Metabolic Capacity and the Evolution of Biogeographic Patterns in Oscine and Suboscine Passerine Birds

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ABSTRACT

Biogeographic analyses of passerine birds demonstrate that suboscines are numerically dominant in South America, whereas oscines are dominant elsewhere. This suggests that oscines generally outcompete suboscines and that suboscine dominance likely persists in South America because of its long isolation from other continents, where oscines have diversified. One hypothesis for oscine competitive superiority is that oscines possess higher metabolic capacities than suboscines, and this favors oscines in most habitats. We tested this hypothesis by comparing summit metabolic rates (M_{sum}, maximum thermoregulatory metabolic rate) between oscines and suboscines using conventional and phylogenetically informed statistical approaches. We predicted that if the metabolic-capacity hypothesis is valid, then oscines should have higher M_{sum} than suboscines. Both conventional and phylogenetically informed ANCOVA on regressions of log M_{sum} against log mass showed that oscines had higher M_{sum} than suboscines: least squares mean M_{sum} was 74% greater for oscines. Moreover, conventional and phylogenetically informed multiple regressions identified log mass, winter-range temperature, and clade (oscines vs. suboscines) as significant effectors of log M_{sum}. Thus, oscines have generally higher M_{sum} than suboscines, which is consistent with the metabolic-capacity hypothesis and suggests that metabolic capacity is one factor influencing the evolution of broad biogeographical patterns in passerines.

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Introduction

Birds of the order Passeriformes are classified into two major suborders, the suboscines and the oscines (Sibley and Ahlquist 1990; Barker et al. 2004). The suboscines are the more ancient lineage and are generally outcompeted by the oscines wherever the two groups come into contact (Feduccia 1999). Biogeographic analyses of passerine birds demonstrate that oscines are dominant in Europe, Asia, North America, Africa, and Australia, whereas suboscines are dominant in South America. In general, suboscines flourish as a group principally in tropical and subtropical regions of the New World, where over 90% of living suboscines are found (Newton 2003). The likely reason that suboscine dominance persists in South America is that the opportunity for interaction between oscines and suboscines has been limited until recently geologically because of the long isolation of South America from other continents, where oscines have diversified. The opportunity for large-scale faunal exchange between North and South America has existed only since the formation of the Central American land bridge in the late Pliocene, between 2 and 4 mya (Feduccia 1999). Even so, Ricklefs (2002) notes that within South America, oscines are typically dominant in forest canopy and open habitats, whereas suboscines are dominant within the forest understory, so the Great American Faunal Interchange following the formation of the Central American land bridge favored North American oscines, which likely displaced South American suboscines from forest canopy and open habitats.

Feduccia (1999) posits that the relatively limited biogeographic "distribution of suboscines is related more to their early acquisition of restrictive tropical physiological adaptations than to any inability to expand their ranges" (p. 369). Feduccia continues, "It was the oscines, with their advanced, more flexible neural parameters, physiological tolerance, and high reproductive potential … that were capable of occupying both temperate and tropical zones" (pp. 369–370). Because this hypothesis focuses on differences in physiological capacities as drivers of passerine biogeographic patterns, we term this hypothesis the "metabolic-capacity hypothesis." In addition to the metabolic-capacity hypothesis, Ricklefs (2002) proposed several other potential hypotheses for why oscine invaders of South America were able to replace suboscines in forest canopy and open habitats. These include differences in morphology (longer legs and toes in oscines) that permit oscines to engage in more active movement through vegetation, more generalized behaviors and diets in oscines that may have been advantageous during the deteriorating climates of the late Tertiary, and the ability of oscines to respond more rapidly to resource fluctuation (as evidenced by shorter incubation periods and lower

investment in immune activity; Ricklefs 2002). These factors are also likely related to metabolic capacities because higher activity levels, shorter incubation periods, and reduced immune-system function are associated with a faster pace of life and elevated basal metabolic rate (BMR) and summit metabolic rate (M_{sum} = maximum thermoregulatory metabolic rate) in temperate relative to tropical birds (Wiersma et al. 2007b). Moreover, not only would more generalized behaviors and diets be beneficial during the climatic cooling of the late Tertiary, but elevated cold tolerance, which is positively correlated with increased M_{sum} (Swanson 2001; Swanson and Liknes 2006), would also be advantageous under such conditions (Swanson and Garland 2009). Thus, differences in metabolic capacities could be an important factor influencing the evolution of biogeographic patterns in oscines and suboscines. However, comparative studies of metabolic capacities of oscines and suboscines have not been undertaken, so no direct tests of the metabolic-capacity hypothesis for passerine biogeography are available.

The broad questions of how physiological traits covary with environmental variability over large geographic distances and how such traits might influence patterns of distribution are significant and have yet to be fully resolved. Consequently, we ask what tropical physiological adaptations might function to restrict suboscine birds largely to tropical and subtropical regions. Tropical birds generally exhibit low clutch sizes, high adult survival rates, and slow growth rates, characteristics that suggest a relatively slow pace of life compared with their temperate-zone counterparts (Martin 1996; McGregor et al. 2007). Wiersma et al. (2007b) conducted a comparative study of BMR, which reflects the minimum energy requirements for maintenance, in tropical and temperature birds and found that tropical birds, on average, had a BMR that was 18% lower than that of temperate-zone species, which suggests that the life-history characteristics present in tropical birds have a metabolic foundation in a low-energy lifestyle. However, it is not immediately apparent why such a low-energy lifestyle would preclude suboscines from tropical and subtropical regions from occupying temperate-zone regions and competing successfully with oscines. Perhaps more pertinent to this question is the capacity of these birds to tolerate the cold temperatures present during temperate-zone winters. Cold tolerance in small birds is positively associated with M_{sum} (Swanson 2001; Swanson and Liknes 2006), which suggests that high heat production capacity is necessary for invasion of cold climates. Furthermore, Wiersma et al. (2007b) showed that tropical birds have lower M_{sum} than temperate-zone birds, and Swanson and Garland (2009) found that temperature within the winter range was inversely correlated with M_{sum} in birds. These comparisons, however, have focused primarily on oscine passerines and other avian orders. Few M_{sum} data are available for suboscine passerines, and much of the available suboscine data are from tropical-resident or tropical-wintering species (Swanson and Liknes 2006; Wiersma et al. 2007b), so available data do not allow appropriate testing of the metabolic-capacity hypothesis for the restricted biogeographic distribution of suboscines. In

this study, we measured metabolic capacities (as M_{sum}) for eight temperate-zone suboscine species and collected additional M_{sum} values from the literature for oscines and suboscines. We then used both conventional and phylogenetically informed comparative analyses to test whether M_{sum} differs between suboscine and oscine passerines. Thus, these data provide the first test of the metabolic-capacity hypothesis for the comparative biogeography of suboscine and oscine passerines.

Material and Methods

Study Species

We measured M_{sum} for eight summer-acclimatized suboscine passerine species from central Chile, namely thorn-tailed rayadito (*Aphrastura spinicauda*), plain-mantled tit-spinetail (*Leptasthenura aegithaloides*), dusky-tailed canastero (*Asthenes humilis*), wren-like rushbird (*Phleocryptes melanops*), fire-eyed diucon (*Xolmis pyrope*), white-crested elaenia (*Elaenia albiceps*), tufted tit-tyrant (*Anairetes parulus*), and many-colored rush-tyrant (*Tachuris rubigastra*). All of these species except white-crested elaenia are permanent residents of the south temperate zone of central Chile (Jaramillo 2003), so these data supplement literature values for M_{sum} in suboscines, which mostly are obtained from tropical resident or tropical-wintering species (Swanson and Liknes 2006; Wiersma et al. 2007b). Thus, our comparisons of M_{sum} in suboscines and oscines include members from each clade that winter in both tropical and temperate zones. We captured all birds by mist net and transported them to laboratories at field stations near the capture location, where we conducted metabolic measurements on the day of capture. Following metabolic measurements, we released all birds at the site of capture.

Because metabolic rates, including BMR and M_{sum}, are flexible phenotypic traits that often show substantial seasonal variation (Bozinovic et al. 1990; Swanson 2010), it is important to standardize M_{sum} measurements to minimize climatic influence on metabolic rates. Summer represents the period of annual minimum metabolic rates for birds wintering in cold climates, and summer birds are acclimatized to similar mild to warm conditions in both temperate and tropical zones, so confounding responses of metabolic rates to climate are expected to be minimal for comparisons of summer-acclimatized birds (Wiersma et al. 2007b; Swanson and Garland 2009). Temperate birds included in our analyses, with the exception of common redpoll (*Acanthis flammea*) from Alaska (Rosenmann and Morrison 1974), were derived from midtemperate latitudes, including the continental United States, southern Canada, central Chile, central Europe, and southeastern Australia (see references in Table A1 in the online edition of *Physiological and Biochemical Zoology*), and M_{sum} in redpolls was consistent with values for other Cardueline finches in this study. Thus, though we acknowledge that differences in climate could affect M_{sum} differences among species, such differences are probably minor in this study because temperate species were collected almost exclusively from midtemperate latitudes with warm summer climates. For this study, we conducted M_{sum} measurements from

January 23 to April 3, during the austral summer, and included literature values for M_{sum} from summer-acclimatized birds or from birds resident in climates without marked seasonal temperature variation (Wiersma et al. 2007*b*; Swanson and Garland 2009).

Metabolic Measurements

We measured M_{sum} by open-circuit respirometry in an atmosphere of 79% helium/21% oxygen (helox), which facilitates heat loss from small birds and induces maximum metabolic rates for heat production at relatively moderate temperatures without affecting normal respiration (Rosenmann and Morrison 1974; Holloway and Geiser 2001). We exposed birds to a series of decreasing temperatures in helox (i.e., sliding cold exposure; Swanson et al. 1996) until they became hypothermic (indicated by a steady decline in oxygen consumption over several minutes), signifying that M_{sum} had been attained. Temperatures in helox at the beginning of the metabolic trials ranged from 17° to 3°C, depending on the size of the bird (higher temperatures for smaller birds). For two individuals each of thorn-tailed rayadito and plain-mantled tit-spinetail, we included measurements of metabolic rates at cold temperatures ($<-2°$C) in air, as we temporarily ran out of helox, and metabolic rates at cold temperatures in air were not noticeably different from those in helox despite not all birds in air becoming hypothermic.

