———, & ———. 1980. Gas exchange in the avian egg: time, structure, and function. Amer. Zool. 20: 477–484.

———, & H. T. HAMMEL. 1982. Incubation water loss, shell conductance and pore dimensions in Adelie Penguin eggs. Polar Biol. 1: 91–97.

———, C. V. PAGANELLI, J. C. T. NISBET, & G. C. WHITTOW. 1976. Regulation of incubation water loss in eggs of seven species of terns. Physiol. Zool. 449: 245–259.

VLECK, C. M., D. VLECK, H. RAHN, & C. V. PAGANELLI. 1983. Nest microclimate, water vapor conductance and water loss in heron and tern eggs. Auk 100: 76–83.

WELLER, M. W., & C. S. SPATCHER. 1965. Role of habitat in the distribution and abundance of marsh birds. Iowa State Univ. Agr. Exp. Station, Spec. Rept. 43.

WHITE, F. N., & J. L. KINNEY. 1974. Avian incubation. Science 186: 107–115.

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Energetics of Free-living Nestling House Finches: Measurements with Doubly Labeled Water

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The total energy metabolism of nestling birds consists of anabolism (the building of body substance) and catabolism (metabolic heat production). Although anabolism has been measured directly as the accumulation of energy in body tissues with time (see Ricklefs 1974), most estimates of nestling catabolism have relied upon extrapolations of laboratory measurements of standard metabolism (based on oxygen consumption) to field conditions. An alternative to the latter technique uses doubly labeled water (DLW) to monitor directly the CO_2 production of nestlings in their natural physical and social environment. We have determined the total energy metabolism of free-living nestling House Finches (*Carpodacus mexicanus*) using DLW. Although the DLW method provides reliable measurements of CO_2 production and water flux in adult birds (see Nagy 1980, Nagy and Costa 1980, Williams and Nagy 1984), it has yet to be validated for use with growing animals. There is potential for error when DLW is used with rapidly growing animals. In growing animals, the total body water volume in which isotopes equilibrate changes regularly as mass changes. If the changes in body water volume are extreme, errors in calculation of isotope turnover can result (see Nagy 1980, Nagy and Costa 1980). In the present study, nestlings averaged 74% of adult mass, a size typically associated with a declining growth rate (Ricklefs 1969). In fact, nestling water volumes increased by <10% initial volume in our study. Such a change is within the limits that theoretically should permit accurate calculation of turnover rates (Nagy 1980, Nagy and Costa 1980). Therefore, we suspect that for nestlings of this size, errors in the DLW method should be small. However, in the absence of direct validation of the DLW method, our results must be regarded as preliminary.

All nestlings used in this study occupied natural nests constructed in and around buildings at the University of California's Philip L. Boyd Deep Canyon Desert Research Center near Palm Desert, California. All measurements were made in May 1980. Thirteen nestlings from 4 nests were studied. Mean nestling mass at the time of isotope injections (see below) was 15.0 ± 0.4 g ($\bar{x}$ ± SE) and did not differ between nests ($F = 1.93$, $P = 0.19$). Eight nestlings from 2 nests received intramuscular injections of tritiated water only (0.1 ml, containing 50 μCi ^3H), and 5 nestlings from 2 other nests received DLW (0.1 ml, containing 50 μCi ^3H in 95 atoms % ^{18}O-enriched water). These injection solutions provided sufficient isotope activity to assure final activities of both ^3H and ^{18}O that did not approach background activity after 48 h (general guidelines for suggested activities of injected isotopes are given in Nagy 1983).

Following injections, labeled nestlings were returned to their nests for 1 h to allow isotope equilibration in body water. At 1, 25, and 49 h postinjection, nestlings were removed from their nests and weighed. Blood (50 μl) was then drawn from a brachial vein, and nestlings were returned to the nest. Blood samples were stored in flame-sealed, refrigerated microhematocrit tubes until returned to the University of California, Los Angeles, for analysis. Blood was distilled according to procedures in Wood et al. (1975). Tritium activity of the distilled water samples was assayed by liquid scintillation spectroscopy (Beckman LS-230). Oxygen-18 was assayed using the proton-activation technique of Wood et al. (1975). Gamma emissions of the resulting fluorine-18 were quantified with a Packard-Gamma Rotomatic system. Carbon dioxide production and water influx were calculated using equations in Nagy (1980, 1983)

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and Nagy and Costa (1980). In all but 4 cases, rates represent means based on 48-h observation periods. The exceptions are 3 instances where ^{3}H-labeled nestlings disappeared between the 25-h and 49-h samples, and 1 instance where the volume of the final blood sample drawn from a doubly labeled nestling was too small to allow ^{18}O analysis. For these cases, calculated rates were based on the initial 24-h periods.

