TEMPERATURE AND THE NORTHERN DISTRIBUTIONS
OF WINTERING BIRDS[1]

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Abstract. Root (1988*b*) proposed that a physiological limit on metabolic rate constrains the northern distributions of wintering birds. Thermoregulation requires that metabolic rate increase as temperature declines, and hence a ceiling on metabolism that is reached before food or other factors become limiting would set the northern extent of a species distribution.

I compared data with two predictions stemming from the proposal. First, there should be close correspondence between the northern range boundaries of species and temperature isotherms. To test this, I re-evaluated the data and found that only 8–42% of the species that Root classified as limited by temperature had northern range boundaries that corresponded to particular temperature isotherms. The second prediction examined was new: Species' northern limits should scale to body mass, because the ceiling on metabolism is stated as a multiple of basal metabolic rate, which itself scales to body mass. Large species should extend farther north than small species. A test of the prediction using Root's data showed little evidence that a constraint strongly affects the distributions of birds. In a second test, I analyzed additional recent Christmas Bird Counts that include areas farther north than were available to Root. I found that species of all sizes occur at the lowest temperatures, indicating that a ceiling on metabolism does not generally constrain the distributions of birds wintering in North America.

My analysis turned up one other unexpected result: Few large passerines in North America have northern distribution boundaries that occur in warm, southerly areas, whereas small species have northern distribution boundaries in southern as well as in northern areas. The pattern might reflect the relationship between body size and the size of a species' geographic range coupled with the geography of North America. Large species tend to have only large geographic ranges, whereas small species are not so restricted. The avifauna of North America north of Mexico is bounded by a barrier formed by the Gulf of Mexico and a turnover in avifauna between the United States and Mexico. To the north of such a barrier, the northern distribution boundaries of large species should be well away from the barrier because of their large size.

Key words: biogeography; birds; energetics; North America; physiological constraint; species distributions; temperature; winter.

INTRODUCTION

Although there is a consensus among ecologists that the influences of abiotic factors and biotic factors interact to determine population abundances (Begon et al. 1986), it has been difficult to explain specific range boundaries. MacArthur (1972) commented that explanations for the distributions of individual species were in terms of the particulars of the biology of each species rather than in a general framework, and he failed to find a general pattern. He was able to marshal many examples of how the southern ends of the ranges of temperate species might be determined by competition. However, the explanations for northern limits or the upper limits along elevational gradients were few and often involved abiotic factors such as temperature. MacArthur argued that climatic factors alone were un-

likely to limit distributions generally because so many species, particularly plants, could be successfully grown well outside of their normal ranges.

Interest in the determinants of geographic range boundaries has been rekindled recently by Root (1988*b*, *c*). She found that 60% of the bird species wintering in the United States and southern Canada have northern range boundaries that coincide with isotherms of minimum daily January temperature (Root 1988*c*). The passerines within that set of species were calculated to have metabolic rates at their northern limits that average 2.5× basal metabolic rate, and Root (1988*b*) argued that the average is a ceiling on metabolic rate that constrains the northern distributions of species. Such a constraint predominates over other biotic processes that might also influence distributions.

Castro (1989) criticized Root's claim on the grounds that 2.5 represents a simple average rather than a constraint on metabolic heat production. He reasoned that any set of northern limits has a mean and that to dem-

onstrate the existence of a constraint it must be shown that the observed mean differs from that expected by chance. Root (1989), in response, tested the hypothesis that 2.5 represents a constraint as follows. First, she compared the slope of the allometric relationship between body mass and metabolic rate at northern range boundaries with the relationship that would be observed if there were a chance association between species and northern range limits. A null distribution of slopes were generated by repeatedly randomizing temperatures at species limits among species and recalculating the metabolic rates at the limits. The observed slope was greater than expected by chance. Secondly, Root found that the variance of metabolic rate at range boundaries, expressed as a multiple of basal metabolic rate, was less than reckoned by chance, as would be expected of a metabolic constraint.

Although Root's (1989) analysis suggests that a constraint exists, it does not indicate how strongly the constraint influences the distributions of species. The situation is analogous to a regression analysis in which a test of the slope may indicate that a relationship exists, but it is the magnitude of the slope and the coefficient of determination that bear out the relevance of the relationship. The test for constraint was carried out using allometric relationships. Those relationships tend to be tight because of the overwhelming influence of body mass on metabolism, and, consequently, tests based on them might be quite powerful. Root (1988b) found the allometric relationship between body mass and metabolic rate at the northern boundaries of species distributions to have a slope of 0.92, and the coefficient of determination to be 0.87. (A slope of 0.80 was used as the basis for calculating the magnitude of the constraint [Root 1988b].) The null expectation of the slope, obtained through randomization, was 0.75 (Root 1989). Clearly, the constraint, represented by the difference between the observed slope and the null slope, is small relative to the effect of body mass. A method for factoring out the influence of body mass is needed to assess the degree of determination associated with the constraint.

The degree to which a ceiling on metabolism constrains species distributions can be assessed by plotting temperature at the northern range limit against body mass. As the result of allometric relationships explained below, small-bodied birds will reach the ceiling on metabolism at warmer temperatures than will large-bodied birds, and their distributions will also be constrained at warmer temperatures (Fig. 1). A priori, the distribution of species around the constraint might vary between two extreme forms. In either case, the metabolic constraint on species distributions is manifested by a lower temperature bound on species occurrences that decreases with increasing body mass (Fig. 1). If many species are constrained by the ceiling, they should tend to be clustered around the lower bound so that the set of points appears to form a line (Fig. 1a). In the
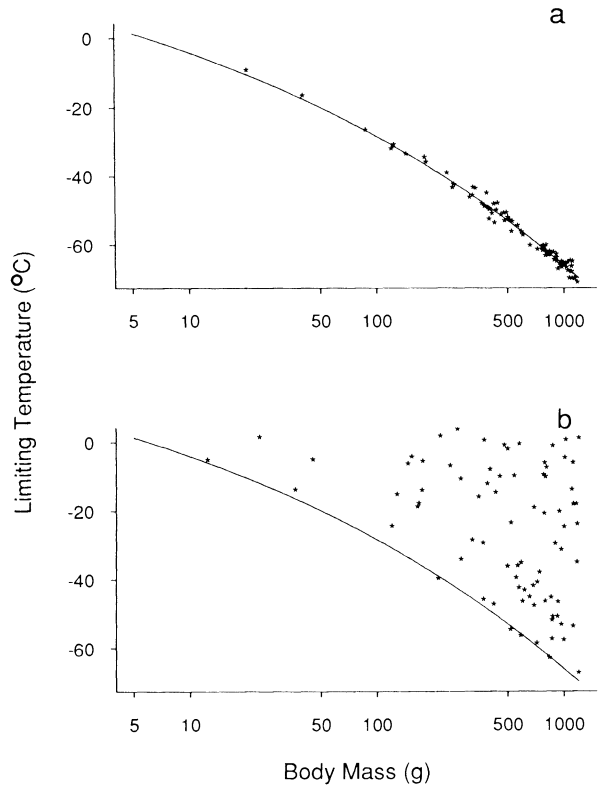

FIG. 1. Alternative hypothetical relationships between coldest temperature along the northern distribution boundary and body mass, assuming that a ceiling on metabolism constrains species distributions. The constraint is illustrated by a line reflecting 2.5 times basal metabolic rate (Root 1988b). In (a) the constraint is pervasive and influences most species. In (b) only a few have northern limits set by the constraint.

other case where relatively few species are constrained, species form a loose cloud of points that is bounded below by the constraint (Fig. 1b).

In this paper, I re-evaluate the extent to which temperature influences the northern distributions of birds. First, I recalculate the match between northern range boundaries and temperature isotherms because I found some discrepancies in Root's (1988b, c) classifications while performing my analysis. Second, I assess Root's metabolic constraint by looking for a lower bound to temperature at the northern limit of species distributions as a function of body mass. I found that only a modest number of species have northern range boundaries that correspond well with temperature, and that the constraint placed by metabolism on the northern limits of species is surprisingly weak. I also discovered a new phenomenon. Although birds of all sizes have range limits at the coldest temperatures studied, only a few large species have northern range limits in warm climes, whereas many small species do so.

PREDICTION OF LIMITING TEMPERATURE

Prediction of the temperature that should limit a species' northern distribution is possible because energy variables scale on body mass. The determinants of metabolic rate are: (1) basal metabolic rate,

$$BMR = 3.19M^{0.73}, \qquad (1)$$

where M is body mass in grams and BMR is in kilojoules per day (Aschoff and Pohl 1970, Root 1988b: Eq. 5); (2) the threshold ambient temperature below which additional energy must be spent to maintain body temperature,

$$TCRIT = TBODY - 11.5M^{0.19},$$

where $TCRIT$ and $TBODY$ (body temperature) are in degrees Celsius (Weathers and van Riper 1982, Root 1988b:Eq. 7); and (3) the rate at which energy expenditure increases as ambient temperature declines,

$$COND = 0.28M^{0.54}, \qquad (2)$$

in kilojoules per day per degree Celsius (Aschoff 1981, Root 1988b:Eq. 6). The rate of maintenance metabolism, hereafter simply metabolic rate (MR), can be calculated as

$$MR = BMR + (TCRIT - TAMB)COND$$

where $TAMB$ is ambient temperature, when the ambient temperature is less than $TCRIT$ (see Calder and King 1974). If MR is expressed as $2.5 \times BMR$ as in Root's (1988b) constraint, this equation can be solved for the ambient temperature that should limit species distributions:

$$TAMB = TCRIT - 1.5BMR/COND.$$
$$TAMB = 40.3 - 28.6M^{0.19}, \qquad (3)$$

given the allometric equations above and an average body temperature of 40.3°C (taken from Root [1988b: Table 1]). Limiting temperature declines as body mass increases (Fig. 1) because $TCRIT$ and $COND$ expressed as a proportion of BMR both decrease as body size increases.

I used previously published estimates of the allometric equations rather than Root's (1988b) estimates of them for two reasons. The range of body masses on which the earlier equations are based is closer to the range of body masses for which I wish to make calculations than the range in Root's data set. Also, Root's equation describing $COND$ differs markedly from previously published allometric equations (W. Weathers and anonymous reviewer, *personal communication*). Note, however, that both sets of equations result in the prediction of declining limiting temperature as body mass increases, and that the analysis that I will employ is not contingent upon the prediction of specific temperatures.

Finally, the prediction that limiting temperature declines with increasing body mass is insensitive to vari-ation in body temperature. Any change in body temperature translates into an equal-sized change in predicted limiting temperature. The effect of variation in body temperature among species, range = 3°C (from Root 1988b:Table 1), is small over a large range of body sizes.

METHODS

Correspondence between isotherms and range boundaries

I found it necessary to assess the correspondence between range boundaries and temperature because 24% of the species that Root classified as having northern boundaries corresponding with isotherms are found in areas $>10°C$ colder than the temperature designated by Root as the limiting temperature (data from Root 1988a, b). Species for which such large deviations occurred are unlikely to be limited by temperature at the temperatures reported by Root (1988b). For example, the Sharp-tailed Sparrow winters in coastal marshes along the Atlantic and Gulf coasts of the United States (Bent 1968, Root 1988a). Its range extends along the Gulf coast east from Texas and continuously up the Atlantic coast into Massachusetts (Root 1988a). The coldest isotherm intersected by the northern boundary was $-6.7°C$, but Root (1988b) reported that the species distribution is bounded by the $+7.2°C$ isotherm, which runs east–west just north of the Gulf coast. Given the species' propensity for coastal areas, habitat rather than temperature probably limits the northern range boundary along the Gulf coast.

I used metrics of agreement between northern boundaries and isotherms that differed from the one used by Root (1988c). She measured the correspondence between a range boundary and a temperature isotherm by calculating the average distance in degrees latitude between the northern range boundary and the isotherm over the length of the boundary. Species for which the mean distance was not $>1°$ of latitude were designated as matching the isotherm. The measure is somewhat unsatisfactory because the change in temperature with a 1° change in latitude varies geographically. I measured the correspondence between range boundaries and isotherms directly in terms of temperature. I used five different measures to quantify the variation in temperature along the northern boundaries of species distributions. The metrics were: the range of temperature spanned by the entire northern boundary; the standard deviation of temperature along the boundary; the mean absolute deviation of temperature along the boundary; as well as the standard deviation and mean absolute deviation in temperature calculated as difference from the temperature at the coldest point along the boundary. Boundaries corresponding closely with temperature should have small values of variability, whereas those corresponding poorly should vary greatly. Multiple measures were used to guard against

the possibility that the results could be an artifact of a single metric. Although the range in temperature is the metric of interest, it is sensitive to outliers. The standard deviation is a measure less sensitive to outliers than the range, and the mean absolute deviation is even less sensitive to outliers. Measurement of deviations from the coldest temperature along range boundaries provided another method for locating outliers. For example, although the northern boundary of a species distribution might follow a particular isotherm quite closely over most of the boundary, a single divergence from the isotherm would have less of an effect on a metric based on deviations from the coldest temperature than it would on metrics based on deviations from the mean temperature. I searched for outliers by ranking species according to each metric and noting large discrepancies in rank between metrics. I recalculated the metrics for species that appeared to be strongly influenced by outliers, after omitting the disparate portions of the range boundaries.

Temperatures along the northern boundaries of species ranges were taken from the maps of species distributions and temperature isotherms in Root (1988a). The maps included the continental United States and southern Canada. Range maps were based on 10 yr of Christmas Bird Count data published between 1963 and 1972. Isotherms on the temperature maps in Root (1988a) were at 5.6°C (10°F) intervals. I interpolated isotherms at ≈2.8°C intervals (5°F) because Root (1988b) reported some species ranges to be bounded by temperatures at the smaller interval. Spurious disjunct populations that appeared on the maps as the result of a few odd sightings were excluded from the analysis (see Appendix). The northern boundary was taken to be the northernmost boundary at any given longitude. Temperature measurements along the northern boundary were made by passing an index card over the map from east to west so that the trailing edge of the card ran north–south. Isotherms intersecting the northern boundary were recorded as they were exposed.

I examined the data for the 50 passerine species that Root (1988b) classified as matching isotherms, and a random sample of 30 passerines from those that Root (1988c) classified as having northern limits that do not correspond with temperature isotherms. Histograms of the measures of correspondence were examined for any bimodality that could be used to distinguish species with northern limits that match isotherms closely from those that do not.

Metabolic constraint on distribution boundaries

A plot of the coldest temperature along a species' northern distribution against body mass should provide the strongest evidence of a metabolic constraint on distributions. It is at the coldest temperature along a range boundary that a ceiling on metabolism should be reached. Deviations of the boundary from that temperature occur as other factors intercede to limit the distribution.

Species were included in the analysis regardless of whether their northern distribution boundaries matched temperature isotherms. All species should be subject to a ceiling on metabolism that scales to body mass. The coldest areas occupied by species with distributions that are constrained should represent the coldest temperatures inhabited by any species of similar size. Finally, a wide range of species is necessary to judge the pervasiveness of the constraint among species (Fig. 1).

I analyzed two sets of data. The first set was the set of species that Root (1988b) designated as temperature limited and the random sample of 30 species from those that Root (1988c) designated as not limited by temperature. As a measure of coldest temperature, I used the coldest isotherm intersected by the northern distribution boundary. Body masses were taken from Root (1988b) or, if not available there, from Dunning (1984). The body mass of the Brewer's Sparrow was not available from either source and was taken from my own field data collected in the Sonoran Desert of southern California. I repeated the analysis in a slightly different manner on a second set of data because the first provided only weak evidence of a constraint. The second data set was from Christmas Bird Counts more recent than those used by Root (1988a, c) and included localities farther north and colder than those of the first set. The data were published in *American Birds* between 1980 and 1989. Count localities were taken from western Canada because counts from the coldest places were available. Localities were chosen on the basis of the number of years of data available and so that a range of temperatures was represented (Table 1). I recorded the temperature at the coldest locality at which a species was "resident," defined as being sighted in at least half of the years in which Christmas counts were conducted. Species satisfying that criterion can be expected to experience the mean temperature at a locality, and species that might occur in a locality only during years of above-average temperature should be excluded from consideration. Temperatures associated with count localities were the mean daily minimum temperature in January, as used by Root (1988c), taken from the Department of Energy, Mines and Resources (1974), which Root also used to generate maps of temperature isotherms. I took the isotherm closest to a count locality to be the temperature at that locality.

RESULTS

Correspondence between isotherms and range boundaries

The different metrics of agreement were highly correlated with one another (all $r > 0.84$) and yielded similar results. I present ranges and standard deviations in Table 2. Standard deviations were less sus-

TABLE 1. Christmas Bird Count localities and the mean minimum daily temperature in January.

Province/territory	Count locality	Temperature (°C)
Manitoba	Winnipeg	−22.8
	Thompson	−32.5
	Churchill	−32.5
Saskatchewan	Squaw Rapids	−25.0
Alberta	Calgary	−15.0
	Edmonton	−20.0
	Ft. McMurray	−25.0
British Columbia	Vernon	−10.0
	Smithers	−12.5
	Quesnel	−15.0
	Ft. St. James	−18.0
	North Pine	−20.0
Northwest Territories	Hay River	−30.0
	Yellowknife	−32.5
Yukon Territory	Marsh Lake	−20.0
	Whitehorse	−22.8
	Kluane	−27.5
	Haines Junction	−27.5

ceptible to outliers than were ranges, but estimates of range derived from them (±2 SD) were actually greater than the observed ranges because the distributions of temperature along the range boundaries of individual species tended to be platykurtic. Therefore, I relied on ranges to judge the closeness with which range boundaries and isotherms correspond.

