

LETTER

Energetic determinants of abundance in winter landbird communities

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Abstract

There is increasing evidence that individual energetics constrain macroecological patterns. Here we model total abundance within winter landbird communities as a function of (1) energy supply, as measured by ecosystem net primary productivity, and (2) energy use of individuals, as influenced by body mass and ambient temperature. Using data from the North American Christmas Bird Count, we find that total abundance increases with productivity to the 0.61 power, and decreases with body mass and environmental temperature as predicted by metabolic theory when individuals are below their thermoneutral zone. We note a negative relationship between ambient temperature and average body mass, and suggest that this community-level pattern, reminiscent of Bergmann's Rule, is related to a tendency for small species to be less-abundant or absent from cold locations. Results from this study emphasize the importance of individual-level metabolism for understanding large-scale ecological patterns.

Keywords

Abundance, birds, body mass, density, energetics, metabolic theory, productivity, temperature.

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INTRODUCTION

Energetic constraints on abundance have been examined in several taxonomic and ecological contexts. A common finding is that abundance varies with the energetic requirements of individuals. This general pattern has been found for mammals (Damuth 1981, 1987), birds (Nee *et al.* 1991), intertidal invertebrates (Marquet *et al.* 1990), land plants (Enquist *et al.* 1998; Enquist & Niklas 2001), and marine phytoplankton (Belgrano *et al.* 2002; Li 2002). In these cases, abundance, N , usually scales with body mass, M , as $N \propto M^{-3/4}$. Since metabolic rate of individuals, B_i , scales with body mass as $B_i \propto M_i^{3/4}$ (Kleiber 1932), these patterns suggest that abundance is constrained by patterns of individual energy use. Here we investigate the influence of energetics on total abundance within assemblages of wintering birds. We ask how much of the variation in total abundance at a locale can be explained by a theoretical model that quantifies the fundamentals of energy flux through a bird community.

It has long been hypothesized that winter bird abundance is energy limited (Lack 1966; Fretwell 1972). It follows that the total rate of energy use by birds, B_{tot} , is proportional to

total energy supply to birds, E , as $B_{\text{tot}} \propto E$. The energy available to a bird community is determined by the total rate of energy supply in the environment, or productivity, P , and the proportion of that energy that birds can use. This relationship can be described as $E \propto P^x$; we use this flexible functional form as a first approximation because it can describe a linear, accelerating, or decelerating relationship. It follows that

$$B_{\text{tot}} \propto P^x \quad (1)$$

Given this general relationship, we can examine how the constraint of energy supply on energy flux through the community may be understood at the level of individuals.

The energy used by an animal community is given by the sum of metabolic needs of its individuals as $B_{\text{tot}} \propto \sum_{i=1}^N B_i$. Several studies have shown that, for birds within their thermoneutral zone, B_i is related to individual body mass in the form $B_i \propto M_i^{3/4}$ (Kleiber 1932; Zar 1969; Nagy *et al.* 1999). Below the thermoneutral zone, however, the scaling relationship is markedly different. This is because heat loss to the environment must be offset by increased metabolic rate in order to maintain a constant body temperature (Scholander *et al.* 1950). Metabolic rate, then, is determined by thermal

conductance, which scales as $M_i^{1/2}$ (Aschoff 1981; Schleucher & Withers 2001), as well as the difference, T_d , between body temperature and ambient temperature (Calder 1984). Thus, in a relatively cold environment, metabolic demands are given as $B_i \propto M_i^{1/2} T_d$. Combined with eqn 1, the overall energy flux through a winter bird community is

$$B_{\text{tot}} \propto \sum_{i=1}^N M_i^{1/2} T_d \propto P^x \quad (2)$$

The sum-of-body-mass term can be replaced by a term representing the average body mass contribution of an individual, $\bar{M}^{1/2}$, times total abundance: $\sum_{i=1}^N M_i^{1/2} = \bar{M}^{1/2} N$ (note that $\sum_{i=1}^N M_i^{1/2} \neq \bar{M}^{1/2} N$ unless all individuals in the assemblage are of equal mass). Substituting this into eqn 2 yields

