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EXERCISE CAPACITY OF HOUSE WREN NESTLINGS: BEGGING CHICKS ARE NOT WORKING AS HARD AS THEY CAN

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ABSTRACT.—We measured the aerobic capacity for exercise in House Wren (*Troglodytes aedon*) nestlings from 3 to 10 days of age. Exercise data were compared with previous measurements of the energy cost of begging (E_{beg}) to determine if begging chicks are working at maximal exercise capacity. We also compared exercise with the peak metabolic rate during digestion and, in older chicks, with thermogenic heat production. Rates of oxygen consumption ($\dot{V}O_2$) during exercise increased rapidly with age, but the factorial aerobic scope for exercise (exercise $\dot{V}O_2$ /resting $\dot{V}O_2$) averaged only 1.4 (at three to four days) to 1.7 (at 8 to 10 days). The mean E_{beg} was consistently lower than exercise $\dot{V}O_2$, but maximal E_{beg} was similar to exercise $\dot{V}O_2$. The peak $\dot{V}O_2$ during digestion was higher than exercise $\dot{V}O_2$ for young chicks (three to six days) but not significantly different for older chicks. In older chicks (8 to 10 days), regulatory thermogenesis at 22°C was significantly higher than exercise $\dot{V}O_2$. These results suggest that some begging by House Wren chicks can be at maximal muscular effort, but the average output during begging probably is not constrained by exercise capacity. The metabolic capacity for muscular activity of any kind is lower than the metabolic capacity for digestion (at least in young chicks), which presumably reflects a high priority for food processing and growth. Received 2 October 1997, accepted 6 February 1998.

THE ENERGY EXPENDITURE associated with animal signaling has been a topic of considerable interest among physiologists and behavioral ecologists. Much of this interest stems from considerations of signal evolution, particularly when the receiver relies on a signal to reveal an otherwise cryptic condition of the sender (such as genetic quality, condition, or hunger). If the sender can benefit from false advertisement (i.e. "dishonesty"), then the relationship between sender and receiver may become evolutionarily unstable because responding to a dishonest signal reduces the receiver's fitness (i.e. there is a conflict of interest). Theoretical analyses indicate that in such a system, honesty is evolutionarily stable only if signal production has a fitness cost—such as energy expenditure—that limits dishonest escalation (Zahavi 1975, 1977, Maynard Smith 1985, Grafen 1990, Godfray 1991, 1995).

The begging behavior of nestling birds is a good system for investigating the evolution of signals. Although chicks and their parents may "disagree" over the amount of food parents de-

liver and how it is allocated among the brood (Parker 1985, Stamps et al. 1985, Smith and Montgomerie 1991, Godfray 1995), several studies indicate that begging is honest (i.e. proportional to hunger level or body condition; Leonard and Horn 1996, Price et al. 1996, Kilner and Johnstone 1997) and that parents use begging to make decisions about food allocation (Leonard and Horn 1996). Given these findings, several investigators have looked for evidence that the energy cost of begging might be sufficient to enforce honesty. Recent work (Leech and Leonard 1996, McCarty 1996, Bachman and Chappell 1998) suggests that begging has a very small (and arguably trivial) energy cost. However, this is mainly due to the small fraction of time devoted to begging. During begging, rates of energy expenditure are elevated substantially above resting metabolism (Bachman and Chappell 1998).

What is not clear from previous work is whether begging chicks are making the largest muscular effort of which they are physiologically capable. This question is interesting because theoretical analyses suggest that a large effort (perhaps up to the maximum possible) might be expected if begging has a low cost, parents respond to begging intensity, and conflicts with siblings or parents favor escalation

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of begging intensity. In this paper, we test this prediction by comparing the energy cost of begging with metabolic rates during intense forced exercise in nestling House Wrens (*Troglodytes aedon*). We also compare metabolism during exercise and begging with metabolism during two other activities that are important for nestlings: regulatory thermogenesis and digestion.

METHODS

Study site and animals.—We worked at the Sierra Nevada Aquatic Research Laboratory (SNARL) on the eastern slope of the Sierra Nevada in Mono County, California. Most House Wrens at SNARL bred in nest boxes, which we checked periodically to determine hatching dates. To avoid inducing premature fledging, we did not disturb nests containing chicks older than 10 days (day 0 = day of hatching).

