ENERGY CONSTRAINTS ON AVIAN DISTRIBUTIONS AND ABUNDANCES

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Abstract. A long-standing hypothesis within ecology states that external environmental factors, such as extreme temperatures, are the primary forces shaping species' biogeographic ranges. On a continent-wide scale, the correlative evidence presented in this study strongly indicates that the locations of winter distribution and abundance patterns of several avian species are directly linked with their physiological demands.

I calculated the metabolic rate at the northern boundary of the distribution (NBMR) for 14 of 51 passerines known to have range boundaries associated with a particular average minimum January temperature isotherm. Based on physiological measures taken from the literature, a regression analysis reveals that the northern boundary metabolic rate (NBMR) is 2.45 times the basal metabolic rate (BMR). The NBMR to BMR ratio shows little interspecific variation; the mean of this ratio is 2.49 with a standard error of ±0.07. Thus, the scalar multiple of BMR ranges from 2.42 to 2.56. This strong association between NBMR and BMR implies that the winter ranges of these 14 birds are restricted to areas where the energy needed to compensate for a colder environment is not greater than ≈2.5 times the BMR.

Body masses of 36 of the remaining 37 birds, those with their range limits associated with isotherms and without physiological measurements, were used to estimate the various physiological parameters. Even when using such crude estimates of these parameters, the approximation of the metabolic rate of individuals at the northern boundaries of their distributions was 2.64 times their BMR. Furthermore, high-density populations of seven of the 14 species with accurately measured physiological parameters were limited to regions where homeostasis requires energy output of no more than 2.13 times their BMR. The range of this scalar extends from 2.08 to 2.34. These findings strongly suggest that on a broad scale the winter ranges of a large number of passerines are limited by energy expenditures necessary to compensate for colder ambient temperatures.

Key words: abundance patterns; avian energetics; biogeographic patterns; distribution boundaries; energy constraints; metabolic rate; northern range limits; passerine energetics; physiological demands; physiological ecology; winter ranges.

INTRODUCTION

Two long-held hypotheses address the question of what shapes biogeographic patterns. One postulates that abiotic factors, such as climate, exert the primary forces determining the distribution and abundance of species (Andrewartha and Birch 1954); the other implicates biotic interactions, such as competition, as the main factors controlling these patterns (MacArthur 1958). Most ecological studies in the past two decades have examined range boundaries within fairly localized areas (Kareiva and Andersen, in press), and in general they have concluded that biotic interactions, such as competition or predation, appear to dictate the biogeographic patterns of species (Connell 1961, Terborgh and Weske 1975, Moulton and Pimm 1983, Gurevitch 1986).

Factors found to limit distributions on large scales (i.e., entire distributions) should not be extrapolated from findings of studies done within small areas, because factors important at larger scales may be obscured by the details of local studies. A good example of this is the effect of temperature, which Krebs (1985: 86) calls one of the "master limiting factors to the distribution of life on earth." Detecting effects on sedentary species, primarily plants, is relatively easy on a local scale, but for mobile species this is not the case (Brown and Gibson 1983). Thus, except in large-scale studies, the importance of temperature as a limiting factor may be overlooked. In general, biotic interactions are probably influencing proximate details of range boundaries, while the ultimate limiting forces are physiological tolerances (Wardle 1981).

Physiologists have broached the subject of factors limiting species' biogeographic patterns with "confidence that knowledge of the energetics of a species can help to explain its distribution and abundance . . ." (Weatherby 1979:81). Such studies have found general associations between metabolic rate on the one hand and, on the other, body mass (Lasiewski and Dawson 1967, Aschoff and Pohl 1970a), time of day (Aschoff and Pohl 1970a), season (Pohl 1969), and latitude

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(Weathers 1979). However, with few exceptions (e.g., McNab 1973, Hayworth and Weathers 1984), physiological stress from environmental extremes, such as cold ambient temperatures, has not been linked directly with species' biogeographic patterns. The general view that behavioral and ecological factors are more important than physiological ones in limiting ranges has undoubtedly hindered such linkage (Bartholomew and Dawson 1954, Bartholomew 1958, Sturkie 1965).

Relating physiological stress directly with species' ranges has been hampered for two reasons. First, ecological studies necessarily focus on relatively small areas, owing to logistical problems of collecting data over large regions. Moreover, broad pervasive effects generated by abiotic factors are difficult to recognize at the local level, because on small scales, biotic interactions largely overshadow the influences of environmental forces. Second, physiologists have not known a priori which species are most likely to be limited by physiological stress from a given environmental factor. For example, 60.2% of 113 avian species wintering in North America have northern range limits associated with a particular isotherm. Thus, a researcher has a 39.8% chance of choosing a species at random that has a range that is not limited by ambient temperature (Root 1988). Thus, physiological ecologists have a relatively high probability of choosing a species with a range that is not influenced by ambient temperature, and when this occurs the link between a species' physiology and its biogeographic pattern cannot be established. Hence, prior knowledge about limiting species' distributions is needed.