$$B_{\text{tot}} \propto \bar{M}^{1/2} N T_d \propto P^x \quad (3)$$

This is a general model for energy flux through winter landbird communities. It describes how energy use derives from interactions between properties of the environment and characteristics of the community. This general model can be solved for N , giving

$$N \propto P^x (\bar{M}^{1/2})^{-1} T_d^{-1} \quad (4)$$

Equation 4 provides a framework for exploring the energetic basis of abundance in winter bird communities. It predicts that abundance, corrected for the effects of productivity and body mass, should scale as T_d to the -1 power. It also predicts that abundance, corrected for the effects of productivity and temperature, should scale with the body mass term to the -1 power. In this paper, we test these predictions using data on abundance of winter landbirds from across North America. We address the following questions: (1) What is the relationship between resource supply rate and landbird abundance? Do wintering landbirds utilize a constant proportion of productivity across all levels of resource supply? (2) Do the effects of temperature and body mass distribution on abundance follow the predictions of our model? (3) Is the full theoretical model more parsimonious than ones including fewer terms?

METHODS

Christmas Bird Counts (CBCs) have been conducted annually across North America for over 100 years and provide standardized counts of winter birds (Bock & Root 1981). During a single day within a 2-week period, volunteer observers cover count circles with a 12-km radius. We acquired data for CBC sites in the continental USA and

Canada from <http://www.nmt.edu/~shipman/z/cbc>. We screened CBC sites to remove those where birds were likely to acquire resources from aquatic or urban habitats. CBC sites were excluded if they were centered within 12 km of a coastline, major water body (>2.5 ha), or major river (>30 m wide), or were within 24 km of locations with human population $>10\,000$. This process left 285 sites for analysis.

Landbirds were defined as all diurnal terrestrial-feeding species from the orders Columbiformes through Passeriformes (Tramer 1974). Owls were excluded because of their nocturnal habit. Species contained in Coraciiformes were excluded because of their tendency to feed in aquatic habitats and the blackbird species *Agelaius phoeniceus* and *Xanthocephalus xanthocephalus* were excluded after Bock & Root (1981) and Root (1988b). This process left 257 bird species for analysis.

To test predictions of eqn 4, we needed estimates of N , $\bar{M}^{1/2}$, P , and T_d for each CBC site. N was calculated for each year from 1978 to 1998 and then averaged over all years. Since all sites were not censused during all years, averages represent data from 2 to 20 years. N was corrected for observer effort by calculating the number of birds counted per observer party hour (Bock & Root 1981). (We checked the relationship between party hours and abundance and found that the two measures were linearly related at the sites used in our study.) $\bar{M}^{1/2}$ for each site was calculated using the abundance and body mass of the j th species as $\sum_{j=1}^S (NM^{1/2})_j / \sum_{j=1}^S N_j$. We used a single, mean body mass (g) for each landbird species (Dunning 1993). P for each site was obtained from estimates of annual net primary productivity (NPP, carbon $\text{g m}^{-2} \text{year}^{-1}$). NPP was an average of estimates from 17 global models (Cramer *et al.* 1999) and had a spatial resolution of 0.50° long/lat (<http://www.pik-potsdam.de/>). We calculated T_d for each site by subtracting the average ambient temperature during December and January from the average avian body temperature of 40°C (Calder & King 1972). Average December and January temperature was interpolated for each site using data from the US National Climate Data Center's Global Historical Climatology Network.

One assumption of our analysis was that the birds, on average, were below their lower critical temperature, T_c , during winter. We calculated T_c for each species using the equation $T_c = 40 - 42.73M^{1/4}$ (Peters 1983), where M is in kilogram. This equation was derived using allometric models for thermal conductance and metabolic rate, where metabolic rate was estimated to be 25% over basal metabolic rate to account for heat produced by moderate activity (Calder 1984). We then calculated the percentage of individuals at each site for which the average December and January temperature was below T_c .

We constructed general linear models with $\log_{10}$ transformed variables (1) to calculate the empirical scaling relationships between N and P , $M^{1/2}$, and T_d in a multivariate statistical context and (2) to compare these empirical relationships to those predicted by eqn 4. The full general linear model took the form $\log(N) \propto b_0 + b_1 \log(P) + b_2 \log(M^{1/2}) + b_3 \log(T_d)$. The estimates for b_1 , b_2 , and b_3 correspond with the scaling exponents in eqn 4 for P , $M^{1/2}$, and T_d , respectively. We used Akaike's Information Criterion (AIC) to compare the utility of the full three-variable model with that of the reduced one- and two-variable models (Burnham & Anderson 1998). When using this criterion, the best model is that with the lowest AIC value; models with ΔAIC values less than 3 ($\Delta AIC_i = AIC_i - AIC_{\text{best}}$) are considered competitive models and those with values greater than six are considered inferior (Burnham & Anderson 1998). We used correlation analyses on $\log_{10}$ transformed variables to check for collinearity between P , $M^{1/2}$, and T_d .

RESULTS

Winter landbird abundance was relatively low at CBCs in cold and dry regions and relatively high in warm and wet regions of North America (Fig. 1). Across the CBC sites included in this study, N varied from 0.30 to 86.34 individuals party per hour. The average number of birds per party hour was nine and the average number of party hours per site was 396; thus approximately 3564 birds were counted during an average CBC. Across CBC sites, P varied from 115.11 to 943.09 $\text{g m}^{-2} \text{ year}^{-1}$, $M^{1/2}$ varied from 4.59 to 19.53 $\text{g}^{1/2}$, and T_d varied from 24.84 to 64.94 $^{\circ}\text{C}$ (Fig. 1).

The average December and January ambient temperature was below the lower critical temperature of moderately active landbirds in a vast majority of cases. For 202 of the 285 sites, average ambient temperature was below T_c for 100% of the individuals. For 63 sites, average ambient temperature was below T_c for 95–99% of the individuals.