Nestlings used for metabolic studies were removed from nest boxes and brought into the laboratory within 5 min. We never took more than three chicks at once from a nest, and we always left chicks behind to prevent parental desertion of the nest. In the laboratory, chicks were kept in warm, padded cups and fasted for 1 to 2 h prior to testing (sufficient to avoid the period of elevated metabolism following feeding; Chappell et al. 1997). At the conclusion of measurements, we fed chicks to repletion and returned them to their nests.

Exercise measurements.—We used open-circuit respirometry to measure rates of oxygen consumption ($\dot{V}O_2$). The metabolism chamber was an acrylic plastic box (internal volume 240 mL) with ports for air flow and an artificial padded nest cup. An environmental cabinet maintained chamber temperature at 31°C (large chicks) to 34°C (small chicks), similar to ambient temperatures (T_a) measured in nest boxes (unpubl. data). The chamber was ventilated with dry, CO₂-free air pumped through a Tylan mass-flow controller at flow rates of 440 to 900 mL/min STP (standard temperature and pressure), depending on the size of the nestling. Flow rates at ambient barometric pressure (580 torr) were approximately 580 to 1,180 mL/min. The mass-flow controller was calibrated against a Singer dry volume meter to an accuracy of $\pm 2\%$.

Excurrent air (ca. 100 mL/min) from the chamber was dried (Dryerite), scrubbed of CO₂ (Ascarite) and redried, and passed through an Applied Electrochemistry S-3A O₂ analyzer. The S-3A was referenced against ambient air before and after each set of measurements with a linear baseline correction between references. Outputs were sampled every 1.5 s by a Macintosh computer equipped with a National Instruments analog-to-digital converter and custom software. Thirty to 60 readings were averaged for

each sample point, yielding a resolution of $\pm 0.001\%$ (relative to total atmospheric pressure) for O₂. Oxygen consumption (mL/min) was calculated as:

$$\dot{V}O_2 = \dot{V} (F_{iO_2} - F_{eO_2}) / (1 - F_{iO_2}), \quad (1)$$

where \dot{V} is flow rate (mL/min STP) and F_{iO_2} and F_{eO_2} are the fractional O₂ concentrations in incurrent and excurrent air, respectively (F_{iO_2} was 0.2095, and F_{eO_2} was always > 0.205). The estimated maximum cumulative error for $\dot{V}O_2$ calculations was less than 5% (based on resolution of the S-3A, the change in O₂ concentration during tests, and the estimated calibration errors of the mass-flow controller).

Tests began when nestlings were placed in the respirometer and left undisturbed for 5 to 10 min. When O₂ consumption was low and stable, we induced vigorous exercise by tilting and shaking the chamber, which caused the birds to struggle to maintain position and balance. Subjectively, the types of movements during these tests resembled behaviors in natural nests when nestlings struggle for position in the nest cup (Bachman and Chappell 1998). Each chick was measured over exercise periods of 5, 10, 15, 30, 45, 60, and 120 s, with each bout of exercise followed by 3 to 5 min of rest. The range of exercise durations overlapped the lengths of typical begging events (5 to 12 s; Bachman and Chappell 1998) and other movements observed in nest boxes (unpubl. data). The order of the seven test periods was randomized for each bird, and chicks from several nests were included in each age category (3 to 10 days old). None of the chicks was injured during testing, and all appeared to develop and fledge normally.

The respirometry system did not attain steady-state conditions during short exercise bouts. We could not use "instantaneous" correction (Bartholomew et al. 1981) because the chicks' rapid movements toward or away from the output ports created transient enrichment and rarefaction artifacts in gas concentration that invalidated the conversion algorithm (which assumes a temporally variable but spatially fixed source of gas exchange; Berrigan and Lighton 1993). We determined cumulative volume of O₂ consumed during exercise by subtracting resting metabolism from the metabolic increase elicited by an exercise bout and integrating the remainder over time (Fig. 1A). These measurements contained all data from the initial increase in $\dot{V}O_2$ until $\dot{V}O_2$ returned to resting levels, and therefore included any short-term repayment of oxygen debt. Measurements were discarded if substantial movement occurred immediately following exercise. Average exercise $\dot{V}O_2$ was obtained by dividing cumulative O₂ consumption by bout duration.