I analyzed the distribution and abundance maps of all terrestrial birds wintering in the conterminous United States and southern Canada (Root 1988). The entire length of the northern range limits of 62 species was tightly associated with a particular average minimum January temperature isotherm. The purpose of this study was to combine these ecological findings with physiological information from the literature and to investigate whether abiotic factors, in this case minimum January temperature, determine the biogeographic patterns of species, specifically the northern range limits of wintering passerine birds. The results indicate that the metabolic rates of several passerines at their northern boundaries are a scalar multiple of their basal metabolic rate (BMR), and this value shows little variation among species. Thus, this study provides strong correlative evidence that on a broad scale, physiological demands restrict the northern boundaries of these wintering birds.

**METHODS**

The most extensive database of animal abundances in North America is provided by the National Audubon Society’s Christmas Bird Counts. These data have been collected annually since 1900 and today cover all of the United States and southern Canada. Ten years of these data, collected from 1962–1963 to 1971–1972, were used to plot abundance maps of 253 species (Root, in press). These include all species wintering in North America, except those seen on <40 census sites, and those that are extremely gregarious or unusually rare and hence imprecisely estimated (Bock and Root 1981). In a previous study I identified those environmental factors associated with the range boundaries of ≈90% of these winter species (nocturnal, nomadic, and extensively managed species were eliminated) (Root 1988). By comparing these species’ maps with a map of the average minimum January temperature having isotherms drawn at roughly 6°C intervals. I found that the entire length of the northern range limits of 11 nonpasserines and 51 passerines was strongly associated with particular temperature isotherms. Such associations were determined by finding the area between the closest isotherm and the northern range boundary of a given species (Fig. 1). This value was then divided by the length of the boundary. If this average deviation was <1° of latitude (i.e., 115 km), then an association was assumed (Root 1988).

The present study further investigates the 51 passerines, ignoring the nonpasserines because of their taxonomic heterogeneity. In-depth physiological studies on winter-acclimatized individuals of 14 of these passerine species are reported in the literature, and one species, the White-crowned Sparrow (Zonotrichia leucophrys), was examined in two different studies (Table 1). Only those species with physiological characteristics determined under winter conditions are included because season may affect some aspects of the physiology of individuals (Aschoff and Pohl 1970b, Kendegge et al. 1977; but also see Dawson and Carey 1976, Weathers 1980). The pertinent information obtained from
studies in the literature includes lower critical temperature (TCRIT, the ambient temperature at which an individual must increase its metabolic rate in order to maintain heat balance), the basal metabolic rate (BMR, the metabolic rate of a resting individual at an ambient temperature above its TCRIT), and conductance (COND, the rate of heat loss of an individual as the ambient temperature drops below the TCRIT). Physiological information for the Northern Cardinal (Cardinalis cardinalis) had to be gleaned from two sources. Dawson (1958) measured winter-acclimated individuals, but resting rates were taken during the day (W. R. Dawson, personal communication). Hinds and Calder (1973), on the other hand, measured only summer-acclimated individuals, but resting rates were recorded at night. Conductance may be influenced by season (Aschoff and Pohl 1970b, Kendig et al. 1977), but seasonal changes in BMR are not significant. Thus, the value for the cardinal’s BMR was taken from Hinds and Calder’s study, and for its COND from Dawson’s. I calculated TCRIT from these two values and the intercept of the COND line at 0°. The COND values for all the species were determined by least-squares fit of a regression line through measured values, and re-calculation was done when another method was used in the original study. The average minimum January temperatures at the northern boundaries of the 14 species’ ranges (TDIST) were determined from the range maps (Table 1).

Fig. 2 depicts the relationship between the measured physiological values, temperature at the northern boundary of the distribution, and the value for the metabolic rate at the northern boundary of the distribution (NBMR). The equation used to derive NBMR is

\[
NBMR = [(TDIST – TCRIT – COND) + BMR] \tag{1}
\]

with BMR and NBMR measured in kilojoules per day, and COND in kilojoules per day per bird per degree Celsius.

