ORIGINAL PAPER

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The heat increment of feeding in house wren chicks: magnitude, duration, and substitution for thermostatic costs

Abstract The heat increment of feeding (HIF), a transient postprandial increase in metabolic rate, is the energy cost of processing a meal. We measured HIF in house wren chicks (*Troglodytes aedon*) ranging in mass from 1.6 to 10.3 g. This mass range (age 2–10 days) spanned a transition from blind, naked, ectothermic chicks through alert, endothermic birds with nearly complete feathering. We fed chicks crickets (2.7–10% of chick body mass) and determined HIF from continuous measurements of oxygen consumption rate ($\dot{V}O_2$) before and after meals. At warm ambient temperatures (T_a) of 33–36 °C, the magnitude of HIF (in ml O_2 or joules) was linearly related to meal mass and was not affected by chick mass. HIF accounted for 6.3% of ingested energy, which is within the range of results for other carnivorous vertebrates. The duration of HIF was inversely related to chick mass; 10-g chicks processed a standard meal approximately twice as fast as 2-g chicks. HIF duration increased with increasing meal mass. The peak $\dot{V}O_2$ during HIF, expressed as the factorial increase above resting metabolism, was independent of body mass and meal mass. In large, endothermic chicks (> 8 g), HIF substituted for thermoregulatory heat production at low T_a.

Key words Digestion · Energetics · Heat increment of feeding · Metabolism · Thermoregulation

Abbreviations F_eO_2 fractional concentration of O_2 in excurrent air · F_iO_2 fractional concentration of O_2 in incurrent air · *HIF* heat increment of feeding · *RMR* resting metabolic rate · T_a ambient temperature · T_b
body temperature · $\dot{V}$ air flow rate · $\dot{V}O_2$ oxygen consumption rate

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Introduction

The heat increment of feeding (HIF; also called specific dynamic action or diet-induced thermogenesis), is the increase in metabolic rate following ingestion of a meal (Rubner 1902; Maynard and Loosli 1969). In most organisms, HIF has been viewed as an unavoidable loss or 'waste' of ingested energy, but several authors have suggested that endotherms might use HIF to substitute for thermostatic heat production in cold environments. Such substitution, which reduces maintenance energy requirements, has been reported for mammals (Simek 1975; Costa and Kooyman 1984). There have been relatively few studies of avian HIF and the extent to which substitution occurs in birds is unclear (Ricklefs 1974; Dawson and O'Connor 1996). Part of the reason for the paucity of data is the high metabolic rate and activity level of most birds. Moreover, many birds eat frequent small meals, and food is often stored in a crop and released slowly and incrementally for actual digestion. For these reasons it is often difficult to differentiate HIF from metabolic increases caused by activity, and to correlate the magnitude and duration of HIF with meal mass.

In this paper we describe the HIF in chicks of an altricial passerine, the house wren *Troglodytes aedon*. House wren chicks are good subjects for studies of HIF. They readily accept large meals relative to body mass, rapidly process ingested food, and tend remain quiescent after feeding (thereby minimizing activity metabolism that might obscure HIF). We examined the magnitude and duration of HIF in house wren chicks ranging in age from 2 to 10 days, encompassing a 6.6-fold range of body mass and a developmental transition from naked, ectothermic hatchlings to alert, endothermic chicks with nearly complete feathering. We tested for substitution of HIF for thermostatic heat production in chicks larger

than 8 g. Since we could not distinguish between muscular, secretory, or synthesis-related increases in metabolism when estimating HIF, we follow the suggestion of Beamish (1974) and use the term "apparent HIF" to refer to all post-prandial processes that contribute to an increase in metabolic rate.

Materials and methods

Study site and animals

We studied a wild population of house wrens at the Sierra Nevada Aquatic Research Laboratory (SNARL), a University of California reserve at 2160 m elevation on the eastern slope of the Sierra Nevada (Mono County, California, USA). House wrens arrive at SNARL in May and set up territories in riparian vegetation (aspen and willow trees). Most pairs utilized nest boxes (10 cm by 10 cm by 20 cm high) constructed of plywood with removable lids. The boxes were inspected periodically to monitor egg laying and chick growth. During our study (1995–96) the first eggs appeared in June. The modal clutch size was 6 (range 4–8), and most chicks fledged at day 13–15 after hatching. To avoid inducing premature fledging, we did not disturb nests containing chicks more than 10 days old.