Energy costs of begging, HIF and thermoregulation data, and resting metabolism.—We used measurements of the energy cost of begging (E_{beg}) gathered in a 1995 study of House Wrens at SNARL (Bachman and Chappell 1998) and reanalyzed for comparison with

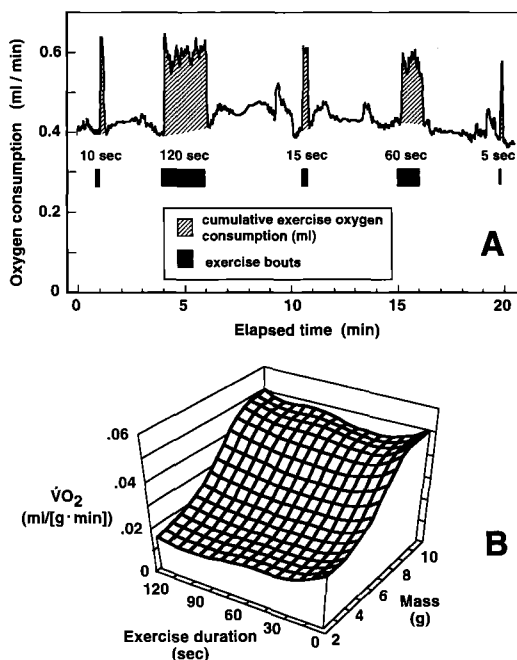


FIG. 1. (A) Oxygen consumption rate ($\dot{V}O_2$) at rest and during forced exercise in a six-day-old House Wren nestling (6.82 g) held at 33°C. Dark bars indicate exercise bouts; shaded areas are integrated cumulative oxygen consumption (mL O_2) after subtracting resting metabolism. The abrupt increases and decreases in measured $\dot{V}O_2$ associated with the start and end of exercise are partially real and partially artifacts of the rapid movement of the nestling with respect to the output port in the metabolism chamber. (B) The combined effect of nestling mass and the duration of exercise bouts on mass-specific exercise $\dot{V}O_2$. The effect of duration (5, 10, 15, 30, 45, 60, and 120 s in these tests) is not significant; $n = 587$ measurements on 66 nestlings (21 individuals were used at two ages). The surface plot was generated using a distance-weighted least-squares algorithm.

the exercise results. The methods used to obtain E_{beg} were similar to those used for the present study (Fig. 1) except that nestlings were stimulated to beg in the respirometer instead of exercised. Begging was elicited by hand clapping, fluctuating light intensity, tapping the chamber, or playbacks of male House Wren song. The occurrence of begging after these stimuli, and its intensity, were scored from bill gaping and movements of the head, neck, wings, and legs (Bachman and Chappell 1998; Table 1).

We obtained data on maximum $\dot{V}O_2$ during the post-prandial elevation in metabolism (heat increment of feeding [HIF]) from a study done at SNARL in 1996 (Chappell et al. 1997). In brief, postabsorptive House Wren nestlings were fed measured quan-

tities of crickets, and the subsequent increase in $\dot{V}O_2$ was recorded until metabolism returned to a low, stable value. For peak HIF, we used the highest 30-s mean of $\dot{V}O_2$ (after subtracting movement artifacts and resting metabolism). Peak HIF was independent of meal mass after correcting for chick mass (Chappell et al. 1997). From the same study, we also obtained thermoregulatory costs for nestlings 8 to 10 days old held at T_a of 22°C (i.e. below the lower critical temperature).

For estimates of aerobic scope (activity $\dot{V}O_2$ /resting $\dot{V}O_2$), we calculated resting metabolic rates from a previously derived equation for SNARL House Wren chicks (resting $\dot{V}O_2$ in mL/min and body mass in g):

$$\text{resting } \dot{V}O_2 = 0.02 \text{ body mass}^{1.565} \quad (2)$$

($r^2 = 0.95$, $P < 0.0001$; Bachman and Chappell 1998).