**RESULTS**

*Metabolic rates at the northern range boundary*

Metabolic rate is strongly associated with body mass (Brody and Proctor 1932, King and Farner 1961, Lasiwski and Dawson 1967, Aschoff and Pohl 1970a, b). This is also true for the 14 passerines examined here.
(Table 1), with 84% of the variation in BMR explained by body mass when both variables are expressed on a log scale. The least-squares fit of a regression line between these two transformed variables (Fig. 3) results in the following equation:

\[
\log(BMR) = \log(2.30) + 0.80 \log(M),
\]

(2)

where BMR is measured in kilojoules per day and body mass (M) in grams. The standard error of the regression coefficient is ±0.10.

Values for NBMR from Eq. 1 regressed on body mass also show a strong positive relationship (Fig. 3), with 87% of the variation in the log-transformed values of NBMR being directly attributable to the similarly transformed body mass of the species. The regression equation is

\[
\log(NBMR) = \log(4.06) + 0.92 \log(M),
\]

(3)

where NBMR is measured in kilojoules per day, and the standard error of the regression coefficient is ±0.10. The slopes of the lines defined in Eqs. 2 and 3 (i.e., 0.80 and 0.92) are not statistically different.

Setting the slope of Eq. 3 to 0.80 necessitates the recalculation of the \( y \)-intercept value. This gives the following equation:

\[
\log(NBMR) = \log(5.65) + 0.80 \log(M).
\]

Rearranging, substituting this into Eq. 2, and transforming out of logarithms gives the following relationship:

\[
NBMR = 2.45 \times BMR.
\]

(4)

Therefore, the energy cost incurred by individuals at the northern limits of these species’ ranges is a scalar multiple of BMR. The ratio of NBMR to BMR shows little variation among species; the mean of this ratio is 2.49 with a standard error of ±0.07. Therefore, the scalar multiple of BMR ranges from 2.42 to 2.56. The small amount of variation among the species in the difference between the NBMR and BMR values is evident in Fig. 3. In fact, the distance between these two values for the outlier, the American Goldfinch (Carduelis tristis), is not significantly different from the distances for the other species.

Species without physiological measurements

I could not find adequate physiological data in the literature for the remaining 37 passerines with northern boundaries associated with certain temperature isotherms. Values for the average body masses of 36 of these birds are available (Dunning 1984), however. These body masses, unfortunately, include both summer- and winter-acclimatized individuals, but for most species, the annual average provides at least a rough estimate of winter body mass. These values can be used to estimate BMR (Aschoff and Pohl’s 1970a), COND (Aschoff 1981), and TCRIT (Weathers and Van Riper 1982) from the following equations:

\[
\log(BMR) = \log(3.19) + 0.73 \log(M),
\]

(5)

\[
\log(COND) = \log(0.28) + 0.54 \log(M),
\]

(6)

\[
\log(TBODY - TCRIT) = \log(11.46) + 0.19 \log(M).
\]

(7)

Again, the BMR is measured in kilojoules per day, COND in kilojoules per day per bird per degree Celsius, TCRIT and TBODY (body temperature) in degrees Celsius, and body mass in grams.

I derived equations similar to these for the 14 species examined in this study:

\[
\log(BMR) = \log(2.30) + 0.80 \log(M),
\]

(2)

\[
\log(COND) = \log(0.13) + 0.82 \log(M),
\]

(8)

\[
\log(TBODY - TCRIT) = \log(7.54) + 0.26 \log(M).
\]

(9)

The respective standard errors of the regression coefficients are ±0.10, ±0.10, ±0.12, and \( r \)’ values are 0.84, 0.84, and 0.25.

I used Eqs. 2, 8, and 9, rather than the equations frequently cited in the literature (Eqs. 5, 6, and 7), to estimate the physiological parameters for the 36 species without values measured directly. Aschoff and Pohl’s (1970a) equation for BMR of night-resting passerines (Eq. 5) is based on 11 species with repeated measurements on two of these, making a total of 14 values, while Eq. 2 was derived from values averaged from several measurements for 14 species, and two separate studies investigated one of these species. Differences in both the slopes and \( y \)-intercepts of these two equations are not statistically significant. Thus, either equation is equally applicable. This is not true, however, for the COND equations.
Table 2. Calculated metabolic parameters* for passerines with northern range limits coincident with an average minimum January temperature isocline and with no physiological measurements (except body mass) available in the literature.

