

# THE EVOLUTION OF HIGH SUMMIT METABOLISM AND COLD TOLERANCE IN BIRDS AND ITS IMPACT ON PRESENT-DAY DISTRIBUTIONS

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Summit metabolic rate ( $M_{sum}$ , maximum cold-induced metabolic rate) is positively correlated with cold tolerance in birds, suggesting that high  $M_{sum}$  is important for residency in cold climates. However, the phylogenetic distribution of high  $M_{sum}$  among birds and the impact of its evolution on current distributions are not well understood. Two potential adaptive hypotheses might explain the phylogenetic distribution of high  $M_{sum}$  among birds. The cold adaptation hypothesis contends that species wintering in cold climates should have higher  $M_{sum}$  than species wintering in warmer climates. The flight adaptation hypothesis suggests that volant birds might be capable of generating high  $M_{sum}$  as a byproduct of their muscular capacity for flight; thus, variation in  $M_{sum}$  should be associated with capacity for sustained flight, one indicator of which is migration. We collected  $M_{sum}$  data from the literature for 44 bird species and conducted both conventional and phylogenetically informed statistical analyses to examine the predictors of  $M_{sum}$  variation. Significant phylogenetic signal was present for log body mass, log mass-adjusted  $M_{sum}$ , and average temperature in the winter range. In multiple regression models, log body mass, winter temperature, and clade were significant predictors of log  $M_{sum}$ . These results are consistent with a role for climate in determining  $M_{sum}$  in birds, but also indicate that phylogenetic signal remains even after accounting for associations indicative of adaptation to winter temperature. Migratory strategy was never a significant predictor of log  $M_{sum}$  in multiple regressions, a result that is not consistent with the flight adaptation hypothesis.

**KEY WORDS:** Allometry, comparative method, energetics, evolutionary physiology, metabolic rate, metabolic theory of ecology, physiology.

The interplay between physiology and climate can have important consequences for animal distributions. Cold climates require high thermoregulatory energy expenditures for endothermic vertebrates, particularly for small species with high surface area to volume ratios and limited insulatory capacities (Schmidt-Nielsen 1984). Basal (BMR) and maximal cold-induced (=summit metabolism,  $M_{sum}$ ) metabolic rates are correlated with climate in mammals, with higher metabolic rates associated with the

higher thermoregulatory demands of cold climates (Bozinovic and Rosenmann 1989; Rezende et al. 2004). A similar correlation of BMR with climate also occurs in birds (Weathers 1979), but such correlations of  $M_{sum}$  with climate for birds have not been established, primarily because measurements of  $M_{sum}$  have mostly been restricted to cold-climate species. The role of winter temperature and the interplay between temperature and metabolism in affecting bird distributions are unclear. Root (1988) found that

the northern range boundary for a number of passerine birds wintering in North America was associated with a mean minimum January temperature eliciting metabolic rates of approximately 2.5 times BMR, thus suggesting a role for winter temperature in limiting passerine distribution. This work, however, has been criticized on various grounds, and further analyses have revealed that the evidence for metabolic ceilings limiting avian distributions is equivocal (Castro 1989; Repasky 1991; Canterbury 2002). These studies have focused on metabolic ceilings calculated as simple multiples of BMR.

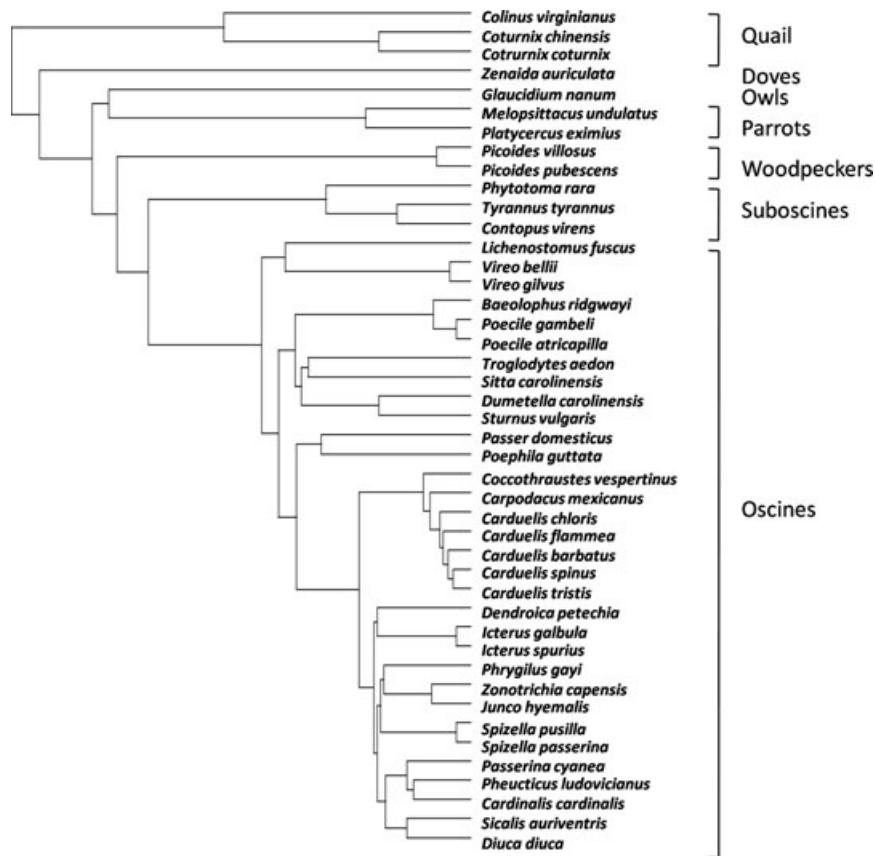
$M_{sum}$  in birds exceeds BMR by three- to ninefold (Saarela et al. 1995; Arens and Cooper 2005). Because of this variability in metabolic expansibility ( $M_{sum}/BMR$ ), a given elevation of metabolic rate for thermogenesis above BMR would result in metabolic rates that represent markedly different fractions of  $M_{sum}$ . For example, a metabolic rate of 2.5-times BMR (the metabolic ceiling proposed by Root 1988) would constitute 83% of  $M_{sum}$  for a bird with a metabolic expansibility of 3, but only 31% of  $M_{sum}$  for a bird with a metabolic expansibility of 8. The fraction of maximum metabolic rates (usually measured by locomotion) that can be sustained for prolonged periods ranges from about 60 to 85% in birds and mammals (Roberts et al. 1996; Guglielmo et al. 2002; McWilliams et al. 2004; Vaanholt et al. 2007). Because fractions of maximum exercise metabolic rates that can be sustained over long periods are apparently less variable than metabolic expansibilities, the fraction of maximum metabolic rates that can be sustained might be a better measure of metabolic ceilings than multiples of BMR. Thus, metabolic ceilings in relation to climate might be determined by the fraction of  $M_{sum}$  that can be sustained, assuming sufficient food is available.  $M_{sum}$  is important to discussion of metabolic ceilings and climate not only because it limits thermogenic performance in birds, but also because increases in  $M_{sum}$  are associated with increases in thermogenic endurance (Marsh and Dawson 1989; Swanson 2001). In this regard,  $M_{sum}$  and thermogenic endurance are related in a similar fashion to the general upscaling of maximal metabolic capacity and endurance in animals generally (Bennett 1991; Rezende et al. 2006).

