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NESTING ENERGETICS OF HOUSE WRENS (*TROGLODYTES AEDON*) IN RELATION TO MAXIMAL RATES OF ENERGY FLOW

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ABSTRACT.—We tested the hypothesis that brood size in House Wrens (*Troglodytes aedon*), which have a mean mass of 10.6 g, is confined by digestive limits to maximal rate of energy flow in parents feeding nestlings. Using doubly-labeled water (DLW), we measured field metabolic rate during feeding of nestlings (FMR_r), tested whether it increased with brood size, and compared it with the wrens' near-maximal rate of intake, digestion, and assimilation measured in the laboratory. To expand the range of House Wrens' effective brood sizes (i.e. brood size/parent), we manipulated some brood sizes by removal of the male parent or by addition of extra chicks or eggs. The rate of nest visits by parent wrens was positively correlated with mass of chicks ($P < 0.001$). Various measures of brood size were regressed against FMR_r. However, when brood size and overnight minimum air temperature were entered together in a stepwise multiple-regression model, only minimum air temperature was significantly related to FMR_r ($P = 0.013$, $r^2 = 0.201$). Mean FMR_r (60.8 ± 2.0 kJ/day) was lower than the near-maximal rate of intake, digestion and assimilation measured in the laboratory (92.7 kJ/day). Therefore, we reject the hypothesis that brood size is limited by digestive constraints on maximum metabolic rate in House Wrens. *Received 6 November 1991, accepted 29 October 1992.*

FACTORS THAT limit clutch size in birds can influence an individual's reproductive success and, thus, are important ecologically. Several hypotheses attempt to explain the limitation of clutch size (Stearns 1976:12, Murphy and Haukioja 1986:141). One involves an energetic constraint on brood size and is based upon the ideas that: (1) parental field metabolic rate during reproduction (FMR_r) increases with increasing numbers of chicks (Drent and Daan 1980:242, Yom-Tov and Hilborn 1981); and (2) there is a physiological limit to the parent's FMR_r that is approached in the field so that maximal metabolic rate sets a limit on brood size (Masman et al. 1989, Peterson et al. 1990).

If maximal sustainable metabolic rate is to be a limiting factor on brood size, FMR_r must increase with brood size. The relationship of FMR_r to brood size or mass is not consistent among species. Parental FMR_r increased with number of young in Savannah Sparrows (*Passer sandwichensis*; Williams 1987) and adult male House Martins (*Delichon urbica*; Hails and Bryant 1979), but has not been shown to be related to brood size in at least seven other species of birds (reviewed by Bryant 1988). We tested the hypothesis that FMR_r will increase with brood mass (and, hence, limits to energy flow could potentially limit brood size).

The second part of the hypothesis is difficult to evaluate, in part because no upper benchmark (i.e. maximum metabolic rate) has been described. In fact, determinants of maximal rate of energy flow are unknown, although maximal rate of energy flow has been proposed to limit reproductive effort (Masman et al. 1989) and various other ecological parameters (Root 1988). Maximal rate of intake, digestion and assimilation may represent maximal energy flow (Kirkwood 1983, Weiner 1992), but it is possible that factors limiting energy expenditure (e.g. mobilization of nutrients, metabolism by tissues) might determine maximal rate of energy flow (Karasov 1986, Peterson et al. 1990).

Some investigators have proposed an upper benchmark of three to five times SMR (Karasov 1990:415), or three to six times fasting metabolic rate (Kirkwood 1983), but there have been few studies designed to experimentally force birds to their maximal rates. Two allometric analyses suggested that the FMR of at least some birds may approach these proposed maximal rates. Karasov (1990:415) found that estimates of maximal rate of energy intake averaged 36% higher than measures of FMR_r in breeding birds. Masman et al. (1989) showed with data from 30 species that maximum sustainable rates of energy flow may be more limiting to FMR_r in small birds than in large birds because the two parameters scale differently with body mass. The smallest bird species (other than hummingbirds) for which FMR_r has been measured are the House Wren (10.6 g; this study) and the Sand Martin (*Riparia riparia*; 12.6 g; Turner 1983).

Additionally, even if an upper benchmark exists, it is not clear how close to the limit a bird must come to be influenced by it. Animals most likely maintain a "safety margin" (sensu Toloza et al. 1991), which may be defined as the amount by which their capacity for energy intake and expenditure (i.e. maximal rate) exceeds their typical daily expenditure (during reproduction). The adaptive significance of such a margin for House Wrens might be to permit an increase in expenditure if the temperature becomes unusually cold or if a nearby food resource is depleted.

In a separate laboratory investigation, we attempted to find the upper benchmark by determining the near-maximal rate of intake, digestion and assimilation in House Wrens (Dykstra and Karasov 1992). In the current study, we examined how closely birds approach their upper benchmark by comparing FMR_r in House Wrens to their energetic ceiling for intake, digestion and assimilation. FMR_r and maximal rates of energy flow have not been compared within a species (Masman et al. 1989).

Of course, there are measures other than comparison to maximum metabolic rate that can be used to evaluate energetic stress; one of these is parental mass loss. We also analyzed mass loss, but did not focus on it, since Freed (1981) suggested that mass loss in breeding female House Wrens may be adaptive, rather than reflect energetic stress.