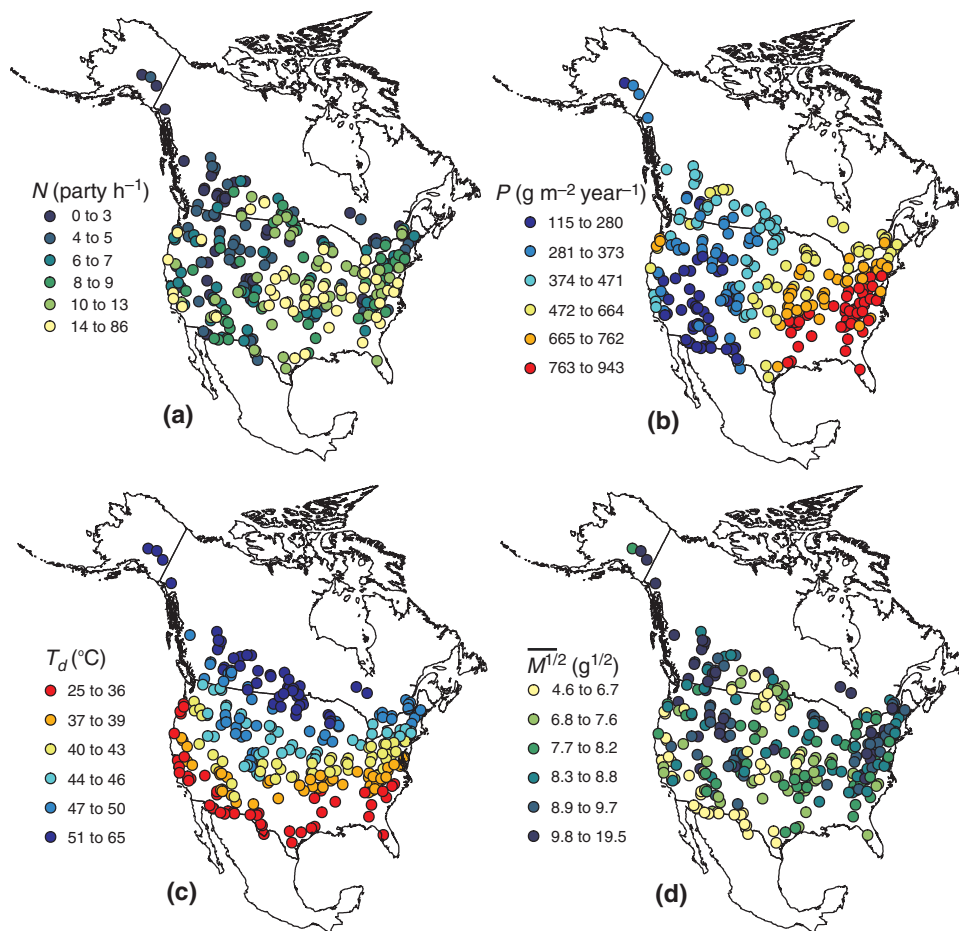


Figure 1 Map of the 285 Christmas Bird Count sites used in this study, together with (a) the associated distributions of N (total landbird abundance); (b) P (annual net primary productivity); (c) T_d (the difference between avian body temperature and December and January mean temperature); and (d) $M^{1/2}$ (average of body masses raised to the $1/2$ power).

Table 1 Summary of AIC values for full and reduced general linear models for $\log(N)$

Model rank	Variables	AIC	Δ AIC
1 (Best)	$\log(P)$, $\log(\overline{M^{1/2}})$, $\log(T_d)$	-642.52	
2	$\log(P)$, $\log(\overline{M^{1/2}})$	-635.08	7.44
3	$\log(P)$, $\log(T_d)$	-623.92	18.60
4	$\log(\overline{M^{1/2}})$, $\log(T_d)$	-606.13	36.39
5	$\log(T_d)$	-597.41	45.11
6	$\log(P)$	-597.22	45.30
7 (Worst)	$\log(\overline{M^{1/2}})$	-596.41	46.11

For the remaining 20 sites, average ambient temperature was below T_c for 85–95% of the individuals.

The best model for predicting winter landbird abundance was the one that included all three terms: productivity, body mass, and ambient temperature ($F_{3,281} = 28.61$, $P < 0.0001$, $R^2 = 0.23$, Table 1). Models that included a productivity and mass term ($F_{2,282} = 37.08$, $P < 0.0001$) and a mass term ($F_{1,283} = 26.88$, $P < 0.0001$) were also significant predictors of abundance, but were inferior alternatives to the full model (see AIC analysis, Table 1).

In the full model, the slope for the productivity term was significantly lower than 1.00, indicating a non-linear relationship between annual productivity and abundance [$\log(P)$, slope $\pm$ 95% CI = 0.61 ± 0.19 , Fig. 2a]. The slope for the body mass term was identical to the exponent predicted by eqn 4 [$\log(\overline{M^{1/2}})$, -1.00 ± 0.43 , Fig. 2b]. Similarly, the slope for T_d was not significantly different from the predicted value of -1 [$\log(T_d)$, -0.85 ± 0.55 , Fig. 2c].

Collinearity among the independent variables was moderate to non-existent. $\log(P)$ was not related to $\log(T_d)$ ($r = -0.02$, $P = 0.80$). There was a weak positive correlation between $\log(P)$ and $\log(\overline{M^{1/2}})$ ($r = 0.15$, $P = 0.01$) and a moderate positive correlation between $\log(T_d)$ and $\log(\overline{M^{1/2}})$ ($r = 0.43$, $P < 0.001$).