A high capacity for cold tolerance in birds, defined as the ability to withstand a particular cold stress for prolonged periods (Dawson and Carey 1976; Dawson et al. 1983a; O'Connor 1995) or the necessity of comparatively low temperatures to induce hypothermia (Swanson and Liknes 2006), is a requirement for overwintering in cold climates (Marsh and Dawson 1989; Swanson, in press). Cold tolerance in birds is positively correlated with  $M_{sum}$  on both intra- and interspecific bases, such that high levels of cold tolerance are accompanied by high  $M_{sum}$  (Swanson 2001; Swanson and Liknes 2006). On a seasonal basis, winter improvements of  $M_{sum}$  and cold tolerance are ubiquitous among small birds wintering in cold climates (Marsh and Dawson 1989;

Swanson, in press). These data strongly suggest that high  $M_{sum}$  is a necessary prerequisite for inhabiting areas with cold winter climates. They also suggest that  $M_{sum}$  is a useful, as well as easily measured, proxy for comparative examinations of cold tolerance among birds.

Assuming that a high  $M_{sum}$  is critical to successful overwintering in cold climates (Marsh and Dawson 1989; Swanson, in press), two adaptive hypotheses exist for explaining the potential distribution of high  $M_{sum}$  and/or cold tolerance among birds. If seasonal cold exposure is most important in defining thermogenic performance and cold tolerance, then species with similar seasonal levels of cold exposure should show roughly similar  $M_{sum}$  (Cold Adaptation Hypothesis). Furthermore, migratory birds that winter in warm climates and tropical residents should demonstrate lower  $M_{sum}$  than temperate residents because they are not seasonally exposed to cold temperatures. Alternatively, because flight metabolic rates in birds typically exceed those for thermogenesis (Marsh and Dawson 1989), birds may be capable, in general, of high rates of thermogenesis as a byproduct of metabolic adaptation for flight, at least for volant species (Flight Adaptation Hypothesis). In this case,  $M_{sum}$  differences should be related to capacity for sustained flight (e.g., long-distance migrants might be expected to show higher  $M_{sum}$  than species that do not engage in sustained flights), rather than to differences in seasonal cold exposure. In addition to these hypotheses, or possibly instead of them, one might expect that mass-adjusted  $M_{sum}$  would exhibit phylogenetic signal (sensu Blomberg and Garland 2002). Blomberg et al. (2003) found significant phylogenetic signal for four of five physiological traits with adequate sample sizes (see also Rezende et al. 2004; Muñoz-Garcia and Williams 2005; Lavin et al. 2008).

Because phenotypic flexibility in  $M_{sum}$  associated with winter acclimatization or migratory disposition occurs among small birds (Dawson et al. 1983a; Swanson, in press), comparative studies require that birds are acclimatized to similar climatic conditions to reduce the effects of phenotypic flexibility (e.g., McKechnie et al. 2006; Wiersma et al. 2007). Ideally, this would involve measurement of  $M_{sum}$  under common garden conditions (Garland and Adolph 1991), but this is not generally feasible for large comparative studies. The inclusion of seasonal phenotypic flexibility of metabolic rates in comparative analyses would also be beneficial, but these data are not available for most species and vary depending on acclimatization state (e.g., Swanson and Olmstead 1999). For temperate-wintering and migratory birds, summer  $M_{sum}$  values represent the annual minimum or baseline  $M_{sum}$  (Swanson and Dean 1999; Swanson, in press). The baseline  $M_{sum}$  may not be the most pertinent factor in defining cold tolerance at other seasons (i.e., winter or migration), but it should effectively address the question of variation in  $M_{sum}$  among taxa. Moreover, seasonal percent changes in  $M_{sum}$  overlap broadly



**Figure 1.** Phylogeny for the 44 species in this study, derived primarily from DNA–DNA hybridization data in Sibley and Ahlquist (1990), but modified based on more recent studies (see text). Branch lengths represent genetic distance from  $\Delta T_{50H}$  values, with modifications as described in the text. An electronic version of the phylogeny, with branch lengths, is presented in the Supporting Information. The seven named lineages were used as the “Clade” variable in statistical analyses and represent different taxonomic orders or suborders (e.g., Table 3).

between migrants (11–27%; Swanson 1995; Swanson and Dean 1999; Vezina et al. 2007) and temperate-zone residents (0–55%, with most values below 30%; Marsh and Dawson 1989; Liknes and Swanson 1996; Swanson, in press). Thus, the baseline  $M_{sum}$  in summer appears to represent a roughly similar fraction of the annual maximum  $M_{sum}$  for both migrants and residents so relative differences among species when  $M_{sum}$  is at an annual maximum should also be reflected, although conservatively, by summer values.

To test these hypotheses for the distribution of high  $M_{sum}$  among birds, we collected  $M_{sum}$  data from the literature from a phylogenetically diverse set of birds acclimatized to summer conditions or from climates that are not strongly seasonal, and then subjected these data to relevant comparative analyses. Such analyses should reveal the relative importance of cold climates, flight capacity, and phylogeny in determining  $M_{sum}$  in birds and help ascertain the role of thermogenic capacities in defining present-day bird distributions.

## Methods

### DATA COLLECTION

We collected  $M_{sum}$  data from the literature for 44 species of birds (Fig. 1, also see Supporting Information) for which measurements were made during spring and summer (warm periods in the annual cycle) or, if the season of measurement was not identified (six species from central Chile, Rezende et al. 2002), for birds from Mediterranean climates in which little or no seasonal variation in metabolic rates occurs (Dawson et al. 1983b; P. Sabat, unpubl. data). Most of the  $M_{sum}$  values were generated by cold exposure in an atmosphere of 79% helium and 21% oxygen (heliox), which promotes heat loss because of its high thermal conductivity and allows maximal levels of heat production to be obtained at relatively modest temperatures (e.g., Rosenmann and Morrison 1974). We also included  $M_{sum}$  values for four species, evening grosbeak (*Coccythraustes vespertinus*) and European starling (*Sturnus vulgaris*, Hart 1962) and greenfinch (*Carduelis chloris*) and Eurasian

siskin (*C. spinus*, Saarela et al. 1995), where  $M_{sum}$  was measured at very cold temperatures in air because values were not obviously divergent from those measured in heliox in related taxa. McKechnie et al. (2006) found that long-term captivity influenced BMR in birds, and by extension, captivity might also influence  $M_{sum}$  in birds, although short-term captivity does not seem to impact  $M_{sum}$  (Hill et al. 1993). We included  $M_{sum}$  values for a few captive birds in this study (*Coturnix coturnix* from Hinds et al. (1993) and outdoor-captive *Colinus virginianus* from Swanson and Weinacht (1997)) because  $M_{sum}$  values for these birds did not differ substantially from other species in that taxon, when corrected for body size. We determined the mean winter temperature for the winter range as the mean January (or July for the Southern Hemisphere) daily temperature for either the locality of capture (for resident species) or for the city nearest to the midpoint of the wintering range (for migrants) using the Hammond Comparative World Atlas (1990).

### PHYLOGENY CONSTRUCTION

We generated a phylogenetic tree for the 44 species with available  $M_{sum}$  data (Fig. 1) primarily from the DNA/DNA hybridization data of Sibley and Ahlquist (1990), which provide branch lengths from  $\Delta T_{50H}$  values. More recent avian molecular phylogenies based on DNA sequence data differ from the topology of Sibley and Ahlquist (1990) in several respects, so results of these more recent studies (Lougheed et al. 2000; Fain and Houde 2004; Barker et al. 2004; Gibb et al. 2007) were incorporated into the phylogeny of Figure 1. Because these recent studies use DNA sequence data, they do not provide comparable branch length data to Sibley and Ahlquist (1990), so we retained  $\Delta T_{50H}$  branch lengths for sister taxa at the tip of the phylogeny when the Sibley and Ahlquist topology was consistent with the more recent studies. To retain the overall height of the tree, we forced branch lengths for lower nodes in the phylogeny to fit the new topology while retaining branch lengths between sister taxa at tips of the phylogeny. Several species were not included in either the Sibley and Ahlquist data or the other molecular phylogenetic studies, but were closely related to species that were included in these studies, so that branch lengths among sister taxa could be approximated. However, for a few species, this was not possible, so we used other data to establish portions of the phylogeny and generated arbitrary branch lengths based on these relationships. Following Swanson and Liknes (2006), we used arbitrary branch lengths of 1.0 for divergences of chipping (*Spizella passerina*) and field (*S. pusilla*) sparrows and Baltimore (*Icterus galbula*) and orchard (*I. spurius*) orioles, and 2.8 for the Bell's (*Vireo bellii*)-warbling (*V. gilvus*) vireo divergence. We extrapolated arbitrary branch lengths of 5.7 for the *C. coturnix*-*C. chinensis* divergence and 6.5 for the *Melospittacus*-*Platycercus* divergence based on the data of Nishibori et al. (2002) and Christidis et al.

(1991), respectively. We used an arbitrary branch length of 2.5 for the *Junco*-*Zonotrichia* divergence because that is the distance between *Junco* and *Melospiza* in Sibley and Ahlquist (1990). Finally, we used data from Arnaiz-Villena et al. (1998) to supplement data in Sibley and Ahlquist (1990) in the derivation of a phylogeny and branch lengths for cardueline finches. We established arbitrary branch lengths of 1.5 between *C. barbatus* and the branch containing Eurasian siskin and American goldfinch *C. tristis* and 1.2 between American goldfinch and Eurasian siskin. The latter value was based on the divergence of 1.2 between American goldfinch and pine siskin *C. pinus* in Sibley and Ahlquist (1990). An electronic version of the phylogeny is available in the Supporting Information (LOGBRKR.BRK, created by the DOS PDTREE.EXE program [Garland et al. 1999]).

### STATISTICAL ANALYSES

We employed both conventional and phylogenetic analyses (e.g., see Garland et al. 1993, 1999, 2005; Clobert et al. 1998; Freckleton et al. 2002; Hutcheon and Garland 2004; Duncan et al. 2007). The latter involved several approaches. We did not attempt to use new methods that incorporate standard errors of the dependent and/or independent variables (Ives et al. 2007) because they were not available for all species. Statistical significance was accepted at  $P < 0.05$  for all tests.

We calculated phylogenetically independent contrasts (Felsenstein 1985; Garland et al. 1992) for log body mass, log  $M_{sum}$ , and winter temperature using the DOS PDTREE.EXE program (Garland et al. 1993, 1999; Garland and Ives 2000). As a test for the adequacy of branch lengths, we regressed the absolute values of standardized contrasts against their standard deviations (Garland et al. 1992). We also compared the means of the absolute values of standardized contrasts between passerines and other birds to test for differences in rates of evolution (Garland 1992; Garland and Ives 2000; Hutcheon and Garland 2004; O'Meara et al. 2006).

To determine whether phylogenetic signal was present for log mass, log mass-adjusted  $M_{sum}$ , or winter temperature, we used the randomization test for the mean-squared error as described in Blomberg et al. (2003, Matlab program PHYSIG\_LL.m). We also calculated their  $K$ -statistic as a measure of the amount of signal. For log mass and log mass-adjusted  $M_{sum}$ , we used the phylogeny with raw branch lengths (Fig. 1), but for similar analyses with winter temperature, we also used the phylogeny with branch lengths rescaled for the passerine clade (see Results for details). For  $M_{sum}$  analyses, we adjusted for mass effects (following Blomberg et al. 2003) by computing:

$$\text{Mass-adjusted } M_{sum} = M_{sum} / \text{mass}^{0.704},$$

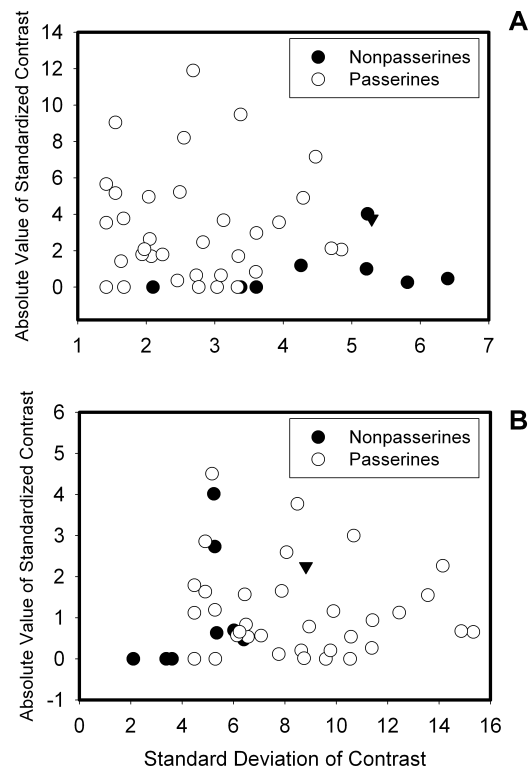
where 0.704 was the exponent of an independent contrasts regression of log  $M_{sum}$  on log body mass.

We then turned to a more general model-fitting approach (e.g., see Duncan et al. 2007) to deduce the “best” model to describe the data when several independent variables were considered in various combinations. We conducted both conventional least-squares and phylogenetically informed regressions using the Matlab program REGRESSIONv2.m (Lavin et al. 2008). These models included a simple linear regression of  $\log M_{sum}$  on log mass and various multiple regressions with independent variables of log mass, winter temperature, migratory strategy (0 = resident, 1 = migrant), and clade (seven lineages composed of separate taxonomic orders or suborders, Fig. 1). For phylogenetically informed regressions, we applied all branch length transformations available in the REGRESSIONv2.m program, including a Brownian motion model (no transformation), Ornstein–Uhlenbeck (OU), Grafen’s  $\rho$ , and Pagel’s  $\lambda$  (Lavin et al. 2008). We then used log likelihood ratio tests (LRT) and the Akaike Information Criterion (AIC) in both its original and corrected forms (AICc; see Burnham and Anderson 2002) to determine which model best fits the multiple regression data (lowest AIC indicates best fit). To our knowledge, application of AICc to regression with parameters in the covariance matrix (e.g., the OU transform model) has not been theoretically justified, but we suspect it is less biased than AIC. We also used partial  $F$  tests to determine the statistical significance of the included independent variables.

## Results

Comparison of the means of the absolute values of standardized phylogenetically independent contrasts indicated no significant difference between passerines and nonpasserines for either log body mass or  $M_{sum}$  ( $t$ -tests or Mann–Whitney tests, depending on whether parametric assumptions of normality and homoscedasticity were met; mass  $P = 0.084$ ,  $M_{sum}$   $P = 0.794$ ), which suggests that rates of evolution of these traits are similar and that differential scaling or transformation of branch lengths between passerines and nonpasserines (e.g., Garland and Ives 2000; Rezende et al. 2002; McKechnie and Wolf 2004) is not necessary in this study. However, the absolute values of standardized winter temperature contrasts (using raw branch lengths) were lower, on average, for nonpasserines than for passerines ( $U = 213.0$ ,  $P = 0.014$ ), suggesting a lower average rate of evolution for winter temperature in nonpasserines (Fig. 2A). Therefore, we multiplied the branch lengths in the passerine subclade by 10, which reduced the difference between winter temperature contrasts to nonsignificant levels ( $P = 0.360$ , Fig. 2B).

Significant phylogenetic signal was present for all traits (Table 1). The  $K$ -statistic indicated much stronger signal for body mass than for the other two traits. For winter temperature, rescaling of the passerine branch lengths had little effect on the signif-



**Figure 2.** Diagnostic graphs (Garland et al. 1992) for absolute values of standardized phylogenetically independent contrasts plotted against their standard deviations (square roots of sums of [corrected] branch lengths) for mean winter temperature. For raw branch lengths (A), nonpasserines (filled circles) had significantly lower values (see text) than for passerines (open circles), indicating lower rates of evolution of winter climate for nonpasserines. The passerine–nonpasserine contrast (filled triangle) was not included in these analyses. When branch lengths for the passerine subclade were multiplied by 10 (B), the difference between passerines and nonpasserines disappeared. The rescaled tree (B) was used for subsequent analyses of phylogenetic signal in winter temperature (Table 1).

icance of phylogenetic signal or the value of the  $K$ -statistic, but it did increase the log likelihood of the model (one measure of the fit of the topology plus branch lengths to the tip data) by 5.0, which suggests a statistically significant improvement.

Considering all 44 species, the nonphylogenetic OLS regression of  $\log M_{sum}$  on log mass was the best (Table 2). Considering models with additional independent variables, migratory strategy was not a significant predictor of  $\log M_{sum}$  for either conventional or phylogenetic models (Table 3). Based on LRTs and AIC, the best fit was provided by an OLS model that included log body mass, winter temperature, and clade (coded as six dummy variables) as independent variables, and all of these were significant predictors of  $M_{sum}$  (Table 3; see also Supporting Information Table S2). As would be expected, given the tendency of AIC to “over-fit” models when  $N/K$  is relative small (where  $K$  is the

**Table 1.** Statistics for randomization tests for significance of phylogenetic signal for log body mass, log mass-adjusted  $M_{sum}$  and winter temperature for the 44 species in this study as calculated with the Matlab program PHYSIG\_LL.m (Blomberg et al. 2003). The phylogenetic tree is shown in Figure 1 and tip data are shown in Supporting Information Table S1. Significant results for the randomization test of the mean squared error (MSE; lower values indicate better fit of tree to data) on the phylogenetic tree indicate the presence of phylogenetic signal for all traits.  $K$ -statistics indicate the amount of phylogenetic signal relative to a Brownian motion expectation (Blomberg et al. 2003).

Trait	Expected MSE <sub>0</sub> / MSE	Observed MSE <sub>0</sub> / MSE	$K$	MSE	MSE <sub>star</sub>	$P$	log maximum likelihood	log maximum likelihood <sub>star</sub>
log Body Mass	2.90	3.58	1.24	0.0765	0.1195	< 0.001	-5.364	-15.181
log $M_{sum}/mass^{0.704}$	2.90	1.39	0.48	0.00512	0.00436	0.016	54.116	57.686
Winter temperature	2.90	0.93	0.32	167.64	156.30	0.004	-174.608	-173.067
Winter temperature <sup>1</sup>	3.40	1.18	0.35	133.40	156.30	0.001	-169.581	-173.067

<sup>1</sup>With branch lengths of passerine clade rescaled as described in the text.

number of independent variables in the model; see Burnham and Anderson 2002), AIC selects a model that has more independent variables compared to AICc. As shown in Table 3, AICc favors the model without Clade. However, the difference in AICc is only 0.40, indicating that the model with Clade also has “substantial support” (Burnham and Anderson 2002). Moreover, the partial  $F$  test for Clade is significant ( $P = 0.025$ ) and the standard error of the estimate is lower for the OLS model with Clade than for the model without Clade.

## Discussion

Body size was a strong positive predictor of  $M_{sum}$  in all models considered (Table 2). Interestingly, for the best-fit model (Table 2), the 95% confidence interval about the slope ( $0.616 < 0.682 < 0.749$ ) just excludes the value of 0.75 that would be predicted by

the so-called metabolic theory of ecology (see also Duncan et al. 2007 and references therein).

After accounting for the association with body size, we found that  $M_{sum}$  was negatively related to winter temperature and differed among clades, but was not significantly related to migratory strategy (Table 3). These results are inconsistent with the flight adaptation hypothesis, which predicts  $M_{sum}$  variation associated with differences in flight capacity. Thus, the presence of metabolic machinery sufficient for long-distance migratory flight is not sufficient, in and of itself, to enable birds to maintain high levels of thermogenesis that may be necessary for overwintering in cold climates.

Our results support the cold adaptation hypothesis, which predicts that bird species wintering in cold climates should have higher  $M_{sum}$  than species wintering in warmer climates. The finding of a significant association between winter temperature and

**Table 2.** Allometric equations as described by conventional ordinary least-squares (OLS) and phylogenetically informed regressions of log  $M_{sum}$  (mL O<sub>2</sub> min<sup>-1</sup>) on log body mass (g). Phylogenetic regressions included models incorporating the different branch length transformations available in the Matlab program REGRESSIONv2.m, including no transformation (=PGLS, Brownian motion evolution of residuals), Ornstein-Uhlenbeck (RegOU), Grafen's rho (RegRho), and Pagel's lambda (RegLambda) (Lavin et al. 2008). All regressions were significant at  $P < 0.001$ . The OLS model showed the lowest AIC value, indicating that it was the best-fit model for these data.  $R^2$  values are not comparable between OLS and phylogenetic regressions (Lavin et al. 2008).

Model	Intercept	SE	log body mass	SE	log maximum likelihood	Transform parameter	$R^2$	MSE	SEE <sup>1</sup>	AIC	AICc
OLS <sup>2</sup>	-0.080	0.039	0.626	0.027	61.720	none	0.928	0.00371	0.0609	-117.44	-116.84
PGLS	-0.244	0.094	0.704	0.040	54.116	none	0.881	0.00524	0.0724	-102.23	-101.63
RegOU	-0.087	0.043	0.629	0.028	61.720	$d = 0.0391$	0.921	0.00373	0.0611	-115.44	-114.41
RegRho	-0.162	0.059	0.665	0.032	61.892	$\rho = 0.2631$	0.910	0.00369	0.0608	-115.78	-114.76
RegLambda	-0.186	0.063	0.676	0.033	62.160	$\lambda = 0.5919$	0.911	0.00365	0.0604	-116.32	-115.29

<sup>1</sup>Standard error of the estimate.

<sup>2</sup>Same as last model in Table 3.

**Table 3.** Partial regression coefficients and *P* values from phylogenetically informed and conventional ordinary least-squares (OLS) multiple regressions with log  $M_{sum}$  (ml O<sub>2</sub> min<sup>-1</sup>) as the dependent variable and log body mass (g), winter temperature (°C), migratory strategy (0=resident, 1=migrant), and clade (corresponding to the seven clades indicated in Fig. 1) as independent variables. Phylogenetic multiple regressions included models incorporating the different branch length transformations available in the Matlab program REGRESSIONv2.m (Lavin et al. 2008), including no transformation (=PGLS, Brownian motion evolution of residuals), Ornstein-Uhlenbeck (RegOU), Grafen's rho (RegRho), and Pagel's lambda (RegLambda). *R*<sup>2</sup> values are not comparable between OLS and phylogenetic multiple regressions (Lavin et al. 2008).

Model	Log mass <sup>1</sup>	SE	Winter temperature	SE	Winter Temperature <i>P</i>	Migratory Strategy <i>P</i>	Clade <i>P</i>	log maximum likelihood	Transform parameter	<i>R</i> <sup>2</sup>	SEE	<i>P</i> for LRT vs. OLS Full Model <sup>2</sup>	AIC	AICc
PGLS	0.6897	0.0390	-0.003388	0.000980	0.002	0.243	0.890	62.569	—	0.919	0.0664		-103.14	-94.89
PGLS	0.6800	0.0357	-0.003449	0.000918	0.001	0.207	—	61.163	—	0.914	0.0632		-112.33	-110.75
RegOU	0.6804	0.0331	-0.002250	0.001028	0.036	0.565	0.036	76.290	9.313e-13	0.963	0.0486		-128.58	-118.52
RegOU	0.6180	0.0264	-0.003204	0.000974	0.002	0.281	—	67.905	0.0479	0.940	0.0544		-123.81	-121.54
RegRho	0.6803	0.0331	-0.002250	0.001028	0.036	0.565	0.036	76.291	2.602e-17	0.963	0.0486		-128.58	-118.52
RegRho	0.6446	0.0302	-0.003031	0.000980	0.004	0.304	—	68.047	0.2663	0.929	0.0550		-124.09	-121.82
RegLambda	0.6803	0.0331	-0.002250	0.001028	0.036	0.565	0.036	76.291	2.602e-17	0.963	0.0486		-128.58	-118.52
RegLambda	0.6532	0.0304	-0.002881	0.000975	0.005	0.329	—	68.047	0.5663	0.930	0.0549		-124.09	-121.82
OLS Full Model	0.6803	0.0331	-0.002250	0.001028	0.036	0.565	0.036	76.291	—	0.963	0.0486		-130.58	-122.33
<b>OLS<sup>3</sup></b>	<b>0.6824</b>	<b>0.0327</b>	<b>-0.001793</b>	<b>0.000657</b>	<b>0.001</b>	—	<b>0.025</b>	<b>76.074</b>	—	<b>0.963</b>	<b>0.0481</b>	<b>0.5093</b>	<b>-132.15</b>	<b>-125.48</b>
OLS	0.6200	0.0245	-0.003040	0.000953	0.003	0.301	—	68.047	—	0.946	0.0541	0.0114	-126.09	-124.52
OLS	0.6152	0.0241	-0.002324	0.000665	0.001	—	—	67.450	—	0.945	0.0541	0.0135	-126.90	-125.88
OLS <sup>4</sup>	0.6259	0.0269	—	—	—	—	—	61.720	—	0.928	0.0609	0.0003	-117.44	-116.84

<sup>1</sup>log mass was significant at  $P < 0.001$  for all models, so *P* values are not included in the table.