Analysis.—We obtained seven measurements of exercise $\dot{V}O_2$ from each of 66 individuals (3 to 10 days old) at 12 nests. Twenty-one of these nestlings were used on two occasions, separated by at least two days. Because there was considerable maturation and mass gain between repeat tests, we treated these data as independent. Results from a few exercise bouts were unusable because of mixing problems or post-exercise activity, yielding 587 data points. Preliminary analysis revealed that rates of oxygen consumption were not significantly influenced by exercise duration, when considered within each age group ($P > 0.06$ for all ages), or for all birds combined ($P > 0.6$; Fig. 1B). Accordingly, to avoid pseudoreplication we computed mean values (averaged across all seven exercise durations) of exercise $\dot{V}O_2$ (mL/min and mL O_2 g $^{-1}$ min $^{-1}$) and aerobic scope for each chick. These means were used for comparisons with costs of begging and HIF.

Growth curves (body mass vs. age) did not differ between years ($P = 0.76$), but variance in age-specific mass was substantial. For convenience, we based most analyses on age instead of mass. We used ANCOVA with mass as the covariate when making age-specific comparisons of the energy costs of exercise, begging, HIF, and thermogenesis. Analyses based on mass (with age as a covariate) yielded qualitatively similar results (see Weathers 1996).

Tests were performed on Statistica 4.1 (StatSoft, Incorporated), a statistical program for the Macintosh. A sequential Bonferroni correction (Rice 1989) was applied to P -values from multiple simultaneous tests in order to avoid Type I errors (significance level = 0.05).

RESULTS

Exercise and aerobic scope.—Nestling House Wrens seemed to recover quickly from forced exercise, although subjectively they appeared

TABLE 1. Comparison of $\dot{V}O_2$ ($\text{mL g}^{-1} \text{min}^{-1}$) during exercise with $\dot{V}O_2$ during begging and the peak $\dot{V}O_2$ during the post-prandial increase in metabolism (heat increment of feeding; HIF). Within each age group, variables were compared using ANCOVA, with mass as the covariate. Sample sizes range from 4 to 12 in each age category. "Ratio" is the ratio of $\dot{V}O_2$ during begging or HIF to $\dot{V}O_2$ during exercise.

Age (days)	Exercise	Begging (maximum)			Begging (mean)			Peak HIF		
	$\dot{V}O_2$	$\dot{V}O_2$	Ratio	P^a	$\dot{V}O_2$	Ratio	P^a	$\dot{V}O_2$	Ratio	P^a
3	0.0264	0.0199	0.76	0.73	0.0090	0.34	0.0003	0.0382	1.45	0.0068
4	0.0252	0.0258	1.02	0.38	0.0143	0.57	0.17	0.0446	1.75	0.0016
5	0.0305	0.0298	0.98	0.50	0.0192	0.63	0.0051	0.0506	1.67	0.0033
6	0.0253	0.0276	1.09	0.69	0.0119	0.47	0.0059	0.0537	2.13	0.0046
7	0.0279	0.0330	1.18	0.73	0.0212	0.76	0.11	0.0432	1.54	0.17
8	0.0457	0.0325	0.71	0.0103	0.0209	0.46	0.0015	0.0415	0.91	0.15
9	0.0395	0.0214	0.54	0.0001	0.0136	0.34	<0.0001	0.0525	1.33	0.40
10	0.0434	0.0365	0.84	0.08	0.0185	0.43	<0.0001	0.0452	1.04	0.38

^a P -values < 0.01 are significant after sequential Bonferroni correction for multiple simultaneous tests.

tired immediately after tests. The order of test durations had no effect on the measured $\dot{V}O_2$, either within age groups or for all birds combined (ANOVA, $P > 0.3$ in all cases).

Although exercise duration did not affect either absolute $\dot{V}O_2$ or mass-specific $\dot{V}O_2$, both of these measures increased rapidly as chicks grew (Figs. 1B, 2A). Between days 3 and 10, absolute exercise $\dot{V}O_2$ increased by a factor of 5.4, and mass-specific exercise $\dot{V}O_2$ increased by a factor of 1.6 (ANOVA, $F = 44.5$ and 23.6, re-

spectively, $df = 7$ and 75, $P < 0.001$ for both comparisons). Similarly, the aerobic scope (Fig. 2B) was fairly small ($1.45 \pm \text{SD of } 0.13$) and constant at ages 3 to 7 days ($F = 0.96$, $df = 4$ and 43, $P = 0.44$), but it increased abruptly during the next three days ($F = 10.4$, $df = 7$ and 75, $P < 0.001$) to a mean of 1.70 ± 0.14 .