Chicks used for HIF studies were removed from nests and transported to the laboratory in warm, padded cups (California Department of Fish and Game/U.S. Fish and Wildlife Service collecting permit # 2203). We took no more than three chicks at a time from a nest and always left at least two chicks in nests to prevent desertion by the parents. At the conclusion of measurements we fed chicks to repletion and returned them to their nests. Chicks were kept outside their nests for a maximum of 5.5 h (the average time was about 3 h). To our knowledge, no chicks were harmed by our procedures.

Measurements of HIF

We used open-circuit respirometry to measure metabolic rates. Metabolism chambers (acrylic plastic boxes) ranged in volume from 340 to 850 ml depending on chick size. Chambers contained padded artificial nest cups and were fitted with ports for air flow. Two chicks could be studied simultaneously in separate chambers. An environmental cabinet maintained chamber temperature ± 0.5 °C. Mass flow controllers (Tylan) supplied dry, CO_2-free air at flow rates of 330 to 1200 ml·min^{-1} STP (depending on chick size). Actual flow rates at ambient temperature and pressure (about 34 °C and 580 torr) were 485–1760 ml·min^{-1}, yielding time constants (the time required for the system to record 67% of a step change in O_2 concentration) of 32–47 s. The flow controllers had repeatabilities of ± 1–2% and were calibrated against a dry volume meter to an absolute accuracy of ± 3%.

About 100 ml·min^{-1} of excurrent air from each chamber was dried (Drierite), scrubbed of CO_2 (Ascarite) and re-dried, and flowed through the sensor of an Applied Electrochemistry S-3A/II dual-channel O_2 analyzer. During measurements the S-3A was referenced against ambient air every 25–40 min. Outputs from the S-3A, flow controllers, and a Bailey BAT-8 thermocouple thermometer measuring chamber temperature were sampled every 2.5 s by a Macintosh computer equipped with a National Instruments analog-to-digital converter and custom software. Multiple readings (20–60) were averaged for each 2.5-s sample point. With digital signal averaging, short-term resolution of O_2 concentration was ± 0.0015%. Signal drift between reference readings was assumed to be linear and averaged about 0.005%; that value is the limit to absolute accuracy of O_2 concentration data. We calculated rates of O_2 consumption ($\dot{V}O_2$; ml·min^{-1}) as: $\dot{V}O_2 = \dot{V} \cdot (F_iO_2 - F_eO_2)/(1 - F_iO_2)$ where $\dot{V}$ is flow rate (corrected to STP), and F_iO_2 and F_eO_2 are the fractional concentrations of O_2 in incurrent and

excurrent air, respectively. The maximum cumulative error for $\dot{V}O_2$ calculations was approximately 5%.

To measure apparent HIF, we fasted chicks in the metabolism chambers until $\dot{V}O_2$ was low and stable and at least 1.5 h had elapsed after removal from the nest box. We made most measurements at T_a of 33–36 °C, similar to those measured in nest boxes (M.A. Chappell, unpublished data). At these T_a, chicks of all ages maintained body temperatures (T_b) of 38 °C or higher (M.A. Chappell unpublished data). As in natural nests, light levels were dim but the chambers were not completely dark. After $\dot{V}O_2$ attained a low, stable level, birds were fed a measured quantity of crickets (*Achaeta domestica*). We removed the insects' head, outer leg segments, and wings (if present). In addition to killing the insects, this made it easier for the wren chicks to swallow large crickets and prevented injury from the crickets' mandibles. Many chicks begged when their chamber was jostled, and were fed simply by giving them crickets held in forceps. Birds that did not beg were fed by gently opening the bill and inserting a cricket, which was always swallowed immediately. Meal mass ranged from 2.7 to 10% of pre-feeding body mass. Immediately after feeding, chicks were returned to the chambers, and $\dot{V}O_2$ was measured until it reached a low, stable level.

As a control for effects of handling, most chicks were subjected to a sham-feeding procedure, identical to the feeding protocol (including insertion of forceps into the mouth) except no food was delivered. After the faux meal, $\dot{V}O_2$ was measured until it returned to pre-handling levels before an actual meal was provided.

House wren chicks larger than 8 g (approximately 8 days old) were endothermic and could maintain high and constant T_b at T_a of 20–22 °C (M.A. Chappell, unpublished data). To determine if heat production from HIF can substitute for thermostatic heat production in these chicks, we measured HIF at both 22 °C and 34–36 °C in 19 individuals (in our analyses we also included data from birds measured in warm conditions only). The order of temperatures for each chick was selected at random. After the completion of measurements at the first T_a, chicks were held at the second T_a until $\dot{V}O_2$ was low and stable, and then fed again. We measured T_b before and after each HIF measurement with a 36-gauge (0.3 mm diameter) esophageal thermocouple connected to a Bailey BAT-8 or BAT-12 thermometer (resolution ± 0.1 °C). All chicks maintained T_b above 37.5 °C throughout measurements. The elapsed time between feedings was 2.5–3 h.

Analysis

Resting metabolic rates (RMR) were calculated as minimum 5-min averages before feeding and after the end of HIF, during periods when chicks were inactive and $\dot{V}O_2$ was stable. We obtained apparent HIF by subtracting RMR from post-prandial $\dot{V}O_2$ during the period when metabolism was elevated above RMR, and then integrating over time to obtain cumulative O_2 consumption in millilitres. Two adjustments were necessary for most individuals (Fig. 1): first, post-feeding RMR was often slightly higher than pre-feeding values, especially in small, rapidly growing chicks. To correct for this, we assumed a linear change in RMR between pre- and post-feeding levels. Second, occasional periods of activity created abrupt 'spikes' in the $\dot{V}O_2$ records (these were confirmed by direct observation of the birds). Activity spikes were deleted and replaced with interpolated data calculated from means of the preceding and following periods of data (assuming a linear change). Where necessary, we also used interpolation to fill the ca. 2-min gaps left by O_2 reference readings. The duration of digestion was estimated as the number of minutes (± 1–2 min) from the initial post-prandial increase in $\dot{V}O_2$ until $\dot{V}O_2$ reached RMR (operationally defined as 1–2 min of stable $\dot{V}O_2$ at values close to pre-feeding RMR, following a sustained decline from peak $\dot{V}O_2$).

We discarded data from several individuals which were too active to allow adequate resolution of HIF. We also discarded data for several chicks that were subsequently found to be hosting botfly larvae (*Protocalliphora* sp.; S. Frommer, personal communication).

The O_2 consumed as HIF (ml) was converted to energy using a factor of 20.1 J per ml O_2. The cost of heating food from room temperature (25–30 °C) to T_b was estimated by multiplying the mass of food by the specific heat of tissue ($4.1 \, J \cdot g^{-1} \cdot °C^{-1}$); this quantity was multiplied by the temperature change and subtracted from the measured total energy consumption to yield actual HIF.

The water and caloric content of crickets were determined by desiccation (50 °C) and bomb calorimetry. The crickets used for these measurements were trimmed of head, wings and legs in the same manner as crickets fed to wren chicks.

Statistics

Correlations in the data were determined by least squares linear regression, covariance analysis (ANCOVA), and multiple regression using Statistica (Statsoft), a statistics program for the Macintosh. Data are expressed as mean ± 1 standard deviation.

Results

We made 105 measurements of HIF, of which 97 yielded useable data. Chicks ($n = 72$, from 16 different nests; chicks were taken from most nests on more than one occasion) ranged in age from 2 to 10 days and in mass from 1.6 to 10.6 g. Some individuals were used more than once, but the minimum time between repeat measurements was 2 days and there were always large changes in body mass and maturation over this interval. There was no apparent relationship between data from siblings. Accordingly, we treated all measurements as independent.

Mean meal size (wet mass) averaged 6.4 ± 1.5% (range 2.3–10.0%) of chick body mass; this percentage did not vary with body mass ($P = 0.53$). We obtained crickets in two sizes, small nymphs (mean mass 0.05–0.1 g) and adults (mean mass about 0.3 g). Wren chicks weighing less than 4 g were fed only nymphs; larger chicks ate a mixture of nymphs and adult crickets. Nymphs contained 76 ± 5% water and had an energy density of $5.2 \, kJ \cdot g^{-1}$ (wet mass). Adult crickets contained 66 ± 5% water and had an energy density of $7.2 \, kJ \cdot g^{-1}$ (wet mass). The mix of nymphs and adults fed to large chicks had an energy density of about 6.2 $kJ \cdot g^{-1}$ (wet mass).

Controls

In most cases we observed no metabolic response following sham-feeding. Some individuals produced a brief peak in $\dot{V}O_2$ associated with increased activity, but this usually declined quickly to resting levels. When similar bursts of activity occurred after actual feedings, the resulting readily identifiable peaks in $\dot{V}O_2$ were subtracted from HIF estimates as described above.

Apparent HIF

In fed chicks studied at high T_a (33–36 °C), $\dot{V}O_2$ usually began to increase above resting levels within 5 min of
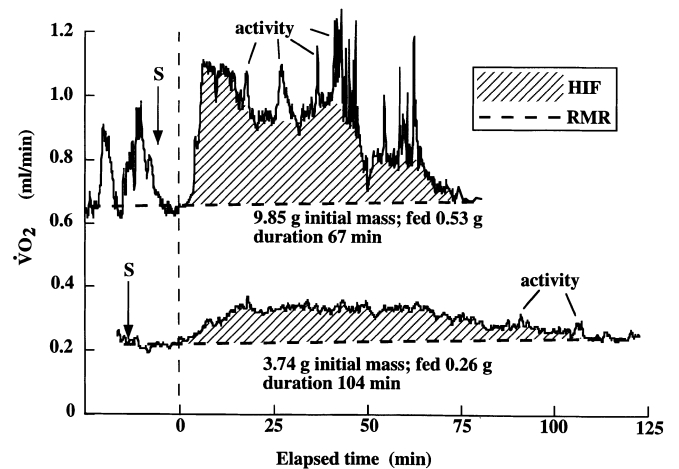
Fig. 1 Examples of the change in $\dot{V}O_2$ over time during feeding trials on two house wren chicks (3.74 and 9.85 g). Both chicks were sham-fed (*S*) prior to consuming an actual meal of crickets at time zero. *Shaded areas* represent the magnitude of the heat increment of feeding (HIF) exclusive of resting metabolic rate (RMR) and $\dot{V}O_2$ peaks caused by activity. Gaps (ca. 2 min) in the $\dot{V}O_2$ records during reference readings (e.g., at *S* and time zero) have been filled by interpolation (see text)

ingestion. In the majority of cases the initial increase was rapid, followed by a gradual decline to resting metabolism (Fig. 1, top). However, there was substantial variation in the shape of the HIF response. Some individuals exhibited a lengthy plateau in $\dot{V}O_2$ (Fig. 1, bottom) while in others the $\dot{V}O_2$ reached a peak and then immediately began to decrease rapidly. In a few chicks, there were two peaks separated by a period of intermediate $\dot{V}O_2$.

The duration of apparent HIF at high T_a was positively correlated to meal mass and negatively correlated to chick mass (Fig. 2; Table 1). For a standardized meal of 6.4% of body mass (the mean meal mass in this study), the predicted duration of HIF decreased from
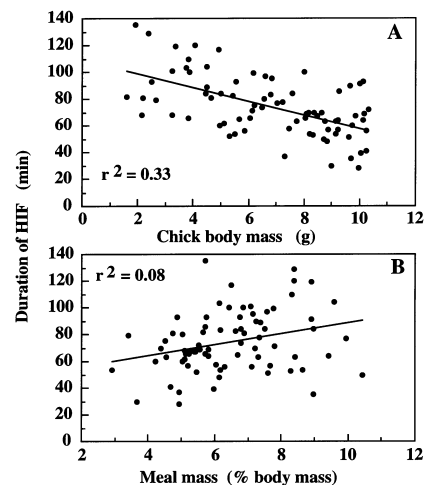
Fig. 2A, B The relationship between the duration of HIF and the size of chicks (**A**) and relative meal size (**B**). Both regressions are significant ($P < 0.05$)

Table 1 Multiple regression equations predicting the magnitude and duration of apparent HIF as a function of chick body mass (g) and meal mass (g). Apparent HIF is expressed in ml O$_2$ or in joules; for the latter the estimated cost of heating ingested food to body temperature has been subtracted from the total. The partial P values indicate the significance levels for partial correlation coefficients for chick mass and meal mass

Variable	Intercept	Chick mass coefficient (partial P)	Meal mass coefficient (partial P)	r^2 (overall P)
HIF (ml O$_2$)	1.44	0.3008 (0.09)	10.2 (0.000013)	0.59 (< 0.00001)
HIF (joules)	28.1	5.86 (0.09)	159.1 (0.00036)	0.51 (< 0.00001)
duration (min)	109	−7.51 (< 0.00001)	37.9 (0.034)	0.35 (< 0.00001)

98 min for a 2-g chick to 58 min for a 10-g chick. For a 10-g chick, a four-fold increase in meal mass (from 0.2 to 0.8 g) is predicted to increase HIF duration from 41 to 64 min. The peak $\dot{V}O_2$ during HIF, expressed as a factorial increase above RMR, was independent of both body size and meal mass ($P = 0.103$ and $P = 0.142$, respectively; Fig. 3) and averaged 1.51 × RMR.

We obtained 78 HIF measurements from chicks studied at warm temperatures (chick mass range 1.59–10.3 g). Multiple regression of the magnitude of apparent HIF as a function of meal mass and chick mass revealed a strongly positive correlation with meal mass (Fig. 4), but no effect of chick mass. Results were qualitatively similar for HIF expressed either as joules (after correction for the cost of heating food to T_b) or as ml O$_2$ (Table 1). Apparent HIF expressed as a percent of the ingested energy in a meal averaged 6.3 ± 1.7%.

Substitution of HIF for thermostatic costs

We obtained 52 HIF measurements for chicks heavier than 8 g, of which 19 were made at 22 °C (below the thermal neutral zone) and 33 were made at 33–36 °C. Values of RMR averaged about twice as high at 22 °C than at the higher T_a (adjusted means 1.41 ml O$_2 \cdot$ min^{-1} and 0.678 ml O$_2 \cdot$ min^{-1}, respectively; $F = 188$, $P < 0.0001$, ANCOVA with mass as the covariate).
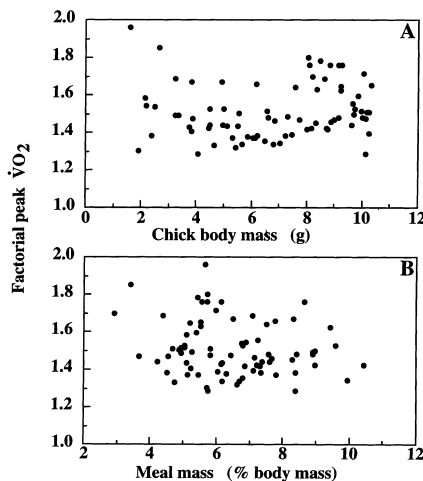

Fig. 3A, B The factorial peak $\dot{V}O_2$ during HIF (peak $\dot{V}O_2$/RMR) is independent of chick size (**A**) and relative meal mass (**B**)

We tested the difference between apparent HIF at 22 °C and at 33–36 °C using ANCOVA with chick mass and meal mass as covariates. The magnitude of apparent HIF at the low T_a was much lower than at high T_a
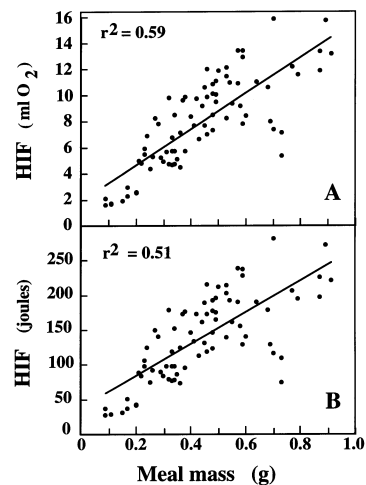

Fig. 4A, B The relationship between HIF and meal mass: **A** HIF expressed as ml O$_2$; **B** HIF expressed as joules, after subtracting the estimated costs of heating ingested food to body temperature. Both regressions are highly significant (P < 0.0001)
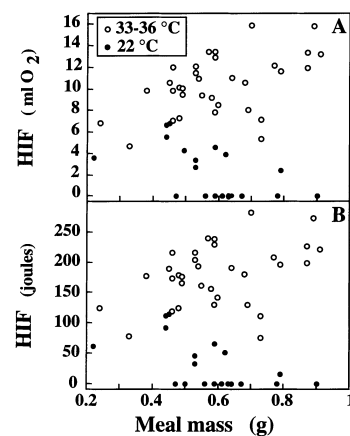

Fig. 5A, B Substitution of HIF for thermostatic heat production in large chicks (> 8 g). *Open circles* show apparent HIF at thermoneutral temperatures (33–36 °C); *filled circles* show apparent HIF at 22 °C: **A** HIF expressed as ml O$_2$; **B** HIF expressed as joules, after subtracting the estimated costs of heating ingested food to body temperature. For both units, HIF at warm temperatures is significantly greater than HIF at 22 °C (P < 0.0001; ANCOVA)

(Fig. 5); the difference was highly significant ($F_{1,49}$ > 100, P < 0.0001 for HIF as both ml O_2 and as joules after correction for heating costs). In many chicks measured at 22 °C we were unable to discern any apparent HIF; in most others the apparent HIF was less than for similar meal sizes at high T_a. We conclude that once house wren chicks have attained endothermy, they are capable of substantial and often complete substitution of HIF for thermostatic costs at low T_a.

Discussion

The phenomenon of HIF appears to occur in all taxa thus far tested, including mammals, birds, reptiles, fish, arthropods, and mollusks (Secor and Diamond 1995; Janes and Chappell 1995 and references therein). The underlying mechanisms responsible for HIF are thought to include mechanical and biochemical processes associated with digestion and assimilation, such as peristalsis, digestive enzyme synthesis, and active transport (Webster et al. 1976; Jobling 1985; Carefoot 1990a, b), but recent work indicates that much of the metabolic increase reflects a cost of protein synthesis (Brown and Cameron 1991a, b). Presumably in consequence, the magnitude of HIF, expressed as a percentage of assimilated energy, is considerably greater for protein diets than for lipid or carbohydrate diets [30%, 13%, and 5%, respectively; Harper (1971)].

The general characteristics of apparent HIF we found in house wren chicks are qualitatively similar to those reported for other carnivorous endotherms. The HIF coefficient of 6.3% of ingested energy for house wrens eating crickets is consistent with that of harbor seals (*Phoca vitulina*) eating fish [4.7%, Ashwell-Erickson and Elsner (1981); 5.1–9.0%, Markussen et al. (1994)], sea otters (*Enhydra lutris*) eating squid and clams [13.2% and 10%, respectively; Costa and Kooyman (1984)], Eurasian kestrels (*Falco tinnunculus*) eating mice [12.9%; Masman et al. (1989)], and Adélie penguin chicks (*Pygoscelis adeliae*) eating the euphausid crustacean *Euphausia superba* [10.0%; Janes and Chappell (1995)]. The metabolizable energy coefficient [(energy ingested−energy excreted)/energy ingested] was 0.716 for adult house wrens held at moderate temperatures and fed a diet of crickets (Dykstra and Karasov 1992). If the same coefficient applies to house wren chicks, HIF accounts for 8.8% of their metabolizable energy intake.

As reported for Adélie penguin chicks (Janes and Chappell 1995), the relationship between meal mass and apparent HIF is linear in house wren chicks (Fig. 4) and there was no effect of chick body mass on the magnitude of apparent HIF. The latter result suggests that the overall energy budget of the digestive process does not undergo large changes as the chicks mature. Unlike the findings for Adélies, the time-course of HIF in house wren chicks was strongly correlated with body size, with large chicks processing 'standard' meals (i.e., normalized for body mass) almost twice as fast as 2-g hatchlings. We speculate that the slow rate of digestion in small chicks (expressed in the time-course of HIF) may be a function of relatively low metabolic intensity (small chicks are ectotherms, whereas large chicks are endotherms). This is consistent with the observation that mass-specific resting metabolism was about 1.7-fold smaller in 2-g chicks than in 10-g chicks (0.0432 vs. 0.0729 ml $O_2 \cdot g^{-1} \cdot min^{-1}$, respectively). This contrasts with expectations based on allometry of basal metabolism for adult birds, which predict mass-specific RMR to be 1.5- to 1.7-fold greater in 2-g chicks than in 10-g chicks (Bucher 1986).

The duration of HIF we observed in large chicks (approximately 40–60 min depending on meal mass) is consistent with the mean digesta retention time of 65–70 min for adult house wrens fed crickets (Dykstra and Karasov 1992). In that study, approximately 80% of an aqueous marker (polyethylene glycol) was excreted within 2 h of ingestion. Retention time in wren chicks is somewhat ambiguous because in nature chicks usually excrete in response to feeding (excreta are contained in a fecal sack, which is removed from the nest by the parent).

Since HIF is in large part a cost of protein synthesis (Brown and Cameron 1991a, b), it can be thought of as a cost of growth. In terms of overall reproductive costs, HIF absorbs a substantial fraction of the food that parents must provide to chicks. Accordingly, it is interesting to compare the amount of energy lost as HIF to the amount of energy chicks deposit in new tissue. Based on the equations in Weathers (1991), a house wren chick requires 396 kJ of metabolizable energy between hatching and fledging at a mass of about 12 g. Of the total, HIF will consume about 35 kJ (8.8%). During this period of growth about 88 kJ are stored as new tissue [based on an estimated energy density of 8 kJ·g^{-1} wet mass at fledging; Robbins (1993)]. Therefore, house wren chicks must expend 0.40 kJ as HIF to deposit 1 kJ of new tissue. This is less than the value of 0.62 kJ per kJ reported for Adélie penguin chicks (Janes and Chappell 1995) but intermediate between the costs of growth measured in grass carp (0.9 kJ/kJ; Carter and Brafield 1992) and in toads (0.35 kJ/kJ) and catfish (0.28 kJ/kJ; Jørgensen 1988).

For most organisms the energy consumed as HIF is an unavoidable cost of processing food and cannot be used to support other physiological requirements. However, several authors have suggested that the heat produced as a result of HIF might serve a functional purpose in endotherms by substituting for the regulatory thermogenesis that would otherwise be necessary at low ambient temperatures. Good evidence of substitution has been obtained for mammals. In golden hamsters (Simek 1975), the measured HIF decreases as T_a declines, indicating that HIF is substituting for thermoregulatory heat production. In muskrats (*Ondatra zibethicus*), HIF is substantial in dry, thermoneutral conditions, but is not measurable when the animals are in cold water and RMR is high (MacArthur and

Campbell 1994). Similarly, sea otters – which live in cold ocean water – apparently substitute HIF for exercise heat production for several hours following a meal (Costa and Kooyman 1984). The extent to which substitution occurs in birds is controversial (Ricklefs 1974; Dawson and O'Connor 1996). Partial or complete substitution has been reported for finches (Meinenberger and Dauberschmidt 1992), Eurasian kestrels (Masman et al. 1989), domestic fowl *Gallus gallus* (Berman and Snapir 1964), and incubating European starlings *Sturnus vulgaris* (Biebach 1984). However, in the latter species substitution did not occur at some temperatures (10 °C) well below the lower critical temperature, and there was no evidence of substitution in Arctic tern chicks *Sterna paradisea* (Klassen et al. 1989). In contrast, we found that large house wren chicks clearly substitute HIF for thermostatic heat production at temperatures below thermoneutrality (Fig. 5). In many cases the substitution was complete at 22 °C (i.e., ingestion of a meal resulted in no apparent HIF). The reason for the difference between the two studies is not clear. Terns are precocial and wrens are altricial, but the wren chicks we studied (> 8 g) were largely feathered and had attained good endothermy. Klassen et al. (1989) did not account for differences in the amount of food or the time since feeding when making their metabolic measurements.

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