<sup>2</sup>In likelihood-ratio tests (LRT) compare fit of the full OLS model including all candidate independent variables with the fit of reduced models. Twice the difference in the log likelihoods is asymptotically distributed as a  $\chi^2$  with df equal to the difference in the number of parameters in the two models. A *P* value  $< 0.05$  indicates that the reduced model has a significantly worse fit to the data than the full model.

<sup>3</sup>Best model based on lowest AIC and lowest SEE; AICc slightly favors the OLS model without Clade. However, LRT for clade indicates  $\chi^2 = 17.25$ , d.f. = 6,  $P = 0.008$ .

<sup>4</sup>Same as first model in Table 2; listed here to facilitate comparisons with more parameter-rich models.

thermogenic capacity is consistent with recent data documenting lower thermogenic capacity in tropical resident birds than in cold-climate resident and migrant birds (Wiersma et al. 2007).

Our results also indicate that phylogenetic position predicts  $M_{sum}$  in birds. The best-fit model (Table 3) included clade ( $P = 0.025$ ) as an independent variable that identified seven different evolutionary lineages (at the ordinal or subordinal level). Models that did not include clade performed significantly worse than those that did, as judged by log likelihood-ratio tests (Table 3). Interestingly, the best-fit model was an OLS model (i.e., depicting the phylogenetic tree as a star with no hierarchical structure), and it fits the data substantially better than any of the phylogenetic models, based on AIC. Thus, phylogenetic signal, in a general sense, is present in log  $M_{sum}$  after statistically controlling for associations with log body mass and winter temperature (or migratory strategy). However, for the present dataset, this signal manifests as differences among lineages, rather than being pervasively distributed throughout the phylogenetic tree.

Univariate randomization tests for phylogenetic signal also indicated its presence in mass-adjusted  $M_{sum}$ , as well as log body mass and winter temperature (Table 1). Winter temperature merits some discussion because it is not a characteristic of the organisms themselves and hence does not actually evolve along a phylogenetic tree. However, as discussed in Garland et al. (1992), habitat preferences and physiological tolerances have inherited components and are organismal characteristics (see also Freckleton et al. 2002 and Blomberg et al. 2003 on “ecological” traits).

$K$ -statistics were higher for body mass than for mass-adjusted  $M_{sum}$  and winter temperature in this study, which is consistent with the general observations of Blomberg et al. (2003) that mass has stronger phylogenetic signal than physiological or behavioral traits, and potentially suggests more evolutionary liability for  $M_{sum}$  and winter climate than for mass, although other factors, such as differences in measurement error (Ives et al. 2007) or phenotypic flexibility, could also account for differences in phylogenetic signal. The value for the  $K$ -statistic for body mass in this study was 1.24, which is slightly lower than other  $K$ -statistics for avian mass, which vary from 1.66 to 1.68 (Reynolds and Lee 1996; Rezende et al. 2002; values reported in Blomberg et al. 2003). However, the  $K$ -statistic in this study still exceeded one, which indicates that body mass in birds shows a greater amount of phylogenetic signal than expected under a Brownian motion evolutionary process along the specified phylogenetic tree. The value for the  $K$ -statistic for mass-adjusted  $M_{sum}$  in this study, 0.48, was higher than  $K$ -statistics for BMR (0.36, data from Reynolds and Lee 1996) and for mass-adjusted  $M_{sum}$  (0.18, data from Rezende et al. 2002) in birds; this latter value was associated with nonsignificant phylogenetic signal. Rezende et al. (2004) also found that mass-adjusted  $M_{sum}$  in rodents did not show significant phylogenetic signal and suggested that  $M_{sum}$  has relatively

high evolutionary liability and changes readily in response to environmental conditions. The relatively low  $K$ -statistic for winter temperature also suggests substantial evolutionary liability in winter thermal conditions among birds. In contrast to previous studies (Rezende et al. 2002, 2004; Blomberg et al. 2003),  $M_{sum}$  in this study did show significant phylogenetic signal. The difference in  $K$ -statistics for  $M_{sum}$  between this study and Rezende et al. (2002) might result from both summer and winter birds being included in  $M_{sum}$  analyses in the Rezende et al.’s study, but only birds acclimatized to relatively warm climates being included in  $M_{sum}$  analyses in this study, so seasonal variation in  $M_{sum}$  is likely reduced in the present study, which might, in turn, reduce noise in the detection of phylogenetic signal.

Bozinovic and Rosenmann (1989) demonstrated that geographic distribution was correlated with maximum cold-induced metabolism in rodents, with high  $M_{sum}$  in cold dwelling species, low  $M_{sum}$  in tropical species, and intermediate  $M_{sum}$  in species from intermediate climates. In addition,  $M_{sum}$  in rodents is negatively correlated with average minimum temperature at their locality of residence (Rezende et al. 2004). It is not known whether an analogous situation occurs in birds because  $M_{sum}$  has been determined principally for species wintering in cold climates, although Wiersma et al. (2007) documented lower  $M_{sum}$  for tropical residents than for temperate-zone breeders. Such a relationship between metabolic rate and climate does occur for BMR in birds, with species from cold climates having higher BMR than species from warm climates (Weathers 1979; Wiersma et al. 2007). These studies have focused on how present physiology (i.e., metabolic ceilings) affects present geographic distributions in endotherms, and the significant effect of winter temperature on  $M_{sum}$  in this study is consistent such a relationship in birds.

Phylogenetic position also significantly predicted  $M_{sum}$  in this study, suggesting that evolutionary history (including dispersal and vicariance events) also plays a role in explaining current distributions, and that historical patterns of physiological characteristics in the ancestors of present-day bird species interacting with past climates exert an important influence on present-day bird distributions. The fossil record suggests that most modern avian orders and families arose during a Tertiary radiation, with much of the diversity in these lineages evolving since the Eocene–Oligocene transition approximately 34 mya (Feduccia 1995, 2003; Blondel and Mourer-Chauviré 1998; James 2005; Mayr 2005). Accompanying this adaptive radiation were marked climatic changes, beginning in the late Eocene, that resulted in much colder climates, the development of polar ice caps, and orogenic episodes that produced cold climates at altitude (Wolfe and Poore 1982; Berggren and Prothero 1992; Blondel and Mourer-Chauviré 1998). Cold climates, therefore, appear as a selective factor in avian evolution during the mid-Tertiary, which is coincident with a major adaptive radiation in modern bird groups.

Blondel and Mourer-Chauviré (1998) conclude that these changes resulted in the withdrawal of tropical birds from the Northern Hemisphere and their progressive replacement by temperate bird assemblages. The present study of the levels of  $M_{sum}$  in extant bird lineages suggests that one factor potentially involved in the colonization of colder climates in the Northern Hemisphere beginning in the Oligocene epoch was a capacity for thermogenesis sufficient for thermoregulation in cold climates. In contrast, taxa that failed to evolve a high thermogenic capacity, and the associated higher capacities for cold tolerance, were potentially restricted to warmer climates. The correlative data we present in this study do not allow distinction of whether the occupation of cold climates drove the evolution of high  $M_{sum}$  in certain taxa or whether the presence of high  $M_{sum}$  in some taxa allowed these taxa to colonize cold climates. Evolutionary lability in  $M_{sum}$ , however, allows further elevation of thermogenic capacity in response to more recent cold periods, resulting in the present situation of the highest levels of thermogenic capacity in cold-climate resident birds. Thus, the current bird distributions and assemblages that occur in cold climates likely reflect a combination of past physiological evolution and current, ongoing selection for high thermogenic capacity.

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## Supporting Information

The following supporting information is available for this article:

**Appendix S1.** Electronic version of phylogeny produced by DOS PDTREE.EXE program.

**Table S1.** Mass (g) and  $M_{sum}$  (ml O<sub>2</sub> min<sup>-1</sup>) data for the species used in the comparative analyses in this study.

**Table S2.** Best-fit model for predicting log Msum (mL O<sub>2</sub> min<sup>-1</sup>).

Supporting information may be found in the online version of this article.

(This link will take you to the article abstract).

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## Online Supplemental Material

**Data Table.** Mass (g) and  $M_{\text{sum}}$  ( $\text{ml O}_2 \text{ min}^{-1}$ ) data for the species used in the comparative analyses in this study. Tip Code column refers to names in the electronic version of the phylogenetic tree (see online supplemental material). Clade refers to seven lineages, representing different taxonomic orders or suborders, identified for multiple regression models shown in Table 4. Strategy refers to migratory and overwintering strategies; W = Warm-climate resident, C = Cold-climate resident, M = Migrant (wintering in warm climates). Winter Temperature refers to the mean daily temperature ( $^{\circ}\text{C}$ ) for January (northern hemisphere) or July (southern hemisphere) for the site of capture (for resident species) or the approximate center of the species' wintering range (for migrant species).

Species	Tip Code	Clade	Strategy	Winter Temperature	Body Mass (g)	$M_{\text{sum}}$ ( $\text{ml O}_2 \text{ min}^{-1}$ )	n	Reference
Order Galliformes								
<i>Coturnix chinensis</i>	kq	1	W	11	43.2	6.57	2	Hinds et al. 1993
<i>Coturnix coturnix</i>	ct	1	M	11	148	20.48	2	Hinds et al. 1993
<i>Colinus virginianus</i>	bw	1	C	-10	220	20.09	12	Swanson and Weinacht 1997
Order Columbiformes								
<i>Zenaida auriculata</i>	Za	2	C	8	124	18.6	-	Rezende et al. 2002
Order Strigiformes								
<i>Glaucidium nanum</i>	Gn	3	C	8	98	10.89	-	Rezende et al. 2002
Order Psittaciformes								
<i>Melopsittacus undulatus</i>	bu	4	W	11	37.9	7.91	2	Hinds et al. 1993
<i>Platycercus eximius</i>	er	4	C	11	89.4	12.79	1	Hinds et al. 1993
Order Piciformes								
<i>Picoides villosus</i>	hw	5	C	-10	62.6	12.67	2	Swanson and Liknes 2006
<i>Picoides pubescens</i>	dw	5	C	-10	25.8	7.72	4	Swanson and Liknes 2006
Order Passeriformes								
Suborder Tyranni								
<i>Phytotoma rara</i>	rp	6	C	8	41.6	8.11	6	Rezende et al. 2001
<i>Tyrannus tyrannus</i>	ek	6	M	22	40.5	8.82	5	Swanson and

								Liknes 2006
<i>Contopus virens</i>	wp	6	M	22	13.7	3.66	5	Swanson and Liknes 2006
Suborder Passeri								
<i>Lichenostomus fuscus</i>	fh	7	W	9	18	4.7	3	Maddocks unpubl. data
<i>Vireo bellii</i>	bv	7	M	19	9.2	2.54	6	Swanson and Liknes 2006
<i>Vireo gilvus</i>	wv	7	M	19	13.4	4.15	6	Swanson and Liknes 2006
<i>Baeolophus ridgwayi</i>	ta	7	C	-4	16.1	4.82	23	Cooper 2002
<i>Poecile gambeli</i>	mc	7	C	-5	11.1	4.26	26	Cooper 2002
<i>Poecile atricapilla</i>	bc	7	C	-10	13.2	4.40	5	Swanson and Liknes 2006
<i>Troglodytes aedon</i>	ho	7	M	22	10.3	3.88	4	Swanson and Liknes 2006
<i>Sitta carolinensis</i>	wb	7	C	-10	19.6	4.88	5	Swanson and Liknes 2006
<i>Dumetella carolinensis</i>	gc	7	M	19	34.8	6.94	7	Swanson and Liknes 2006
<i>Sturnus vulgaris</i>	es	7	C	-13	79.6	17.33	15	Hart 1962
<i>Passer domesticus</i>	pd	7	C	-10	26.8	8.42	6	Swanson and Liknes 2006
<i>Poephila guttata</i>	zf	7	W	11	11.8	4.03	2	Hinds et al. 1993
<i>Coccothraustes vespertinus</i>	eg	7	C	-13	58	12.33	8	Hart 1962
<i>Carpodacus mexicanus</i>	hf	7	C	-10	21.3	6.03	5	Swanson and Liknes 2006
<i>Carduelis chloris</i>	gr	7	C	-2	27.1	6.33	14	Saarela et al. 1995
<i>Carduelis flammea</i>	re	7	C	-24	14	5.09	5	Rosenmann and Morrison 1974
<i>Carduelis barbatus</i>	bs	7	C	8	15	3.95	-	Rezende et al. 2002
<i>Carduelis spinus</i>	sg	7	C	-2	12.8	4.27	3	Saarela et al. 1995
<i>Carduelis tristis</i>	ag	7	C	-10	12.1	4.16	8	Swanson and Liknes 2006
<i>Dendroica petechia</i>	Dp	7	M	19	9.3	2.90	5	Swanson and Liknes 2006
<i>Icterus galbula</i>	lg	7	M	19	31.0	7.48	5	Swanson and Liknes 2006

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<i>Icterus spurius</i>	Is	7	M	19	20.4	5.02	5	Swanson and Liknes 2006
<i>Phrygilus gayi</i>	Pg	7	M	8	27	6.21	-	Rezende et al. 2002
<i>Zonotrichia capensis</i>	Zc	7	C	8	18.8	5.17	9	Novoa et al. 1990
<i>Junco hyemalis</i>	Jh	7	C	4	16.9	5.78	20	Swanson 1990
<i>Spizella pusilla</i>	Sp	7	C	3	12.5	4.54	5	Swanson and Liknes 2006
<i>Spizella passerina</i>	Cs	7	M	11	11.7	3.57	5	Swanson and Liknes 2006
<i>Passerina cyanea</i>	Pc	7	M	19	13.9	3.89	5	Swanson and Liknes 2006
<i>Pheucticus ludovicianus</i>	Pl	7	M	22	40.0	7.45	5	Swanson and Liknes 2006
<i>Cardinalis cardinalis</i>	Cc	7	C	-10	41.4	8.10	5	Swanson and Liknes 2006
<i>Sicalis auriventris</i>	Sa	7	M	15	31	7.77	-	Rezende et al. 2002
<i>Diuca diuca</i>	dd	7	C	8	34	9.1	-	Rezende et al. 2002

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Best-fit model for predicting  $\log M_{\text{sum}}$  ( $\text{ml O}_2 \text{ min}^{-1}$ ) (see Table 2).

Variable <sup>a</sup>	Coefficient	SE	<i>F</i>	<i>P</i>
Y intercept	-0.1376	0.0437	9.90	0.0034
$\log_{10}$ Body Mass <sup>b</sup>	0.6824	0.0327	436.71	< 0.0001
Winter Temperature	-0.001793	0.000657	7.44	0.0099
Clade 1	-0.1097	0.0382	8.25	0.0069
Clade 2	-0.007018	0.055828	0.02	0.9007
Clade 3	-0.1698	0.0543	9.77	0.0036
Clade 4	-0.0445	0.0391	1.30	0.2620
Clade 5	0.0203	0.0371	0.30	0.5884
Clade 6	-0.0178	0.0311	0.33	0.5716

For all variables, d.f. = 1, 35. Total Sum of Squares = 2.167762, Error Sum of Squares = 0.08114056, Model Sum of Squares = 2.086622, Model Mean Squares = 0.2608277,  $R^2$  for model = 0.962569.

<sup>a</sup> The oscine passerine clade (see Fig. 1) is arbitrarily chosen as the base group for comparison and so does not appear as a separate coefficient. Thus, *P* values for the individual Clade 1 - Clade 6 dummy variables are relative to the passerine clade (while controlling for log body mass and winter temperature). As shown in Table 4, the overall clade effect was significant at *P* = 0.025.

<sup>b</sup> The 95% confidence interval about the partial regression slope for  $\log_{10}$  body mass ( $0.616 < 0.682 < 0.749$ ) just excludes the value of 0.75 that would be predicted by the so-called metabolic theory of ecology (see also Duncan et al. 2007 and references therein).

Phylogenetic tree shown in Figure 1 (LOGBRKR.BRK) produced by the DOS PDTREE.EXE program

```
((kq: 5.700E+00,ct: 5.700E+00): 9.400E+00,bw:
 1.510E+01): 1.290E+01,(Za: 2.630E+01,(Gn:
 2.210E+01,(bu: 6.500E+00,er: 6.500E+00): 1.560E+01
): 1.000E+00,(hw: 2.200E+00,dw: 2.200E+00):
 1.940E+01,(rp: 8.900E+00,(ek: 4.600E+00,wp:
 4.600E+00): 4.300E+00): 1.080E+01,((fh: 1.140E+01,
(bv: 1.400E+00,wv: 1.400E+00): 1.000E+01):
 1.400E+00,(((ta: 2.400E+00,(mc: 1.000E+00,bc:
 1.000E+00): 1.400E+00): 8.400E+00,(ho: 1.000E+01,
wb: 1.000E+01): 4.000E-01,(gc: 5.700E+00,es:
 5.700E+00): 4.700E+00): 4.000E-01): 1.000E+00,((
pd: 9.200E+00,zf: 9.200E+00): 1.500E+00,(eg:
 3.000E+00,(hf: 2.600E+00,(gr: 2.000E+00,(re:
 1.800E+00,(bs: 1.500E+00,(sg: 1.200E+00,ag:
 1.200E+00): 3.000E-01): 3.000E-01): 2.000E-01):
 6.000E-01): 4.000E-01): 3.900E+00,(Dp: 5.800E+00,
(Ig: 1.000E+00,Is: 1.000E+00): 4.800E+00):
 2.000E-01,(((Pg: 5.400E+00,(Zc: 2.500E+00,Jh:
 2.500E+00): 2.900E+00): 2.000E-01,(Sp: 1.000E+00,
Cs: 1.000E+00): 4.600E+00): 2.000E-01,((Pc:
 4.000E+00,(Pl: 3.600E+00,Cc: 3.600E+00): 4.000E-01
): 1.300E+00,(Sa: 4.000E+00,dd: 4.000E+00):
 1.300E+00): 5.000E-01): 2.000E-01): 9.000E-01):
 3.800E+00): 1.100E+00): 1.000E+00): 6.900E+00):
 1.900E+00): 1.500E+00): 3.200E+00): 1.700E+00):
 0.000E+00;
```