Begging vs. exercise.—From our earlier study (Bachman and Chappell 1998), we obtained 65 records of $\dot{V}O_2$ during begging (expressed as $\text{mL g}^{-1} \text{min}^{-1}$) from House Wren nestlings aged 3 to 10 days (a few chicks were used more than once; these repeats were treated as described for exercise tests). There was considerable inter- and intraindividual variation in E_{beg} . The mean E_{beg} (mean value for all begs by a given nestling) was consistently lower than exercise $\dot{V}O_2$ (Fig. 3). The difference was significant for six of the eight age groups (Table 1). Across the eight ages tested (3 to 10 days), mean E_{beg} averaged about 50% of exercise $\dot{V}O_2$. In contrast, the maximum power output during begging (i.e. the highest single E_{beg} from each nestling) was quite similar to exercise $\dot{V}O_2$ for most of the age groups tested, being significantly lower only on day 9 (Fig. 3, Table 1). From day 3 to day 7, the average maximum E_{beg} was almost exactly equal to exercise $\dot{V}O_2$ (the former was 1% higher). Maximum E_{beg} fell to 70% of exercise $\dot{V}O_2$ for days 8 to 10.

Exercise vs. HIF.—From our 1996 data (Chappell et al. 1997), we obtained peak $\dot{V}O_2$ during the period of HIF for 73 House Wren chicks aged 3 to 10 days. The mass-specific peak HIF $\dot{V}O_2$ did not differ significantly with age (ANOVA, $P = 0.09$). Until nestlings were about seven days old, peak HIF $\dot{V}O_2$ was significantly high-

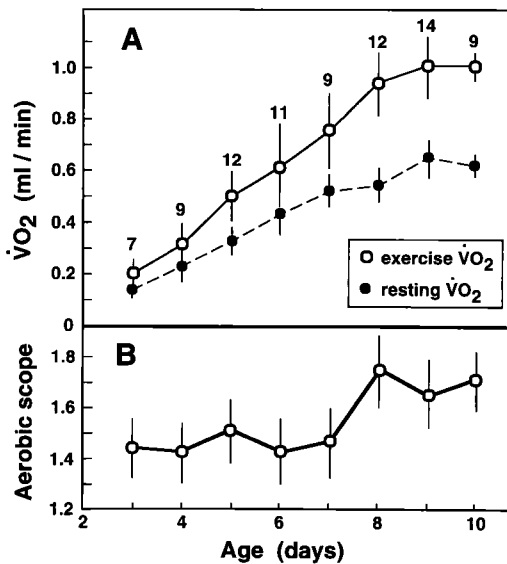


FIG. 2. (A) Exercise and resting oxygen consumption ($\dot{V}O_2$), and (B) exercise aerobic scope (exercise $\dot{V}O_2$ /resting $\dot{V}O_2$) as a function of age in House Wren nestlings. Values are $\bar{x} \pm \text{SD}$. See text and Bachman and Chappell (1998) for calculation of resting $\dot{V}O_2$.

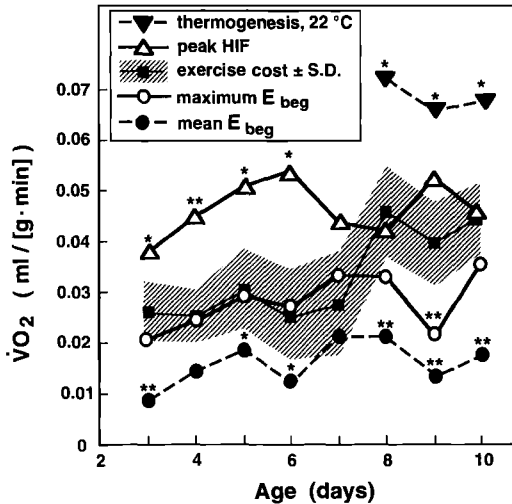


FIG. 3. Comparison of exercise $\dot{V}O_2$ with $\dot{V}O_2$ during begging (E_{beg} ; Bachman and Chappell 1998), thermoregulation at 22°C, and the post-prandial heat increment of feeding (HIF; Chappell et al. 1997). Shaded areas are ± 1 SD around the mean for exercise $\dot{V}O_2$. For clarity, SD values are not shown for the other variables. *, differences from exercise $\dot{V}O_2$ significant at $P < 0.05$; **, differences significant at $P < 0.01$. A sequential Bonferroni correction was applied to avoid Type I errors in multiple simultaneous tests.

er than $\dot{V}O_2$ during both forced exercise and begging (Fig. 3, Table 1). From day 3 to day 6, peak HIF $\dot{V}O_2$ averaged 71% higher than exercise $\dot{V}O_2$. Subsequently (days 7 to 10), the difference fell to an average of 9% and was not significant.

Exercise vs. thermoregulation.—Previous work showed that House Wrens of age 8 to 10 days are endothermic and have substantial thermoregulatory ability (Chappell et al. 1997). From that study, we obtained $\dot{V}O_2$ at 22°C for 16 nestlings aged 8 to 10 days (all chicks exposed to this T_a maintained normal body temperature). Thermostatic costs ($\dot{V}O_2$ at 22°C – resting $\dot{V}O_2$ in thermoneutrality) were significantly higher than exercise costs (Fig. 3). At these ages, the aerobic scope for thermogenesis (1.91) averaged 12% higher than the scope for exercise (1.70; ANOVA, $P = 0.0003$); the increase above resting metabolism during HIF was 30% higher than during exercise. House Wren chicks in this age range probably are capable of additional thermostatic heat production, but we did not test them at lower T_a .

DISCUSSION

The purpose of our study was to compare the aerobic exercise capacity of House Wren chicks with rates of energy consumption during other activities, especially begging. Before those issues are discussed, two methodological questions must be considered: (1) did the exercise protocol elicit a maximal physiological effort, and (2) was there a substantial anaerobic component to exercise metabolism?

Several pieces of indirect evidence suggest that the exercise protocol produced maximal (or near maximal) muscular performance. First, during the exercise tests we attempted to generate the most vigorous activity possible without harming the birds. Second, the range, frequency, and intensity of movement during exercise (which was maintained over periods of up to 2 min) equaled or exceeded that seen during the most intense bursts of activity in 120 h of video records of behavior in nest boxes (Bachman and Chappell 1998, G. C. Bachman unpubl. data). Finally, chicks showed behavioral signs of exhaustion (i.e. lack of movement, absence of normal rest posture) for 10 to 30 s following exercise, particularly after the longer-duration tests (i.e. >15 s). These symptoms did not occur after brief bouts of less-intense activity, either spontaneously or experimentally induced.

The question of an anaerobic contribution to power production during exercise (e.g. McCarty 1997, Weathers et al. 1997) cannot be answered rigorously without whole-body lactate analyses. However, we saw little indirect evidence of substantial anaerobiosis. There was no consistent sustained post-exercise elevation of $\dot{V}O_2$ that would indicate repayment of a large oxygen debt (e.g. Fig. 1); in nearly all cases, $\dot{V}O_2$ returned to resting levels within 15 to 20 s of the cessation of exercise. Moreover, the order of test durations had no detectable effect on exercise $\dot{V}O_2$, even though rest periods were short (5 min or less). If there was a large anaerobic component to exercise, a reduced exercise capability would be expected in late versus early tests, but this did not occur. Given these data, we conclude that the exercise protocol provided useful estimates of maximal aerobic exercise metabolism.

Exercise capacity, HIF, and thermoregulatory costs.—As expected from their altricial growth

pattern, nestling House Wrens at 3 to 10 days of age have a low metabolic scope for activity, presumably because their skeletal musculature is relatively undeveloped until they approach the time of fledging (about 18 days old at SNARL). Although absolute and factorial exercise capacities increased rapidly with age (Fig. 3), the maximal aerobic scope attained between days 3 and 10 was about 1.7. In contrast, typical aerobic scopes for adult birds are 5 to 7 for thermoregulatory heat production and 7 to 15 for flight or running exercise (Dawson and Marsh 1989, Chappell et al. 1996, Norberg 1996). The comparison is imperfect because the adult scopes were computed from basal metabolism, whereas scopes for the wren chicks were computed from minimal resting metabolism in rapidly growing animals. Nevertheless, it is clear that young House Wren nestlings have a very limited capacity for exercise.