Species with northern range limits corresponding with a particular isotherm were not easily identified. Histograms of temperature ranges and standard deviations were unimodal and lacked clear break points to distinguish range boundaries that match isotherms from those that do not (Fig. 2). There was also broad overlap in the frequency histograms of species that Root (1988b, c) classified as limited by temperature and the set classified as limited by other factors (Fig. 2) even though the sets were statistically different (one-tailed Wilcoxon two-sample tests: range: $S = 1375.0$, $P = .0558$; standard deviation: $S = 1398.0$, $P = .0230$). Thus, Root's set of temperature-limited species is only slightly better than a random sample of species. There are not two sharply distinguishable groups of species—those that are limited by temperature and those not so limited.

Given the absence of two distinct groups of species, it is necessary to establish the metabolic significance of variation in temperature along northern boundaries before deciding which species have distribution boundaries that match isotherms closely. I used two criteria, one conservative and one liberal, to designate species with northern distributions that correspond well with isotherms. The conservative criterion was a range in temperature that would change metabolic rate by 10% of Root's ceiling on metabolism, or 25% of basal metabolism, and the liberal criterion was a range of temperature changing metabolism by 20% of Root's ceiling, or 50% of basal metabolism. Ranges of temperatures

corresponding to these criteria scale on body mass; variation in metabolic rate expressed as a proportion of basal metabolic rate is $0.088M^{-0.19}\,\Delta TAMB$ (the ratio of Eqs. 2 and 1), where M is body mass in grams and $\Delta TAMB$ is the range in ambient temperature in degrees Celsius along the northern distribution boundary.

Relatively few species had northern limits that corresponded well with temperature isotherms. Eighteen of the 50 species that Root (1988b) classified as limited by temperature had range boundaries along which metabolism should vary by 50% of basal metabolic rate or less. Only 4 species had range boundaries along which metabolism should vary by 25% of basal metabolic rate or less. Inspection of the different metrics of correspondence revealed three species that were unduly affected by outliers: the Northern Mockingbird, American Tree Sparrow, and Eastern Meadowlark. After removing the disparate portions of each species' range boundary, the expected change in metabolic rate due to variation in temperature along the northern boundary was between 50 and 25% of basal metabolism in each case. I conclude that only 4–21 of the 50 species (8–42%) that Root (1988b) classified as matching isotherms actually have northern range boundaries that correspond well with temperature isotherms. Those species represent 5–30% of the passerines having northern range boundaries that Root (1988c) found to fall within the study area.

Metabolic constraint on distribution boundaries

That so few species have northern distributions corresponding with isotherms does not discount the existence of a metabolic constraint on avian range boundaries. It suggests that fewer species than were expected might be limited by such a constraint along their entire northern boundaries. More species might be constrained at the coldest points along their range boundaries, where, if anywhere, a ceiling on metabolism should be reached. I investigated that possibility by plotting the coldest isotherm intersected by species' northern boundaries against body mass. A metabolic constraint on northern boundaries should be manifested as a negatively sloping lower bound on the scatter of points.

The initial result, from Root's data set, indicated that a ceiling on metabolic rate might weakly influence northern distribution limits. However, it was not definitive because the data set was restricted to relatively warm climes. Fifty-nine percent of the species occurred at temperatures colder than expected from Root's (1988b) estimated ceiling on metabolism (Fig. 3a), and some occurred in areas in which estimated metabolic rate was >3.5× basal metabolic rate. The overall relationship between coldest temperature and body size was negative (Fig. 3a, one-tailed t test, $b = -6.54$, $t = -3.12$, df = 78, $P = .0012$) although it accounted for only a small amount of the variation in temperature

($r^2 = 0.11$). Removal of the two extremely heavy species, which might have had excessive influence on the regression analysis, did not change the result. Note that the upper bound appears to decline more steeply than the lower bound, which was relatively flat and showed species from 6 to 450 g occurring at the coldest recorded temperature, $-23.3°C$.

I investigated trends in the upper and lower bounds of the data quantitatively using nonparametric techniques. First, I estimated the 10th, 50th, and 90th percentiles across the range of body masses by running a "window" 12 observations wide across the range of body masses from left to right, one observation at a time. Percentiles were estimated only for those "windows" for which there were 12 observations, and they were calculated as weighted averages using definition 1 of the SAS univariate procedure (SAS Institute 1985). I then fit smooth lines through the series of percentile estimates using the scatterplot smoothing algorithm Lowess (Becker et al. 1988) at the default parameters