<table>
<thead>
<tr>
<th>Species</th>
<th>Mass (g)</th>
<th>BMR (kJ/d)</th>
<th>COND (kJ d^-1 °C^-1 )</th>
<th>TCRIT (°C)</th>
<th>TDIST (°C)</th>
<th>NBMR (kJ/d)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Black-tailed Gnatcatcher</td>
<td>5.0</td>
<td>8.4</td>
<td>0.1</td>
<td>28.5</td>
<td>-1.1</td>
<td>22.2</td>
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<td>Blue-gray Gnatcatcher</td>
<td>6.0</td>
<td>9.6</td>
<td>0.1</td>
<td>28.0</td>
<td>1.7</td>
<td>23.9</td>
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<td>Golden-crowned Kinglet</td>
<td>6.2</td>
<td>10.1</td>
<td>0.1</td>
<td>27.9</td>
<td>-17.8</td>
<td>35.6</td>
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<td>Ruby-crowned Kinglet</td>
<td>6.7</td>
<td>10.5</td>
<td>0.1</td>
<td>27.6</td>
<td>-3.9</td>
<td>29.3</td>
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<td>Prairie Warbler</td>
<td>7.7</td>
<td>11.7</td>
<td>0.2</td>
<td>27.2</td>
<td>7.2</td>
<td>25.1</td>
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<td>Northern Parula Warbler</td>
<td>8.6</td>
<td>13.0</td>
<td>0.2</td>
<td>26.8</td>
<td>7.2</td>
<td>27.2</td>
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<td>Sedge Wren</td>
<td>9.0</td>
<td>13.4</td>
<td>0.2</td>
<td>26.7</td>
<td>4.4</td>
<td>30.1</td>
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<td>9.0</td>
<td>13.4</td>
<td>0.2</td>
<td>26.7</td>
<td>1.7</td>
<td>32.2</td>
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<td>Yellow-throated Warbler</td>
<td>9.4</td>
<td>13.8</td>
<td>0.2</td>
<td>26.5</td>
<td>4.6</td>
<td>31.4</td>
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<td>Carolina Chickadee</td>
<td>10.1</td>
<td>14.7</td>
<td>0.2</td>
<td>26.2</td>
<td>-6.7</td>
<td>42.3</td>
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<td>Brown-headed Nuthatch</td>
<td>10.2</td>
<td>14.7</td>
<td>0.2</td>
<td>26.2</td>
<td>-1.1</td>
<td>37.7</td>
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<tr>
<td>House Wren</td>
<td>10.9</td>
<td>15.5</td>
<td>0.2</td>
<td>26.0</td>
<td>-1.1</td>
<td>39.8</td>
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<td>White-eyed Vireo</td>
<td>11.4</td>
<td>16.3</td>
<td>0.2</td>
<td>25.8</td>
<td>4.4</td>
<td>36.0</td>
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<td>Field Sparrow</td>
<td>12.5</td>
<td>17.2</td>
<td>0.2</td>
<td>25.5</td>
<td>-6.7</td>
<td>49.4</td>
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<td>Rock Wren</td>
<td>16.5</td>
<td>21.8</td>
<td>0.3</td>
<td>24.4</td>
<td>-9.4</td>
<td>64.1</td>
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<td>Solitary Vireo</td>
<td>16.6</td>
<td>21.8</td>
<td>0.3</td>
<td>24.3</td>
<td>1.7</td>
<td>50.2</td>
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<td>Lincoln Sparrow</td>
<td>17.4</td>
<td>22.6</td>
<td>0.3</td>
<td>24.2</td>
<td>-6.7</td>
<td>62.8</td>
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<tr>
<td>Dark-eyed Junco (Junco hyemalis argus)</td>
<td></td>
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<td></td>
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<td></td>
</tr>
<tr>
<td>Dark-eyed Junco</td>
<td>19.6</td>
<td>24.7</td>
<td>0.3</td>
<td>23.7</td>
<td>-15.0</td>
<td>80.4</td>
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<td>(J. h. hyemalis)</td>
<td>19.8</td>
<td>25.1</td>
<td>0.3</td>
<td>23.6</td>
<td>-15.0</td>
<td>81.2</td>
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<td>Sharp-tailed Sparrow</td>
<td>19.8</td>
<td>25.1</td>
<td>0.3</td>
<td>23.6</td>
<td>-7.2</td>
<td>49.0</td>
</tr>
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<td>American Tree Sparrow</td>
<td>20.1</td>
<td>25.5</td>
<td>0.3</td>
<td>23.5</td>
<td>-17.8</td>
<td>86.3</td>
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<td>Carolina Wren</td>
<td>21.0</td>
<td>26.4</td>
<td>0.4</td>
<td>23.4</td>
<td>-9.4</td>
<td>76.2</td>
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<td>Water Pipit</td>
<td>21.3</td>
<td>26.8</td>
<td>0.4</td>
<td>23.3</td>
<td>1.7</td>
<td>59.9</td>
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<td>Tufted Titmouse</td>
<td>21.6</td>
<td>26.8</td>
<td>0.4</td>
<td>23.2</td>
<td>-13.3</td>
<td>83.7</td>
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<td>Seaside Sparrow</td>
<td>23.9</td>
<td>29.3</td>
<td>0.4</td>
<td>22.8</td>
<td>7.2</td>
<td>55.7</td>
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<td>Western Bluebird</td>
<td>28.1</td>
<td>33.1</td>
<td>0.5</td>
<td>22.1</td>
<td>-6.7</td>
<td>88.8</td>
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<td>Hermit Thrush</td>
<td>31.0</td>
<td>36.0</td>
<td>0.5</td>
<td>21.6</td>
<td>-3.9</td>
<td>89.6</td>
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<td>Eastern Bluebird</td>
<td>31.6</td>
<td>36.4</td>
<td>0.5</td>
<td>21.3</td>
<td>-6.7</td>
<td>96.7</td>
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<td>Cedar Waxwing</td>
<td>32.5</td>
<td>37.3</td>
<td>0.5</td>
<td>21.4</td>
<td>-20.6</td>
<td>128.9</td>
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<td>Townsend’s Solitaire</td>
<td>34.0</td>
<td>38.5</td>
<td>0.5</td>
<td>21.1</td>
<td>-20.6</td>
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<td>Gray Catbird</td>
<td>36.9</td>
<td>41.5</td>
<td>0.6</td>
<td>20.7</td>
<td>4.4</td>
<td>80.8</td>
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<td>Northern Mockingbird</td>
<td>48.5</td>
<td>51.5</td>
<td>0.7</td>
<td>19.3</td>
<td>-6.7</td>
<td>130.2</td>
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<td>Brown Thrasher</td>
<td>68.8</td>
<td>67.8</td>
<td>1.0</td>
<td>17.3</td>
<td>-9.4</td>
<td>175.9</td>
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<td>Eastern Meadowlark</td>
<td>93.9</td>
<td>87.1</td>
<td>1.2</td>
<td>15.4</td>
<td>-9.4</td>
<td>216.5</td>
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<tr>
<td>Western Meadowlark</td>
<td>99.6</td>
<td>91.3</td>
<td>1.3</td>
<td>15.1</td>
<td>-12.2</td>
<td>240.3</td>
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<tr>
<td>American Crow</td>
<td>448.0</td>
<td>304.4</td>
<td>4.5</td>
<td>3.1</td>
<td>-17.8</td>
<td>696.7</td>
</tr>
</tbody>
</table>