Interestingly, the peak metabolic rate during HIF greatly exceeded exercise $\dot{V}O_2$ in younger nestlings, as did thermogenic $\dot{V}O_2$ in older chicks (Fig. 3, Table 1). The relatively high HIF reflects the necessity for quick digestion of large quantities of food to support rapid growth: House Wrens at age 3 to 6 days (3.4 to 6.9 g) have a daily food intake equal to about 50% of their body mass, process meals in less than 2 h, and add almost 1 g/d of new tissue (Chappell et al. 1997, Bachman and Chappell 1998). The higher capacity for heat production than for exercise in chicks at 8 to 10 days is more difficult to explain, because skeletal muscle is the principal effector organ for both regulatory thermogenesis and exercise (Dawson and O'Connor 1996). Possibly, chicks can use a greater fraction of muscle power output during coordinated shivering than during forced exercise, although in most adult birds the power output during flight activity exceeds thermogenic capacity considerably (Dawson and Marsh 1989).

Are begging chicks working maximally?—Previous studies (Leech and Leonard 1996, McCarty 1996, Bachman and Chappell 1998) have shown that the energy cost of begging in passerine chicks is low when expressed as a fraction of the daily energy budget. These data do not reveal whether the low cost is due in part to physiological constraints; i.e. when begging, do chicks work as vigorously as their physi-

ogy permits, or is begging effort submaximal? Our results suggest that a begging House Wren nestling can achieve metabolic rates close to those attained during vigorous forced exercise. However, begging nestlings more typically expend energy at rates of about one-half of their metabolic capacity for exercise. Therefore, the average begging intensity is not a consequence of physiological constraints, although maximum intensity may be.

How do these findings fit into current models of signal evolution? In theory, parents that require begging signals to be costly are less likely to be fooled by dishonest nestlings, which in turn may request more food than is optimal for their parents to deliver (Grafen 1990; Godfray 1991, 1995). Direct fitness costs of begging include energy expenditure and increased predation risk (Haskell 1994). In our wrens, the energy costs of begging (expressed as a fraction of the daily energy budget or of the energy deposited in new tissues) are very low (Bachman and Chappell 1998), and nest predation is rare (only two possible instances of nest loss to predators in more than 100 nests during three seasons). Given these seemingly low fitness costs, one would expect little selection against signal escalation if food is scarce and nestlings beg as a primary means of competing for food (Harper 1986, Smith and Montgomerie 1991). Accordingly, it is worth considering why mean E_{beg} is well below the chicks' physiological capacity for exercise. At SNARL, only a subset of the chicks begs during a typical parental nest visit, and parents occasionally cannot elicit begging from any chick (Bachman and Chappell 1998). This suggests that, at least for chicks less than 11 days old in this population, adequate food was available and competition among chicks was not severe, which would reduce selection for escalation. It is also possible that begging intensity is constrained by indirect costs, such as loss of inclusive fitness when successful begs deprive siblings of food (Briske et al. 1994, Godfray 1995).

Although the maximum E_{beg} attained by young House Wrens may be physiologically constrained, it is unlikely that energy costs of begging would comprise an important fraction of these chicks' energy budgets even if exercise capacity—and E_{beg} —were much higher. In House Wrens, begging is a short-duration event because parents decide which chick to feed

within 4 to 7 s after arriving at the nest (chicks generally cease begging once one of them has been fed). As a result of this (and because individual chicks do not beg at every parental visit), begging has a very low "duty factor," consuming at most 3% ($\bar{x} = 0.3$ to 1%) of a 24-h day, even though the number of parental visits may be impressively large (up to 350/day). For a 10-day-old chick begging at the highest observed rates (4 times the mean rate; Bachman and Chappell 1998), E_{beg} would need to be 3.3 times higher than the measured exercise $\dot{V}O_2$ (and 3.9 times higher than the maximum observed E_{beg}) in order to comprise just 5% of the daily energy budget. In other species, the effect of begging energetics on daily energy budgets could be of greater importance, but this would require either a substantially higher rate of energy expenditure during begging (i.e. greater muscular exertion), or a considerably larger duty factor resulting from more frequent or more prolonged begging events.

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