DAILY ENERGY EXPENDITURE OF NESTLING BALD EAGLES IN NORTHERN WISCONSIN

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Abstract. We measured field metabolic rate of nestling Bald Eagles (Haliaeetus leucocephalus) in northern Wisconsin, using doubly-labeled water. In inland northern Wisconsin and along the Wisconsin Lake Superior shore, eaglets aged 39–60 days, weighing 3.08–4.85 kg, expended an average of 2,427 ± 100 kJ day⁻¹. Nestling field metabolic rate was weakly correlated with nestling age, but not with mass. Field metabolic rate of eaglets can be used to estimate the biomass of food that adult eagles must provide from their environment, a datum that is important for determination of habitat suitability.

Key words: Bald Eagle, doubly-labeled water, energy expenditure, field metabolic rate, Haliaeetus leucocephalus, Lake Superior, nestling.

Habitat suitability for Bald Eagles (Haliaeetus leucocephalus) has been studied for both the winter season and the breeding season (Peterson 1986, Hansen 1987, Bowerman 1993). One critical factor of habitat suitability during the breeding season is food availability in the area of the nest (Peterson 1986); an area with ideal nest trees and minimal human disturbance is unsuitable to breeding eagles if they cannot find enough food to raise nestlings. However, it has been difficult to assess the adequacy of food supplies for raising nestlings, in part because the energy needs of Bald Eagle nestlings have never been determined.

One way to approximate nestling energy requirements is to estimate energy intake from observations of the number and type of prey deliveries brought to the nestlings. A few investigators have monitored prey delivery rates to nestling Bald Eagles (Cain 1985, Kozie 1986, Dykstra et al. 1998). Although observations can be an inexpensive, non-intrusive way to monitor food intake, it is possible that the number of prey items delivered to the nest does not correspond in a uniform way to the amount of energy delivered, and energy delivered is the critical variable which must be measured.

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A more direct technique to determine energy requirements of nestlings uses doubly-labeled water (DLW) to measure nesting energy expenditure, in a technique which has been validated for Bald Eagle nestlings in the laboratory (Dykstra et al. 1997). In order for the DLW measurements to represent typical eaglet expenditures for any region, the nestlings studied should be in average-size broods located in representative habitat for that region. Thus, we selected eaglets in nests located in typical habitat in northern Wisconsin: continuous hardwood-conifer forest with supercanopy white pines (Pinus strobus), numerous lakes and rivers, and low human populations. Eagles nesting in these areas had excellent productivity (1.1 young per occupied territory, 1987–1996; Meyer, Dykstra, and Warnke, unpubl. data), very low organochlorine contaminant exposure (Dykstra et al. 1998), and seemed to have adequate food availability, based on the adult and nestling behaviors (i.e., food delivery rates and time nestlings spent feeding, Warnke 1996).

For comparison, we also studied eaglets in nests along the Wisconsin shoreline of Lake Superior, the least contaminated of the Great Lakes (International Joint Commission 1985). Wisconsin Lake Superior eagles have significantly lower reproductive rates than eagles nesting in inland Wisconsin (Dykstra et al. 1998). Habitat for eagles may be less suitable at Lake Superior than at inland lakes, because Lake Superior is both cooler (Palm and deSouza 1983) and more oligotrophic (Great Lakes Basin Commission 1976) than inland breeding habitats.

METHODS

STUDY SITES

Northern Wisconsin inland nests were located along the shores of natural lakes, reservoirs, or large rivers in Vilas, Iron, Douglas, and Oneida Counties, Wisconsin. Lake Superior nests studied were <8 km from the Lake Superior shore, in Iron, Bayfield, and Douglas Counties, Wisconsin. Inland sites and most of the Lake Superior shore are in mixed conifer-hardwood forests (Curtis 1959), while a few Lake Superior nests lie within the interphase of the boreal and conifer-hardwood zones (Curtis 1959). Conifers are primarily white pine, with lesser quantities of red pine (P. resinosa) and hemlock (Tsuga canadensis), as well as balsam fir (Abies balsamea), spruces (Picea spp.) and white cedar (Thuja occidentalis). Deciduous species include aspens (Populus spp.), sugar maple (Acer saccharum), yellow birch (Betula alleghaniensis), white birch (Betula papyrifera), and others. All eagle nests studied were in white pine, red pine, or aspen.

ENERGY EXPENDITURE

We measured nesting energy expenditure, or field metabolic rate (FMR), in 16 nesting Bald Eagles, aged 39–60 days. At this age eaglets are endothermic, and are probably near their maximal energy requirements due to rapid growth (Ricklefs 1974, Stalmaster 1987). The nesting period in Bald Eagles is 10–12 weeks (Stalmaster 1987), and nesting fledging mass is approximately 4.10 kg (males) and 5.20 kg (females, Bortolotti 1984a). Normal brood size for eagles is one or two, with three being rare (4%, Stalmaster 1987).

In 1992, we measured FMR of six eaglets in inland nests; in 1993, we measured an additional six inland eaglets. In 1994, we measured FMR of four Lakeshore eaglets, which represented the entire production of Lake Superior eaglets in Wisconsin, with the exception of two in a nest in a dead tree, which was unsafe to climb.

At each nest, a qualified climber retrieved one or more nestlings. Each nestling was weighed to the nearest 50 g with a 10.0-kg Pesola spring scale. Nestlings were aged and sexed by measurement of eighth primary length and footpad length (Bortolotti 1984b). A background blood sample (ca. 1 ml) was taken from the brachial vein using a plastic 3-ml syringe tipped with a 20-ga needle. The dose of DLW for each chick was calculated and weighed in a glass Hamilton syringe (in 1992) or sterile plastic syringe (in 1993 and 1994) on a portable field balance. Doses of DLW were as follows: 1992, 0.27 g DLW kg⁻¹ body mass (0.12 g kg⁻¹ of 99% D₂O and 0.15 g kg⁻¹ of 97% H₂¹⁸O); 1993, 0.256 g DLW kg⁻¹ body mass (0.084 g kg⁻¹ of D₂O and 0.171 g kg⁻¹ of H₂¹⁸O); 1994, 0.28 g DLW kg⁻¹ body mass (0.09 g kg⁻¹ of D₂O and 0.19 g kg⁻¹ of H₂¹⁸O). Doses were injected into the pectoralis or the brachial vein, and the birds were kept on the ground for 30 min–2 hr, a sufficient time for equilibration according to pilot studies (Dykstra et al. 1997). One nesting was returned to the nest without a background blood sample; the single-sample technique (Webster and Weathers 1989) was used for this nesting. On the ground, unstrained young nestlings sat quietly, while older nestlings were placed in nylon bags in the shade for the duration of the equilibration. After the equilibration period, 1-ml blood samples were taken from the brachial veins, and the chicks were returned to the nest.

When we returned to the nests 4.5–5.1 days later, we weighed and remeasured nestlings. A final blood sample (1 ml) was taken from the brachial vein of each chick, and chicks were returned to their nests. All field research was conducted under appropriate federal and state permits.

Blood samples were kept on ice throughout the day. Each blood sample was centrifuged the evening it was collected, and the plasma was drawn off, flame-sealed into 75 µl capillary tubes (1992 and 1993) or disposable pipettes (1993 and 1994), and refrigerated for later analysis.

Plasma samples were analyzed by isotope-ratio mass spectrometry at the University of Wisconsin-Madison, Department of Chemistry (1992) or by Metabolic Solutions Inc., Merrimack, New Hampshire (1993 and 1994). Isotope-ratio measurements were reported as differences from the Vienna-standard mean ocean water (VSMOW), delta per mil versus VSMOW, and so used in calculations. Most samples were analyzed in duplicate, with additional samples analyzed if CV was >5.0%. CVs for initial and final samples averaged 1.16% for H₂¹⁸O and 2.11% for deuterium. Isotopic enrichments of samples were well elevated above background levels (all initial and final samples >3.2 × background).

Total body water content was estimated by H₂¹⁸O dilution space. CO₂ production was calculated using
TABLE 1. Doubly-labeled water measurements in Bald Eagle nestlings, 1992–1994. Trial lengths were 4.5–5.1 days. FMR = Field metabolic rate.

<table>
<thead>
<tr>
<th>Year</th>
<th>Location</th>
<th>Chick</th>
<th>Nest</th>
<th>Sex</th>
<th>Age (d)</th>
<th>Initial mass (kg)</th>
<th>Final mass (kg)</th>
<th>Brood size</th>
<th>FMR (kJ d⁻¹)</th>
<th>Water influx (ml kg⁻¹ d⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1992</td>
<td>INLAND</td>
<td>58</td>
<td>Stone’s Bridge</td>
<td>F</td>
<td>50</td>
<td>4.59</td>
<td>4.65</td>
<td>2</td>
<td>2,690</td>
<td>149</td>
</tr>
<tr>
<td>1992</td>
<td>INLAND</td>
<td>59</td>
<td>Stone’s Bridge</td>
<td>F</td>
<td>44</td>
<td>4.24</td>
<td>4.40</td>
<td>2</td>
<td>1,870</td>
<td>167</td>
</tr>
<tr>
<td>1992</td>
<td>INLAND</td>
<td>66</td>
<td>Lt. St. Germaine</td>
<td>M</td>
<td>41</td>
<td>3.08</td>
<td>3.15</td>
<td>3</td>
<td>2,392</td>
<td>190</td>
</tr>
<tr>
<td>1992</td>
<td>INLAND</td>
<td>62</td>
<td>Blair Lk.</td>
<td>M</td>
<td>47</td>
<td>3.29</td>
<td>3.15</td>
<td>1</td>
<td>1,929</td>
<td>108</td>
</tr>
<tr>
<td>1992</td>
<td>INLAND</td>
<td>86</td>
<td>Horsehead Lk.</td>
<td>F</td>
<td>41</td>
<td>3.70</td>
<td>3.90</td>
<td>2</td>
<td>2,773</td>
<td>188</td>
</tr>
<tr>
<td>1993</td>
<td>INLAND</td>
<td>48</td>
<td>Haunted Is.</td>
<td>M</td>
<td>60</td>
<td>3.95</td>
<td>4.05</td>
<td>2</td>
<td>2,896</td>
<td>120</td>
</tr>
<tr>
<td>1993</td>
<td>INLAND</td>
<td>49</td>
<td>Haunted Is.</td>
<td>M</td>
<td>54</td>
<td>3.90</td>
<td>3.85</td>
<td>2</td>
<td>2,834</td>
<td>138</td>
</tr>
<tr>
<td>1993</td>
<td>INLAND</td>
<td>50</td>
<td>Aurora Lk.</td>
<td>F</td>
<td>47</td>
<td>4.60</td>
<td>4.70</td>
<td>1</td>
<td>2,356</td>
<td>189</td>
</tr>
<tr>
<td>1993</td>
<td>INLAND</td>
<td>51</td>
<td>Star Lk.</td>
<td>M</td>
<td>56</td>
<td>4.00</td>
<td>4.00</td>
<td>2</td>
<td>2,816</td>
<td>170</td>
</tr>
<tr>
<td>1993</td>
<td>INLAND</td>
<td>52</td>
<td>Star Lk.</td>
<td>M</td>
<td>54</td>
<td>3.95</td>
<td>3.95</td>
<td>2</td>
<td>2,300</td>
<td>148</td>
</tr>
<tr>
<td>1993</td>
<td>INLAND</td>
<td>60</td>
<td>Lost Canoe</td>
<td>F</td>
<td>54</td>
<td>4.85</td>
<td>4.40</td>
<td>2</td>
<td>2,721</td>
<td>127</td>
</tr>
<tr>
<td>1994</td>
<td>LK SUP.</td>
<td>28</td>
<td>Saxon Harbor</td>
<td>F</td>
<td>55</td>
<td>4.48</td>
<td>4.36</td>
<td>1</td>
<td>2,183</td>
<td>98</td>
</tr>
<tr>
<td>1994</td>
<td>LK SUP.</td>
<td>29</td>
<td>Amnicon</td>
<td>F</td>
<td>39</td>
<td>4.03</td>
<td>4.19</td>
<td>2</td>
<td>1,776</td>
<td>172</td>
</tr>
<tr>
<td>1994</td>
<td>LK SUP.</td>
<td>30</td>
<td>Amnicon</td>
<td>F</td>
<td>44</td>
<td>4.22</td>
<td>4.24</td>
<td>2</td>
<td>2,732</td>
<td>144</td>
</tr>
<tr>
<td>1994</td>
<td>LK SUP.</td>
<td>31</td>
<td>Reefer Cr.</td>
<td>F</td>
<td>53</td>
<td>4.37</td>
<td>4.46</td>
<td>1</td>
<td>2,712</td>
<td>130</td>
</tr>
</tbody>
</table>

Nagy’s (1980) equation (validated in eaglets, Dykstra et al. 1997). The datum from the single nestling for which the initial blood sample was obtained was analyzed by the single-sample DLW technique (Webster and Weathers 1989). Rates of CO₂ production were converted to kJ day⁻¹ using the relationship 25.7 J ml⁻¹ CO₂ for a proteinaceous food source (Ricklefs 1974). Water influx was calculated using Nagy’s (1983) equation (#3).

ENERGY RETAINED IN GROWTH

For nestlings for which we measured FMR, we measured mass gain over the same 5-day period and determined the amount of energy deposited as new tissue by multiplying mass gain by the energy content of the new tissue. Tissue energy content (6.8–8.1 kJ g⁻¹ for nestlings aged 39–60 days) was calculated from a regression for several species of birds (Weathers 1996, equation 13.10).

STATISTICAL ANALYSES

Values are reported as means ± SE. Standard statistical tests were performed with Systat (Wilkinson 1988). A P-value < 0.05 was considered significant.

RESULTS

ENERGY EXPENDITURE OF INLAND NESTLINGS

Average inland FMR determined by doubly-labeled water was 2,452 ± 114 kJ day⁻¹ (values for individual nestlings in Table 1). Average water influx was 611.7 ± 31.8 ml day⁻¹ (or 15.3% of body mass). Siblings were treated as independent data points. To determine covariates of FMR we used forward stepwise multiple regression, with acceptance criteria of t-statistic and Mallow’s C_p (Ott 1988). We tested whether FMR varied with age, mass, sex, brood size, or year. FMR was significantly related only to nestling age (r² = 0.38, P = 0.03, n = 12, slope = 36.1 ± 4.2, intercept = 686 ± 206, Fig. 1). Neither additional variables nor interactions of age with other variables significantly improved the fit of age with FMR.

Because siblings may not represent independent measurements, we reanalyzed the data using means for the FMRs, masses, and ages of each sibling pair. With siblings averaged, there was no relationship of FMR to age (r² = 0.24, P = 0.22, n = 8) or to any other variable. However, mean FMR remained the same (2,450 ± 118 kJ day⁻¹).

ENERGY EXPENDITURE OF LAKE SUPERIOR NESTLINGS

FMR of four nestlings averaged 2,351 ± 230 kJ day⁻¹ (Table 1). Data from Lake Superior and inland nestlings were combined for stepwise multiple regression as described above, with the additional factor of location (inland or Lake Superior). FMR did not differ between locations and was significantly related only to nestling age (F₁₃,₁₅ = 6.09, r² = 0.33, P = 0.02).

ENERGY RETAINED IN GROWTH

Mean mass change during the 5-day trial was +10 ± 50 g for inland nestlings and +35 ± 59 g for Lake Superior nestlings. Mass differences of <100 g were near the limit of our measurement sensitivity and probably were not biologically meaningful because the birds themselves vary daily in mass due to food in the crop. Nonetheless, we calculated the energy deposited as new tissue for each chick whose FMR was measured. Means were 104 ± 32 metabolizable kJ day⁻¹ for inland nestlings and 110 ± 60 metabolizable kJ day⁻¹ for Lake Superior nestlings, assuming no energy devoted to growth for nestlings with no mass gain over the 5-day trial. Thus, resired energy (FMR) + energy retained in the observed growth averaged 2,556 ± 116
metabolizable kJ day\(^{-1}\) for inland nestlings, 2,461 \(\pm\) 207 metabolizable kJ day\(^{-1}\) for Lake Superior nestlings, and 2,532 \(\pm\) 98 metabolizable kJ day\(^{-1}\) for all nestlings combined.