* BMR = estimated basal metabolic rate; COND = estimated conductance (the rate of heat loss as the ambient temperature drops below TCRIT); TCRIT = estimated lower critical temperature (the ambient temperature at which the animal must increase metabolic rate in order to maintain heat balance); TDIST = average minimum January temperature at the northern boundary of the species' range; NBMR = estimated metabolic rate at northern boundary of the species' distribution.

Aschoff’s (1981) equation for COND of night-resting passerines (Eq. 6) is based on 22 species with four repeated measures. However, these values, which were obtained from studies in the literature, were not all measured in the same manner. Several were determined by the best least-squares fit of a regression line, but for those studies not reporting values for COND, Aschoff calculated them by dividing the oxygen consumption at temperatures below thermoneutrality by the difference between body and ambient temperature. Such values are usually larger than those obtained with a least-squares fit, because when oxygen consumption is zero the line must pass through the point where ambient temperature is equal to body temperature (McNab 1980). In addition, estimates of COND from at least one of the studies used by Aschoff were derived in yet another manner: Lasiwski (1963) used lines drawn along the lower limits of the measured values.

Another possible reason for the statistically significant discrepancy between Eqs. 6 and 8 is that Aschoff included measurements from both summer- and winter-acclimated individuals, whereas I included only winter-acclimated individuals in my derivations.

Weathers and Van Riper (1982) derived an equation (Eq. 7) that relates metabolism with conductance and temperature differences by substituting Eqs. 5 and 6 into the Scholander-Irving equation (Scholander et al. 1950:247). Thus Eq. 7 has the same unfortunate drawbacks as Eq. 6. In addition, the applicability of the Scholander-Irving equation to free-living individuals is questionable (Dawson and Carey 1976). When the log transformation of the difference between body temperature and lower critical temperature is regressed on the logarithm of body mass for the 14 passerines examined in this study (Eq. 9), only 25% of the variance in the temperature differences is explained by body
Fig. 4. Plot of the association between the metabolic rates at the edge of species' distributions, which were derived from estimates of the various physiological parameters, and body mass. The line is the regression between log(\(NBMR\)) and log(M) for the 14 species with measured physiological parameters (Eq. 3).

mass. The slope of this line is not significantly different from zero, or from 0.19, which is the slope of the line defined by Eq. 7. Neither of these equations (7 or 9) is a good predictor of \(TCRIT\), but for this study Eq. 9 is more applicable than Eq. 7. Therefore, because of the doubtful applicability of Eqs. 6 and 7, I used the equations derived in this study (Eqs. 2, 8, and 9) rather than those cited in the literature (Eqs. 5, 6, and 7) to estimate the physiological values of the 36 species without such measurements (Table 2). Certainly, even Eqs. 2, 8, and 9 can provide only crude estimates of these physiological parameters, because these equations are obtained from regressions that do not account for 100% of the variation in the data.