Mean water influx of 11 nestlings was 343.3 ± 11.6 ml $H_2O \cdot kg^{-1} \cdot day^{-1}$, or ~42% of the total body water pool per day (based on a body water volume of 72.7% of carcass wet mass determined by oven drying at 70°C). This influx rate is 66% of the rate reported for Savannah Sparrow (*Passerculus sandwichensis*) nestlings (Williams and Nagy pers. comm.). Measurements on these two species represent the only available data on H_2O influx in free-living nestlings. The nestling House Finch influx rate is 83% of that predicted for a 15-g adult bird in captivity (416 ml $H_2O \cdot kg^{-1} \cdot day^{-1}$; Degen et al. 1982), which, unlike nestlings, would have access to drinking water.

Labeled nestlings produced 4.17 ± 0.15 ml $CO_2 \cdot g^{-1} \cdot h^{-1}$ ($n = 5$), which is equivalent to ~37 kJ/day (assuming 24.66 J/ml CO_2 for a mixed seed diet; Weathers and Nagy 1984). Nestlings gained 1.6 ± 0.3 g wet mass during the 2-day measurement period. Energy allocated to growth can be determined from these mass changes if carcass energy content is known. Because nestlings were not killed at the conclusion of our study, we did not measure energy contents. However, altricial passerines display characteristic changes in body energy content during the course of their development (Ricklefs 1974). We used data for a representative passerine, the Rufous-winged Sparrow (*Aimophila carpalis*, Ricklefs 1974), to estimate that House Finch nestlings contained 6.3 kJ/g wet mass, and that they accumulated 10.1 kJ in body energy during the 2-day study period. This is 14% of total energy metabolized by nestlings. During our 2-day observations, nestlings averaged 15.8 g, 77% of the adult mass (20.4 g, Weathers 1981). Ricklefs (1974: Fig. 26) predicted that, for a hypothetical small nestling sparrow at 77% of adult mass, growth should equal ~40% of total metabolic rate—nearly 3 times the value we observed. Ricklefs ignored the cost of thermoregulation and activity in developing his model, however, and this probably accounts for most of the discrepancy.

With this information, we can estimate the rate at which the parent finches supplied metabolizable energy to a nest containing 3 large nestlings. A single nestling metabolized 37 kJ/day and invested 5 kJ/day into production of new body tissue, for a total of 42 kJ/day. Three 15-g nestlings thus would receive 126 kJ/day of metabolizable energy as food provided by their parents. For comparison, we predicted daily energy expenditure of an adult weighing 20 g to be 81 kJ/day using Walsberg's (1983) equation (#10) for birds that do not forage in flight. Walsberg's equation was derived from data for breeding and nonbreeding birds, so it may underestimate energy expenditure of adult birds feeding large nestlings. However, similar-sized Savannah Sparrow females (17.3 g) feeding 5-day-old nestlings metabolized only 68 kJ/day (Williams and Nagy pers. comm.). Either estimate indicates that the food requirement of 3 large nestling finches is about equivalent to that of 1.5 adult finches. If both adults share equally in feeding the nestlings, then each adult would need to gather about 1.75 times as much food each day as it would need for self-maintenance alone. Hence, adult House Finches feeding large nestlings must capture food at a rate nearly twice that of nonbreeding adults.

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Literature Cited

Degen, A. A., B. Pinshow, & P. U. Alkon. 1982. Water flux in Chukar Partridges (*Alectoris chukar*) and a comparison with other birds. Physiol. Zool. 55: 64–71.

Nagy, K. A. 1980. CO_2 production in animals: analysis of potential errors in the doubly-labeled water method. Amer. J. Physiol. 238: R466–R473.

———. 1983. The doubly-labeled water method ($^{3}HH^{18}O$): a guide to its use. Univ. California (Los Angeles) Publ. No. 12-1417.

———, & D. P. Costa. 1980. Water flux in animals: analysis of potential errors in the tritiated water method. Amer. J. Physiol. 238: R454–R465.

Ricklefs, R. E. 1969. Preliminary models for growth rates in altricial birds. Ecology 50: 1031–1039.

———. 1974. Energetics of reproduction in birds. Pp. 152–292 *in* Avian energetics (R. A. Paynter, Jr., Ed.). Publ. Nuttall Ornithol. Club No. 15.

Walsberg, G. E. 1983. Avian ecological energetics. Pp. 161–220 *in* Avian biology, vol. 7 (D. S. Farner, J. R. King, and K. C. Parkes, Eds.). New York, Academic Press.

Weathers, W. W. 1981. Physiological thermoregulation in heat-stressed birds: consequences of body size. Physiol. Zool. 54: 345–361.

———, & K. A. Nagy. 1984. Daily energy expenditure and water flux in Black-rumped Waxbills (*Estrilda troglodytes*). Comp. Biochem. Physiol. 77A: 453–458.

Williams, J. B., & K. A. Nagy. 1984. Validation of the doubly labeled water technique for measuring energy metabolism in Savannah Sparrows. Physiol. Zool. 57: 325–328.

Wood, R. A., K. A. Nagy, N. S. MacDonald, S. T. Wakakuwa, R. J. Beckman, & H. Kaaz. 1975. Determination of oxygen-18 in water contained in biological samples by charged particle activation. Anal. Chem. 47: 646–650.

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