We used a FoxBox-C Field Gas Analysis System (Sable Systems, Las Vegas, NV) for open-circuit respirometry in this study. We passed both incurrent and excurrent gas streams through columns of Drierite and Baralyme to remove water and CO_2, and we maintained helox flow rates at 520–780 mL min^{-1} STPD with the FoxBox-C mass flowmeter, depending on the size of the bird (lower flow rates for smaller birds). We fashioned metabolic chambers from Plexiglas cylinders (9 cm diameter × 15 cm length) and provided temperature control within the metabolic chambers by immersion into a water/antifreeze bath capable of regulating temperature to $\pm 0.1°$C (Rezende et al. 2001). We conducted M_{sum} measurements during the day from 0800 to 1430 hours Atlantic Standard Time. We measured oxygen concentration in excurrent air every 5 s and calculated oxygen consumption as instantaneous oxygen consumption (Bartholomew et al. 1981). We considered M_{sum} as the highest 5-min average oxygen consumption over the test period (Wiersma et al. 2007*b*).

Following metabolic measurements, we measured body temperature cloacally with a copper-constantan thermocouple and a Digi-Sense DuaLogR digital thermometer (Cole-Parmer, Vernon Hills, IL) inserted to a depth (ca. 1 cm) where further insertion did not alter the temperature reading. We considered birds with body temperatures less than 36°C at the end of the metabolic trial as hypothermic (Swanson and Liknes 2006). The presence of hypothermia at the termination of the cold-exposure trial verified that maximum metabolic rate was attained. We weighed birds to the nearest 0.1 g both before and after metabolic tests on a Soehnle Ultra 200 balance (Backnang,

Germany), we assumed constant mass loss over the period of metabolic measurement, and we used the body mass corresponding to the 5-min period during which M_{sum} was obtained for mass versus metabolic rate regressions.

Data Analysis

To test whether M_{sum} differed between oscines and suboscines, we employed both conventional and phylogenetically informed statistical analyses, the latter of which adjusts for phylogenetic nonindependence of raw data (Felsenstein 1985; Garland et al. 1999). We first generated separate conventional least squares regressions of log M_{sum} against log body mass (M_b) for oscines ($n = 44$; see Table A1) and suboscines ($n = 16$; see Table A1) and compared regression lines by ANCOVA.

For phylogenetically informed analyses, we generated a phylogenetic tree (Fig. 1) derived primarily from the DNA/DNA hybridization data of Sibley and Ahlquist (1990) but modified from DNA sequence data as in Wiersma et al. (2007*a*, 2007*b*) and Swanson and Garland (2009). To fit additional suboscines for which we measured M_{sum} in this study into the phylogeny, we derived branching patterns from recent molecular data (Irestedt et al. 2006; Ohlson et al. 2008) and scaled branch lengths according to $\Delta T_{50}H$ (the difference in 50% dissociation temperatures between homoduplex DNA hybrids from the same individual and heteroduplex DNA hybrids from different species) values from Sibley and Ahlquist (1990). Specifically, for the tyrannid clade, we scaled branch lengths by equating the $\Delta T_{50}H$ value for the Contingid-Tyrannid node from Sibley and Ahlquist (1990) with the timescale and branching pattern provided in Ohlson et al. (2008), then applying $\Delta T_{50}H$ values to the nodes in the Tyrannid phylogeny. For the Furnariid clade, we used the $\Delta T_{50}H$ value for the split from the Thamnophilidae clade and then divided this value by the number of subsequent branch points for lower taxa (branching pattern from Irestedt et al. 2006), assuming equal branch lengths ($\Delta T_{50}H = 1.65$) between successive nodes. Only two unresolved polytomies remained in the phylogeny: the vireo clade and the variable seed-eater/crimson-backed tanager/blue-black grosbeak clade. We reduced degrees of freedom in subsequent phylogenetically informed analyses by two to account for these polytomies (Purvis and Garland 1993; Garland and Diaz-Uriarte 1999).

To determine whether phylogenetic signal (i.e., the condition where trait values for closely related species are more similar than those of distantly related species) was present in the log M_b or log mass-adjusted M_{sum} data, the presence of which would indicate that phylogenetically informed methods are necessary for subsequent data analyses, we used the PHYSIG_LL.m Matlab program (Blomberg et al. 2003). We adjusted M_{sum} for M_b as in Blomberg et al. (2003) according to the equation

$$\text{mass-adjusted } M_{sum} = \frac{M_{sum}}{M_b^{0.655}},$$

where the exponent represents the slope of the phylogenetically generalized least squares (PGLS) regression of log M_{sum} on log
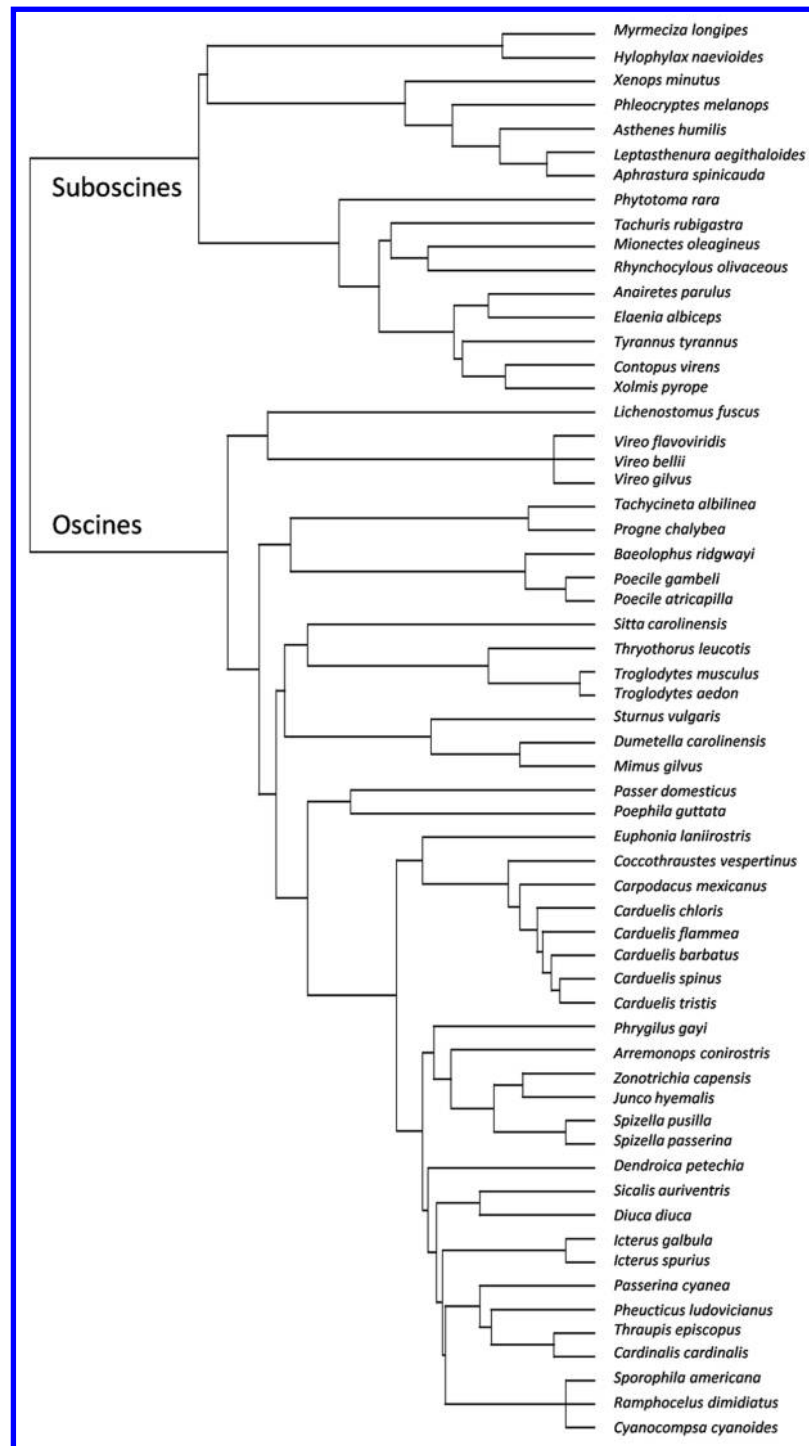
Figure 1. Phylogeny for the 60 species of passerines for which M_{sum} data are available from summer-acclimatized birds or birds from climates that are not strongly seasonal. The phylogeny was derived from the DNA-DNA hybridization data of Sibley and Ahlquist (1990) but modified by more recent DNA sequence data, where such data differed from the DNA-DNA hybridization phylogeny (see text for details).

M_b for all species combined. We used the slope of the PGLS regression rather than the slope from the conventional least squares regression for adjusting M_{sum} for M_b because it fit the data better than the ordinary least squares regression (see below). To test for phylogenetic signal, we used the randomization test (1,000 replicates) for the mean square error (MSE) and also calculated the K statistic (which measures the strength of the phylogenetic signal; Blomberg et al. 2003) for each variable. To determine whether Ornstein-Uhlenbeck (OU) transformation (which simulates stabilizing selection) of branch lengths

in the phylogeny better fit the data than a star phylogeny (i.e., conventional nonphylogenetic model) or a Brownian motion evolutionary model, we compared MSEs for log M_b and log mass-adjusted M_{sum}, calculated by the PHYSIG_LL.m Matlab program, among OU-transformed and untransformed trees (Brownian motion model) and a star phylogeny.

Because phylogenetic signal was present in the data (see "Results"), we calculated phylogenetically independent contrasts (PICs; Felsenstein 1985; Garland et al. 1992) for log M_b, log M_{sum}, and winter-range temperature. We considered winter-range temperature as the mean daily temperature for January (Northern Hemisphere) or July (Southern Hemisphere) for either the locality of capture (resident species) or the city nearest the midpoint of the wintering range (for migrants), using the Hammond Comparative World Atlas (1990), as in Swanson and Garland (2009). We then plotted absolute values of standardized contrasts against their standard deviations (branch lengths) to test for the adequacy of branch lengths for standardizing contrasts. No significant correlations between branch lengths and standardized contrasts were apparent for any variable—for either the entire phylogenetic tree or for suboscine or oscine clades—indicating that contrasts were sufficiently standardized, so we used raw branch lengths for phylogenetically informed analyses. We positivized log M_{sum} contrasts on log M_b contrasts and then generated least squares regressions of log M_{sum} contrasts against log M_b contrasts through the origin for both oscines and suboscines according to Garland et al. (1992). We then mapped the log M_{sum} against log M_b PIC regressions back onto the original data space to provide PIC regression equations (Fig. 2; Garland and Ives 2000). We also tested whether rates of evolution for any of the variables differed among oscines and suboscines by comparing the means for absolute values of PICs for the two clades with Student's t-test (Garland 1992; Garland and Ives 2000; O'Meara et al. 2006).