Using these admittedly crude estimates for \(BMR\), \(COND\), and \(TCRIT\), along with the temperatures at the northern boundaries of the 36 species' distributions, I estimated the metabolic rates at the northern boundaries (Table 2). Regressing these log-transformed values on the similarly transformed mass values gives the following equation:

\[
\log(NBMR) = \log(6.11) + 0.79 \log(M).
\]

The units of these parameters are the same as above (see Eq. 3). The standard error of the regression coefficient is \(\pm 0.03\) and the \(r^2\) value is 0.95. The slope and the intercept of this line are not statistically different from those of Eq. 3. Fig. 4 graphically portrays how well these points cluster along the regression line expressed in Eq. 3.

Even using such crude estimates of the various physiological parameters, the mean of the ratio of \(NBMR\) to \(BMR\) is 2.64, with a standard error of only \(\pm 0.07\). This average is a bit higher than the 2.45 value of the 14 species. This striking similarity suggests that all those passerines with northern distributional boundaries associated with a particular average minimum January temperature isocline have winter ranges that are restricted to areas where the metabolic cost of keeping warm is not over \(\approx 2.5 BMR\).

**Metabolic rates at the edges of areas of abundance peaks**

For each of seven of the 14 species for which physiological information could be found, the boundaries of the area where populations of high abundance spend the winter also coincides with a specific average minimum January isotherm. The boundary of each species' area of high density is defined as the location where \(\geq 20\%\) of the maximum density of individuals occurs. An example is provided in Fig. 5, showing the association between the northern boundary of the region where the Eastern Phoebe (S. phoebe) occurs in high density and the 4°C isotherm. There were too few species to allow extensive analysis, but the metabolic rates at the northern edges of these abundant areas which I designated \(\Delta EMR\) (abundance edge metabolic rate), were calculated in the same manner as were the \(NBMR\) values (Table 3). For the seven species in the sample, the regression equation of log(\(BMR\)) on log(M) is:

\[
\log(BMR) = \log(2.18) + 0.81 \log(M),
\]

which is equivalent to the equation relating \(BMR\) to body mass for the 14 species (Eq. 2). The percentage of variation in \(BMR\) explained by body mass for the seven species is 97\%, in contrast to 84\% for all 14 species. The standard error of the regression coefficient is \(\pm 0.06\).

The slope of the regression line between log(\(NBMR\)) and log(M) for these seven species is not statistically different from that for the 14 species (Eq. 3), and again the explained variation in \(NBMR\) due to body mass is higher when fewer species are considered (\(r^2 = 0.97\).
TABLE 3. Metabolic parameters* for passerines with the northern edge of their high-density area coincident with an average minimum January isotherm.

<table>
<thead>
<tr>
<th>Species</th>
<th>Mass (g)</th>
<th>BMR (kJ/d)</th>
<th>NBMRI (kJ/d)</th>
<th>TABUN (°C)</th>
<th>AEMR (kJ/d)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Palm Warbler</td>
<td>9.8</td>
<td>13.4</td>
<td>29.7</td>
<td>7.2</td>
<td>24.7</td>
</tr>
<tr>
<td>Common Yellow-throat Warbler</td>
<td>10.6</td>
<td>15.1</td>
<td>31.8</td>
<td>4.4</td>
<td>29.3</td>
</tr>
<tr>
<td>Yellow-rumped Warbler</td>
<td>11.5</td>
<td>16.3</td>
<td>42.3</td>
<td>4.4</td>
<td>34.3</td>
</tr>
<tr>
<td>Song Sparrow</td>
<td>19.1</td>
<td>21.8</td>
<td>69.5</td>
<td>−6.7</td>
<td>62.0</td>
</tr>
<tr>
<td>White-throated Sparrow</td>
<td>20.2</td>
<td>24.3</td>
<td>67.0</td>
<td>−1.1</td>
<td>58.6</td>
</tr>
<tr>
<td>Eastern Phoebe</td>
<td>21.6</td>
<td>29.7</td>
<td>71.6</td>
<td>4.4</td>
<td>59.9</td>
</tr>
<tr>
<td>Northern Cardinal</td>
<td>41.0</td>
<td>43.5</td>
<td>121.4</td>
<td>−6.7</td>
<td>99.6</td>
</tr>
</tbody>
</table>

