick FMR was negatively correlated with mean

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TABLE 1. Field metabolic rate and water influx in House Wren chicks, 1989 and 1990.

Chick	Nest	Date	Brood size	Age (days)	Minimum air temperature (C)	Mean maximum air temperature (C)	Mean mass (g)	Water influx (ml/day)	FMR (kJ/day)
b23	Q	7/17/89	5	12	17	25.5	10.65	3.6	21.1
b19	Q	7/17/89	5	12	17	25.5	10.08	4.5	26.6
b20	Q	7/17/89	5	12	17	25.5	10.14	4.3	22.2
b22	Q	7/17/89	5	12	17	25.5	9.82	4.3	25.5
p21	N44	8/6/90	5	13	10	22.5	10.11	*	38.4
p22	N44	8/6/90	5	13	10	22.5	9.34	6.2	34.0
b41	N18	8/7/89	6	14	13	21.5	11.39	5.7	35.3
b44	N18	8/7/89	6	14	13	21.5	9.81	4.2	29.9
b42	N18	8/7/89	6	14	13	21.5	10.28	4.5	27.5
b43	N18	8/7/89	6	14	13	21.5	10.61	6.6	35.5
b40	N18	8/7/89	6	14	13	21.5	9.34	5.5	28.3
b39	N18	8/7/89	6	14	13	21.5	9.05	5.2	33.2
p5	SP	8/9/90	6	14	12	24.5	8.45	5.7	35.4
p2	SP	8/9/90	6	14	12	24.5	7.98	5.3	28.0
b33	BP	7/17/89	5	11	17	25.5	9.51	4.5	19.7
b29	BP	7/17/89	5	11	17	25.5	8.89	3.7	18.3
b31	BP	7/17/89	5	11	17	25.5	8.54	4.3	17.1

*. Water influx was not calculated because a small amount of water leaked out of the skin upon injection.

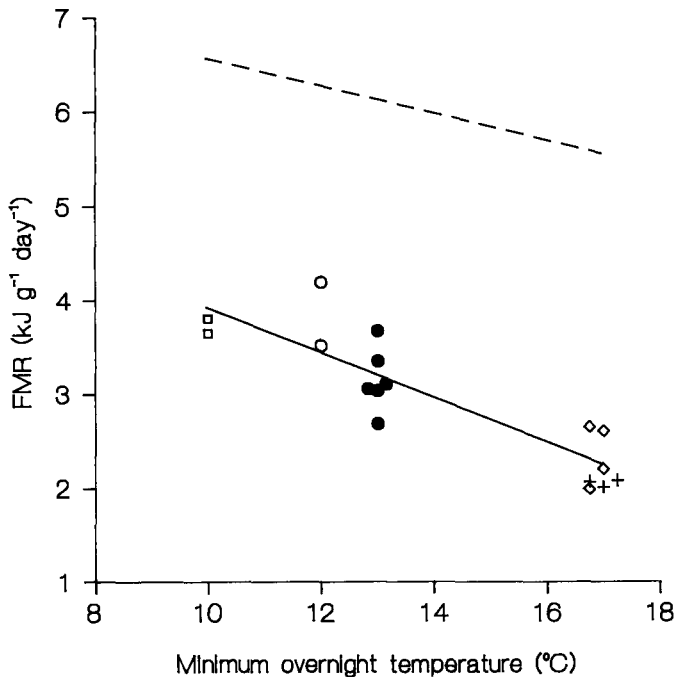


FIGURE 1. House Wren chick FMR in $\text{kJ g}^{-1} \text{day}^{-1}$ as a function of minimum overnight temperature ($r^2 = 0.787$, $P < 0.001$, $n = 17$). Least-squares linear regression slope = -0.24 ± 0.03 (SEM) $\text{kJ g}^{-1} \text{day}^{-1} \text{ } ^\circ\text{C}^{-1}$, y-intercept = 6.37 ± 0.47 . The dashed line is the relationship between FMR and minimum air temperature in adult House Wrens (slope = -0.15 ± 0.06 [SEM], y-intercept = 8.04 ± 0.87). Slopes of the lines were not significantly different (two-tailed $P = 0.295$). Symbols represent chicks of various ages. Circles, 14 days; triangles, 13 days; diamonds, 12 days; squares, 11 days. Among 14 day chicks, solid symbols represent chicks from one brood, while open symbols represent chicks from a second brood. For 13 day, 12 day and 11 day chicks, each age is represented by chicks from only one brood. Some symbols have been displaced horizontally to clarify graph; overnight minimum temperatures were 10°C, 12°C, 13°C, and 17°C on the four days of the study.

maximum temperature ($r^2 = 0.519$, $P = 0.001$), and with minimum overnight temperature ($r^2 = 0.787$, $P < 0.001$; Fig. 1). In this analysis we did not include age as a covariate, because Kendeigh (1939) showed in a controlled laboratory study that metabolic rate did not vary between House Wren chicks of age 12 and 15 days (equivalent to 11 and 14 days in our study since Kendeigh's hatch day = day 0). In addition, sibling measurements were treated as independent. Although brood FMRs cluster fairly tightly (Fig. 1), this may be due to other factors such as heritability of FMR or additional microclimate variables (solar radiation, average wind speed).

FMR also increases with decreasing air temperature in adult House Wrens (Dykstra and Karasov, in press) and another small species, the Bank Swallow (*Riparia riparia*; Westerterp and Bryant 1984), but not in several larger passerine species (Bryant and Westerterp 1983, Ricklefs and Williams 1984, Westerterp and Bryant 1984, Williams 1987). The slope of the relation in House Wrens was not statistically different between nestlings and adults (-0.241 ± 0.03 vs. -0.147 ± 0.06 $\text{kJ g}^{-1} \text{day}^{-1} \text{ } ^\circ\text{C}^{-1}$, two-tailed t -test $P = 0.295$; Dykstra and Karasov 1992, Fig. 1).

Chick FMR can be used to calculate the energy which must be collected by parents at this stage in the nesting cycle (i.e., age = 11–14 days, mass change minimal). For a brood of seven chicks at this age, each parent must collect enough food for itself and the needs of 3.5 chicks:

$(28.0 \text{ kJ day}^{-1} \times 3.5) + 60.8 \text{ kJ day}^{-1} = 158.8 \text{ kJ day}^{-1}$. Assuming a metabolizable energy coefficient equal to that measured in captive adult wrens eating crickets (0.72, Dykstra and Karasov 1992), we calculate from the above requirements that an adult wren collects an average 221 metabolizable kJ day^{-1} . If wild insects' energy content and water content approximately equal those of domestic crickets, (22.8 kJ/g dry mass, Dykstra and Karasov 1992) then each adult wren must collect 9.7 g dry mass of insects day^{-1} , or 38.8 g wet mass day^{-1} to maintain itself and its nestlings. (We do not know how many hours per day the wrens foraged, but the maximum daylength during the breeding season was about 16 hr.) Similar calculations for other species in which FMR has been measured with DLW indicate that breeding Yellow-eyed Juncos (*Junco phaeonotus*, 19.5 g) collect approximately 240 metabolizable kJ/day (Weathers and Sullivan 1989, 1991) and that breeding Savannah Sparrows (*Passerculus sandwichensis*, 17.3 g) collect 170 kJ/day (Williams and Nagy 1985, Williams and Prints 1986).

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