FIG. 3. Relationship between the coldest temperature isotherm intersected by the northern boundary of a species and body mass. (a) The data. Symbol "T" represents species designated by Root (1988b, c) as limited by temperature, and "O" represents a random sample of 30 species from those designated as limited by other factors by Root (1988c). —— represents the temperature that ought to constrain northern limits under the 2.5×-basal-metabolic-rate ceiling on metabolic rate proposed by Root (1988b). — — — below represent expected limiting temperatures for constraints at 3, 3.5, and 4× basal metabolic rate, respectively. (b) Smoothed estimates of the 10th, 50th, and 90th percentiles of the coldest isotherm intersected as a function of body mass (see *Results: Correspondence between isotherms and range boundaries*). The points (★) along the lower curve are the running estimates of the 10th percentile to which the corresponding curve was fit.
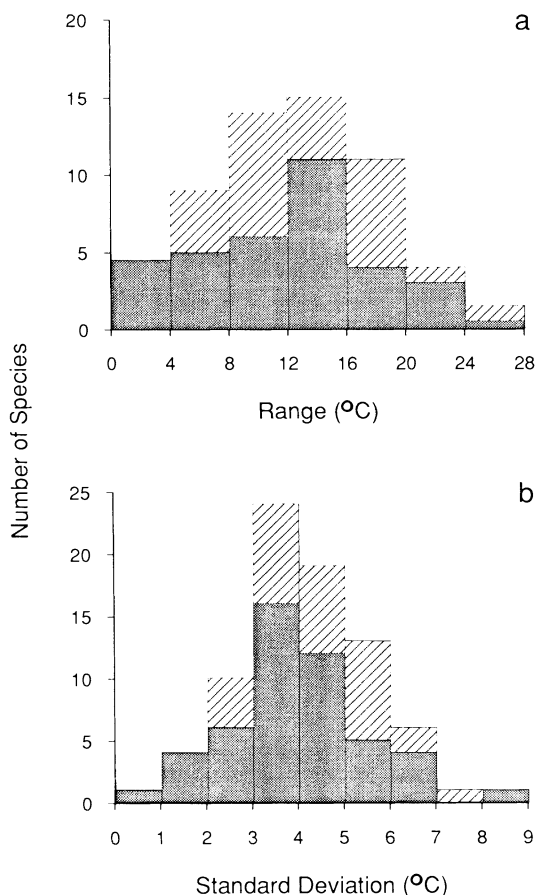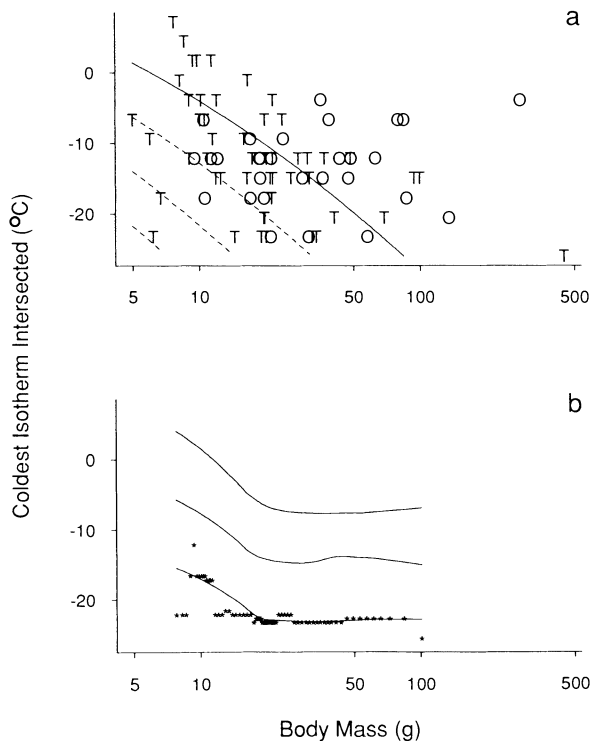

FIG. 2. Range and standard deviation of temperature isotherms intersected by northern boundaries of wintering birds. The filled portion of each bar represents species designated as limited by temperature by (Root 1988b); hatched portions represent a random sample of species not limited by temperature according to Root (1988c).

for smoothing. Lines fit to the upper and lower percentiles had negative slopes at small body mass and then levelled off and remained relatively constant at larger body masses (Fig. 3b).

Data from more northerly areas are critical to determine whether a ceiling on metabolism influences northern distribution boundaries, and if so, whether it influences birds of all body sizes. It is well known that small birds occur in places colder than the coldest in Root's data set, and that they are able to do so by spending large amounts of energy. Redpolls (*Carduelis hornemanni* [12.7 g] and *C. flammea* [13.0 g]), for example, occur regularly in Fairbanks, Alaska (Brooks 1968), where mean minimum daily temperature during January is $-26.6°C$ (Hartman and Johnson 1984) and temperature can drop as low as $-60°C$ (Brooks 1968). These species appear to lack peculiar adaptations that

TABLE 2. Temperatures at the northern boundaries of species distributions. Included in the table are 50 species listed by Root (1988b) as having northern boundaries corresponding with a particular isotherm (TDIST) and limited by that temperature (limitation "T") and a random sample of 30 species from those listed by Root (1988c) as having northern boundaries that do not correspond with temperature isotherms (limitation "O").

Species	Body mass* (g)	Limitation	TDIST (°C)	Isotherms intersected by northern boundary†		
				Coldest (°C)	Range (°C)	SD (°C)
Prairie Warbler, *Dendroica discolor*	7.7	T	7.2	7.2	0.0	0‡
Carolina Chickadee, *Parus carolinensis*	10.1	T	−6.7	−6.7	0.0	0.0
Eastern Phoebe, *Sayornis phoebe*	21.6	T	−3.9	−3.9	2.8	1.3
Northern Parula Warbler, *Parula americana*	8.6	T	7.2	4.4	2.8	1.4
Pine Warbler, *Dendroica pinus*	12.0	T	−1.1	−3.9	5.6	1.5
White-eyed Vireo, *Vireo griseus*	11.4	T	4.4	1.7	5.5	1.7
Solitary Vireo, *Vireo solitarius*	16.6	T	1.7	−1.1	8.3	2.2
Yellow-throated Warbler, *Dendroica dominica*	9.4	T	4.4	1.7	5.5	2.3
Palm Warbler, *Dendroica vitellina*	9.8	T	−1.1	1.7	5.5	2.5
Brown-headed Nuthatch, *Sitta pusilla*	10.2	T	−1.1	−3.9	5.6	2.5
Savannah Sparrow, *Passerculus sandwichensis*	15.9	T	−1.1	−9.4	8.3	2.6
Yellow-rumped Warbler, *Dendroica coronata coronata*	11.5	T	−3.9	−9.4	8.3	2.7
Brewer's Sparrow, *Spizella breweri*	10.5	O	⋯	−6.7	8.4	2.8
White-breasted Nuthatch, *Sitta carolinensis*	21.1	O	⋯	−23.3	8.3	2.9
Phainopepla, *Phainopepla nitens*	24.0	O	⋯	−9.4	11.1	2.9
Harris' Sparrow, *Zonotrichia querula*	36.3	O	⋯	−15.0	8.3	2.9
Sedge Wren, *Cistothorus platensis*	9.0	T	4.4	−3.9	11.1	3.1
Black and White Warbler, *Mniotilta varia*	8.2	T	1.7	−1.1	8.3	3.1
White-throated Sparrow, *Zonotrichia albicollis*	20.2	T	−6.7	−12.2	13.9	3.2
Northern Mockingbird, *Mimus polyglottos*	48.5	T	−6.7	−12.2	13.9	3.2
Yellow-rumped Warbler, *Dendroica coronata auduboni*	12.1	O	⋯	−12.2	11.1	3.2
Swamp Sparrow, *Melospiza georgiana*	17.0	O	⋯	−9.4	8.3	3.2
Tufted Titmouse, *Parus bicolor*	21.6	T	−13.3	−15.0	11.1	3.3
White-crowned Sparrow, *Zonotrichia leucophrys*	26.1	T	−9.4	−15.0	8.3	3.3
Golden-crowned Kinglet, *Regulus satrapa*	6.2	T	−17.8	−23.3	11.1	3.3

TABLE 2.　Continued.

Species	Body mass* (g)	Limitation	TDIST (°C)	Isotherms intersected by northern boundary†		
				Coldest (°C)	Range (°C)	SD (°C)
Eastern Meadowlark, *Sturnella magna*	93.9	T	−9.4	−15.0	13.9	3.3
Cactus Wren, *Campylorhynchus brunneicapillus*	38.9	O	⋯	−6.7	11.1	3.4
Hermit Thrush, *Catharus guttatus*	31.0	T	−3.9	−12.2	11.1	3.4
Field Sparrow, *Spizella pusilla*	12.5	T	−6.7	−15.0	13.9	3.5
Song Sparrow, *Melospiza melodia*	19.1	T	−12.2	−23.3	11.1	3.6
Carolina Wren, *Thryothorus ludovicianus*	21.0	T	−9.4	−15.0	13.9	3.6
Western Bluebird, *Sialia mexicana*	28.1	T	−6.7	−12.2	11.1	3.7
Dark-eyed Junco, *Junco hyemalis caniceps*	19.6	O	⋯	−17.8	11.1	3.7
Sage Thrasher, *Oreoscoptes montanus*	43.3	O	⋯	−12.2	13.9	3.8
Pyrruloxia, *Cardinalis sinuatus*	35.5	O	⋯	−3.9	11.1	3.8
California Thrasher, *Toxostoma redivivum*	84.4	O	⋯	−6.7	11.1	3.8
Common Yellowthroat, *Geothlypis trichas*	10.6	T	−1.1	−6.7	13.9	3.9
Eastern Bluebird, *Sialia sialis*	31.6	T	−6.7	−15.0	13.9	3.9
Ruby-crowned Kinglet, *Regulus calendula*	6.7	T	−3.9	−17.8	13.9	3.9
Lesser Goldfinch, *Carduelis psaltria*	9.5	O	⋯	−12.2	13.9	3.9
Black-tailed Gnatcatcher, *Polioptila melanura*	5.0	T	−1.1	−6.7	13.9	4.0
Chestnut-collared Longspur, *Calcarius ornatus*	18.9	O	⋯	−12.2	13.9	4.1
Black Phoebe, *Sayornis nigricans*	18.7	O	⋯	−12.2	11.1	4.2
Brown Thrasher, *Toxostoma rufum*	68.8	T	−9.4	−20.6	16.7	4.2
Fish Crow, *Corvus ossifragus*	285.0	O	⋯	−3.9	11.1	4.3
House Wren, *Troglodytes aedon*	10.9	T	−1.1	−12.2	13.9	4.3
Vesper Sparrow, *Pooecetes gramineus*	21.5	T	−1.1	−12.2	16.6	4.4
American Goldfinch, *Carduelis tristis*	14.5	T	−17.8	−23.3	16.6	4.4
Seaside Sparrow, *Ammodramus maritimus*	23.9	T	7.2	−6.7	13.9	4.5
Dark-eyed Junco, *Junco hyemalis hyemalis*	19.8	T	−15.0	−20.6	16.7	4.5
American Tree Sparrow, *Spizella arborea*	20.1	T	−17.8	−23.3	16.6	4.5

TABLE 2. Continued.

Species	Body mass* (g)	Limitation	TDIST (°C)	Isotherms intersected by northern boundary†		
				Coldest (°C)	Range (°C)	SD (°C)
Blue-gray Gnatcatcher, *Polioptila caerulea*	6.0	T	1.7	−9.4	13.8	4.5
Curve-billed Thrasher, *Toxostoma curvirostre*	79.4	O	⋯	−6.7	13.9	4.5
Crissal Thrasher, *Toxostoma dorsale*	62.7	O	⋯	−12.2	13.9	4.6
Loggerhead Shrike, *Lanius ludovicianus*	47.4	O	⋯	−15.0	19.4	4.7
Rufous-crowned Sparrow, *Aimophila ruficeps*	18.7	O	⋯	−12.2	16.6	4.8
Western Meadowlark, *Sturnella neglecta*	99.6	T	−12.2	−15.0	16.7	4.8
Sharp-tailed Sparrow, *Ammodramus caudacutus*	19.8	T	7.2	−6.7	13.9	4.8
Rock Wren, *Salpinctes obsoletus*	16.5	T	−9.4	−15.0	19.4	4.9
Orange-crowned Warbler, *Vermivora celata*	9.0	T	1.7	−12.2	16.6	5.1
Dark-eyed Junco, *Junco hyemalis oregonus*	19.6	T	−15.0	−20.6	16.7	5.1
Chipping Sparrow, *Spizella passerina*	11.9	T	−1.1	−15.0	16.7	5.2
American Dipper, *Cinclus mexicanus*	57.8	O	⋯	−23.3	19.4	5.2
Plain Titmouse, *Parus inornatus*	17.0	O	⋯	−17.8	16.7	5.2
Brown Towhee, *Pipilo fuscus*	48.6	O	⋯	−12.2	16.6	5.3
Cedar Waxwing, *Bombycilla cedrorum*	32.5	T	−20.6	−23.3	22.2	5.6
Say's Phoebe, *Sayornis saya*	21.2	O	⋯	−12.2	19.4	5.7
American Crow, *Corvus brachyrhynchos*	448.0	T	−17.8	−26.1	19.4	5.7
Green-tailed Towhee, *Pipilo chlorurus*	29.4	O	⋯	−15.0	19.4	5.8
Sage Sparrow, *Amphispiza belli*	18.9	O	⋯	−15.0	19.4	5.8
Marsh Wren, *Cistothorus palustris*	11.3	O	⋯	−12.2	19.4	5.9
Canyon Wren, *Catherpes mexicanus*	10.6	O	⋯	−17.8	19.5	5.9
Water Pipit, *Anthus spinoletta*	21.3	T	1.7	−17.8	22.2	6.0
Lincoln's Sparrow, *Melospiza lincolni*	17.4	T	−6.7	−12.2	19.4	6.1
Gray Catbird, *Dumetella carolinensis*	36.9	T	4.4	−12.2	19.4	6.4
Horned Lark, *Eremophila alpestris*	31.3	O	⋯	−23.3	27.7	6.4