*BMR = basal metabolic rate; NBMRI = metabolic rate at northern boundary of the species’ distribution; TABUN = average minimum January temperature at the edge of the species’ area of high density (see Results: Metabolic Rates at the Edges of the Areas of Abundance Peaks); AEMR = metabolic rate at the northern edge of the abundance peak.

and \( r^2 = 0.87 \). The equation for the seven species is

\[
\log(NBMRI) = \log(3.43) + 0.98 \log(M),
\]

where the standard error of the regression coefficient is \( \pm 0.08 \).

The regression equation relating log(AEMR) with log(M) is \( (r^2 = 0.96) \):

\[
\log(AEMR) = \log(3.14) + 0.96 \log(M),
\]

and the slope of this line, with a standard error of \( \pm 0.11 \), is not significantly different from that found between log(NBMRI) and log(M) (Eqs. 3 and 10). Setting the slope of the line described in Eq. 11 to 0.98, which is the slope of Eq. 10, the y-intercept changes, resulting in the following equation:

\[
\log(AEMR) = \log(2.97) + 0.98 \log(M).
\]

Transforming Eq. 10 out of logarithms, rearranging, and substituting into this equation gives the following relationship:

\[
AEMR = 0.87 \text{ NBMRI}.
\]

Substituting 2.45 \text{ BMR} for NBMRI gives

\[
AEMR = 2.13 \text{ BMR}.
\]

As with the NBMRI to BMR ratio, the AEMR to BMR ratio shows little variation among the species. The mean of the latter ratio is 2.21 with a standard error of \( \pm 0.13 \). Thus, the scalar multiple of BMR that describes the metabolic rate at the edge of the species’ area of high abundance is 2.08 to 2.34.

The seven species are typical representatives of the 14 species because the slopes of the lines relating body mass with BMR and with NBMRI are not statistically different between the two groups of species. The energy cost incurred by individuals in the high-density habitats is only 87% of that incurred by individuals at the northern range boundaries; in terms of BMR, the metabolic cost is a bit more than twice that of the basal rate (Fig. 3). Also, the energy costs at the edges of the high-density areas show little variation among all seven species, with a standard error of only ±0.13 on the mean of the AEMR to BMR ratio.

DISCUSSION

Scale is an important consideration when investigating factors that shape distribution and abundance patterns of species. Most ecological studies in the last two decades have provided evidence for the hypothesis that the important factors are primarily biotic interactions. This preponderance of evidence, however, does not preclude the possibility that abiotic factors are the primary forces determining the distribution and abundance patterns of species. Indeed, 80% of recent ecological studies have examined areas that are <100 m² ( Kareiva and Andersen, in press). In these relatively small areas, factors such as competition and predation are more obvious, and thereby overshadow the possible importance of climate and other external factors.

The broad pervasive effects of environmental factors are most easily recognized in large-scale studies, and such studies are fairly rare because of the logistical difficulties of obtaining data. The lack of results demonstrating the effects of abiotic factors is, therefore, not evidence that they are not important, but merely a testimony to the difficulty of executing large-scale ecological studies. Likewise, the paucity of physiological data directly linking energy constraints to species’ biogeographic patterns is not evidence that such a link does not occur. The lack of large-scale ecological studies has prevented physiologists from knowing a priori which species are most likely to have ranges constrained by a particular environmental factor. A total of 60.2% of 113 bird species wintering in North America have northern range boundaries associated with average minimum January temperature (Root 1988). Thus, almost 40% of the species examined have northern ranges that are not associated with ambient temperature. If a species falling into this latter group were chosen for physiological study, then the links between energy constraints due to temperature and the species’ biogeographic pattern would not be evident.

The results of the present study indicate that on a continentwide scale biogeographic patterns of some species are directly linked with physiological demands. The estimated metabolic rate at the northern boundary of the winter distribution of the 14 passerines examined is 2.45 times their BMR (Eq. 4; Fig. 3). This means that these species are restricted in their winter distributions to areas where the birds need not raise their metabolic rate >2.45 times their BMR to meet thermal requirements in a colder climate. This correlative evidence supports the hypothesis that on a large scale the northern limits of these distributions are determined by the physiological demands of the colder ambient temperatures. This type of investigation cannot detect
the effects of biotic interactions such as competition and predation. The low interspecific variation in the increase of BMR to the metabolic rate at the northern boundary (NBMR) indicates that biotic interactions are doing little more than “fine tuning” the shapes of the ranges of these species on a continentwide scale. The diversity among the species examined implies that this relationship between NBMR and BMR among passerines demonstrates a physiological limit imposed by ambient temperature regardless of body size, diet, or general habitat; the body masses of the species examined vary from 8.2 to 41.0 g, their diets range from seeds to insects, and the northern boundaries of their distributions occur from northern Florida to southern Canada.