DISCUSSION

Based on the energetic model given by eqn 4, we hypothesized that total abundance in winter landbird communities would scale inversely with the metabolic needs of individuals, so that N would scale as $(\overline{M^{1/2}})^{-1}$ and T_d^{-1} . These predictions were supported by data from CBCs, implying that energetic constraints on individuals are manifested in large-scale abundance patterns. Previous support for such an energetic hypothesis has come from studies showing that N scales as $M^{-3/4}$. Our results provide strong and unique support for the energetic hypothesis by showing that a model incorporating environmental temperature to estimate the metabolic cost of thermoregulation

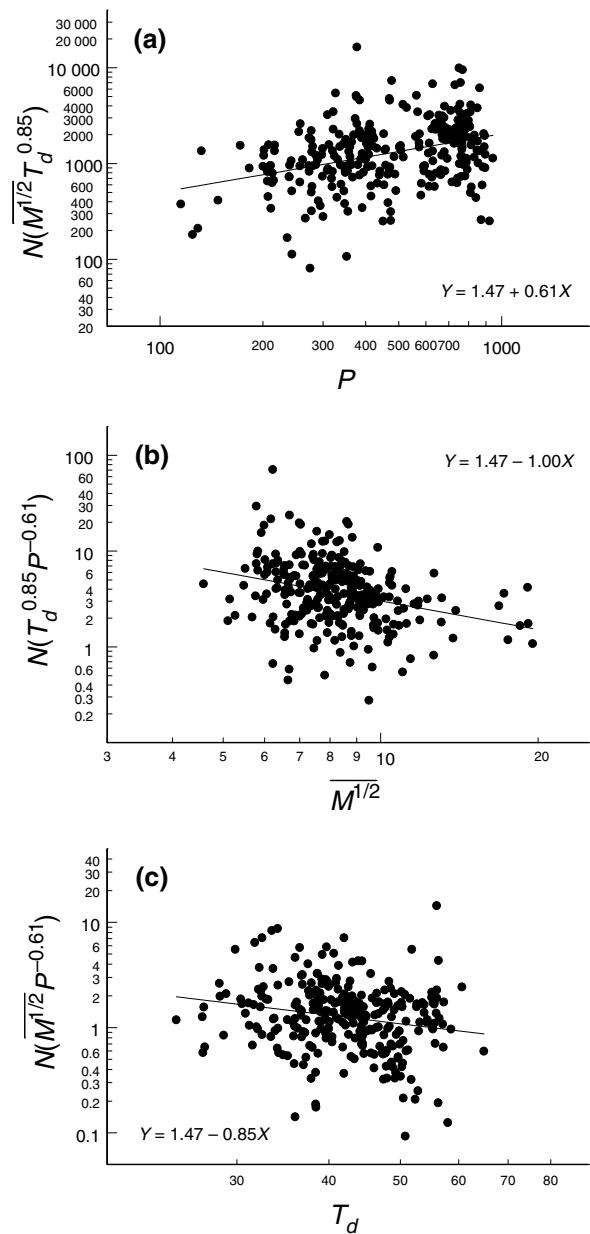


Figure 2 Logarithmic plots showing (a) the scaling of N (total landbird abundance, individuals party per hour) with P (annual net primary productivity, carbon $\text{g m}^{-2} \text{ year}^{-1}$), where N is corrected for $\overline{M^{1/2}}$ (average of body masses raised to the $1/2$ power, $\text{g}^{1/2}$) and T_d (the difference between avian body temperature and December and January mean temperature, $^{\circ}\text{C}$); (b) the scaling of N with $\overline{M^{1/2}}$, where N is corrected for T_d and P ; and (c) the scaling of N with T_d , where N is corrected for $\overline{M^{1/2}}$ and P . Scaling exponents used to correct abundance estimates were from general linear model results. Linear equations are of the form $\log(Y) = b_0 + b_1 \log(X)$.

during winter gives better predictions of bird abundance than a model including body mass alone.