We assume that the nestling stage is the energetic bottleneck that constrains reproductive output in House Wrens. It may seem *a priori* that other stages, such as egg-laying or fledgling stages, might be important bottlenecks for wrens. However, experimental studies have shown that House Wrens are indeterminate layers early in the summer and may lay up to 32 eggs in succession (Kendeigh et al. 1956, pers. observ.); hence, it appears that egg laying is not a constraining stage for wrens. The postfledging stage may be more important, as it is in Yellow-eyed Juncos (*Junco phaeonotus*; Weathers and Sullivan 1989), and it has not been studied in House Wrens.

Clearly, if FMR_r varied with brood size and were near the maximal rate of energy flow (i.e. intake and/or expenditure), the physiological limits to maximal rate could be limiting reproductive output (brood size). Alternatively, if FMR_r were substantially below the maximal rate of energy flow, we could reject the hypothesis that physiological limits to maximal rate of energy could limit reproductive output. However, between these two alternatives lies a "gray area" in which one cannot determine whether the hypothesis should be rejected; in this zone one could invoke the idea of "safety margins" and examine the size of these margins.

METHODS

Study site and species.—Fieldwork was conducted in 1989 and 1990 along the Wisconsin River at the Leopold Memorial Reserve, near Baraboo, Wisconsin. The Reserve is about 570 ha, of which about two-thirds is flood-plain forest and marsh lands, and one-third is upland oak-hickory-pine forest and old fields.

The House Wren is a 10- to 11-g monomorphic passerine that is strictly insectivorous. An edge species, the House Wren is tolerant of human disturbance and commonly nests near residences. Single House Wren chicks become strictly homeothermic at eight to nine days of age (Kendeigh and Baldwin 1928, Dunn 1976), although broods of five or six chicks become effectively homeothermic on days 3-4 (Dunn 1976). For more details of the wren's life history, see Bent (1948:113) or Kendeigh (1941).

Nests.—One hundred nest boxes (most with dimensions 14 cm × 10 cm × 12.5 cm deep, with a 2.5-cm diameter entrance hole) were nailed to trees in open forested areas and along edges of fields at a height of 1.1 to 1.4 m. Later in the season, we located wren nests built in the Reserve's bluebird boxes (14 cm × 14 cm × 28 cm deep) that were located in open fields; these nests also were used in the study. Both types of boxes had doors that could be closed from a distance, allowing investigators to trap the birds inside.

Nest boxes were checked twice per week and more often when eggs were close to hatching. Broods were aged such that day 1 was the day all or most of the eggs hatched (if equal numbers of eggs hatched on two consecutive days, the day the first eggs hatched was designated day 1).

At most nests, both the male and female fed the chicks, as observed by Kendeigh (1941). Of 17 nests in 1989 at which we observed feeding, 15 had a male feeding the chicks until at least day 5, when we trapped and removed three males; 12 nests had males feeding until at least day 9. Of six nests in 1990, all had a male present until at least day 5, when males were trapped. Others have reported that the feeding effort of the male varies among nests (Freed 1981, Finke et al. 1987).

Brood-size manipulation and FMR_r.—To study the effect of brood size on FMR_r, we manipulated the brood size per parent in five nests in 1989 and six nests in 1990. Brood size was increased by transferring eggs or chicks from donor nests to experimental nests. We removed one to three eggs at a time from the donor nest (always leaving at least one egg in an attempt to induce donor females into laying extra eggs (Kendeigh et al. 1956:51). The donor eggs were added to nests with at least three (unincubated) eggs. In six cases, young chicks were transferred to experimental nests with chicks of similar age and weight, at least one week before the FMR_r of parents was measured.

At the manipulated nests, males were captured and removed about three days before the FMR_r was to be measured, so the females were required to care for the entire brood. Males were brought to the University of Wisconsin-Madison for a laboratory study. At one nest in 1989 and one in 1990, the males were trapped and removed, but no extra chicks or eggs were added.

FMR_r of 19 adults was measured when broods were age 7 to 14 days. FMR_r in one male and four females was measured twice, once when broods were seven to nine days and again four to five days later, in an attempt to determine if FMR_r increased in individuals as brood mass increased. All chicks in each brood were weighed to the nearest 0.01 g on a portable electronic balance (Ohaus). Birds were captured between 0700 and 1500 CST; we captured both adult birds, if possible, or just the female. Birds were sexed by the presence or absence of the brood patch, weighed to the nearest 0.01 g, and banded with a numbered, colored, plastic band (A.C. Hughes, Hampton Hills, Middlesex, Great Britain).

Each bird was injected in the pectoralis with 60 μL doubly-labeled water containing 95% ^{18}O and 1 mCi ^{3}H per ml. After a 1-h equilibration period (Moreno et al. 1988), the initial blood sample of about 100 to 150 μL was taken from the brachial vein (occasionally the jugular). The initial sample was omitted in 16 birds. Blood samples were collected in 75-μL heparinized capillary tubes, temporarily sealed with clay, and flame-sealed in the laboratory in the evening.