TABLE 2. Continued.

Species	Body mass* (g)	Limitation	TDIST (°C)	Isotherms intersected by northern boundary†		
				Coldest (°C)	Range (°C)	SD (°C)
Townsend's Solitaire, *Myadestes townsendi*	34.0	T	−20.6	−23.3	22.2	6.7
Clark's Nutcracker, *Nucifraga columbiana*	135.0	O	···	−20.6	22.3	6.8
Scrub Jay, *Aphelocoma coerulescens*	86.4	O	···	−17.8	27.8	7.1
Northern Cardinal, *Cardinalis cardinalis*	41.0	T	−17.8	−20.6	25.0	8.0

* Body masses were taken from Root (1988*b*) or, if not available there, from Dunning (1984). The body mass of Brewer's Sparrow was not available from either source and was taken from the author's unpublished data.
† The coldest isotherm intersected, range in isotherms intersected, and standard deviation of isotherms intersected by northern range boundaries were taken from the distribution maps presented by Root (1988*a*).
‡ Only one intersection of northern range boundary and an isotherm; assigned value 0.

might avert a ceiling on metabolism through energy conservation. Redpolls are well insulated but not inordinately so (Pohl and West 1973), and they undergo nocturnal hypothermia only when deprived of food (Steen 1958, Reinersten and Haftorn 1986). Instead, they raise their basal metabolic rate during winter, rely on a rich food source, have a food storage pouch that permits them to roost with a good store of food, and begin foraging extremely early in the morning (Brooks 1968, Pohl and West 1973). Data from colder areas should indicate whether redpolls are the norm or an exception.

Analysis of the data set of recent Christmas Bird Counts from western Canada did not yield evidence of a metabolic constraint on the distributions of birds (Fig. 4). There was no overall tendency for the coldest count locality to be negatively related to body mass (Fig. 4, one-tailed test, $r^2 = 0.02$, $b = -2.49$, df = 50, $P = .1566$). Species of all sizes could be found at the coldest localities (Fig. 4a), and running estimates of the 10th percentile did not decline as body size increased (Fig. 4b). Thus, a ceiling on metabolism, at best, only weakly influences the northern distributions of birds within the study area.

As in Fig. 3a few large birds had northern distribution boundaries at warm temperatures (Fig. 4a). The 90th percentiles in Figs. 3b and 4b exhibit downward trends that reflect the scarcity with which large birds have northern limits at warm temperatures. A downward sloping upper bound in the absence of a downward sloping lower bound does not represent Root's constraint, and it was not expected.

DISCUSSION

Temperature and the northern distributions of species

A priori, it is easy to imagine that a ceiling on metabolic rate might constrain the distributions of birds.

For any species, there is apparently a ceiling on metabolism that cannot be exceeded regardless of food availability (Peterson et al. 1990), and cold temperatures requiring metabolic rates greater than the ceiling cause death, presumably from hypothermia. The extent to which such a physiological limit actually de-
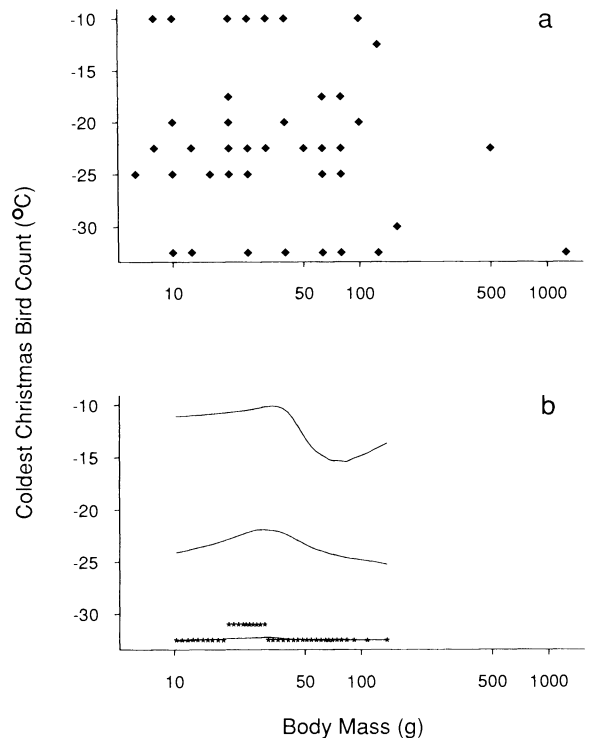

FIG. 4. The coldest temperature at which a species occurred regularly in Christmas Bird Counts vs. body mass. (a) The data. (b) Smoothed estimates of the 10th, 50th, and 90th percentiles of coldest temperature as a function of body mass. Methods as in Fig. 3b.

termines the distributions of species depends on where it occurs relative to other factors affecting distributions. Below the absolute physiological limit, temperature must still influence species distributions through its effect on energy budgets, because more energy is required for thermoregulation and survival at lower temperatures. Yet food abundance may determine the actual range boundary of a species along a temperature gradient: the boundary would occur at that point where sufficient food cannot be obtained to offset the greater energy demand of colder temperatures. Interspecific competition, predation, and habitat characteristics could also modify the northern boundary through their effects on food availability and energy expenditure. Range boundaries set in this manner might follow isotherms only loosely because of geographic variation in food, habitat, predators, and competitors, whereas those set by the physiological limit should follow isotherms closely. In the latter case, isotherms should also be related to body mass, whereas if food and other factors control boundaries, no relationship between body mass and temperature at the northern boundary is expected.

My analysis did not support the contention that a physiological limit generally sets the northern distributions of birds. Species distributions are likely to be determined by the interactions of temperature and biotic factors rather than by simply a metabolic constraint. Relatively few species had northern range boundaries that corresponded closely with temperature isotherms, and the prediction from the constraint hypothesis that small birds would be restricted to warm areas, whereas only large birds could inhabit cold areas, was not supported by the data. Birds of all sizes occurred at the lowest temperatures in the study area. The results also suggest indirectly that the ceiling on metabolic rate might be $>2.5\times$ basal metabolic rate because most species occurred at temperatures colder than the limiting temperatures predicted from that ceiling.

Evidence of a physiological constraint on species distributions might be found if areas colder than the study area could be included in the analysis. However, that is unlikely to occur in North America. My analysis included the coldest sub-tundra areas on the continent. The progression to yet colder temperatures is confounded with radical changes in habitat structure that might also constrain species distributions. Nevertheless, even if the inclusion of colder regions yielded favorable evidence, only a small portion of the continental avifauna would be affected.

Although the northern distribution boundaries of most species are probably shaped primarily by the interaction of biotic and abiotic factors, it is still not possible to draw definitive conclusions about the relative strengths of the two types of factors. First, an association between a range boundary and an isotherm is not necessarily causal (Lack 1971). It could be correlative, or it could be due to chance. Suppose, how-

ever, that the association is causal. It has two different interpretations. The first is that the effect of temperature dwarfs the effect of variation in biotic factors along the range boundary. Alternatively, there may simply be little variation in the important biotic factors over the length of the boundary. Clearly, it is not factors along the boundary alone that determine the location of the boundary, but also factors perpendicular to the boundary. By the same reasoning, poor correspondence between a range boundary and a temperature isotherm does not necessarily mean that temperature is unimportant or less important than biotic factors in determining the boundary. The relative importances of the factors are determined by both the sensitivity of the species to the factors and the amount of variation in the factors perpendicular to the boundary. It is necessary to have information about more than just temperature to determine relative importances. Data concerning other factors are necessary. In lieu of data, even qualitative predictions about distributions resulting from different factors (e.g., Terborgh 1971, 1985) would be a substantial first step.

Northern distributions and geographic range size

To my knowledge the observation that few large birds have northern distribution boundaries in warm places has not been reported previously. What causes that pattern? It might be a consequence of the geography of North America and a nonmetabolic consideration, the relationship between body size and size of geographic range. Range sizes of breeding birds tend to increase with increasing body size because few large species have small geographic ranges (Brown and Maurer 1987). That pattern and a biogeographic barrier could order the avifauna north of the barrier as follows. Few large species would have northern range boundaries near the barrier because the barrier would form the southern boundaries of those species occurring near it and large range sizes would force the northern boundaries to be well away from it. Small species, on the other hand, having small geographic ranges, could easily have northern range boundaries located near the barrier. The Gulf of Mexico formed a large portion of the southern boundary of the study area. Its effect as a barrier could be complemented by a large turnover in avifauna between Mexico and the United States to produce a paucity of large species with northern range boundaries in warm, southerly areas of the United States.

To conclude, my analysis fails to support earlier findings that a metabolic constraint limits the northern distributions of birds and that a large fraction of wintering birds have northern distributions governed principally by temperature. Temperature probably plays a pervasive although less acute role determining distributions through interactions with biotic factors such as food, competition, predation, parasitism, and hab-

itat, and less pervasively through the peculiarities of the biology of individual species that render them vulnerable to temperature.

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APPENDIX. DISJUNCT POPULATIONS OMITTED FROM THE ANALYSIS

The decision to omit specific populations was made on the basis of the descriptions that accompany the range maps in Root (1988a). Populations resulting from odd or infrequent sightings were omitted. All scientific names are provided in Table 2.

Species	Population(s)	Reason for omission
Say's Phoebe	Colorado, Illinois	Sighted 1 yr only
Plain Titmouse	E. Texas, Colorado–Kansas	Sighted 1 yr only
House Wren	Illinois, Kentucky–W. Virginia	Irregular sightings
Sedge Wren	All disjuncts but w. Texas	Unusual sightings
Carolina Wren	Québec	Sighted 1 yr only
Marsh Wren	Two western disjuncts	Sighted in no more than 4 of 10 yr
Hermit Thrush	Northern Idaho	Two birds in 1 yr
Townsend's Solitaire	Québec	One odd sighting
Gray Catbird	All disjuncts	Sighted in 3 of 10 yr or less
Solitary Vireo	West-central Texas	One odd sighting
Yellow-throated Warbler	Nevada and California	Infrequent sightings
Pine Warbler	Texas	Observed 1 yr only
Northern Parula Warbler	All disjunct populations	Sighted in 1 or 2 yr at most
Black and White Warbler	All disjunct populations	Probably late migrants rather than winter residents
Prairie Warbler	All populations n. of Florida	Irregular observations