While our predictions were supported, there was considerable variation in the data not accounted for by the energetic model (Fig. 2). Some of this variation might be explained by other biological variables operating at local scales. Other variation may be related to the inherent difficulties of estimating parameter values. For example, environmental temperature and net primary productivity used in this analysis are mean estimates generated from course-scale climate data. While these estimates provide approximate environmental conditions, they do not give an indication of microclimate opportunities or fine-scale resource availability. Furthermore, field abundances are difficult to measure with high precision. We used data from the CBC, which is known to vary in quality across sites due to observer effort and ability (Bock & Root 1981). While observer effort and ability likely added random variation to our analysis, there are no obvious systematic relationships between observer effort or species detectability and our core predictor variables that would influence the scaling relationships we observed.

Our results support the increasing body of information suggesting that winter bird assemblages are energy limited (Lack 1966; Fretwell 1972). We found that winter landbird abundance was positively related to resource availability, as was shown previously for wintering sparrows in southwestern North America (Pulliam & Brand 1975; Dunning & Brown 1982). While we found a positive association between N and P , the relationship was not linear (exponent significantly less than 1). By combining eqns 3 and 4, we can show that the total energy flux through a winter landbird assemblage was also a positive, decelerating function of productivity. This could imply that in warmer and more productive environments, a smaller fraction of energy resources are available to winter birds, perhaps because of increased diversity and abundance of competing taxa, such as ectothermic insects, reptiles, and amphibians (Currie 1991). Alternatively, this could imply that resources available to winter birds are, simply, not directly proportional to annual production.

We found that average body mass increased with decreasing temperature, as reflected in the positive correlation between T_d and $M^{1/2}$. This pattern could not be attributed to Bergmann's rule (Meiri & Dayan 2003), because we assumed that individuals of a given species had the same body mass at all locations. Rather, the positive relationship between T_d and $M^{1/2}$ was due to changes in species composition and relative abundance, a community-level version of Bergmann's rule. Root (1988a) concluded that the northern range limits of certain bird species are related to winter ambient temperature through its effect on metabolic demands. That work would predict the commu-

nity-level pattern we observed due to several small-bodied species decreasing in abundance or being absent from communities at relatively cold locations.

In conclusion, data on winter landbird abundance supported predictions for the scaling relationships between abundance, resource availability, and resource use derived from a general model for energy flux through communities. Further, the model that included the independent effects of ambient temperature, body mass, and productivity performed better than one with body mass as the only predictor of metabolic needs. We take these results as evidence for the role of energetics in determining abundance across different kinds of organisms and environments and for the value of metabolic scaling theory for understanding large-scale ecological patterns (Brown *et al.* in press).

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REFERENCES

- Aschoff, J. (1981). Thermal conductance in mammals and birds: its dependence on body size and circadian phase. *Comp. Biochem. Phys.*, 69, 611–619.
- Belgrano, A., Allen, A.P., Enquist, B.J. & Gillooly, J.F. (2002). Allometric scaling of maximum population density: a common rule for marine phytoplankton and terrestrial plants. *Ecol. Lett.*, 5, 611–613.
- Bock, C.E. & Root, T.L. (1981). The Christmas Bird Count and avian ecology. *Stud. Avian Biol.*, 6, 17–23.
- Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M. & West, G.B. (in press). Toward a metabolic theory of ecology. *Ecology*.
- Burnham, K.P. & Anderson, D.R. (1998). *Model Selection and Inference: A Practical Information-Theoretic Approach*. Springer-Verlag, New York.
- Calder, W.A. (1984). *Size, Function, and Life History*. Dover Publications, Mineola, New York.
- Calder, W.A. & King, J.R. (1972). Body weight and the energetics of temperature regulation: a re-examination. *J. Exp. Biol.*, 56, 775–780.
- Cramer, W., Kicklighter, D.W., Bondeau, A., Moore, B. III, Churkina, G., Nemry, B. *et al.* (1999). Comparing global models of terrestrial net primary productivity (NPP): overview and key results. *Global Change Biol.*, 5 (Suppl. 1), 1–15.
- Currie, D.J. (1991). Energy and large-scale patterns of animal-species and plant-species richness. *Am. Nat.*, 137, 27–49.
- Damuth, J. (1981). Population density and body size in mammals. *Nature*, 290, 699–700.