The strong link between winter ranges and physiological demands is evident even for the 36 passerines for which there were no measured physiological parameters available. Estimates of these parameters can be obtained from the body masses of the species. Even using these estimates, the derived values of the metabolic rates at the boundaries of their ranges were very similar to those from birds having accurately measured physiological parameters (Fig. 4). This implies that the metabolic rates at the northern edges of the distributions of a large number of passerines are associated with the energy demands of the species. These birds restrict their winter ranges to areas where they need not increase their metabolism >2.42–2.56 times their BMR. The physiology of the 36 species without exact physiological measurements, however, needs to be directly investigated. Such examination will help to determine the robustness of the relationship NBMR = 2.45 BMR. In addition, studies need to be done on these species to investigate how physiological demands in general shape their biogeographic patterns.

It is not obvious why species restrict their winter ranges to areas where they need not raise their metabolic rate over 2.42–2.56 BMR in order to compensate for the ambient temperature. As already noted, interspecific interactions are adding only a small amount to the strong correlation between NBMR and BMR, but other ecological factors may be involved. For example, the length of daylight could influence length of available foraging time, which in turn may help regulate the daily accumulation of body fat. Moreover, foraging rate also influences how full the crop of an individual will be in the evening, and thus, how much heat will be provided from the digestive process through the night (Diamond et al. 1986). The northern expansion of the ranges of many species that frequent feeding stations (e.g., Tufted Titmouse [Parus bicolor] and House Finch [Carpodacus mexicanus]) is to some extent facilitated by digestive heat (Beddall 1963). In the late afternoon, individuals can visit feeders and fill their crops full of seeds, which will provide digestive heat throughout the night.

When determining avian energy expenditures, other investigators have found multiples of BMR similar to those found in this study. Drent and Daan (1980) referred to an unpublished study by Drent and Doornbos, which shows the daily existence energy for nonmolting, nonreproducing birds to be ≈2.6 BMR. Walsberg (1983) derived a relationship between body mass and average annual daily energy expenditure (DEE). Using the minimum and maximum body masses of the species I examined, the DEE values range from 2.62 to 3.18 BMR. These estimates are for annual DEE, which includes the energy-expensive reproductive period, when metabolic demands may be as high as 4.0 BMR (Drent and Daan 1980). Unfortunately, there are insufficient data to determine the winter DEE, but Walsberg (1980: 303) indicates that “... contrary to what is frequently assumed, winter is not necessarily a period of relatively high energy expenditure.” This implies that the winter DEE may be somewhat less than the range given above. Of course, the metabolic rates at edges of species’ distributions determined in this study are based on resting metabolic rates, and they do not account for extra heat generated during digestion or activity. One of the assumptions of these calculations is that ambient temperature is an adequate index of an individual’s thermal environment. Certainly, microhabitats and wind conditions have great influence on the energy expended to keep warm (Buttemer 1985). To a first approximation, average minimum January temperature, however, appears to describe adequately the wide-scale thermal environment of species, but certainly more study is needed. Further investigations will help determine if there is a connection between the ubiquitous value of 2.45 BMR for the metabolic rate at the northern edge of winter distributions found in this study and daily energy expenditures expounded by other workers, or if the similar values are just an unusual coincidence.

Results of this study indicate that the energetics of these passerines influence abundance patterns as well as distributions. Although data are available for only seven species, all of them have areas of high abundance that are restricted in the north to regions where raising their metabolic rate from 2.08 to 2.34 times their basal rate compensates for colder ambient temperatures (Eq. 12). This is a 13% energy savings over that needed at the northern edge of the distribution (Fig. 3). Therefore, strong correlative evidence indicates that both the distribution and abundance patterns of selected passerines are directly linked with the physiological demands of those species. More study needs to be done to determine if the individuals in the less energy-costly areas have different metabolisms, say for instance, a lower BMR, than those individuals at the northern edges of distributions, or if these individuals have “extra” energy available, which may be expended on competitive interactions. Answers to such questions might provide some information on why various species exhibit a north-south gradient in the sex ratio of wintering populations. For instance, adult male Dark-eyed Juncos...
(Junco hyemalis) remain farther north in the winter than females and juveniles (e.g., Ketterson and Nolan 1976, 1979, 1982).

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Literature Cited


Walsberg, G. E. 1980. Energy expenditure in free-living birds: