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CONSTRAINTS ON DISTRIBUTIONS AND DIVERSITY IN BIRDS AND MAMMALS OVER VARIABLE ENVIRONMENTS

by

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B.A. Biology, University of Oregon, 2008

DISSERTATION

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CONSTRAINTS ON DISTRIBUTIONS AND DIVERSITY IN BIRDS AND MAMMALS OVER VARIABLE ENVIRONMENTS

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ABSTRACT

The distributions of species are determined by intrinsic factors such as physiological tolerances as well as extrinsic factors of the environment such as the availability of resources. While physiological tolerances generally change over evolutionary time scales, changes in environmental productivity due to processes such as succession or seasonal progression often occur over ecological times. I address both physiology and resource availability as drivers of the distributions and diversity of endothermic birds and mammals using a macroecological approach and a metabolic perspective. Migratory birds, altering communities over seasonal cycles, provide a unique opportunity to investigate the drivers of distributions and diversity that act over ecological time scales. In my first chapter, I show that energy use by migrants in North American breeding bird communities tracks the seasonal dynamics of resource availability. Migrants dominate consumption in tundra and boreal forests where the summer pulse of resources is large relative to winter productivity. While migrants are more prominent during the breeding season, many species overwinter throughout the temperate zone where their role in communities is understudied. In my second chapter, I quantify the contribution of migrants to diversity and energy use in North American

winter bird communities. Overwintering migrants contribute little to diversity but dominate energy use in many temperate communities.

My third chapter represents the efforts of myself and colleagues to understand the physiological adaptations that determine the thermal environments in which species can persist. By expanding on the Scholander-Irving model of heat transfer, we show that mass independent changes to basal metabolic rate and thermal conductance allow endotherms to inhabit nearly the full breadth of thermal environments on Earth.

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INTRODUCTION

Understanding the factors that determine the distributions of species is the fundamental goal of biogeography and an important step in elucidating the drivers of biological diversity. Intrinsic characteristics of species such as physiological tolerances limit the environments in which they can survive. Extrinsic factors of the ecosystem, such as the availability of resources, place constraints on the number and identities of species that can persist in a given area. These co-acting drivers influence distributions over differing time scales. The adaptations that confer physiological tolerances to environmental conditions generally occur over evolutionary time scales. In contrast, changes in environmental productivity can occur over ecological time scales through processes such as ecological succession or the progression of seasons. In my dissertation, I use a macroecological approach and a metabolic perspective to investigate the role of physiology and resource availability in determining distributions and diversity in endothermic birds and mammals.

Because migratory birds cause significant seasonal changes to the structure of communities across the temperate zone, they provide a unique opportunity to investigate the determinants of distributions and diversity that act over ecological time scales. In my first chapter, I use data from the North American Breeding Bird survey to understand the role of seasonal dynamics of resource availability in structuring avian communities. By focusing on energy use and highlighting the role of migrants as consumers within ecosystems, I show that these birds take advantage of the summer pulse of resources occurring in high latitudes to breed during the northern summer. While most migrants leave temperate communities after breeding, many species of short-distance migrants, many of which are the most abundant in North America, will redistribute to overwinter throughout the temperate zone. In my second chapter, along with James H. Brown, I use data from the Audubon Society Christmas Bird Count to quantify the contribution of migrants to diversity and energy use in North American winter bird communities. While migrants dominate energy use in many temperate communities, they contribute little to diversity. In winter communities, the resources that allow migrants to persist alongside year-round residents are not allocated to greatly increase diversity.

In order to investigate the contribution of physiological tolerances in influencing the geographic distributions of species, I focused on adaptations that allow endotherms to persist over a wide range of thermal environments. While body size plays a large role in determining thermal physiology, in my third chapter, along with Joseph Burger, Meghan Balk, Imran Khaliq, Christian Hof, and James H Brown, we extend the Scholander-Irving model of heat transfer to examine mass-independent thermal adaptations. In a macrophysiological study of 211 birds and 178 mammals, we show that species of all body sizes occupy nearly the full breadth of environmental temperatures by changing basal metabolic rate and thermal conductance independently of body size.

By investigating drivers that act over differing time scales, these three chapters further elucidate the factors that allow endotherms to persist over variable environments.

CHAPTER 1: Energy use by migrants and residents in North American breeding bird communities

Trevor S Fristoe

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ABSTRACT

Aim: On the order of 5 billion birds comprising more than 700,000 tonnes of biomass migrate across North America every year to exploit seasonal resource pulses at high latitudes during breeding. Despite this impressive scale, little is known about the metabolic role of these migrants on their breeding grounds across temperate ecosystems. I estimate the energy use of short and long distance migrant passerines as well as residents in over 2,000 breeding bird communities covering the geographic scope of North America. My aim was to characterize the geographic patterns of energy use by each migratory group and test the hypothesis that seasonal patterns of resource availability structure temperate breeding bird communities.

Location: North America from 25-69 °N.

Methods: I estimated the energy use of migrant and resident passerines using abundance data from the North American Breeding Bird Survey and scaling relationships for field metabolic rate as a function of body size. Linear regression was used to test the relationship between energy use by each migratory group and latitude as well as indirect measures of environmental productivity during different seasons.

Results: Energy use by all groups showed a strong relationship with latitude except for long-distance migrants, which were surprisingly invariant across geography. Energy use by migrants was highest in environments with low winter productivity and high seasonality while resident energy use was highest where annual productivity was the highest.

Main conclusions: Migrant passerines contribute significantly to temperate breeding bird communities, especially in high latitudes. They account for 78% of consumption in habitats north of 50°N compared to 1.7% in the subtropics south of 35°N. Short-distance migrants are especially important to community energy use in the habitats where migrants consume the most. Future shifts in breeding bird community composition are likely to occur as climate change alters seasonal cycles of resource availability.

INTRODUCTION

Avian migration is perhaps the most conspicuous seasonal change that occurs in vertebrate communities of the temperate zone. In North America alone, on the order of 5 billion birds comprising more than 300 species and 700,000 tonnes of biomass travel from the tropics to breed during the brief northern summer every year (Cox, 1985; Rappole, 1995; Appendix s1 in Supporting Information). Additionally, more than 100 species of short-distance migrants travel between overwintering and breeding grounds within the continent (Gough *et al.*, 1998). It is well documented that these migrants comprise a major component of temperate breeding bird communities, especially at the highest latitudes (Newton & Dale, 1996; Hurlbert & Haskell, 2003). Largely missing, however, has been an explicit focus on the energetic impact of migrants across habitats and over large geographic scales.

Here, I take a metabolic perspective to quantify the energetic contribution of migrant passerines within breeding bird communities across North America, from Florida to Alaska. I investigate how short-distance migrants, which overwinter within the temperate zone, long-distance migrants, which overwinter primarily in the tropics, and year-round residents differentially contribute to energy use in order to understand the ecological factors that structure these communities. By taking into account the metabolic requirements as well as the abundances of individuals, this approach moves beyond documenting species composition to highlight the roles of migrant birds as consumers within ecosystems (Morlon *et al.*, 2009).

Building on a framework developed by Herrera (Herrera, 1978), a simple graphical model (Fig. 1) predicts how the energy consumption of migrants and residents sharing a common pool of resources (e.g., passerines feeding on arthropods) varies with seasonal cycles of resource availability. Throughout the year, total community energy use is limited by the current resource supply. Because many bird populations are regulated largely during winter, when food supplies are short and low temperatures increase energy demands and abiotic stress (Holmes *et al.*, 1986), resource supply during this season should limit energy use by residents. As productivity increases through the spring and summer, migratory populations can move in and exploit the seasonal pulse of resources for breeding. Therefore, only habitats where the summer pulse in productivity is large relative to winter resource availability are predicted to support a substantial proportion of migrants as shown in Fig. 1. The relative magnitude of this pulse increases with latitude, but also varies with local and regional climate (Schloss *et al.*, 1999). There are some additional complications. For example, energy budgets vary over an annual cycle depending on the expenditures for thermoregulation, reproduction and other activities. Despite these complexities, I make the qualitative prediction that the energy use of migrants relative to residents should increase with latitude and additionally with environmental seasonality.

The shorter migration distances of intra-continental migrants coupled with their ability to detect and respond to regional changes in environmental conditions means that these species often arrive on breeding grounds earlier than long-distance migrants traveling from the tropics (Butler, 2003; Biaduń *et al.*, 2011). If migrants departing from winter ranges within the temperate zone have first access to the resource pulse and territories occurring at high latitudes, it is predicted that the energy use of these birds should increase with latitude. It is unclear how the energy use of tropical migrants will vary over geography. Seasonal habitats in the North are predicted to provide the greatest opportunities for breeding migrants but metabolic and mortality costs as well as the race to establish high quality territories may limit how far they travel before settling to breed (Alerstam & Lindström, 1990). Therefore, I expect the proportion of energy used by long-distance relative to short-distance migrants to decrease with latitude as short-distance migrants increasingly dominate avian communities towards the pole. Alternatively, if short-distance migrants, arriving first, occupy opportunities in nearby locations in the Southern portions of the region, long-distance migrants may be forced to move farther and settle in more Northern communities. This would result in the opposite pattern of increasing proportional energy use by long-distance migrants with increasing latitude. Additionally, because migrants show a high degree of habitat fidelity between winter and the breeding season (Böhning-Gaese & Oberrath, 2003), energy use by migrants from the largely forested Neotropics should be greater in forested than in open grassland or shrubland habitats.

To test these predictions I used data from the North American Breeding Bird Survey (BBS) and scaling relationships for field metabolic rate as a function of body size to quantify the energy use of migrant and resident passerines in 2,274 temperate breeding bird communities across the continent. These communities cover the breadth of habitats and nearly the entire latitudinal extent of the North American continent north of Mexico. By including only passerines, which are primarily insectivorous during the breeding season (Ehrlich *et al.*, 1988), I restrict my analyses to a group of species that share a common pool of resources, a requirement of the model above.

METHODS

Site selection

Species composition and abundance data for 2,274 avian communities came from the BBS. The BBS is an annual, standardized survey of avian abundances coordinated by the United States Geological Survey and Canadian Wildlife Service. Each roadside route is surveyed during the height of the breeding season (usually June) by experienced volunteers across the US and Canada. To control for the effect of surveys conducted during anomalous years, these communities are composed of routes surveyed seven or more times between the years 2001-2011. All surveys fulfilled BBS quality criteria (i.e., runtype = 0). For analyses correlating energy use variables with environmental productivity, only the 1,888 routes with available actual evapotranspiration (AET) data were used.

Migratory status

Using a function that I developed with the MATlab Mapping Toolbox™ and range map data provided by NatureServe.org (Ridgely *et al.*, 2003), each of 3,356,065 passerine species observations within the dataset was assigned as either migrant or resident depending on the location where it occurred. A species was considered migrant at a route if the survey start coordinates fell within the summer portion of its range and assumed resident if they were in either the year-round or winter portions of its range. Because many intra-continental migrants have portions of their range where they are year-round residents and others where they occur only during breeding, this method allows for the same species to be considered as resident at some locations within the study area and migratory others. This eliminates the risk of counting species as migratory in portions of their range where some individuals remain as year-round residents, but increases the chance of counting individuals as resident that are actually migrating within this area. When route coordinates fell outside all portions of the species' range map, it was considered vagrant and not included in calculating community energy use.

While I acknowledge that migration distances vary along a continuum, I chose to follow Gough *et al*, 1998 in using a geographic boundary to categorize each migratory species into one of two distinct groups for simplicity and practicality (Gough *et al.*, 1998). If a species overwinters entirely outside of North America North of Mexico it was designated as a long-distance migrant. This geographic cut-off closely corresponds to the boundary between the Neotropics and Nearctic and was chosen over a separation criteria based on an arbitrary migration distance. The species categorized as long-distance migrants can be thought of as tropical-Nearctic migrants. All other species were considered short-distance migrants and can be considered Nearctic-Nearctic migrants.

To compliment this geographic based approach, I also looked at how the average migration distance of birds within a community varied over geography and with the proportion of migrants. For each species, a single estimate of migration distance was calculated by measuring the distance between the geographic centers of the breeding and winter ranges (winter range included both winter and year round portions of the range). Migratory distances for all migrant individuals observed were averaged for every year that a route was surveyed, and the means of these are reported.

Energy use calculations

The energetics of breeding bird communities were estimated quantitatively using the relationship between field metabolic rate (B) and body mass (M): $B = cM^b$, where c is a taxon-specific normalization constant and b is the allometric scaling exponent (Brown *et al.*, 2004; Sibly *et al.*, 2012). I use values provided from empirical studies for passerine birds under natural conditions of c = 10.5kJ/day/g and b = 0.713 (Nagy, 2005; McNab, 2009). There are factors such as within species variation in energy use for which this relationship is unable to account. However, values estimated using this method should provide a reasonable representation of breeding bird community energetics as body size alone has been shown to account for over 90% of the variation in avian field metabolic rates (Nagy, 2005). Body masses (M) were taken from Dunning's *Handbook of Avian Body Masses Second Edition* (Dunning, 1993).

The energetic requirement for the local species population (E) is simply NB, where N is abundance as reported from BBS surveys. Summing across all species gives the total energy use of the entire passerine community (E_{TOT}). The energy use of residents, short-distance, long-distance, or all migrants (E_{RES}, E_{SDM}, E_{LDM}, and E_{MIG} respectively) was determined by summing E for all species belonging to each particular group. The relative metabolic contribution of migratory species within the community was estimated as $P_{MIG} = E_{MIG}/E_{TOT}$, which potentially ranges from 0, for a community with no migrants, to 1, for a community composed entirely of migrants. The proportion of energy consumed by long-distance migrants within the migrant community is $P_{LDM} = E_{LDM}/E_{MIG}$.

Values reported for each energy use variable are averages of all years that a route was surveyed between 2001 and 2011.

Environmental data

I used global data on actual evapotranspiration (AET; mm time^{-1}) to approximate the rate of resource supply to the passerine community at each BBS route location during different seasons (Ahn, 1994). June (the height of the breeding season and the month when BBS surveys are conducted), January, and annual AET at the start coordinates of each BBS route were extracted from the 55km^2 resolution grid. Resource seasonality was calculated as the difference between June and January AET.

To look at differences between forested and open regions I used data on the terrestrial ecoregion of each BBS route location. Ecoregions were categorized as either open or forested as follows: tundra, desert, xeric shrublands, flooded grasslands, flooded savannas, temperate grasslands, temperate savannas, temperate shrublands, and tropical or subtropical grasslands, savannas, and shrublands = open; Mediterranean forests or woodlands, boreal forests/taiga, temperate conifer forests, and temperate broadleaf and mixed forests = forested (Nature Conservancy data available at: http://maps.tnc.org/gis_data.html).

Statistical analysis

I ran all statistical tests in R 3.1.0 (R Development Core Team, 2014). I used correlations as determined by OLS regression to quantify the relationships between the total and proportional energy use of the various migratory groups and latitude, June AET, January AET, annual AET, and seasonality. To reduce heteroscedasticity and fulfill the assumptions of regression analysis, values of total energy use (E_{TOT}, E_{RES}, E_{SDM}, E_{LDM}, and E_{MIG}) were always log transformed while values of proportional energy use (P_{MIG} and P_{LDM}) were logit transformed. The package *modttest* was used to implement Dutilleul’s correction in order to account for the inflated degrees of freedom resulting from spatial autocorrelation (Dutilleul *et al.*, 1993).

To test whether P_{LDM} was higher in forested than in open habitats, I used analysis of covariance (ANCOVA) to compare the relationships between P_{LDM} and latitude in each habitat type.

RESULTS

In many boreal forest and Arctic habitats as well as the Northern Great Plains, the vast majority of passerine energy use can be attributed to migrants (average $P_{MIG} = 0.78 \pm 0.21$ at sites above 50°N; maximum $P_{MIG} = 1$ at seven sites above 64.00°N). In contrast, migrants account for almost none of the consumption in southern temperate and subtropical communities (average $P_{MIG} = 0.17 \pm 0.01$ at sites below 35°N; minimum P_{M} $_{IG}$= 0.0003 at 26.56°N). In high latitude communities, where migrants account for a large proportion of energy use, the majority of energy being used by migrants was consumed by short-distance migrants that winter within the temperate zone (average $P_{LDM} = 0.30 \pm 0.19$ at sites above 50°N ; minimum $P_{LDM} = 0$ at 50.45°N; $P_{LDM} = E_{LDM}/E_{MIG}$). At low latitudes, where energy use by migrants was the lowest, long-distance migrants, which varied little over geography, were primarily responsible for this consumption (average $P_{LDM} = 0.86 \pm 0.18$ at sites below 35°N; maximum $P_{LDM} = 1$ at 14 sites throughout the latitudinal extent).

Total energy use in the passerine breeding community was highest in the Great Plains and Eastern deciduous forests. The lowest levels of avian energy use occurred in the Intermontane West, Western Canada, and Alaska (Fig. 2a). Overall energy use, E_{TOT}, was not significantly correlated with latitude. Resource availability during the breeding season, June AET, was the best significant predictor of energy use by the total breeding bird community as hypothesized (Table 1; Fig. 3a).

Energy use of residents reached the highest levels in Eastern deciduous forests, was lowest in the most Northern habitats and the Intermontane West (Fig. 2b), and showed a significant, negative correlation with latitude. Contrary to predictions, January AET was weakly correlated with resident energy use, while annual AET accounted for the largest amount of variation (Table 1; Fig. 3b).

Total migrant energy use and short-distance migrant energy use were significantly correlated with latitude and both peaked in the plains of the Northern US and Canada (Fig. 2c and d). Latitude was not correlated with energy use by long-distance migrants, which showed very little spatial pattern (Table 1, Fig. 2e). AET seasonality was strongly correlated with E_{MIG}, but January AET emerged as the best predictor (Table 1, Fig. 3c). Winter AET was also the best predictor of energy use by short-distance migrants, while AET seasonality was the best predictor of energy use by long-distance migrants (Table 1, Fig. 3d and e).

A map of P_{MIG} for all breeding bird communities reveals that the proportion of energy consumed by migrants increases with increasing latitude as predicted (Fig 4a). Latitude was revealed as a strong correlate of P_{MIG}, accounting for about half of observed variation (Table 1). This geographic pattern in P_{MIG} can be explained by differing energy use of both residents and migrants over latitudes. While migrant energy use increased consistently until all but the very highest latitudes, energy use by residents declined with latitude, reaching negligible amounts in the far North, keeping P_{MIG} high throughout these habitats (Fig. 4b).

The quantity of energy consumed by long-distance relative to all migrants, P_{LDM}, decreased with latitude (Fig. 4c). Latitude explained about one third of observed variation in P_{LDM} (Table 1). This pattern is caused primarily by the increasing energy use of short-distance migrants with increasing latitude. Energy use of long-distance migrants varied little across latitudes (Fig. 4d). However, average migration distance did not show a strong latitudinal signal, but was highest along the west and gulf coasts as well as in Northern temperate forests. Migration distances were lowest in the Desert Southwest, the Great Basin, and the Great Plains (Fig. 5a). There was a significant negative relationship between migration distance and P_{MIG} ($r = -0.31$, $df = 86$, $p = 0.003$), indicating that migrants were traveling relatively shorter distances to reach the habitats where they played the largest role in community energetics (Fig. 5b).

The relationship between P_{LDM} and latitude differed between open and forested habitats. ANCOVA revealed that forested habitats had a significantly shallower slope than open ($F_{1, 2270} = 49.1$, $p << 0.001$). Forested habitats had higher relative energy use by long-distance migrants at all but the lowest latitudes (Figure s1 in supporting information).

DISCUSSION

Taking a macroecological and metabolic perspective highlights the role of migrant birds in avian communities and ecosystem energetics across the geographic scale of the North American continent. Migrants are especially important in high latitude communities, accounting for an average of 78% of passerine energy consumption in boreal forest and arctic tundra communities north of 50°N. As latitude increases, fewer resources are available throughout the year to support resident birds. At the same time, the relative magnitude of the seasonal pulse of productivity during the breeding season increases, providing resources for migratory species. Despite the smaller body sizes of migrants relative to resident birds in Northern habitats (Ramirez *et al.*, 2008), these resources are utilized by high abundances of incoming birds, leading to the energy use patterns observed. These high abundances likely have the potential to support a greater number of viable species populations (Brown, 2014). As a result, these patterns of energy use are reflected in the distribution of migrant richness over latitudes (Morales-Castilla *et al.*, 2013). Overall, my results for North America are consistent with those reported for Europe (Herrera, 1978). So, the importance of bird migration in community energetics is likely a widespread phenomenon, at least in the Northern Hemisphere.

While June AET was the strongest correlate of total energy use as predicted, energy use of residents was determined primarily by annual AET and not by winter productivity. This unexpected result can likely be attributed to a number of factors. First, since productivity during winter months is close to zero across much of North America, resident birds must persist on resources produced but not consumed during more productive seasons (Mönkkönen *et al.*, 2006). Locations with high productivity throughout the year likely provide a greater surplus of resources that can be exploited by birds when times are lean. Second, resident species are not the only birds present in winter bird communities. The short-distance migrants that inhabit high-latitude habitats during the breeding season winter at lower latitudes within the temperate zone. It is unclear what environmental factors allow for the persistence of both residents and overwintering migrants in non-breeding communities, but it is likely that each group impacts the resource use of the other. To add to complications, many passerine species change diet from insects during breeding to seeds and fruits during the non-breeding season (Ehrlich *et al.*, 1988). So the food available to birds during the non-breeding season can vary substantially depending on location, habitat, current environmental conditions and diet (Dunning & Brown, 1982; Laurance & Yensen, 1985). Other factors to be considered are the energy budgets and physiological tolerances of both migrants and residents on the wintering grounds (Root, 1988; Meehan *et al.*, 2004).

Energy use by migrants was highest in environments with low winter productivity and high seasonality, characteristics that typify habitats of the far North. This is consistent with the hypothesis that incoming migrants are able to insert themselves into temperate breeding communities by taking advantage of the seasonal pulse of resources, but is inconsistent with previous research that found seasonality to be a weak predictor of migrant energy use in both North America and Europe (Mönkkönen *et al.*, 2006). The reason for this difference may be due to how I classified migratory status. Previous macroecological studies on avian migration have generally either classified each species into a single migratory category no matter where it occurred, or restricted analyses to only tropical (i.e. long-distance) migrants (MacArthur, 1959; Willson, 1976; Herrera, 1978; Mönkkönen *et al.*, 2006). Because my analysis considers any individual that was not present in a community outside of the breeding season as a migrant, it will elucidate the greater impact of migrants across all latitudes (compared to studies that considered only tropical migrants) and better estimate the impact of migrants where some populations of a species may remain as year-round residents (compared to studies that used one classification for each species). I believe this method captures a more accurate representation of the role of migrants in avian community energetics.

As winter AET and AET seasonality explained less than a third of the variation in energy use by migrants, other factors associated with high-latitudes may contribute to the observed patterns. Short growing seasons often produce concentrated pulses of abundant insects that provide food for many species of birds (Herrera, 1978). Another possible influence is day length, which affects the time available for diurnal passerines to forage. Round-the-clock daylight during the arctic summer provides ample foraging time for migrants and residents rearing offspring (Marshall, 1938). Diminishing daylight and foraging time during the winter adds to the burden of residents that must deal with the energetic stresses of limited food and low temperatures (Root, 1988).

In the Northern habitats where migrants are the prominent consumers in breeding communities, short-distance migrants account for a majority of energy use. This supports the hypothesis that their shorter migrations and earlier arrivals to breeding grounds allow them to take advantage of the opportunities for reproduction in these seasonal environments, thereby reducing the potential resources available to the later arriving tropical migrants. As a result, the quantity of energy used by these tropical migrants was surprisingly invariant across latitudes. They appear to fill vacancies and use resources left by short-distance migrants. Short-distance migrants were more important in open compared to forested habitats, where P_{LDM} was generally higher and migration distances longer. This is consistent with previous work that has shown that the majority of tropical migratory species in the new world are forest birds (Böhning-Gaese & Oberrath, 2003).

The fact that the various components of the avian community are so closely tied to seasonal patterns of resource availability raises concerns as climate change affects abiotic conditions and biotic interactions. Results of this study agree with previous research which suggests that more moderate climates should allow more birds to overwinter while a diminishing seasonal pulse of resources should decrease the availability of food for migratory species to exploit during the breeding season (Lemoine & Böhning-Gaese, 2003). These changes are predicted to be most pronounced in the Northern latitudes which provide the greatest opportunities for migratory birds (Hinzman *et al.*, 2005).

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TABLES

	Resource availability variable				
Energy use variable	Jan AET	June AET	AET Seasonality	Annual AET	Latitude
E_{TOT}	$r = -0.018$ $df = 196$ $p = 0.8$	**$r = 0.334$** $df = 289$ $p << 0.001$	$r = 0.329$ $df = 666$ $p << 0.001$	$r = 0.37$ $df = 18.1$ $p = 0.11$	$r = -0.13$ $df = 55.3$ $p = 0.32$
E_{RES}	$r = 0.19$ $df = 286$ $p = 0.001$	$r = 0.25$ $df = 320$ $p = 0.002$	$r = 0.10$ $df = 819$ $p = 0.003$	**$r = 0.37$** $df = 20$ $p = 0.03$	$r = 0.001$ $df = 62$ $p << 0.001$
E_{MIG}	**$r = -0.49$** $df = 375$ $p << 0.001$	$r = 0.25$ $df = 588$ $p << 0.001$	$r = 0.41$ $df = 687$ $p << 0.001$	$r = -0.18$ $df = 218$ $p < 0.001$	$r = 0.524$ $df = 289$ $p << 0.001$
E_{SDM}	**$r = -0.55$** $df = 315$ $p << 0.001$	$r = 0.24$ $df = 629$ $p << 0.001$	$r = 0.33$ $df = 850$ $p << 0.001$	$r = -0.30$ $df = 124$ $p < 0.001$	$r = 0.64$ $df = 200$ $p << 0.001$

$\boldsymbol{E_{LDM}}$	$r = -0.30$ $df = 799$ $p << 0.001$	$r = 0.23$ $df = 673$ $p << 0.001$	$\underline{\boldsymbol{r = 0.32}}$ $df = 838$ $p << 0.001$	$r = 0.11$ $df = 214$ $p = 0.11$	$r = 0.11$ $df = 403$ $p = 0.03$
$\boldsymbol{P_{MIG}}$	-	-	-	-	$r = 0.70$ $df = 66$ $p << 0.001$
$\boldsymbol{P_{LDM}}$	-	-	-	-	$r = -0.57$ $df = 163$ $p << 0.001$

Table 1: Results for linear regressions of energy use in each migratory group (total community energy use [E_{TOT}]; resident energy use [E_{RES}]; migrant energy use [E_{MIG}]; short-distance migrant energy use [E_{SDM}]; long-distance migrant energy use [E_{LDM}]; proportion of migrant energy use [P_{MIG}]; proportion of long-distance migrant energy use [P_{LDM}]) against each measure of seasonal resource availability and latitude (actual evapotranspiration [AET] is used as a proxy for resource availability). For AET variables with significant relationships, the highest value of Pearson's correlation coefficient (r) for each group is bold and underlined. Degrees of freedom (*df*) are calculated from the effective sample sizes resulting from Dutilleul's correction to account for spatial autocorrelation.

FIGURES

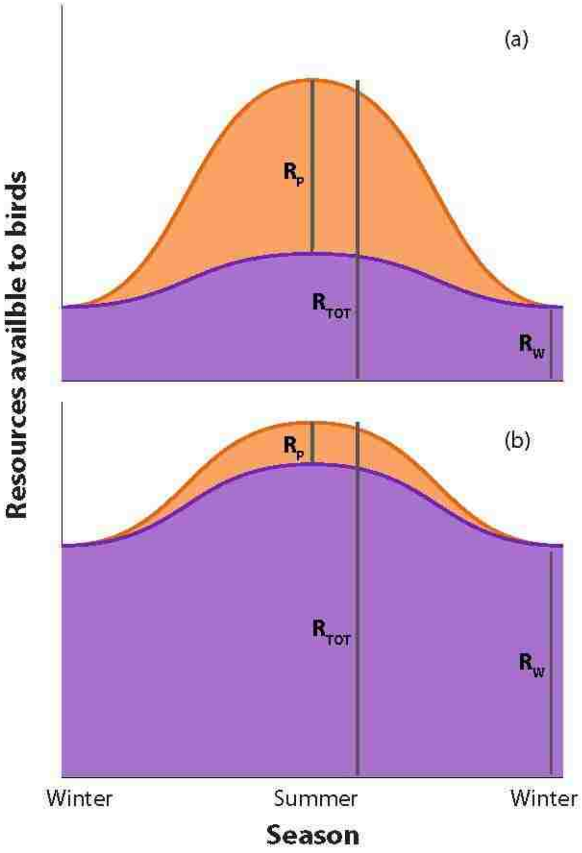

Figure 1: A graphical model showing how resource seasonality in high (a) and low (b) latitude communities is predicted to affect the energy use of migrant and resident birds. The area under the topmost curve represents the resources available to birds throughout the year. Resources utilized by resident (E_{RES}) and migrant birds (E_{MIG}) are depicted in purple and orange respectively. Resident birds should ultimately be limited by the resources available during the winter months (R_W). While residents should have some capacity to utilize the summer pulse of resources to produce offspring during breeding, the remaining excess (R_P) will be available for exploitation by incoming migrants. The proportion of energy used by migrants (P_{MIG}) is predicted to be correlated to the

magnitude of R_P relative to the total available resources during the breeding season, R_{TOT}. Highly seasonal environments at high latitudes (*a*) should have the largest values of P_{MIG} and the less seasonal environments closer to the equator (*b*) are predicted to have low values of P_{MIG}.

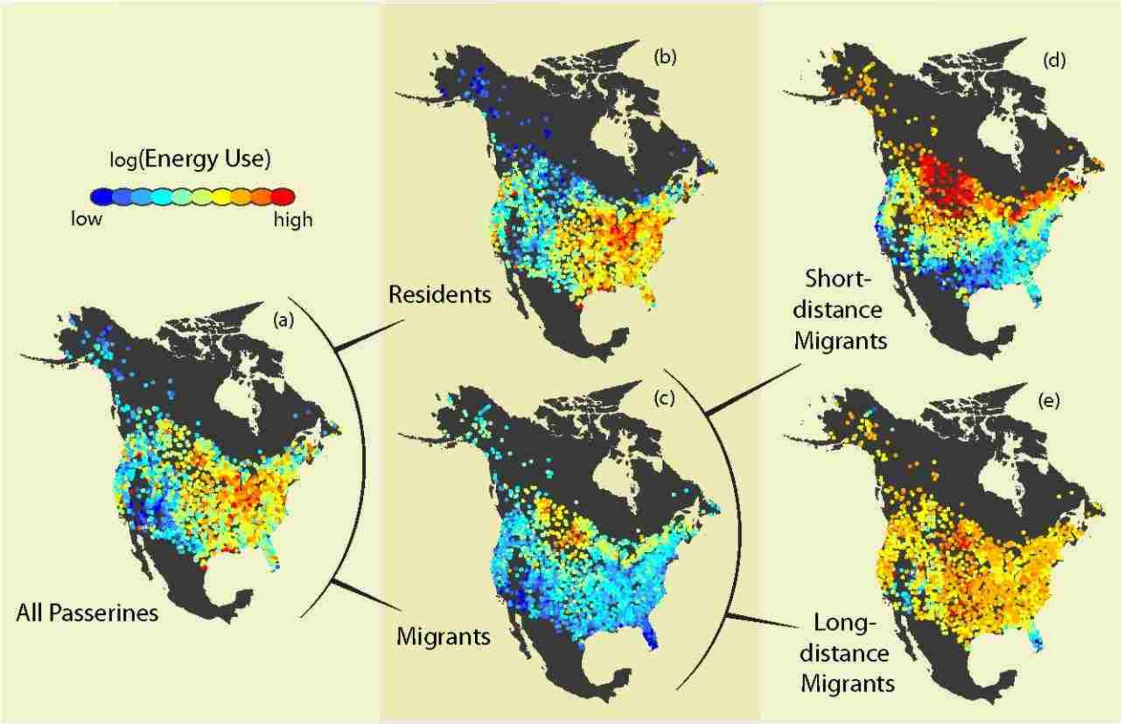

Figure 2: Geographic patterns of energy use by various migratory groups for each of 2,274 North American breeding bird communities. The color scale is equivalent within each column of maps. The energy use depicted in maps (a) and (c) are comprised of the energy use of all groups in columns to the right. Energy use (with highest levels in red and lowest in blue) within the total passerine community (E_{TOT}) was highest in Eastern deciduous forests and the Great Plains; lowest in many northern habitats and much of the Intermontane West (a). Energy use by residents (E_{RES}) decreased with latitude and, like total energy use, was highest in the productive deciduous forests of the eastern US (b). Energy use increased with latitude in migratory species (E_{MIG}), reaching highest levels in the northern Great Plains (c). Energy use by short-distance migrants (E_{SDM}) increased steeply with latitude and was high throughout northern habitats (d) while energy use by long-distance migrants (E_{LDM}) showed no strong geographic pattern (e).

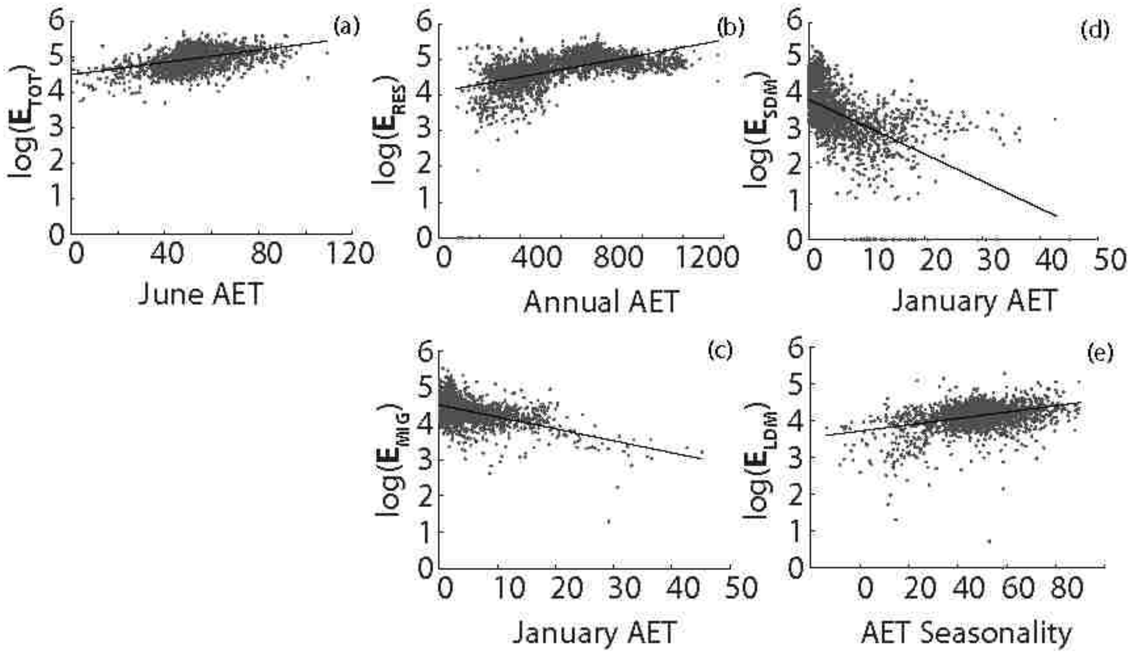

Figure 3: The relationship between energy use by each migratory group and the productivity measure that best predicted it. Energy use in the entire community (E_{TOT}) (a) was best explained by summer actual evapotranspiration (AET) ($r = 0.34$, $df = 289$, $p << .001$). Resident energy use (E_{RES}) (b) was best explained by annual AET ($r = 0.37$, $df = 20$, $p = 0.03$). Energy use by all migrants (E_{MIG}) (c) as well as short-distance migrants (E_{SDM}) (d) were best explained winter AET ($r = -0.49$, $df = 375$, $p << .001$; $r = -0.55$, $df = 315$, $p << .001$). Energy use by long-distance migrants (E_{LDM}) (e) was best explained by AET seasonality ($r = 0.32$, $df = 838$, $p << .001$). Slope lines were fitted with simple OLS models, not accounting for spatial autocorrelation, because slope estimates are thought to be unaffected by spatial pseudo replication.

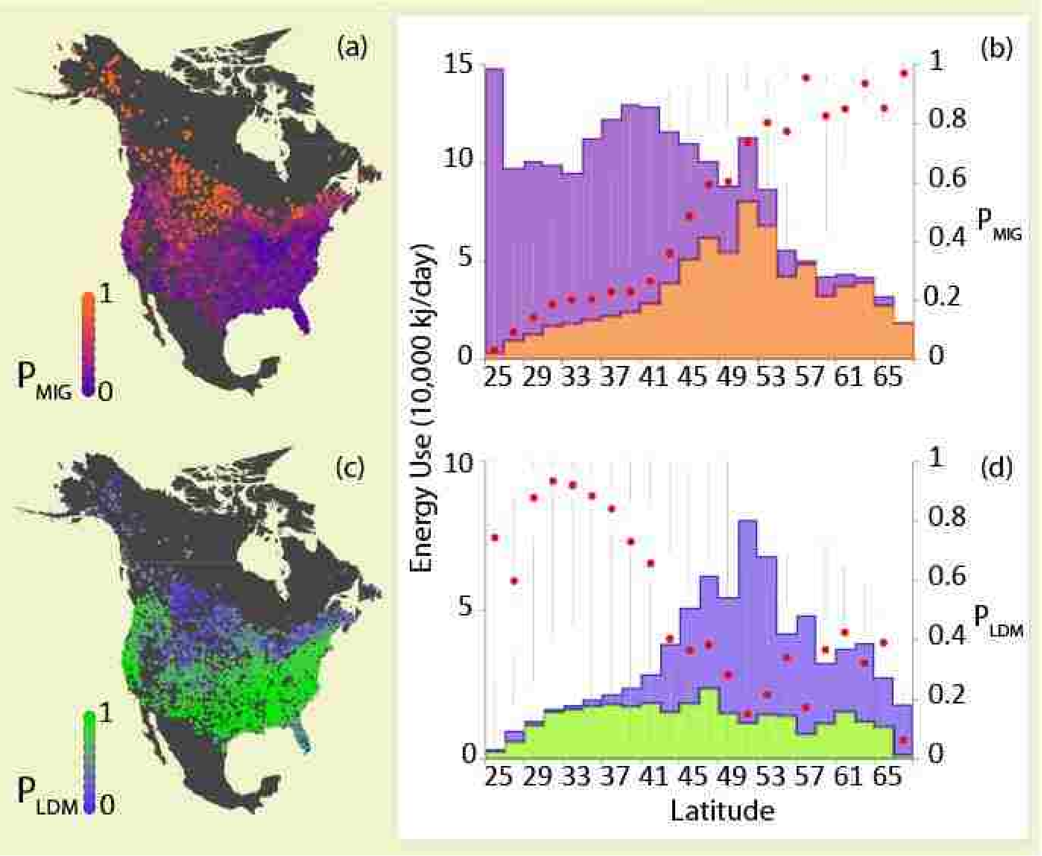

Figure 4: The proportion of energy used by migrants (P_{MIG}), depicted as a gradient from purple (P_{MIG} = 0) to orange (P_{MIG} = 1), increased dramatically with increasing latitude (a). A stacked bar graph of energy use by residents (E_{RES} in purple) and energy use by migrants (E_{MIG} in orange) averaged over 2° latitude bins shows that this pattern was due to decreasing E_{RES} coupled with increasing E_{MIG} at all but the highest latitudes (b). Red points indicate average P_{MIG} within each latitudinal bin while grey bars depict the upper and lower quartiles. The space above and below red dots and between grey bars shows the combined range of the second and third quartiles. Within the migratory community, a map depicting the proportion of energy used by long-distance migrants (P_{LDM}) from blue (P_{LDM} = 0) to green (P_{LDM} = 1) shows that the proportion of energy used by long-distance migrants decreased with increasing latitude (c). A stacked bar graph of the energy use by

short-distance migrants (migrants which overwinter within the temperate zone; E_{SDM} in blue) and energy use by long-distance migrants (migrants that overwinter outside of the temperature zone; E_{LDM} in green) averaged over 2° latitude bins reveals that this pattern was driven by generally increasing E_{DSM} with latitude while E_{LDM} remained relatively constant (d). Red points indicate average P_{LDM} within each latitudinal bin while grey bars depict the upper and lower quartiles.

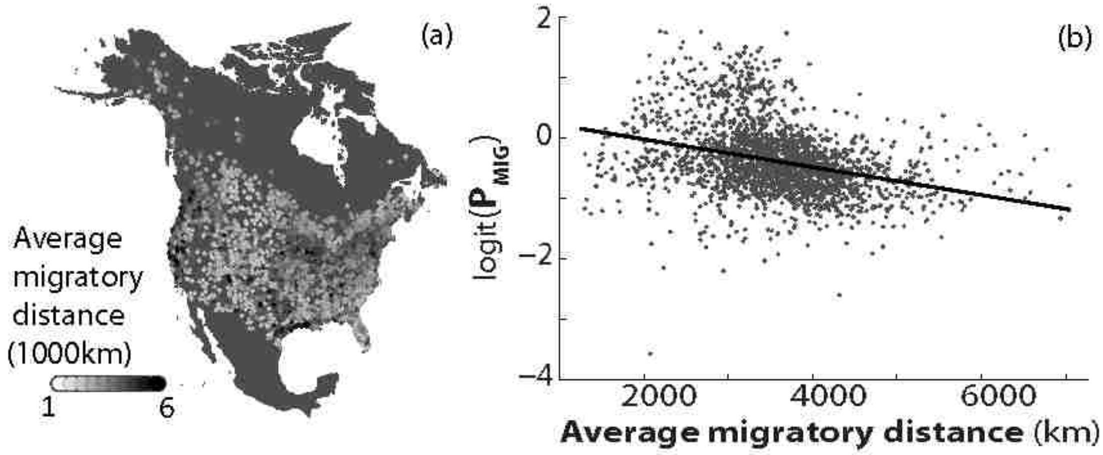

Figure 5: The average migration distance of individuals within breeding bird communities over geography (a) and its relationship with proportion of energy use by migrants (P_{MIG}) (b). Migrants traveled the longest distances (depicted in black) to reach breeding communities along the West and gulf coasts as well as the Northern temperate forest. The shortest migration distances (depicted in white) were found throughout the open habitats of the Great Plains and desert southwest (a). There is a negative correlation between P_{MIG} and average migratory distance (r = -0.31, df = 86, p = 0.003). This relationship indicates that birds in the habitats that support the largest portion of migrants are migrating from relatively close winter ranges.

SUPPLEMENTAL MATERIALS

To estimate the total biomass of all tropical migratory birds breeding in North America (T), I used:

$$T = NM$$

The number of individuals (N) was based on Cox's (1985) rough estimation of 5,000,000,000. The mass used for each individual (M) was 151g; the mean mass of all migratory individuals observed during the North American Breeding Bird Survey. All surveys with a runtype of 1 (designating high quality surveys) were used in this calculation. The mean mass of an individual was averaged over the survey years between 2000 and 2009. Individuals of each species were designated as a migrant based on the methodology outlined in the "Migratory status" subheading of the methods section. The calculated value of T = 775,400,000,000g was rounded down to 700,000,000,000g.

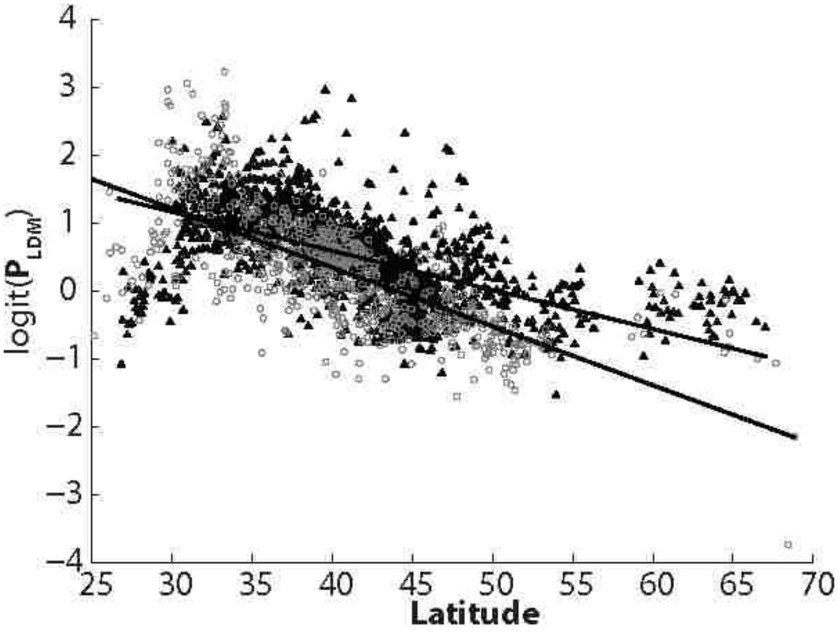

Figure S1: Relationship between the proportion of energy used by tropical migrants within the migratory community *(P_{LDM})* and latitude in forested (black triangles) and open (grey circles) habitats. Both habitats show a pattern of decreasing P_{TM} with latitude, but forested habitats had higher values over all but the lowest latitudes.

CHAPTER 2: The contribution of migrants to North American winter bird communities

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ABSTRACT: Migration dramatically changes the structure of bird communities over seasonal time scales. After breeding and with the approach of winter, some arctic and temperate zone species depart for the tropics, but many others redistribute to overwinter within the temperate zone. Despite the fact that such short-distance migrants include some of the most abundant species in North America, little is known about their contribution to winter bird communities. Using data from the Audubon Society Christmas Bird Count we quantify the diversity and energy use of migratory and resident birds in winter communities from Alaska to Florida. We find that migrants contribute little to overall species diversity but often dominate community metabolism because of their generally high abundances and relatively large body sizes. In communities where migrants account for the greatest portion of consumption, energy use is dominated by individuals of one or a few species, which often join conspecifics which have remained as year-round residents. Resources that support a great influx of migrants are not allocated to support a commensurate increase in diversity.

INTRODUCTION:

Over the course of the year, migratory birds cause dramatic changes in community composition across the temperate zone (Newton & Dale, 1996a,b). These changes are most conspicuous during the breeding season, when a relatively large influx of migrants may substantially increase both abundance and diversity. So, most attention has focused on understanding impacts of migrants on the structure and function of breeding bird communities during summer months (MacArthur, 1959; Herrera, 1978; Hurlbert & Haskell, 2003; Fristoe, 2015). While the majority of migratory species that breed in North America winter in the tropics, more than 100 species of short-distance migrants redistribute to overwinter within the temperate zone (Gough *et al.*, 1998). Since many of these species are among the most abundant birds in North America (Sauer *et al.*, 2014), they should have major impacts on structuring winter communities as they move in and coexist alongside year-round residents, consuming and potentially competing for resources (Salewski *et al.*, 2003; Sherry *et al.*, 2005). Despite potential importance, little is known about how short-distance migrants contribute to community composition and ecosystem processes during the winter across the broad geographic scale of the temperate zone.

A metabolic perspective can provide valuable insights into the mechanisms that structure ecological communities, including those of winter birds (Brown & Maurer, 1989; Brown *et al.*, 2004). Focusing on the currency of energy, by taking into account metabolic requirements as well as abundances, highlights the role of migrant and resident birds as consumers within ecosystems (Morlon *et al.*, 2009). A metabolic perspective can also address questions about how resources – in this case, those available to overwintering birds - are allocated among species to support biodiversity. In many species of short-distance migrants, some individuals will remain as year-round residents across large portions of the geographic range. During winter, these birds may be joined by even larger numbers of conspecifics moving in after breeding in other parts of the species' range. This influx of individuals means that migrants of these species add to the metabolic demands of the winter bird community without increasing species diversity. This disparity between migrant energy use and species diversity may be compounded if resource use and community composition are dominated by just a few species.

Here, we use data from the National Audubon Society's Christmas Bird Count (CBC), a large-scale citizen-science project to quantify the contribution of migrant passerines to species diversity and energy use in ~1800 North American winter bird communities. We compile and analyze CBC from Alaska to Florida over a 10-year period. In those communities where migrants dominate community metabolism, we quantify how energy is distributed among migratory species.

METHODS:

Site selection

Species composition and abundance data for 1814 winter bird communities were compiled from the National Audubon Society's Christmas Bird Count (CBC). The CBC is conducted once per site per year between December and January at locations across the Americas, with volunteers counting all birds seen or heard within a circular area 24km in diameter over a 24-hour period. Data were included only for locations that had been surveyed seven or more times between the years 2001-2011. Because the number of volunteers and duration of surveys is inconsistent between locations and years, all abundances from CBCs were dividing by party-hours to correct for survey effort. Party-hours are calculated as the number of volunteers taking part in the survey multiplied by the number of hours they participated (Bock & Smith, 1971; Raynor, 1975).

Diversity

For each winter bird community, we calculated species richness of migrants (S_M) and residents (S_R) and the proportion of migratory species (P_S) averaged across all years that the site was surveyed. To determine whether a species was either migratory or resident at each CBC location, we developed a measure using the MATlab Mapping Toolbox^{TM} and range map data provided by NatureServe.org (Ridgely *et al.*, 2003). A species was considered as migrant at a survey location if the coordinates of the midpoint of the count circle fell within the winter (only) part of its mapped geographic range and considered as resident if it was in either the year-round or breeding parts of its range. When a species was recorded in a count circle outside all parts of its range map, it was considered as vagrant and not included when calculating community diversity or energy use (Fristoe, 2014).

Community metabolism

Energy use in winter bird communities was estimated quantitatively using the relationship between field metabolic rate (B) and body mass (M):

$B = cM^b$

where c is a taxon-specific normalization constant and b is the allometric scaling exponent (Brown *et al.*, 2004; Sibly *et al.*, 2012; Fristoe, 2015). Calculations used values of $c = 10.5\text{kjday}^{-1}$ and $b = 0.713$ based on empirical studies for passerine birds under natural conditions and body masses (M) from the second edition of Dunning's *Handbook of avian body masses* (Dunning Jr, 1992; Nagy, 2005; McNab, 2009). The energy use of all migrants (E_M) or residents (E_R) in a community was the sum of B for all migratory or resident individuals respectively. The relative contribution of migrants to community metabolism estimated as the proportion of total energy used:

$$P_E = E_M / (E_M + E_R)$$

which ranged from 0, for a community with no overwintering migrants, to 1, for a community composed entirely of migrants.

Many short-distance migrants are widely distributed across large geographic ranges in the breeding season, and then congregate in the winter in parts of the range where some individuals have remained throughout the year. In order to calculate the proportion of individuals that were migratory within the year-round parts of species ranges, abundances were compared between summer and winter months. Summer abundance data came from the North American Breeding Bird Survey (BBS). The BBS is an annual, standardized survey of avian abundances coordinated by the United States Geological Survey and the Canadian Wildlife Service. Each roadside route is surveyed during the height of the breeding season (usually June) by experienced volunteers across the United States and Canada. Only routes surveyed seven or more times between the years 2001-2011 and meeting BBS quality criteria (i.e. runtype = 0) were included in the analysis.

Because the CBC and BBS use different methodologies and have differing geographic distributions, abundances could not be directly compared between seasons. We used differences between the numbers of individuals recorded in CBC and BBS surveys of known non-migratory species as a baseline to correct for the different abundances reported in winter and summer. This correction factor allowed us to estimate of the proportions of individuals of each migratory species that were actually year-round residents and overwintering migrants. We designated species whose mapped breeding and winter ranges overlapped completely as non-migratory. As indicated above, we designated species whose winter ranges did not encompass all of the breeding range as migratory, and we estimated the proportion of migratory individuals of each of these migratory species (M_P) counted at CBC sites where the breeding and winter ranges overlapped as:

$$M_P = (M_W R_W^{-1} - M_S R_S^{-1})/(M_W R_W^{-1})$$

where M_W and M_S are the average abundances of the migratory species during winter and summer (from CBC and BBS data), respectively, within 5° latitude bins from 25-55 °N, and R_W and R_S are the average abundances during winter and summer of a reference sample of non-migratory species across the same latitude band. The minimum value of M_P was restricted to zero. As a simple example, this means that if a migratory species is twice as abundant as the non-migratory species during summer but four times more abundant during winter, then half of these individuals were categorized as overwintering migrants (i.e. $M_P = 0.5$). Only non-migratory species which occurred in 80% or more of the CBC and BBS routes within a latitude band were included in the reference sample used for this calculation (see table S1 for a list of non-migratory species used). Values of

R_W and R_S used in the above calculation were the average of all of the non-migratory species in the reference sample for a given latitudinal band. The above equation was used to estimate the number of migratory individuals of each migratory species for each CBC site falling within the overlapping breeding and wintering part of its geographic range. Within the winter-only portion of the range, all individuals recorded in CBCs were assumed to be migrants. In order to restrict comparisons across latitude bands to similar environments, we calculated M_P and community energy use only in the central ("grassland"; n = 307) and eastern ("forests"; n = 985) regions of North America. Calculations in each region were performed separately. Values reported for E_M, E_R, and P_E are averages of all years that a location was surveyed between 2001 and 2011.

Analysis

All statistical analyses were performed in MATlab. To characterize geographic patterns in species diversity and energy use of migrants, smoothing splines were fit to the relationships between S_M, S_R, P_S, E_M, E_R, and P_E with latitude using a smoothing parameter of 0.1.

To quantify the differential contribution of migrants to community diversity and energy use, the relationship between P_S and P_E was analyzed by OLS regression. A slope differing significantly from 1, as determined by 95% confidence intervals, indicates that migrants allocate resources among species richness differently than resident birds. We additionally analyzed species-energy relationships of migratory and resident birds. Species-energy relationships quantify the rate at which diversity (S) increases with increasing energy use (E) and, like species-area relationships, generally follow a power law of the form:

$$S = kE^z$$

where k is a constant and z is the scaling exponent (Wright, 1983). A value of $z = 1$ indicates that diversity and energy use increase at the same rate, $z <$ that energy use increases faster than, *vice versa* for $z > 1$, and $z = 0$ (no significant slope) indicates no relationship between diversity and energy use.

To quantify the division of energy among migratory species, relative energy use within the migratory community was calculated for all species in the 20% of communities where P_E was highest. These communities were categorized geographically as northern plains, southern plains, northeast, or southeast. Relative energy use of each species compared to the total energy use of all migrants was averaged across sites within each region.

RESULTS:

Validation of the method for estimating M_P

In some cases, values of M_P varied depending on which non-migratory species was used for comparing winter and breeding abundances. However, this variation was low when M_P was the highest (Fig. S1). This means that our method of determining the proportion of migratory individuals worked well in detecting regions where the breeding and winter parts of a species range overlap and the majority of individuals were in fact overwintering migrants.

Diversity

Migrant passerines only modestly contributed to species diversity of most winnter bird communities; they accounted for < 50% of species richness in only 2.5% of communities surveyed. However, migrants comprised a substantial portion of the species certain geographic regions: Great Plains (mean $P_S = 0.36$ in grassland habitats), desert southwest, gulf coast, and Florida (mean $P_S = 0.44$ south of 33°N; maximum $P_S = 0.59$ at 29.8°N; Fig. 1a). The contribution of migrants to species richness was relatively low in the far north and throughout mountainous regions of the West (mean $P_S = 0.08$ north of 55°N; minimum $P_S = 0$ at 7 sites, 5 of which were above 53°N). Throughout most of North America, the proportion of migratory species generally declined with increasing latitudes. However, in grassland regions of central North America, the proportion of migratory species was high in the south, declined at mid latitudes, and increased again in the northern Great Plains (Fig. 1b).

Species diversity of resident was highest along the West Coast of the US and in the desert southwest, but also relatively high along the East Coast. Along both coasts, richness of resident species peaked at mid latitudes (Fig. 2b). Diversity of residents was generally low across the Great Plains, where migrants contributed relatively more to species richness (Fig. 2d). Overall, richness of resident species decreased significantly with increasing latitudes (Fig. 2c). Richness of migratory species declined sharply with increasing latitude (Fig. 2a); it was highest across the southern US, especially along the Gulf Coast.

Community metabolism

Winter migrants accounted for the majority of community energy use throughout the southern US as well as in the northern Great Plains and boreal forests (mean $P_{E} =$ 0.79 south of 33°N; 0.49 north of 46°N; maximum P_E = 0.98 at 20.13°N; Fig. 3a). Winter migrants contributed less to community metabolism throughout mid latitudes, but their energy use was rarely below 20% (mean P_E between 40-46°N = 0.37). The result was a distinctly U-shaped relationship between the proportion of energy used by migrants as a function of latitude (Fig. 3b).

Absolute energy use by migrants and residents showed opposite geographic patterns (Fig. 4a and b). Resident energy use peaked at mid latitudes where migrants accounted for a smaller proportion of community metabolism (Fig. 4c). Absolute energy use by migrants reflected their proportional energy use, being highest throughout the southern US, northern Great Plains, and boreal forests.

The distribution of energy among species

On average, migrants contributed over twice as much to community energy use as they did to species richness (mean P_E/P_S = 2.11 ± 2.23). There was a significant relationship between the proportion of migratory species in a community and the proportion of energy used by migrants but the slope was substantially < 1 (slope = 0.26 [95% confidence intervals: 0.24 – 0.28]; Fig. 5a). Because migrant diversity showed no significant relationship with migrant energy use (i.e. z did not differ significantly from 0; $p = 0.11$; Fig. 5b), the increase in P_S with increasing P_E was driven primarily by the species-energy relationship of the resident species (Fig. 5a). The z-value of 0.11 for resident species, indicating a slightly more than 10-fold increase in richness for a 100-fold increase in energy use, was similar to previous studies of winter birds (Evans *et al.*, 2006).

Energy use by migrants was generally dominated by one or a few species in the 20% of communities where P_E was the greatest (Table 1), but which species was dominant varied geographically. In the south, influxes of individuals of species with large, generally more northerly breeding ranges were responsible for the vast majority of consumption. In winter communities of the northern Great Plains, consumption was dominated by species which breed in the Far North and move south into exclusively winter ranges in southern Canada and northern US. In boreal forests where migrants dominated community metabolism, common ravens (*Corvus corax*) were almost exclusively responsible.

DISCUSSION:

After breeding at high latitudes, short-distance migrants redistribute and contribute substantially to community metabolism in winter bird communities across many regions of North America. Although migrants increased species richness of nearly all winter communities, their contribution was generally low, usually accounting for less than half of the species. On the other hand, over much of North America, migrants dominated community metabolism. By taking an energetic perspective and emphasizing the metabolic demands of migrants, we have highlighted the importance of short-distance migrants in winter bird communities across the temperate zone.

The general decline in the proportion of migratory species with increasing latitude across most of the continent is consistent with previous results for eastern North America (Newton & Dale, 1996b). However, migrants generally made up a greater portion of winter bird diversity throughout grassland habitats of central US and Canada. Over much of this region, migrants accounted for a third of species; in the northern Great Plains and throughout the South, they often comprised half of all species. The bird communities of northern plains are unique in being dominated by migratory species throughout the year. They are a hotspot of migrant diversity during the summer (Hurlbert & Haskell, 2003), and then species that breed in this region migrate south in winter and are replaced by migrants that bred throughout the tundra and boreal forests.

Across eastern North America, migrant passerines accounted for the majority of community metabolism throughout the South, but also in some northern communities. Outside of the Great Plains where many of the winter migrants were small granivores or frugivores, high energy use in high latitude communities was almost entirely due to common ravens (*Corvus corax*). CBC count circles tend to be located near population centers and this result may to some extent be a consequence of ravens congregating during winter to take advantage of anthropogenic food subsidies (Restani *et al.*, 2001; Dunn *et al.*, 2005), rather than broad scale movements across latitudes. Regardless of the cause, because CBC sampling is low in northern Canada and Alaska, it is not clear if the pattern of increasing P_E with increasing latitude would continue to the far North. This is unlikely, however, because migratory species were virtually absent from the northernmost communities with available data in western North America.

Where winter migrant energy use was highest, it was generally dominated by one or a few species. In northern communities of the Great Plains, snow buntings (*Plectrophenax nivalis*) and bohemian waxwings (*Bombycilla garrulous*) together accounted for over two thirds of total community metabolism. These species breed farther north and are present only during the winter. In contrast, the dominant winter migrant species across southern North America occur in parts of their breeding ranges, where some individuals remain throughout the year and are joined in winter by an influx of conspecifics from northerly breeding ranges. This pattern accounts in part for the disproportionate contribution of the migrants to community metabolism compared to species diversity; the influx of large numbers of migratory individuals in the winter causes them to dominate community metabolism without increasing species diversity.

Our method for calculating the proportion of migratory individuals within the resident portion of species ranges allows only rough estimates of migrant energy use. For example, the sharp transitions in P_E across 5° latitude bins (Fig. 3b) highlight our inability to capture the gradual changes in the proportion of migratory individuals that likely occur in most species. Regardless, our method represents a significant step forward in understanding the contribution of migrants to winter bird communities, especially those in the temperate zone of North America where an influx of migrants adds to the abundances of species that are year-round residents. Considering all individuals within the area of overlap between breeding and winter parts of a species range as resident is unrealistic, and it may greatly underestimate energy use by migrants, especially in southern communities. The alternative extreme, counting all individuals of potentially migratory species as migrants regardless of geographic location, runs the opposite risk; overestimating energy use by migrants in the northern portions of overlapping breeding and winter ranges. While more accurate estimates will likely become possible as available data improves, our results provide the most complete analysis of the energetic impact of migrants in winter bird communities over a broad continental scale.

Besides elucidating the importance of migrants as consumers within winter communities, these results highlight the unique opportunity that avian migration provides for investigating the drivers of abundances, distributions, and diversity of species that act over ecological time scales (Mönkkönen *et al.*, 2006). Environmental productivity has been proposed as a key driver of biodiversity, with more resources supporting more individuals that can be divided into viable populations of more species (Connell & Orias, 1964; Pianka, 1966; see discussion in Currie, 1991; Lomolino *et al.*, 2010; Brown, 2014). While a correlation between resource availability and species diversity has been shown at many ecological scales (Wright, 1983; Currie *et al.*, 2004; Hurlbert, 2006), overwintering migrants in winter bird communities seem to provide an interesting exception where diversity is largely decoupled from energy use. Understanding the environmental factors that work independently of productivity in order to support diversity in overwintering migrants may provide insights into the complex ecological and historical factors that combine to determine diversity across different taxa and spatial and temporal scales.

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TABLES

Southeast (n = 179)

Species	Average relative energy use	COVAR	Frequency of occurrence
Quiscalus quiscula	0.28	0.06	1.00
Agelaius phoeniceus	0.26	0.06	1.00
Sturnus vulgaris	0.14	0.07	1.00
Turdus migratorius	0.10	0.07	1.00
Corvus ossifragus	0.05	0.13	0.77
Tachycineta bicolor	0.04	0.15	0.52
Quiscalus major	0.02	0.10	0.40
Corvus brachyrhynchos	0.02	0.06	0.98
Molothrus ater	0.02	0.11	0.99
Setophaga coronata	0.02	0.11	1.00

Northeast (n = 19)

Species	Average relative energy use	COVAR	Frequency of occurrence
Corvus corax	0.86	0.08	1.00
Pinicola enucleator	0.07	0.09	1.00
Acanthis flammea	0.03	0.11	1.00
Plectrophenax nivalis	0.02	0.20	0.95
Bombycilla garrulus	0.01	0.13	0.89
Coccothraustes vespertinus	< 0.01	0.33	0.89
Lanius excubitor	< 0.01	0.12	0.95
Carduelis hornemanni	< 0.01	0.15	0.79
Spizella arborea	< 0.01	0.25	0.37
Poecile hudsonicus	< 0.01	0.22	0.89

Southern plains (n =142)

Species	Average relative energy use	COVAR	Frequency of occurrence
Agelaius phoeniceus	0.30	0.06	1.00
Sturnus vulgaris	0.18	0.07	1.00
Quiscalus mexicanus	0.08	0.10	0.77
Turdus migratorius	0.08	0.08	1.00
Quiscalus quiscula	0.08	0.10	0.96
Corvus brachyrhynchos	0.07	0.13	0.92
Molothrus ater	0.03	0.09	0.95
Junco hyemalis	0.03	0.08	0.97

Bombycilla cedrorum	0.02	0.09	0.98
Zonotrichia leucophrys	0.01	0.17	1.00

Northern plains (n = 25)

Species	Average relative energy use	COVAR	Frequency of occurrence
Plectrophenax nivalis	0.37	0.10	1.00
Bombycilla garrulus	0.31	0.10	1.00
Carduelis flammea	0.07	0.10	1.00
Corvus corax	0.06	0.20	0.96
Poecile atricapillus	0.06	0.10	1.00
Cyanocitta cristata	0.03	0.11	0.88
Pinicola enucleator	0.02	0.11	0.80
Loxia leucoptera	0.01	0.17	0.80
Corvus brachyrhynchos	0.01	0.38	0.64
Loxia curvirostra	0.01	0.28	0.44

Table 1: Dominant migrant species within four geographic regions: the southeast, the northeast, the southern plains, and the northern plains. The ten species that had the greatest relative energy use across the 20% of sites with the highest proportional energy use by migrants (P_E) are listed for each region. COVAR is the coefficient of variation in relative energy use for the species across sites in the region. Frequency of occurrence is the frequency of sites that the species occurred in across the region.

FIGURES

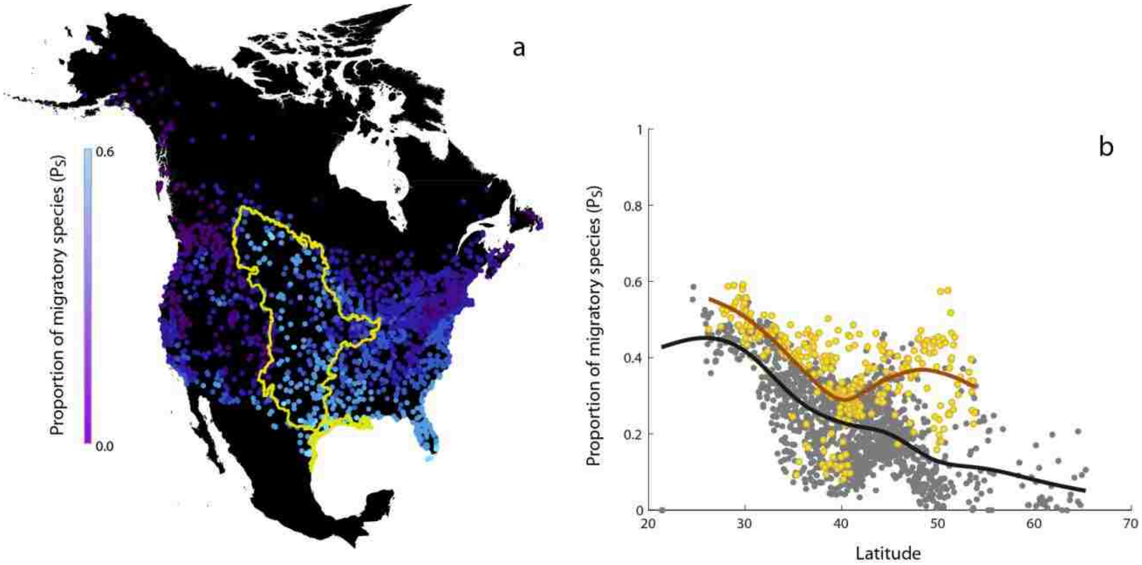

Figure 1: The proportion of migratory species (P_S) for 1814 North American winter bird communities (a) and its relationship with latitude (b). Migrants made up a substantial portion of species richness in communities throughout central grasslands (outlined in yellow), the desert southwest, gulf coast, and Florida (a). Migrants contributed little to communities in the far north or throughout mountainous regions of the west. In general, P_S declined with latitude (b; grey points with black spline), but in grassland habitats (yellow points with brown spline) was highest in communities at high as well as low latitudes. Smoothing splines fit with a smoothing parameter of 0.1.

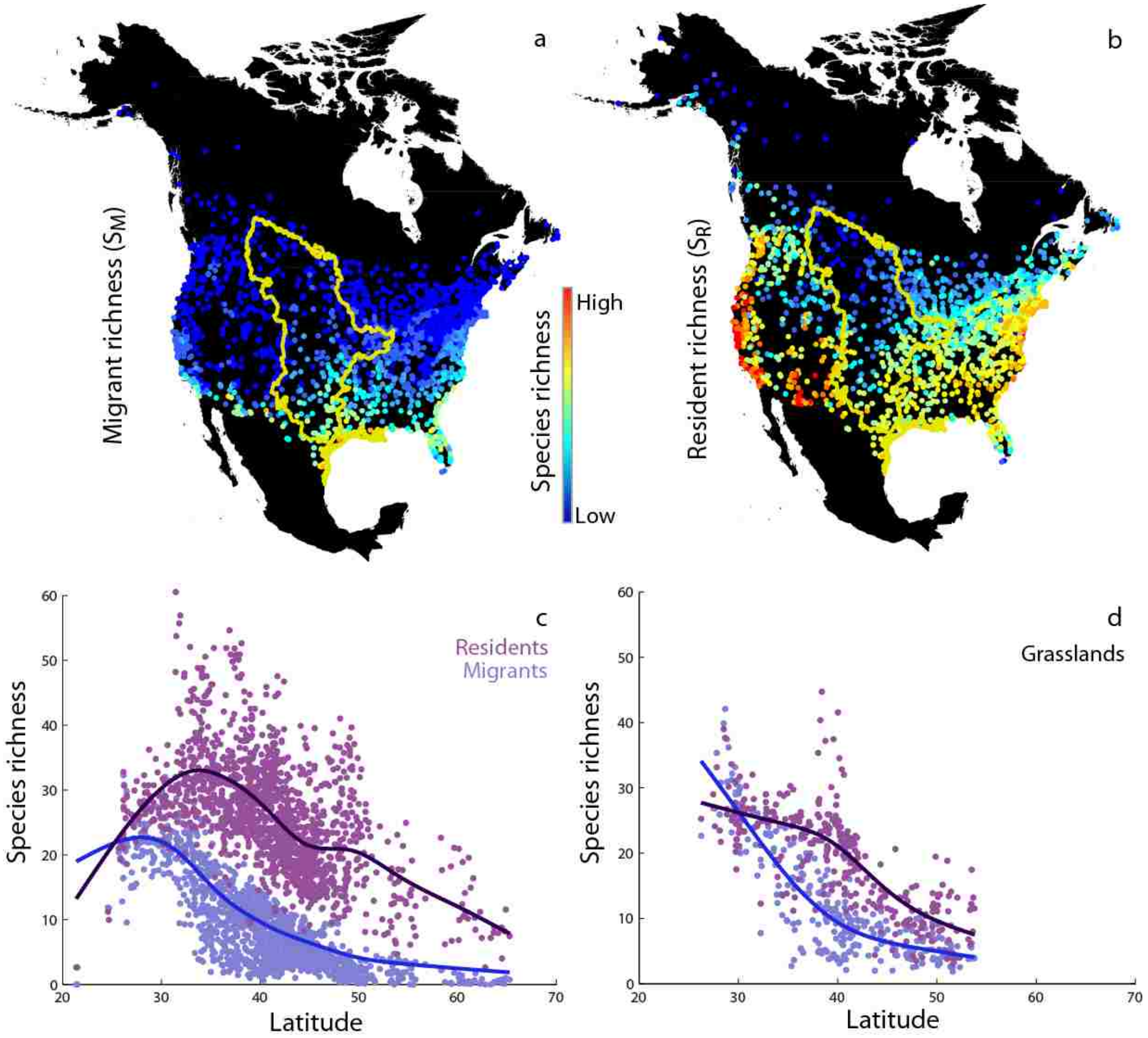

Figure 2: Species richness of migrants (S_M; a) and residents (S_R; b) in North American winter bird communities. Across the continent, migrants showed a pattern of steeply declining species richness with latitude (a, c). Residents were most diverse along the west coast of the US and in the desert southwest (b). Along both coasts, resident richness peaked at mid latitudes. Species richness of both residents and migrants declined with latitude with residents generally being more diverse (c). This difference between migrant and resident species richness was reduced across grassland habitats (on maps, outlined in yellow; d). Smoothing splines were fit with a smoothing parameter of 0.1.

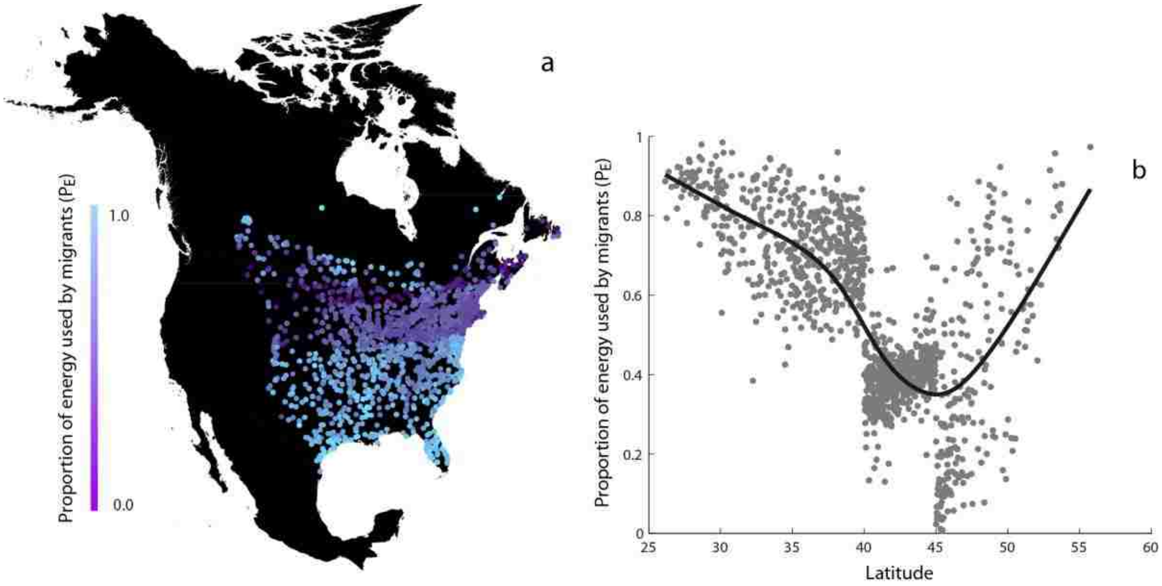

Figure 3: The proportion of energy used by migrants (P_E) in winter bird communities across North America (a) and its relationship with latitude (b). Migrants accounted for the majority of energy use throughout the southern US but also in communities in the northern Great Plains and in boreal forests (a). P_E was generally high but migrants contributed less to energy use at mid latitudes, causing P_E to have a U-shaped pattern over latitude. Smoothing spline fit with a smoothing parameter of 0.1.

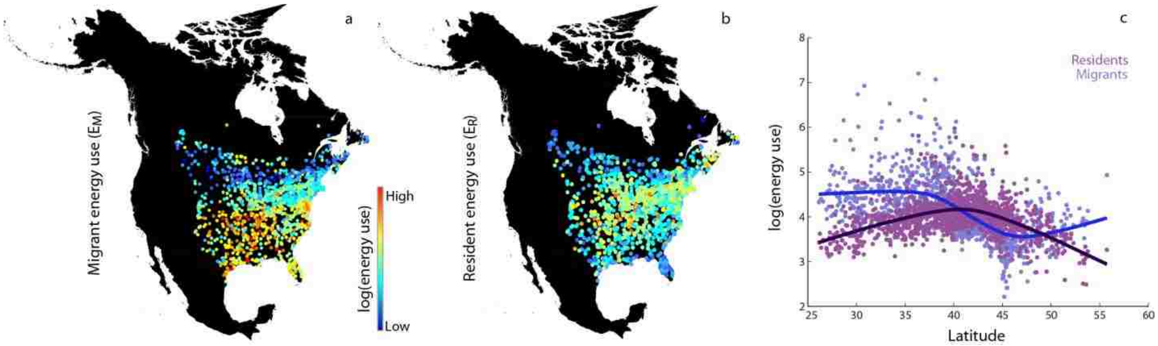

Figure 4: Energy use by migrants (E_M; a) and residents (E_R; b) in winter bird communities of North America. Resident energy peaked in communities across mid latitude, while migrant energy use showed the opposite pattern (c); peaking across the southern US and increasing again at the highest latitudes sampled. Smoothing splines fit with a smoothing parameter of 0.1.

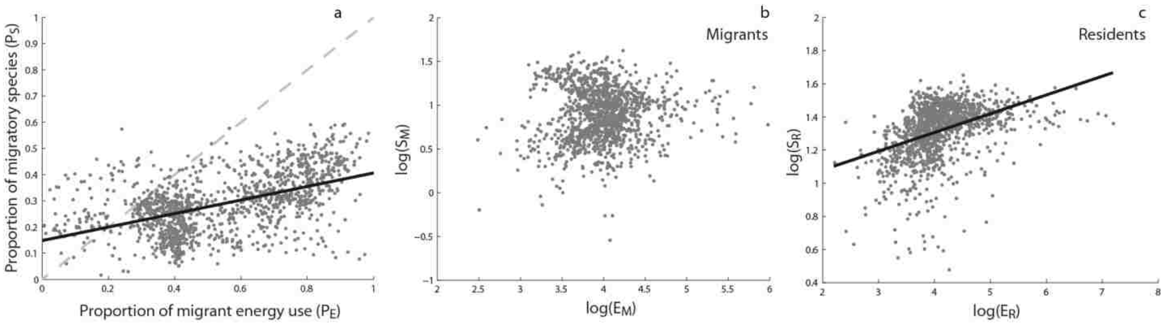

Figure 5: The relationship between proportional (a) and absolute diversity and energy use by migrant (b) and resident birds (c). There was a significant relationship between the proportion of migratory species (P_S) and the proportion of energy used by migrants (P_E) but the slope was significantly less than 1, indicating that migrants contribute disproportionately to energy use compared to species richness (a). Because migrants did not show a significant relationship between species richness (S_M) and energy use (E_M; $p = 0.11$; b), the pattern between P_S and P_E was driven by the species-energy relationship of resident birds (c). A slope of $z = 0.11$ means that species richness increases by slightly more than 10-fold as total energy use increases by 100-fold.

SUPPLEMENTAL MATERIALS:

Eastern sites	**Latitude bins (°N)**					
Species	25-30	30-35	35-40	40-45	45-50	50-55
Carolina chickadee		x	x			
Black-capped chickadee				x	x	x
Tufted titmouse	x	x	x			
Brown-headed nuthatch		x				
Carolina wren	x	x	x			
Northern cardinal	x	x	x	x		
House finch			x	x		
House sparrow	x	x	x	x		

Plains sites	**Latitude bins (°N)**					
Species	25-30	30-35	35-40	40-45	45-50	50-55
Carolina chickadee	x					
Northern cardinal	x					
House finch		x	x	x		
House sparrow	x	x	x	x	x	x

Table S1: The largely resident species used in calculating the proportion of migratory individuals (M_P) of potentially migratory species in sites of eastern portion and the central plains of North America. Largely resident species were used in calculations for a latitude bin only if they occurred in at least 80% of breeding and winter survey sites (indicated by ‘x’).

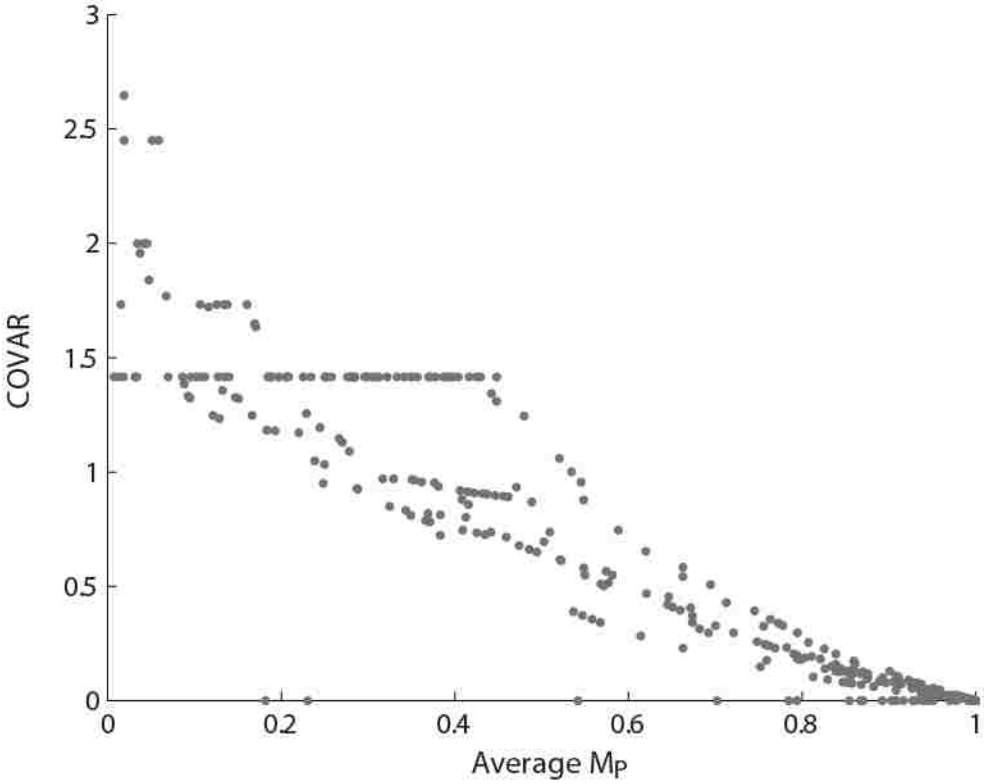

Figure S1: The coefficient of variation (COVAR) in M_P calculated by comparisons with different largely resident species against average M_P. When M_P was small, calculations varied widely, but when it was large, variation was very low.

CHAPTER 3: Metabolic heat production and thermal conductance are mass-independent adaptations to thermal environment in birds and mammals

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ABSTRACT:

The extent to which different kinds of organisms have adapted to environmental temperature regimes is central to understanding how they respond to climate change. The Scholander-Irving (S-I) model of heat transfer lays the foundation for explaining how endothermic birds and mammals maintain their high, relatively constant body temperatures in the face of wide variation in environmental temperature. S-I shows how body temperature is regulated by balancing the rates of heat production and heat loss. Both rates scale with body size, suggesting that larger animals should be better adapted to cold environments than smaller animals and *vice versa*. However, the global distributions of approximately 9000 species of terrestrial birds and mammals show that the entire range of body sizes occurs in nearly all climatic regimes. Using physiological and environmental temperature data for 211 bird and 178 mammal species, we test for mass-independent adaptive changes in two key parameters of the S-I model: basal metabolic rate and thermal conductance. We derive an axis of thermal adaptation that is independent of body size, extends the S-I model, and highlights interactions among physiological and morphological traits that allow endotherms to persist in a wide range of temperatures. Our macrophysiological and macroecological analyses support our

predictions that shifts in basal metabolic rate and thermal conductance confer important adaptations to environmental temperature in both birds and mammals.

Significance statement:

How different kinds of organisms adapt to environmental temperature is central to understanding how they respond to past, present, and future climate change. The Scholander-Irving (S-I) model predicts how rates of heat production and heat loss can be modified to maintain the relatively high, constant body temperatures of birds and mammals. We apply this model to data to assess the contributions of three avenues of adaptation, body size, basal metabolic rate, and thermal conductance, in hundreds of species. Adaptation via changes in body size is limited and the entire ranges of body sizes of birds and mammals occur in nearly all climatic regimes. Using physiological and environmental temperature data for 211 bird and 178 mammal species, we demonstrate thermal adaptation through mass-independent changes in two key parameters of the S-I model: basal metabolic rates and thermal conductance. We derive a measure of thermal adaptation that is independent of body size and measures the separate and combined contribution of the other avenues. Results of our analyses support model predictions that birds and mammals adapt to environmental temperature regimes by concerted changes in both basal metabolic rate and thermal conductance.

INTRODUCTION:

A fundamental problem in ecology and biogeography is to elucidate the physiological processes that determine the environmental tolerances and influence the distributions of species (1). Across their nearly worldwide distributions, endothermic birds and mammals maintain near-constant body temperatures in the face of extreme and fluctuating environmental temperatures. Revealing the morphological and physiological adaptations that allow species to inhabit such a wide spectrum of thermal environments is important for understanding the distribution of biodiversity and predicting responses of species to climate change (2, 3).

In a seminal paper, Scholander et al. (4) showed how endotherms balance rates of heat production and heat loss so as to maintain a constant body temperature in the face of varying environmental temperatures. The essence of their model (S-I model) is the equation:

$$T_b - T_a = B/C$$

where T_b is body temperature, T_a is ambient temperature, B is the rate of metabolic heat production, and C the rate of heat loss or thermal conductance (5). For a resting animal which has minimized heat loss by maximizing insulation and optimizing body posture, $C = C_{MIN}$, B = basal metabolic rate (BMR), and $T_a = T_{lc}$, where T_{lc} is the lower critical temperature or the lower limit of the thermal neutral zone (TNZ). The TNZ is ecologically important because it is the range of environmental temperatures where energy expenditure is minimal; outside of the TNZ an organism must expend additional energy on thermoregulation to maintain homeostasis (6). Here we focus on adaptive responses to varying degrees of cold stress that shift the lower limit of the thermal neutral zone, where the S-I model makes straightforward predictions. Endotherms can theoretically modify T_{lc} by changes in BMR, C_{MIN}, or both (Fig. 1 b and c).

The situation is complicated, however, because BMR and C_{MIN} scale predictably with body size in birds and mammals (Fig. 2). Rates of both heat production and heat loss are higher in larger than in smaller animals (*7*), but *BMR* increases with mass more rapidly than C_{MIN}, so larger organisms are predicted to have a higher ratio of BMR/C_{MIN}, a lower T_{lc}, and be better able to tolerate colder temperatures than smaller organisms (8). This logic underpins Bergmann's hypothesis to explain geographic variation in body size within closely related taxa of mammals and birds (9). In the colder environments at high latitudes and elevations, natural selection should favor larger individuals because they expend relatively less energy on thermoregulation. This prediction is generally supported by the examples of intraspecific variation in body size consistent with Bergmann's rule that have been documented in many, but by no means all kinds of mammals and birds (10, 11).