- Damuth, J. (1987). Interspecific allometry of population density in mammals and other animals: the independence of body mass and population energy-use. *Biol. J. Linn. Soc.*, 31, 193–246.
- Dunning, J.B. (1993). *CRC Handbook of Avian Body Masses*. CRC Press, Boca Raton, FL.
- Dunning, J.B. & Brown, J.H. (1982). Summer rainfall and winter sparrow densities: a test of the food limitation hypothesis. *Auk*, 99, 123–129.
- Enquist, B.J. & Niklas, K.J. (2001). Invariant scaling relations across tree-dominated communities. *Nature*, 410, 655–660.
- Enquist, B.J., Brown, J.H. & West, G.B. (1998). Allometric scaling of plant energetics and population density. *Nature*, 395, 163–165.
- Fretwell, S.D. (1972). *Populations in a Seasonal Environment*. Princeton University Press, Princeton, NJ.
- Kleiber, M. (1932). Body size and metabolism. *Hilgardia*, 6, 315–353.
- Lack, D. (1966). *Population Studies of Birds*. Clarendon Press, Oxford.
- Li, W. (2002). Macroecological patterns of phytoplankton in the northwestern North Atlantic Ocean. *Nature*, 419, 154–157.
- Marquet, P.A., Navarrete, S.A. & Castilla, J.C. (1990). Scaling population-density to body size in rocky intertidal communities. *Science*, 250, 1125–1127.
- Meiri, S. & Dayan, T. (2003). On the validity of Bergmann's Rule. *J. Biogeog.*, 30, 331–351.
- Nagy, K., Girard, I. & Brown, T. (1999). Energetics of free-ranging mammals, reptiles, and birds. *Annu. Rev. Nutr.*, 19, 247–277.
- Nee, S., Read, A.F., Greenwood, J.J.D. & Harvey, P.H. (1991). The relationship between abundance and body size in British birds. *Nature*, 351, 312–313.
- Peters, R.H. (1983). *The Ecological Implications of Body Size*. Cambridge University Press, Cambridge, UK.
- Pulliam, H.R. & Brand, M.R. (1975). The production and utilization of seeds in the plains grassland of southwestern Arizona. *Ecology*, 56, 1158–1166.
- Root, T. (1988a). Energy constraints on avian distributions and abundances. *Ecology*, 69, 330–339.
- Root, T. (1988b). Environmental factors associated with avian distributional boundaries. *J. Biogeog.*, 15, 489–505.
- Schleucher, E. & Withers, P.C. (2001). Re-evaluation of the allometry of wet thermal conductance for birds. *Comp. Biochem. Phys.*, 129, 821–827.
- Scholander, P.F., Hock, R., Walters, V. & Irving, L. (1950). Adaptation to cold in arctic and tropical mammals and birds in relation to body temperature, insulation, and basal metabolic rate. *Biol. Bull.*, 99, 259–271.
- Tramer, E.J. (1974). An analysis of the species density of U.S. landbirds during the winter using the 1971 Christmas Bird Count. *Am. Birds*, 28, 563–567.
- Zar, J.H. (1969). The use of the allometric model for avian standard metabolism-body weight relationships. *Comp. Biochem. Phys.*, 29, 227–234.

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