Birds were released, and recaptured about 24 h later ($\bar{x} = 23.5 \pm$ SE of 0.3 h, range 20.4-26.8 h), when the final blood sample was obtained. Recapture sometimes required the use of mist nets and House Wren song recordings, when birds would not enter the nest box in the presence of the investigators.

Feeding behavior.—Feeding behavior of color-banded adult wrens at the nest was observed, typically the day following recapture. Observations were made for 1.5 h, between 0700 and 1200. An observer 20 to 30 m away from the nest box recorded the number of times a parent entered the box. Although we attempted to determine the percentage of visits made by the male and by the female at nests for which both were present, we could identify the sex by band color or behavior for only 70% of the visits.

Weather.—Daily maximum and minimum temperatures, as well as precipitation, were recorded at the Bradley Study Center on the Leopold Memorial Reserve. Because most injections and recaptures were done in midday, the maximum temperatures for the injection day and the recapture day of a given experiment were averaged to obtain a mean maximum temperature for our analysis.

Sample analysis and calculations.—Blood samples were microdistilled by the methods of Nagy (1983a:21). The water samples were pipetted with micropipettes (Drummond "gold-label"). Two 5- or 2-μL replicates for each sample were analyzed for ^{3}H activity by liquid scintillation. Three 7-μL replicates of each sample were measured for ^{18}O content by proton activation at K. A. Nagy's laboratory (University of California-Los Angeles).

CO_2 production, water influx, and water efflux were calculated using Nagy's (1983a:32) equations (1, 2, and 3). When initial blood samples were omitted, data were analyzed by the single-sample DLW technique (Webster and Weathers 1989). Body-water content was estimated based on the percent body water measured in five males by drying ($\bar{x} = 67.0 \pm$ SE of 0.6%). CO_2 production rates were converted to kJ g^{-1} d^{-1} using the relationship 25.7 J/mL CO_2 for an insectivorous food (Nagy 1983b:28). For birds that lost more than 4% of their initial body mass ($n = 3$; other mass losses of more than 4% were suspect due to time of weighing; Table 1), we calculated metabolic rate following Weathers and Sullivan (1989). Because errors were small ($\bar{x} = 0.9 \pm 0.4\%$) we used the uncorrected values in statistical analyses.

Metabolic water production of each wren was calculated using the conversion factor 0.026 μL/J metabolized (Schmidt-Nielson 1990:333). In order to make our results comparable with those of others, we also normalized FMR_r to standard metabolic rate (SMR; Koteja 1991). We calculated the House Wren's SMR during the inactive phase as the standard metabolism during the active phase (1.14 kJ/h; Kendeigh 1939) divided by 1.24 (Aschoff and Pohl 1970).

We used t-tests for simple comparisons. Regressions and ANCOVAs were computed using SYSTAT (Wilkinson 1988:457). One-tailed tests were used to test the *a priori* prediction that FMR_r increases with brood size; two-tailed tests were used elsewhere. The 0.05 probability level was considered significant.

RESULTS

Nests.—In Table 2, nests are divided into early and late breeding periods as described by Kendeigh (1941) and Freed (1981). The early period includes nests in which the clutch was completed before 29 June; the late-period

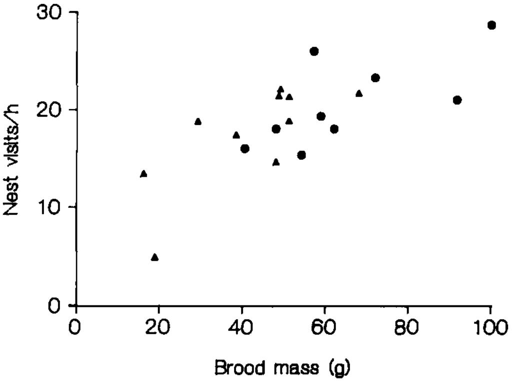

Fig. 1. Total nest visits per hour by adult House Wrens in 1989 and 1990 as a function of increasing brood mass ($r^2 = 0.551, P < 0.001$). Triangles represent natural nests and circles manipulated nests.

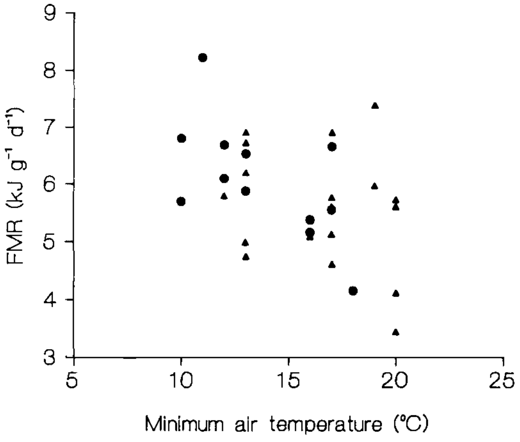

Fig. 2. FMR_r (in kJ g^{-1} day^{-1}) in adult House Wrens as a function of overnight minimum air temperature in 1989 and 1990 ($r^2 = 0.201, P = 0.013$, slope of -0.147 ± 0.056, intercept of 8.038 ± 0.870). Circles represent manipulated nests and triangles natural nests.

clutches were completed after 6 July. The numbers of natural clutches and broods in the late part of the season were small due to nest manipulations during July and August. There were no unmanipulated clutches studied in 1990.

Feeding behavior.—Total parental visits to the nest among both natural and manipulated nests averaged 18.9 ± 1.2 visits/h ($n = 19$ observations at 16 nests, range 4.8–28.7). The total number of parental visits to the nest per hour varied significantly with increasing brood mass ($r^2 = 0.551$, one-tailed $P < 0.001$; Fig. 1) and with brood mass per number of parents ($r^2 = 0.466$, $P < 0.001$), whether brood mass was evaluated simply in grams or as "metabolic brood mass" (i.e. brood $mass^{0.66}$; Hails and Bryant 1979). The number of visits per hour also was significantly related to the age of chicks ($P = 0.041$, $r^2 = 0.169$), the number of chicks in the nest ($P = 0.027$, $r^2 = 0.202$), and the number of chicks/number of parents ($r^2 = 0.386$, $P = 0.003$).

The rate of visitation by House Wrens feeding nestlings falls within the range found in other studies (255 visits/day for 13- to 15-day-old chicks, or about 17/h, depending on day length; Kendeigh 1952:52, Freed 1981). We take this as evidence that our handling of the birds did not appreciably disturb their normal behavior.

Parental mass balance.—The mean mass of House Wrens was 10.53 ± 0.12 g ($n = 31$; males 10.51 ± 0.12; females 10.59 ± 0.33, $P = 0.817$). Mean mass change over the one-day release-recapture period was −0.15 ± 0.08 g, which was not significantly different from 0 ($t = 1.85$, df $= 22$, $P > 0.05$). Mean body mass change was not significantly correlated with any measure of brood size.

Energy expenditure and brood size.—Repeat measures of FMR_r for five individuals were treated as separate measures. The mean FMR_r for parent House Wrens ($n = 7$ males and 23 females) was 5.77 ± 0.19 kJ g^{-1} day^{-1} (60.8 ± 2.0 kJ/day) with a range of 39.4 to 84.0 kJ/day (Table 1). Male FMR_r (56.2 ± 3.2 kJ/day) did not vary significantly from that of females (62.2 ± 2.3 kJ/day; t-test, $P = 0.156$), whether compared on a whole-animal basis or corrected for body mass. Therefore, we combined the sexes in the regression analyses below. Mean FMR_r was not statistically different in 1989 and 1990 ($P = 0.151$), so years were combined. Mean FMR_r in natural and manipulated nests did not vary (among natural nests, $\bar{x} = 58.4 \pm 2.5$ kJ/day; among manipulated nests, $\bar{x} = 64.3 \pm 3.0$; $P = 0.145$). Means and variances of FMR_r did not differ between birds measured with the single-sample technique and those with a double sample ($P = 0.684$ and 0.279, respectively).

FMR_r in kJ/day was inversely associated with overnight minimum temperatures ($r^2 = 0.136$, two-tailed $P = 0.045$, $n = 30$), as was FMR_r in kJ g^{-1} day^{-1} ($r^2 = 0.201, P = 0.013$; Fig. 2). FMR_r (kJ/day) was not significantly associated with mean maximum air temperature ($P = 0.327$) or the amount of precipitation ($P = 0.271$).

Because FMR_r was significantly related to minimum air temperature and laboratory stud-

TABLE 1. Summary of adult birds injected in 1989 and 1990.