**DISCUSSION**

Mean FMR of nesting Bald Eagles in this study, 2,427 kJ day\(^{-1}\), was 13% higher than mean daily energy expenditure measured by DLW in four wild eaglets 51–56 days old held temporarily in captivity (2,148 kJ day\(^{-1}\), Dykstra et al. 1997). Slightly higher rates of energy expenditure in the field may be due to greater activity or higher thermoregulatory costs in the field than in captivity. However, small differences such as these may also be due to limitations inherent in the DLW technique, which can produce individual errors >10% (Dykstra et al. 1997). Nestlings in captivity or in the field had much higher rates of energy expenditure than adult Bald Eagles in captivity. Two captive adults averaged 1,203 kJ day\(^{-1}\) (mean mass of 4,785 g; Dykstra et al. 1997). Four captive adults, measured on a per-kg basis, averaged 258 kJ kg\(^{-1}\) day\(^{-1}\) and 221 kJ kg\(^{-1}\) day\(^{-1}\) when consuming mammalian and fish diets, respectively, (corresponding to 1,235 and 1,057 kJ day\(^{-1}\) for a bird of 4,785 g; Stalpaster and Gessaman 1982).

There was some evidence that FMR was lower in broods of two nestlings on Lake Superior and in broods of three nestlings inland than in all other brood sizes. On Lake Superior, for broods of two, FMR averaged 2,254 \(\pm\) 478 kJ day\(^{-1}\) (n = 2 sibs), while for broods of one, FMR averaged 2,448 \(\pm\) 265 kJ day\(^{-1}\) (n = 2 nests). Similarly, FMR for inland nestlings in broods of three averaged only 2,119 kJ day\(^{-1}\) (n = 2 sibs in one nest of three), compared to 2,519 kJ day\(^{-1}\) for other inland nestlings (Table 1). Although the sample sizes were too small to make any conclusions, the observed trend is consistent with other data which suggest that these brood sizes may be somewhat energy-deficient (i.e., food-stressed). Both Lake Superior broods of two and inland broods of three received fewer prey deliveries per nesting and less energy per nesting than did inland broods of one or two and Lake Superior broods of one (Warnke 1996, Dykstra et al. 1998). For Lake Superior broods of two, adult and nesting behaviors also suggested food shortage (Warnke 1996, Dykstra et al. 1998). Alternatively, the lower FMR of larger broods might be explained by thermal benefits nestlings derived from huddling.

Nesting FMR can be used to calculate the energy which must be collected for the nestlings by parents at this stage in the nesting cycle (age = 30-60 days). For a typical brood of two, each parent must collect enough food for the FMR plus energy retained in growth of one chick, 2,532 metabolizable kJ day\(^{-1}\), in addition to fulfilling its own requirements. For ease of calculation, we assume a strictly fish diet (fish made up 80–97% of inland and Lake Superior eagles’ prey deliveries in 1992 and 1993, Warnke 1996). Assuming a metabolizable energy coefficient (MEC) equal to that measured in captive nestling eagles eating wild-caught bullheads (*Ictalurus* spp.), 0.82, we calculated that each parent must collect 3,088 metabolizable kJ day\(^{-1}\) for the chicks. If the energy content and water content of wild fish are approximately equal to those of the above bullheads (19.7 kJ g\(^{-1}\) dry weight and 78.5% water, Dykstra et al. 1997), then each adult eagle must collect 729 g wet mass of fish day\(^{-1}\) for each nestling. Additionally, each adult must collect food for its own energy requirements. Although FMR of breeding adults is unknown, we can conservatively assume that it would be a minimum of 1,203 kJ day\(^{-1}\), the daily energy expenditure measured in captive, non-breeding adults (Dykstra et al. 1997). This would add an additional 346 g wet mass of fish day\(^{-1}\) for each adult to collect, bringing the total to 1,075 g fish day\(^{-1}\) per adult, equivalent to four 28-cm bullheads or eight 20-cm bluegills (*Lepomis macrochirus*; calculated using length-mass relationships in Carlander 1969, 1977). We should note that this is a conservative estimate in two ways. As described above, the adult FMR is unknown, but is probably higher than the captive energy
expenditure we used. Also, field MEC for both nestlings and adults may be lower than the 0.82 used in this calculation. The fish eaten in the feeding trial used to determine this MEC were small bullheads (Dykstra et al. 1997), which may have been more digestible than some larger types of prey fish. In a study of adult eagles eating fish, average MEC was 0.75 (Stalmaster and Gessaman 1982).

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LITERATURE CITED