We used two different phylogenetic approaches to test whether M_{sum} differed among oscines and suboscines and whether any such differences were statistically robust. First, we conducted phylogenetically informed ANCOVA (PI-ANCOVA) to compare regression lines from log-transformed M_{sum} and M_b data between oscines and suboscines (Garland et al. 1993). For the PI-ANCOVA, we used PDSIMUL (Garland et al. 1993) to generate 1,000 data sets of simulated data for log M_b and log M_{sum} along the phylogeny for the 60 birds in this study (Fig. 1). We used six models (gradual Brownian with bounds, correlation set by program; gradual Brownian with bounds, correlation set to 0; speciational Brownian with bounds, correlation set to 0; gradual OU with bounds, correlation set by program; gradual OU with bounds, correlation set to 0; and speciational OU with bounds, correlation set to 0) for evolutionary change along the phylogeny and used the flip algorithm, with no trends, when values approached bounds. For OU simulations, we used default values for decay constants and adaptive peaks set by the program. We used bounds for M_b of 3 g and 1,500 g to cover the range of body sizes in passerines (Dunning 2008) and bounds for M_{sum} of 1.5 and 86.5 mL O_2 min^{-1}, as predicted for body sizes of 3 g and 1,500 g from the
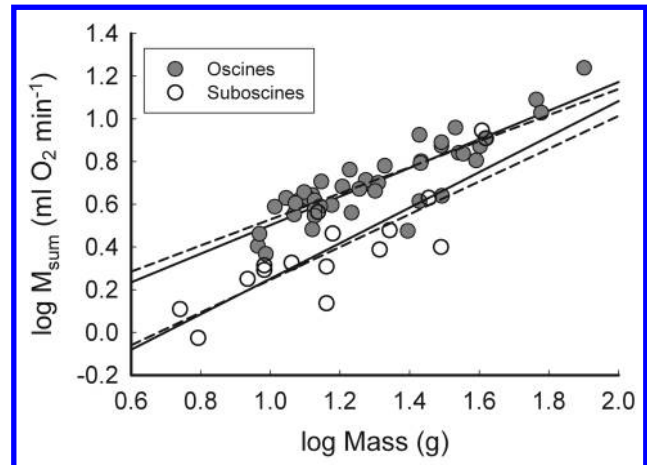

Figure 2. Relationships of log M_b versus log M_{sum} for oscine (*filled circles*) and suboscine (*unfilled circles*) passerine birds. Solid lines represent least squares regression on raw data, whereas dashed lines represent regressions of phylogenetically independent contrasts (PICs) mapped back onto the original data space (Garland and Ives 2000). PIC regression equations were $\log M_{sum} = -0.520 + 0.768 \log M_b$ and $\log M_{sum} = -0.082 + 0.611 \log M_b$ for suboscines ($n = 15$) and oscines ($n = 43$), respectively. Oscine M_{sum} was significantly greater than suboscine M_{sum} for conventional ANCOVA and for phylogenetically independent ANCOVA employing gradual Ornstein-Uhlenbeck evolutionary models.

allometric equation for M_{sum} in Rezende et al. (2002). We then used PDANOVA to analyze the simulated data for comparisons with actual regressions of log M_{sum} versus log M_b.

Finally, we used a multiple-regression model–fitting approach to describe the model that most effectively fit the data. For multiple regressions, log M_{sum} was the dependent variable, and we used various combinations of log M_b, winter-range temperature, and clade (0 = suboscines, 1 = oscines) as separate independent variables, including simple regressions of log M_{sum} on log M_b. We performed conventional and phylogenetically informed multiple regressions with the Matlab program REGRESSIONv2.m (Lavin et al. 2008). We applied all branch-length transformations available in REGRESSIONv2.m, which included a Brownian motion model (no transformation, PGLS), OU, Grafen's ρ, and Pagel's λ. To determine the best-fit model for multiple-regression data, we used log-likelihood ratio tests and the Akaike Information Criterion in both its original (AIC) and corrected (AIC$_C$) forms (Burnham and Anderson 2002; Lavin et al. 2008). We considered the best-fit model as that model with the lowest AIC score and the highest log maximum likelihood (Lavin et al. 2008; Swanson and Garland 2009). Moreover, we used partial F-tests to determine which independent variables significantly influenced log M_{sum}. We considered tests with $P < 0.05$ as statistically significant.

Results

Significant positive correlations of log M_{sum} with log M_b occurred for both suboscines and oscines (Fig. 2). Conventional

regression equations were as follows: subosines ($n = 16$): $\log M_{sum} = -0.580 + 0.832 \log M_b$, $R^2 = 0.729$, $P < 0.001$; oscines ($n = 44$): $\log M_{sum} = -0.167 + 0.670 \log M_b$, $R^2 = 0.762$, $P < 0.001$.

Slopes of these regression equations did not differ significantly ($F_{1,56} = 1.8$, $P = 0.188$), and conventional ANCOVA revealed that oscines had a significantly higher M_{sum} than did suboscines ($F_{1,57} = 46.4$, $P < 0.001$; Fig. 2). Least squares mean M_{sum} for oscines exceeded that for suboscines by 74%.

Significant phylogenetic signal was present for log M_b and log mass-adjusted M_{sum} under both Brownian motion and OU evolutionary models (Table 1), indicating that closely related species had more similar values for these traits than is expected by chance. For Brownian motion models, K statistics for the three traits were all less than 1 (Table 1), which indicates that the traits are less similar among taxa than predicted on the basis of genetic distance under the assumption of Brownian motion evolution. MSEs for log M_b and log mass-adjusted M_{sum} for the phylogenetic trees following OU transformation were lower than those for the untransformed trees and for a star phylogeny (Table 1), indicating that the OU transformation provides a better fit to the log M_b and log mass-adjusted M_{sum} data than either the original untransformed tree or a star phylogeny. K statistics for log M_b and log mass-adjusted M_{sum} were higher under OU evolutionary models, suggesting that phylogenetic signal is stronger under evolutionary models simulating stabilizing selection.

Mean absolute values of PICs for log M_b ($P = 0.291$), log M_{sum} ($P = 0.324$), or winter-range temperature ($P = 0.067$) did not differ between oscines and suboscines, suggesting similar rates of evolution for these traits in the two taxa. Therefore, differential transformation of branch lengths for the two groups in subsequent phylogenetic analyses (Garland and Ives 2000) was not necessary in this study. PI-ANCOVA indicated that oscines had a significantly higher M_{sum} than suboscines under gradual OU models of evolution but not under Brownian motion evolutionary models. Critical ($\alpha = 0.05$) F statistics derived from PI-ANCOVA models must be less than the F statistic

from conventional ANCOVA (46.4 in this study) for the PI-ANCOVA to be considered significant (Garland et al. 1993). Critical F statistics from the different models for PI-ANCOVA in this study were 59.8 ($P = 0.077$) for gradual Brownian with bounds, with correlation set by the program; 63.8 ($P = 0.087$) for gradual Brownian with bounds, with correlation set to 0; 48.5 ($P = 0.057$) for speciational Brownian with bounds, with correlation set to 0; 36.8 ($P = 0.033$) for gradual OU with bounds, with correlation set by the program; 38.9 ($P = 0.034$) for gradual OU with bounds, with correlation set to 0; and 46.8 ($P = 0.051$) for speciational OU with bounds, with correlation set to 0.

The full multiple-regression models—with log M_b, winter-range temperature, and clade (oscines and suboscines) as independent variables—had lower AIC and AIC_C scores than any of the reduced models and thus fit the data better than the reduced models (Table 2). All three independent variables had significant effects on log M_{sum} in all models, with the exception of clade in the PGLS model, but this model provided a substantially worse fit than other models (Table 2). The best-fit model was the OU model with log M_b, winter-range temperature, and clade as independent variables, but the ordinary least squares model also received substantial support (Table 2).

Discussion

OU evolutionary models, which simulate stabilizing selection, consistently provided the best fit for the data for phylogenetically informed (PI) analyses in this study, so we concentrate our discussion of PI analyses on results from the OU transformation. Oscines exhibited higher M_{sum} than did suboscines for both conventional and phylogenetically informed analyses, although not all phylogenetically informed models resulted in significant differences (gradual OU models provided significant differences, but Brownian motion models did not). In addition, the best-fit multiple-regression models all included clade (oscines vs. suboscines) as a significant effector of log M_{sum}, which also indicates significant differences in M_{sum} between oscines

Table 1: Statistics for randomization tests for significance of phylogenetic signal for log M_b, log mass-adjusted M_{sum}, and winter temperature for the 60 species studied

Trait	Expected MSE_0/MSE	Observed MSE_0/MSE	K	MSE	MSE_{star}	P	ln ML	ln ML_{star}
Log M_b	2.65	.91	.34	.06842	.06168	.001	−4.168	−1.059
Log M_b (OU)	1.17	1.02	.87	.06149	.06263	.023	−.964	−1.059
Log $M_{sum}/M_b^{0.655}$	2.65	1.59	.60	.01493	.02091	<.001	41.491	31.389
Log $M_{sum}/M_b^{0.655}$ (OU)	1.45	1.87	1.29	.01270	.02914	<.001	46.362	31.389
Winter temperature	2.65	1.18	.44	167.66	192.55	<.001	−238.291	−242.443

Note. Calculated with the Matlab program PHYSIG_LL.m (Blomberg et al. 2003). Statistics for log M_b and log mass-adjusted M_{sum} are presented for both the original phylogenetic tree (Fig. 1) and for the original tree with branch lengths transformed according to the Ornstein-Uhlenbeck (OU) model using $d = 0.684$ for log M_b and $d = 0.846$ for log mass-adjusted M_{sum}, the transformation parameters calculated with the Matlab program PHYSIGOU.m (Blomberg et al. 2003). Tip data used in these analyses are presented in Table A1 in the online edition of *Physiological and Biochemical Zoology*. 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 amount of phylogenetic signal relative to a Brownian motion expectation (Blomberg et al. 2003). ML = maximum likelihood.

Table 2: Partial regression coefficients and *P* values from phylogenetically informed and conventional ordinary least squares (OLS) multiple regressions

Model	Log M_b[a] (SE)	Winter Temperature (SE)	Winter Temperature *P*	Clade *P*	ln ML	Transform Parameter	R^2	SEE	AIC	AIC_C
OLS	.8037 (.0958)	...	...	...	33.44	...	.671	.1410	−60.87	−60.44
OLS	.7914 (.0673)	−.00435 (.00120)	.0006	...	39.63	...	.732	.1282	−71.26	−70.54
OLS	.7190 (.0517)	−.00324 (.00092)	.0009	<.0001	57.28	...	.851	.0964	−104.55	−103.44
PGLS	.6552 (.0613)	...	...	...	41.53	...	.663	.1232	−77.06	−76.63
PGLS	.6477 (.0572)	−.00362 (.00115)	.0027	...	46.29	...	.713	.1148	−84.58	−83.85
PGLS	.6466 (.0571)	−.00356 (.00115)	.0031	.2815	46.92	...	.719	.1146	−83.83	−82.72
Reg OU	.6873 (.0623)	...	...	...	44.69	.65443	.677	.1169	−81.38	−80.65
Reg OU	.6780 (.0583)	−.00363 (.00117)	.0029	...	49.40	.64705	.724	.1090	−88.80	−87.69
Reg OU	**.7142 (.0525)**	**−.00312 (.00100)**	**.0029**	**<.0001**	**58.68**	**.09556**	**.844**	**.0943**	**−105.36**	**−103.77**
Reg ρ	.7156 (.0601)	...	...	...	47.06	.44455	.710	.1124	−86.11	−85.39
Reg ρ	.7068 (.0568)	−.00327 (.00113)	.0054	...	51.19	.42928	.747	.1058	−92.37	−91.26
Reg ρ	.7173 (.0526)	−.00312 (.00100)	.0028	<.0001	57.28	.12542	.809	.0977	−102.55	−100.97
Reg λ	.7195 (.0590)	...	...	...	47.06	.72884	.720	.1124	−86.11	−85.39
Reg λ	.7150 (.0558)	−.00318 (.00110)	.0054	...	51.17	.64812	.757	.1059	−92.35	−91.24
Reg λ	.7187 (.0521)	−.00322 (.00095)	.0012	<.0001	57.28	.13313	.816	.0980	−102.55	−100.97

Note. Log M_{sum} (mL O_2 min^{-1}) was the dependent variable, and various combinations of log M_b (g), winter temperature (°C), and clade (0 = suboscine, 1 = oscine) were 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 ρ (Reg ρ), and Pagel's λ (Reg λ). R^2 values are not comparable between OLS and phylogenetic multiple regressions (Lavin et al. 2008). ML = maximum likelihood. Bolded row highlights the best-fit model according to SEE, AIC, and AIC_C.

[a]Significant at $P < 0.0001$ for all models, so *P* values are not included in the table.

and suboscines independent of M_b and winter temperature effects on M_{sum}. Thus, in general, maximum cold-induced metabolic rates are higher in oscines than in suboscines, so these data support the metabolic-capacity hypothesis for the evolution of biogeographic patterns in passerine birds (Feduccia 1999) and suggest that metabolic capacity may have been one factor contributing to the ability of oscines to outcompete suboscines to become the dominant land bird assemblage on all continents except South America. Such a result is consistent with the idea that metabolic capacity may influence broad biogeographic trends in birds generally (Swanson and Garland 2009).

Tropical birds have a slow pace of life that is correlated with a lower BMR and a lower metabolic capacity than that in temperate birds (Wiersma et al. 2007*a*, 2007*b*). This suggests that high metabolic rates are not required for tropical life histories but are favored in temperate climates and by temperate life histories. The prevalence of suboscines in South America is probably due to the long isolation of that continent from other continents after the breakup of Gondwana in the Cretaceous period and the subsequent radiation of suboscines there without interference from oscines (Feduccia 1999; Raikow and Bledsoe 2000; Ericson et al. 2003). However, even in South America, oscines appear to have largely replaced suboscines in open and forest canopy habitat guilds (Ricklefs 2002). Higher metabolic capacities are likely favored by the life histories of birds in these guilds, which are characterized by generally higher activity levels than lifestyles of birds in the forest understory (Ricklefs 2002).

Thus, the higher metabolic capacities of oscines are consistent with their apparent competitive replacement of suboscines in open habitat and forest canopy guilds in South America.

If the metabolic-capacity hypothesis is a valid explanation for patterns of passerine biogeography, then the expectation is that oscines will outcompete suboscines wherever conditions, such as cold climates, favor high metabolic capacity. However, despite the lower M_{sum} for suboscines than for oscines documented in this study, suboscines are not excluded from regions with cold climates in South America (i.e., high Andean habitats and Patagonia; Fjeldså and Krabbe 1990). Moreover, the percentage of suboscines (i.e., suboscine species as a percentage of all passerine species) occupying Patagonian habitats overlaps with that for tropical forest habitats in South America, ranging from 55% to 65% in Patagonia (Ralph 1985; Vuilleumier 1985; Jaksic and Feinsinger 1991; Estades 1997; Couve and Vidal 2003; Ridgely and Tudor 2009), compared with 62%–71% in tropical forest habitats of South America (Ricklefs 2002 and references cited therein). Thus, oscines do not appear to achieve a competitive advantage compared with suboscines in cold climates in South America, which seems inconsistent with the metabolic-capacity hypothesis.

An alternative but not mutually exclusive hypothesis for patterns of passerine biogeography relative to climate is that climate shapes M_{sum} similarly in both oscines and suboscines such that M_{sum} is elevated in cold climates for both groups. The results from this study partially support such a claim, as winter-range temperature was a significant predictor of M_{sum} in mul-

tiple-regression models including both suboscines and oscines. Nevertheless, clade (suboscine vs. oscine) was also a significant predictor of M_{sum} in multiple-regression models, with oscines having higher values even when winter-range temperature was included in the model, so clade has a significant effect on M_{sum} independent of winter temperature. This suggests that for a given climate, oscines have higher M_{sum} than that of suboscines, which should favor oscines in cold climates given that M_{sum} is positively correlated with cold tolerance in birds (Swanson 2001; Swanson and Liknes 2006). Noteworthy in this regard is that temperatures for cold climates in South America do not reach the temperature extremes of continental climates in the Northern Hemisphere (Hammond 1990). For example, average daily winter (January) temperatures for Vermillion, South Dakota (43°N, http://climate.sdstate.edu/climate_site/climate.htm) and Edmonton, Alberta (53°N, http://www.climatetemp.info) are −7°C and −14°C, respectively. Average daily winter (July) temperatures for similar latitudes in South America are 1°C for Esquel, Argentina (43°S, http://en.allmetsat.com/climate), and 3°C for Punta Arenas, Chile (53°S, http://www.climatetemp.info). Therefore, South American birds, even those inhabiting the coldest climates on the continent, are not subject to the same extremes of temperature for birds at similar latitudes in the Northern Hemisphere. Moreover, the avifauna of Patagonia has been described as relatively impoverished compared with North American avifaunas (Vuilleumier 1985; Jaksic and Feinsinger 1991; Newton 2003), suggesting that suboscines, as the dominant land birds of South America, have been less successful in this cold region than oscines in similarly cold or colder regions in North America. Irestedt et al. (2002) suggest from biogeographic and molecular genetic evidence for the diverse tracheophone suboscines (including the families Furnariidae, Dendrocolaptidae, Formicariidae, Thamnophilidae, Rhinocryptidae, and Conopophagidae) that Patagonia was relatively recently invaded by this taxon and only by the tapaculo and Furnariid lineages, thus supporting the view that suboscines underwent only relatively minor radiations in cold climates.

In addition, cold temperatures became a prominent selective factor in avian evolution only since the terminal Eocene cooling, approximately 35–40 mya (Swanson and Garland 2009). Competition between oscines and suboscines began during or relatively soon after this period on all continents except South America (Ericson et al. 2003), providing South American suboscines more time to radiate into regions with cold climates, without interference from oscines, than on other continents. Thus, the relatively recent advent of competition between oscines and suboscines in South America compared with other continents and the large suboscine adaptive radiation on that continent, including species occupying high Andean and Patagonian cold climates, before competitive interactions with later oscine invaders might render such competitive interactions less decisive than on other continents. We argue that the potential exists for metabolic capacity to act as an "intrinsically superior trait" (Ricklefs 2002) leading to a competitive advantage for the oscines in many situations, including cold climates or other conditions favoring high metabolic output, and that elevated metabolic capacity may contribute to a general ability of oscines to outcompete suboscines. Such a claim is consistent with the pattern of oscine dominance on all continents except South America.

Significant phylogenetic signal was present for log M_b and log mass-adjusted M_{sum} in this study under both Brownian motion and OU evolutionary models, indicating that these traits were more similar among related species than is expected by chance. The value of K (a measure of the strength of phylogenetic signal) for M_b in this study (0.34 for the original phylogeny) was lower than that for M_b in several other broad interspecific studies including multiple avian orders. Values of K for log M_b in such studies range from 1.24 to 1.68 (Reynolds and Lee 1996; Rezende et al. 2002; Blomberg et al. 2003; Swanson and Garland 2009). Interestingly, studies focusing on smaller taxonomic levels in birds generate lower values for K for log M_b, with values of 0.75 for shorebirds ($n = 58$), 0.82 for Anseriformes ($n = 55$), 0.29 for swallows ($n = 13$), and 0.89 for Phasianids ($n = 4$; Blomberg et al. 2003). In this respect, the low value for K in this study, which limits comparisons to Passeriformes, is consistent with values focusing on the ordinal level or below in other avian taxa and suggests that stabilizing selection reduces phylogenetic variation in M_b at finer phylogenetic scales. Morphology in passerines is strongly canalized such that morphological differences separating passerine families are not as great as those separating other avian genera (Feduccia 1999). Perhaps, then, it is not surprising that the OU evolutionary model, which simulates stabilizing selection, fits the data for log M_b (a morphological trait) and log M_{sum} (a physiological trait) better than other evolutionary (or nonevolutionary) models. This suggests that physiology may also be canalized among passerines so that members of this order show a low degree of physiological divergence similar to the low degree of morphological divergence. Moreover, given the significant difference in M_{sum} between oscines and suboscines in this study, such physiological canalization may also extend to passerine suborders and thereby affect large-scale biogeographic patterns in these taxa.

Acknowledgments

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