Box	Bird	Sex	Date	No. chicks	Age chicks (days)	Brood mass (g)	No. parents	DS or SS[a]	FMR (kJ/day)	Mass change (g/day)	Mean mass (g)	H_2O influx (mL/day)
Natural (1989)												
4	Y1	F	19 June	7	9	—	2	1	69.8	—	10.14	10.3
17	Y3	F	22 June	6	8	49.4	2	2	39.4	0.02	11.51	9.0
17	R3	M	22 June	6	8	49.4	2	1	59.3	—	10.61	8.9
BA	Y4	F	22 June	7	10	70.2	1	2	65.5	0.09	11.46	11.0
11	Y5	F	22 June	8	10	74.5	2	2	42.8	−0.15	10.43	9.4
PP	R7	M	29 June	4	8	34.1	1	2	64.8	0.24	11.22	11.3
16	Y8	F	2 July	7	8	50.0	2	2	60.2	0.07	10.80	10.2
YY	Y10	F	10 July	5	9	45.5	2	2	72.9	−0.15	9.90	11.4
YY	R10	M	10 July	5	9	45.5	2	2	67.5	−0.27	11.33	11.0
Q	Y11	F	13 July	5	8	42.5	2	1	64.6	−0.11[b]	9.57	9.1
Q	R11	M	13 July	5	8	42.5	2	2	52.1	—	10.50	9.5
Q	Y11	F	17 July	5	12	50.6	2	1	55.9	0.17	9.74	9.3
BPN	Y12	F	13 July	6	7	49.9	2	2	52.0	−0.93[b]	10.54	8.4
BPN	R12	M	13 July	6	7	49.9	2	2	57.5	−1.32[b]	9.30	7.8
BPN	Y12	F	17 July	5	11	47.0	2	1	78.6	−0.27	11.42	10.6[c]
BPN	R12	M	17 July	5	11	47.0	2	1	44.2	0.73	9.64	7.8[c]
13	Y20	F	10 August	5	9	44.3	1	2	52.3	−0.18	10.34	9.3
13	Y20	F	14 August	5	13	52.4	1	1	52.7	−0.60	10.33	9.6
Manipulated (1989)												
CC	Y2	F	7 August	11	10	97.5	2	1	66.0	−0.68	11.23	8.5
SS	R16	M	27 July	1	10	10.0	2	2	48.1	−0.47	11.60	10.1
18	Y17	F	7 August	6	14	63.9	1	1	69.8	−0.12	10.69	12.8
YY	Y18	F	10 August	6	7	36.4	1	1	55.1	−0.34	10.70	9.3
YY	Y18	F	14 August	6	11	57.3	1	1	72.6	−0.94	10.91	10.2
40	Y19	F	14 August	6	10	60.0	1	1	57.1	−0.41[b]	10.08	10.3[c]
Manipulated (1990)												
CC	Y21	F	11 June	5	10	49.4	1	2	73.0	−0.22	10.91	11.7
BA	Y4	F	18 June	10	10	99.6	1	2	67.5	—	11.08	11.2
BA	Y4	F	21 June	10	13	—	1	1	—	−0.22	10.77	16.3
A	Y24	F	2 July	6	10	58.8	1	2	84.0	−0.3	10.21	11.6
YY	Y23	F	24 July	7	9	58.9	1	1	54.0	−0.12	10.04	13.2
SP	Y25	F	6 August	8	11	74.7	1	1	67.8	−0.08	9.96	13.9[c]
48	Y27	F	6 August	8	10	67.8	1	1	56.5	−0.38	9.91	12.4

[a] DS or SS refers to the double-sample (2) or single-sample (1) DLW method.

[b] Mass change may be inaccurate because one or both masses taken before 0900 CST, and birds are lighter in morning than in afternoon.

[c] Water flux may be high by 6% or more because a small amount of water leaked from bird after injection. The initial ^3H was estimated (on basis of mass) rather than measured in initial blood sample.

TABLE 2. Reproductive characteristics of House Wren population at Leopold Memorial Reserve, 1989.

	Clutch size			Brood size		
	n	Mean	Mode	*n*	Mean	Mode
Total	26	6.46	7	17	5.76	7
Early[a]	23	6.61	7	13	5.92	7
Late[b]	3	5.33	5	4	5.25	6

[a] Before 30 June.

[b] After 6 July.

ies have shown the dependance of energy expenditure on temperature, we analyzed the effect of brood size on FMR$_r$ (kJ g^{-1} day^{-1}), with weather as a covariate. We fitted the overnight minimum temperature with various measures of brood size as covariates in a linear-regression model. Of the various measures (number of chicks, chick age, brood mass, number of chicks/number of parents, and brood mass/number of parents), brood mass/parent had the greatest statistical significance and was ecologically the most relevant. The model indicated that there was no interaction between the variables brood mass/parent and overnight minimum air temperature (two-tailed $P = 0.994$). When fitted without the interaction term in stepwise regression, the variable brood mass/parent was not significant (two-tailed $P = 0.376$), while the variable minimum air temperature was significant and was included in the model (two-tailed $P = 0.013$), and the entire model was significant (overall $P = 0.013$; $r^2 = 0.201$; $n = 30$). Simple linear regression revealed that overnight minimum temperature was inversely correlated to brood mass/parent ($P = 0.037$, $r^2 = 0.146$). Hence, there was a coincidental relationship between overnight minimum temperatures and brood mass, but not a meaningful relationship between FMR$_r$ and brood mass/parent.

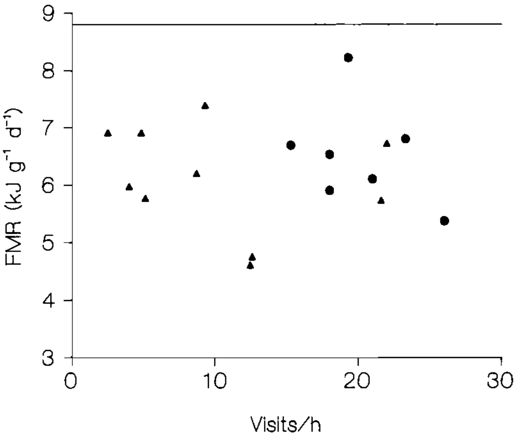

Fig. 3. FMR$_r$ as a function of number of nest visits per hour ($P = 0.908$). Triangles represent natural nests, and circles manipulated nests. Line at 8.8 kJ g^{-1} day^{-1} represents the near-maximal rate of intake, digestion, and assimilation measured in House Wrens in the laboratory.

Reproductive "cost" often cannot be demonstrated among natural nests, but has been demonstrated for manipulated nests (Partridge and Harvey 1985, 1988, Reznik 1985, Gustafsson and Sutherland 1988). However, in our study the results for manipulated nests alone ($n = 12$) were similar to those for all nests; overnight minimum temperature was significantly related to FMR$_r$ ($P = 0.017$, $r^2 = 0.381$), while brood mass/parent was not.

Energy expenditure and nest visits.—The number of visits per hour was not related to kJ/day expended by the parents (two-tailed $P = 0.908$, $n = 17$ measurements; Fig. 3). At boxes where both parents fed chicks, the total visits per hour was proportioned between the sexes. The sex of the bird visiting was known for most visits

TABLE 3. Water influx data for House Wrens (1989 and 1990).[a]

	1989			1990		
	Rainy days	No-rain days	*P*	Rainy days	No-rain days	*P*
n	6	16		4	3	
Mass (g)	10.56 ± 0.30	10.62 ± 0.15	0.842	10.57 ± 0.72	10.03 ± 0.13	0.325
H_2O influx (mL/d)	10.5 ± 0.6	9.6 ± 0.2	0.208	12.8 ± 1.2	12.4 ± 0.5	0.754
Metabolic H_2O produced (mL/d)	1.6 ± 0.1	1.5 ± 0.1	0.479	2.0 ± 0.5	1.7 ± 0.2	0.663
Other influx (food and drink; mL/d)	9.0 ± 0.6	8.1 ± 0.2	0.227	10.9 ± 0.8	10.7 ± 0.7	0.903

[a] P-values are for significance of difference between rainy and no-rain days. "Other influx" is subtraction of metabolic water from total water influx, and is obtained through diet and drinking. Water influx was significantly higher in 1990 ($P = 0.004$). Water efflux is not reported because water influx and efflux were nearly equal.

(70% on average); the ratio of male visits/female visits for those visits where sex was known was assumed to be equal to the ratio of male visits/female visits for all visits.

Water influx.—Water influx was correlated to FMR_r (Fig. 4). Average water influx is reported in Table 3. Water influx on rainy days did not differ statistically from that on days without precipitation (Table 3); this result was expected because drinking water was readily available to wrens.

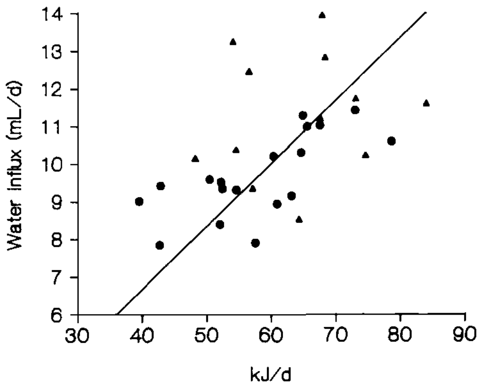

Fig. 4. Water influx in adult House Wrens as a function of FMR_r. Water influx significantly correlated to energy expenditure ($r^2 = 0.975$, $P < 0.001$). Line indicates: water influx (mL/d) = 0.167FMR_r (kJ/day). Triangles represent natural nests and circles manipulated nests.

DISCUSSION

Weather.—For House Wrens, FMR_r increased with decreasing air temperatures, a relationship rarely observed in field studies. In other studies FMR_r increased with decreasing temperatures only for the smallest avian species studied (Westerterp and Bryant 1984), while numerous studies have not shown such a relationship (Hails and Bryant 1979, Bryant and Westerterp 1980, Ricklefs and Williams 1984, Westerterp and Bryant 1984, Williams 1987). Interestingly, the slope of the relationship between overnight air temperature and FMR_r (-0.147 ± 0.056 kJ g^{-1} day^{-1} $°\text{C}^{-1}$) is nearly identical to that for energy assimilated/day and air temperature in the laboratory (-0.150 ± 0.060 kJ g^{-1} day^{-1} $°\text{C}^{-1}$; Dykstra and Karasov 1992) and only 10% higher than the conductance value calculated from Kendeigh's (1939) measurements of resting metabolism as a function of temperature (-0.133 ± 0.020 kJ g^{-1} day^{-1} $°\text{C}^{-1}$).

Does adult maximal energy flow limit brood size?—For House Wrens, we reject the hypothesis that FMR_r and, hence, brood size may be limited by a digestive limit to the maximum rate of energy flow. First, if maximum rate of energy flow is to limit brood size, then FMR_r must be positively correlated with brood size. Although there seemed to be evidence that FMR_r increased with increasing brood mass, further analysis revealed that this apparent relationship was merely coincidental with the relationship of FMR_r to overnight minimum temperatures. The relationship between FMR_r and brood size seems to vary among species. In Bryant's (1988) summary of nine studies, four species showed increased FMR_r in relation to increased brood number or increased numbers of nest-visits per hour or both: European Starlings (*Sturnis vulgaris*; Westerterp and Drent 1986), Pied Kingfishers (*Ceryle rudis*; Reyer and Westerterp 1985), House Martins (Bryant and Westerterp 1983), and female Savannah Sparrows (Williams 1987). Other species showed no relationship (Bryant et al. 1984, Ricklefs and Williams 1984, Westerterp and Bryant 1984, Williams and Nagy 1985, Bryant 1988). Bryant (1988) noted that studies showing no relationship had small sample sizes, while those where FMR_r was correlated with brood size had sample sizes greater than 23. Despite a sample size of 30, we found no strong relation between FMR_r and nest visits per hour (Fig. 3). We did find a relationship between feeding visits and brood mass or size (Fig. 1), as have other investigators (Bryant and Gardiner 1979:293, Hails and Bryant 1979, Freed 1981, Williams 1987).

There are both biological and technical explanations for the lack of relationship between nest visits and FMR_r. First, wrens may compensate behaviorally for the increased expenditure of extra flights by decreasing expenditure in some other activity. Second, the effect of flying extra trips on the energy budget of adult wrens may be too small to be resolved. Third, all observations were made during the same short time period (0700–1200); individual wrens may have different daily periods of increased activity. Fourth, we may have incorrectly divided the "unknown" nest visits between male and female; there may have been systematic errors (e.g. at some nests the male and female have identifiably different behaviors for approaching and entering the nest box; in some cases, more female visits than male visits may have been classified as "unknown" because of the rapid way in which the female entered the box).

Thus, we did not show that FMR_r varied with brood size. Additionally, comparison of FMR_r with maximal rates of intake, digestion and assimilation leads us to reject the energetics hypothesis. Although Peterson et al. (1990) have suggested that limits to rate of energy flow might limit species' reproductive output, and Masman et al. (1989) showed that smaller species, thus, are more likely to be limited than larger birds, digestive limits to energy intake and assimilation do not seem to limit brood size in House Wrens. The FMR_r of House Wrens was considerably below the mean near-maximum rate of intake, digestion and assimilation that we measured in the laboratory (92.7 ± 6.6 kJ/day) in House Wrens exposed to cold and forced to exercise. The increased feeding rate of the laboratory wrens was accompanied by, and perhaps permitted by, a 21% increase in small intestine length (Dykstra and Karasov 1992). It may seem incongruous to compare field metabolic rates measured in the breeding season with those measured under conditions of cold and exercise, but cold and exercise should be seen merely as the most practical device for forcing a sustained elevated metabolic and feeding rate. Overall, the result of our comparison is that in the smallest passerine in which FMR_r has been measured, maximal rates of digestion and assimilation, which may represent maximal rates of energy flow, did not limit FMR_r. One might argue that our manipulated clutches represented unrealistic conditions ecologically, but even if so, our overall conclusion that the effect of additional chicks was small remains unchanged. Mock (1991) also concluded for Western Bluebirds (*Sialia mexicana*) that additional chicks had only a small effect on daily energy expenditure. FMR_r of larger species may be even further below their maxima and limits to maximal rates of energy flow may be important only to species with a mass less than 10 g (Masman et al. 1989).

FMR_r of House Wrens (61 kJ/day or 2.8SMR) was close to Masman et al.'s (1989) allometrically-predicted FMR_r for breeding birds (64.1 kJ/day for a 10.6-g bird) and was similar to other breeding passerines in the wild (mean 3.4SMR, range 1.9–5.0SMR; Weathers and Sullivan 1989: 236). However, the near-maximum rate of intake, digestion and assimilation for the wrens was 43% greater than Masman et al. (1989) predicted using Kirkwood's (1983) equation (i.e. 64.9 kJ/day). The Kirkwood equation was based on a few studies in which animals were held in energetically expensive conditions; these studies were not specifically designed to measure maximal energy flow and, therefore, the values obtained were not necessarily maximal.

Additional evidence that birds' FMR_r may be far below maximal rates is found in Williams' (1987) observations of breeding Savannah Sparrows. Even when brood sizes were doubled, experimentally widowed females were able to feed chicks at twice the level of paired birds (with feeds per hour being positively correlated with FMR_r). Single wrens also fed chicks at the same level of total feeds per hour provided by paired birds.

Our discussion has focused on the energetic demands of feeding nestlings, but there is evidence that energetic demands on parents may be greater in the postfledging period. Weathers and Sullivan (1989:233) found FMR_r in parent Yellow-eyed Juncos to be 14% higher in the postfledging stage than when birds were feeding nestlings, although the authors attributed most of the increase to higher costs of thermoregulation. If House Wrens similarly increased their metabolic rate during the postfledging stage, the average FMR_r would have been 68 kJ/day (3.1SMR), still well below the near maximal rate of digestion/assimilation of 93 kJ/day.

Other hypotheses of brood-size limitation.—Several other hypotheses for brood-size limitation have been proposed. Stearns (1976) suggested that clutch sizes are limited by the number of eggs that birds can successfully incubate. However, this was rejected by Baltz and Thompson (1988) in an experimental study.

Another hypothesis involves a positive correlation between clutch size and adult mortality. Therefore, lifetime reproductive success may be optimized by laying a clutch smaller than the most productive size (Charnov and Krebs 1974). Recent studies have expanded this hypothesis to include not only adult mortality, but also other factors that reduce reproduction (Finke et al. 1987). Large clutch sizes have been hypothesized to be positively correlated with lower chick mass at fledging, lower fledgling survival, reduced chance of initiating a second brood (in multiple-brooded species), and decreased adult body "condition." Finke et al. (1987) found no evidence that raising an additional chick affected future reproductive success of females or the mass of fledglings, although it increased the number of fledglings produced. Conversely, Robinson and Rotenberry (1991) found that, although experimentally enlarged House Wren nests produced more fledglings than control nests, chicks reared in enlarged nests were significantly lighter than chicks produced at control nests. We also found evidence that nestlings reared in enlarged nests were lighter, although our results were not statistically significant due to small sample size (below).

An alternative hypothesis of brood-size limitation states that birds lay clutches smaller than the most productive size in a "bet-hedging" strategy. Among natural House Wren nests, the most productive clutch size is larger than the most common clutch size (Finke et al. 1987, Robinson and Rotenberry 1991). Because environmental conditions vary temporally, and making too large a reproductive effort can result in disaster (death of all young and maybe parents), birds should be conservative in clutch size.

We suggest two environmental factors that may be unreliable against which the wrens might be "hedging their bets." The first is food (insect) availability, which can be influenced by weather (Taylor 1981:1, Bart and Tornes 1989). In a male-removal study with House Wrens, Bart and Tornes (1989) found that in three breeding periods out of four the presence of a male feeding the chicks did not change the survivorship of the nestlings. However, in the fourth period, survivorship of nestlings with only a female feeding them was 63% lower than that in nests with two parents. Bart and Tornes (1989) qualitatively related the fourth period to a time of cold, wet weather and, hence, low insect availability. They concluded that male help may benefit the young only during unfavorable periods. Thus, food availability might be limiting House Wren reproductive output at some times. Conceivably, clutch size might be adjusted to the poorer conditions, so that under "average" conditions wrens can fledge extra chicks (Finke et al. 1987), and the help of the male is not needed (Baltz and Thompson 1988).

Additional evidence that food availability might be a crucial factor on which House Wrens may "hedge their bets" was our observation that nest-provisioning rate increases in relation to brood mass (Fig. 1) and brood size. It is likely that there is some upper limit of food delivery that cannot be exceeded. An important factor that may limit nest provisioning is food availability (Martin 1987:470).

A second uncertainty against which House Wrens might be "hedging their bets" is male desertion. Although we found that most males (89%) helped females feed chicks, there were some nests at which no male was ever observed. Kendeigh (1941) found that 17% of males deserted the nest before the chicks fledged (Bart 1990). Others noted that the males fed chicks sporadically for the first few days only, and fed later only if the female disappeared (Freed 1981), or that males were more difficult to catch because they visited nests infrequently (Finke et al. 1987). Thus, clutch size might be adjusted to the number of chicks that the female can raise alone, if necessary. This would represent a conservative, "bet-hedging" strategy.

Upper limit to food-collection rate.—Our experimental manipulations also allowed calculation of an upper limit to food collection rate for adult wrens. At two manipulated nests, experimentally widowed females with 10 chicks each were unable to provide enough food for all, as demonstrated by successive deaths of three chicks at one nest and four at the other. A male at a natural nest was able to raise only six of eight chicks after his mate was accidentally killed. Another experimentally widowed female was probably unable to raise 10 chicks successfully. The chicks were somewhat lighter than usual (mean mass = 7.9 g at day 14) and experienced a mass loss of 14% between days 11 and 14. Similarly, a male at an experimental nest was abandoned by his mate on day 11, and raised 10 of 11 chicks at least two more days, but the chicks experienced similar mass loss (10% in two days) and were lighter than average (mean mass = 8.4 g at day 13). The chicks' masses and mass losses were not significantly different from those at natural nests, possibly due to small sample size.

Thus, we estimated that a single wren could not raise 10 chicks successfully (or perhaps fewer), and we conservatively calculated an upper limit to food collection as the food required to sustain 10 chicks' daily energy expenditure, plus adult daily energy expenditure. At days 11–14 (when chick mass gain is minimal), chicks expend 28.0 ± 1.6 kJ bird^{-1} day^{-1} (Dykstra and Karasov 1993). Thus, we calculate metabolizable energy required as

$$(10 \times 28.0 \text{ kJ/day}) + 60.8 \text{ kJ/day} = 340.8 \text{ kJ/day}$$

metabolized. Assuming a metabolizable energy coefficient equal to that measured in captive adult wrens eating crickets (0.72; Dykstra and Karasov 1992), we calculate that 340.8 kJ/day metabolized requires a collection rate of 473 kJ/day. If the energy content of wild insects approximately equals that of domestic crickets (22.8 kJ/g dry mass, Dykstra and Karasov 1992), an upper limit to food collection is 20.7 g dry mass/day.

However, most of our manipulated nests had single female parents, and Charles Thompson (pers. comm.) reported that male House Wrens are more likely than females to increase their feeding rate in response to an increased brood size. In addition, in our study the parent with the highest observed feeding rate was a male (Fig. 1). Hence, the calculations above should be viewed with caution. Nonetheless, we conclude that it is far more likely that food availability limits brood mass in House Wrens than do constraints associated with parental maximal metabolism.

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