If body size is the predominant means of thermal adaptation, however, it would be predicted that only large-bodied species inhabit the coldest environments and only small bodied species occur in the hottest environments. This is not the case as shown by compiling and analyzing data on the geographic ranges of 6714 species of birds and 2649 species of mammals (Fig. 3). In mammals, the smallest-bodied species (2.3 – 10 g) occur across the entire breadth of environmental temperatures, and – contrary to prediction – the largest species (100 – 325 kg) occur only in relatively warm temperatures (5 - 35°C; Fig. 3a). In birds, the smallest body sizes (1.9 – 10 g) support the prediction, because they are missing from the coldest environments (-35 - -5°C; Fig. 3b). Contrary to prediction and similar to mammals, however, the largest bird species (10 – 111 kg) occur only in environments with temperatures ranging from moderate to the hottest (5 – 45°C). These patterns support previous studies suggesting that adaptive shifts in body size are not a major avenue of climatic adaptation in birds and mammals, except perhaps at the species level (12, 13).

Theory: extensions of the S-I model

The S-I model straightforwardly predicts adaptations to environmental temperature regimes that are independent of body size (5, 14). In colder environments, birds and mammals are predicted to have higher *BMR* and lower C_{MIN}, or perhaps some combination of these. Such adaptations should explain some of the considerable variation around the allometric relationships in figure 2. For any species, the variation in these traits independent of body size can be measured statistically as the residuals orthogonal to the body size axis (*log(BMR) residuals* or $log(C_{MIN})$ *residuals*). A species that falls above the regression lines in figure 2a or 2c has a relatively higher BMR for its size (*log(BMR) residuals* > *0*) and should therefore be better adapted to colder temperatures (i.e., more cold-tolerant). Conversely, species below the line (*log(BMR) residuals* < *0*) should be adapted to warmer temperatures (i.e., more hot-tolerant). The opposite is true in the case of C_{MIN}; species below the regression lines in figure 2b or 2d have lower rates of heat loss than similarly sized species ($log(C_{MIN})$ *residuals* < *0*) and should be better able to tolerate colder temperatures and vice versa for species above the line ($log(C_{MIN})$ *residuals* > *0*). The magnitude of thermal adaptation depends not only on *BMR* or C_{MIN} alone, but on how the two traits change relative to one another (14, 15). For example, a species with both a higher *BMR* and lower C_{MIN} than expected for its body size should be especially well cold-adapted, whereas a species with a higher *BMR* and higher C_{MIN} than expected might be no more cold-tolerant than an average species of the same size. Deviations in both *BMR* and C_{MIN} can be combined into a single quantitative measure of **mass independent thermal adaptation (*A*)**:

$$A = log(C_{MIN})\ residuals - log(BMR)\ residuals$$

According to this parameterization, species with $A > 0$ should be adapted to warmer temperatures than expected for their body size (i.e., hot-tolerant) and species with $A < 0$ should be better adapted to colder temperatures (i.e., cold-tolerant). This is illustrated in the conceptual diagram in figure 4a.

Because changes to *BMR* or C_{MIN} may not contribute equally to mass-independent thermal adaptation, we have constructed an index of avenues of adaptation (*I*) to the thermal environment to quantify the relative contribution of either the residuals of $log(C_{MIN})$ or *log(BMR)* to the value of *A*. When the magnitude of *A* is due entirely to changes in C_{MIN}, $I = 1$ ($log(C_{MIN})$ *residuals* contribute 100% to $|A|$; *log(BMR) residuals* reduce or contribute 0% to $|A|$). On the other hand, when the residuals of *log(BMR)* solely contribute to the magnitude of *A*, $I = 0$ ($log(C_{MIN})$ *residuals* decrease or contribute 0% to $|A|$; *log(BMR) residuals* contribute 100% to $|A|$). These situations may represent compromising selective pressures on traits affecting rates of heat production and heat loss due to factors not related directly to the thermal environment. An example would be lower conductance in colder environments to compensate for a BMR that is also lower due to adaptation to low environmental productivity and food supply (16, 17). When changes to both C_{MIN} and *BMR* contribute to the magnitude of *A*, then *I* is calculated as:

$$I = (log(C_{MIN})\ residuals)/A$$

In these cases, the contributions of $log(C_{MIN})$ or $log(BMR)$ residuals may not be equal, and I will fall somewhere between 0 and 1. The value of I can be depicted as the position of a species in the thermal adaptation space represented in figure 4b.

The above theoretical framework based on the S-I model makes several testable predictions:

1) If body size is an important mechanism of thermal adaptation across species, larger species of birds and mammals should occur in colder environments and vice versa for warmer environments. Previous studies and our analyses of geographic distributions (Fig. 3) generally do not support this prediction.

2) Species have responded to thermal environments independently of body size through shifting BMR, C_{MIN}, or both (Fig. 2b).

3) Combining shifts in BMR and C_{MIN} into a single measure of variation should provide additional evidence for the importance of these two mechanisms, singly and in combination together. The overall magnitude of mass-independent thermal adaptation, A, is predicted to be significantly correlated with variation in environmental temperature.

Empirical evidence

We used published data on the thermal physiology of 211 species of birds and 178 species of mammals and environmental temperatures to evaluate the theoretical framework outlined above and test its predictions. Our objectives were: first, to quantify which body size independent avenues of adaptation, changes in BMR, C_{MIN}, or both, are more common and whether these adaptations are phylogenetically conserved; and second, to test whether the magnitudes of mass-independent shifts in these variables correspond to the thermal environments of the species, thereby reflecting physiological adaptations.

I) Avenues of adaptation (*I*) in hot and cold tolerant species:

For hot-tolerant mammals ($A > 0$), low *BMR* was the most common avenue of adaptation (Fig. 5a). However, the distribution of species across the four categories was not significantly different from random (C_{MIN} only: 24 species; primarily C_{MIN}: 22 species; primarily *BMR*: 18 species; *BMR* only: 30 species; $p = 0.36$). In cold-tolerant mammals ($A < 0$), there were significantly more species with low C_{MIN} than any other avenues of adaptation (C_{MIN} only: 33 species; primarily C_{MIN}: 13 species; primarily *BMR*: 14 species; *BMR* only: 24 species; $p = 0.005$). Few species of cold-tolerant mammals had low C_{MIN} combined with high *BMR*.

Low *BMR* was also the most common pattern of residuals exhibited by hot-tolerant birds (Fig. 5b; C_{MIN} only: 33 species; primarily C_{MIN}: 18 species; primarily *BMR*: 16 species; *BMR* only: 41 species; $p = 0.001$). Few species of hot-tolerant birds showed both low *BMR* as well as high C_{MIN}. In cold-tolerant birds, most species showed shifts in both variables. Positive residuals of $log(BMR)$ were generally greater than negative residuals of $log(C_{MIN})$, although the distribution of species across categories was not significantly different from random (C_{MIN} only: 19 species; primarily C_{MIN}: 24 species; primarily *BMR*: 32 species; *BMR* only: 29 species; $p = 0.29$).

There was little evidence of an influence of phylogenetic relatedness on our index of avenue of adaptation. Blomberg's K calculated for *I* was not significantly different from 1 in either mammals or birds (mammals: $K = 0.16$, $p = 0.28$; birds: $K = 0.01$, $p = 0.81$; see Fig. S1 for the phylogenetic distribution of *I*).

II) Thermal adaptation (*A*) vs. environmental temperature:

In both birds and mammals, our measure of mass-independent thermal adaptation (A) was significantly correlated with maximum and minimum environmental temperatures (Fig. 6; Table 1). In birds, values of *A* were more strongly correlated with maximum than minimum temperature (max: $R^2 = 0.18$, $p << 0.001$; min: $R^2 = 0.13$, $p << 0.001$) while the opposite was true for mammals (max: $R^2 = 0.12$, $p << 0.001$; min: $R^2 = 0.14$, $p << 0.001$). These results remained unchanged when using PGLS analyses to account for phylogenetic relationships among species, except in the case of the relationship between *A* and minimum environmental temperature in mammals, which was no longer significant (Table 1).

Discussion

Despite the large effect of body size on thermal physiology, size alone only modestly influences the range of environmental temperature regimes where a species can occur. Nearly the full spectrum of mammalian body sizes occurs across the entire range of environmental temperatures in terrestrial regions on Earth. The exceptions are the very largest mammals, which contrary to predictions based on the relationship between body size and thermal physiology (8, 9), occur only in relatively warm environments. It is possible that the current distributions of the largest-bodied mammals and their absence from cold environments are the result of large-size bias in human-caused extinctions of megafauna outside of Africa (18, 19). In the case of birds, the smallest species do not occur in the coldest environments. Burrowing and hibernation, which allow small mammals to escape extreme temperatures in cold environments, are rare in birds (20, 21). As in mammals, the largest birds occur only in moderately warm to very hot environments. Considering that body size affects many other ecologically relevant traits in addition to thermal physiology (7, 22–24), it is not surprising that body size alone cannot account for all thermal adaptations.

In contrast to the patterns in body size, our data and analyses for variation in both BMR and thermal conductance in both birds and mammals provide strong evidence that these are important mechanisms of adaptation to environmental temperature. The empirical patterns of residual variation orthogonal to the body size axis in these two measures of thermal performance support theoretical predictions based on the S-I model. The overall magnitude of mass-independent thermal adaptation (A) in both birds and mammals varies with environmental temperatures as predicted. In birds, maximum environmental temperatures were the best predictor of A, explaining nearly 20% of variation. Before accounting for phylogeny in mammals, minimum temperatures best explained variation in A. This difference between birds and mammals, as well as the stronger correlation between A and environmental temperature in birds may reflect differences in lifestyle. For example, a large proportion of mammals are nocturnal, burrowing, and hibernators; attributes that tend to reduce exposure to extreme temperatures. This interpretation is consistent with results found by Khaliq et al., 2014 (2). In both birds and mammals, adaptive body-size independent changes to *BMR* and thermal conductance in combination with additional behavioral and physiological traits allow species to occur in a wide range of thermal environments.

The present analysis focuses on how shifts in *BMR* and C_{MIN} confer thermal adaptations by affecting the lower limit of the thermal neutral zone. Our results show that different species of birds and mammals use multiple avenues of adaptation to respond to similar thermal environments. Certain avenues were more common than others, however: cold-tolerant mammals used low C_{MIN} most frequently, and hot-tolerant birds used low *BMR* as the primary avenue. Lack of phylogenetic signal for *I*, our index of the relative contribution of C_{MIN} and *BMR*, implies that closely related species do not rely on one particular avenue of adaptation. We caution that our focus on C_{MIN} and *BMR* directly addresses adaptation to only the cold end of the spectrum of thermal environments experienced by these species. Physiological responses to cold stress may be complicated by tradeoffs in responses to other biological constraints and environmental conditions. For example, birds use feathers for both insulation and flight, so changes that affect conductance may compromise flight and vice versa (25). Adaptations may also reflect the range of environmental temperatures encountered by a species over its geographic range and over diel and seasonal cycles. The extreme environmental temperatures, both cold and warm, actually experienced may be modified by physiological and behavioral adjustments such as hibernation, estivation, torpor, migration, and microclimate selection. Additionally, whereas responses of endotherms to cold stress usually primarily involve changes in insulation and metabolic rate which are reflected relatively straightforwardly in C_{MIN} and *BMR*, responses to heat stress are more complicated and may also include changes in body temperature and evaporative water loss. So, although it may seem surprising that so few species change both C_{MIN} and *BMR* in ways predicted by our adaptive hypotheses, these traits may be under a variety of sometimes conflicting selective pressures, some with offsetting effects directly on heat exchange and thermoregulation, and some reflecting other selective pressures on metabolism, integumentary and vascular systems, life history, behavior, and ecology (17, 26, 27).

Our results build on the Scholander-Irving model of heat transfer by developing theoretically and testing empirically avenues of thermal adaptation independent of body size. This approach highlights the complex interactions among physiological and morphological traits that allow endotherms to persist in a wide range of thermal regimes. Many aspects of structure and function, anatomy, physiology, ecology, and behavior are highly constrained by allometric scaling relationships and consequently vary predictably with body size. For this reason, it is easy to understand why mass-independent variations in *BMR* and C_{MIN} are important avenues of adaptation to environmental temperature regimes, which vary widely and predictably over the geographic ranges of birds and mammals. Understanding the interactive effects of body size and other morphological, physiological, and behavioral traits on thermal tolerances and performances will be an important step in predicting how birds and mammals respond to past, present, and future climate change.

Materials and Methods

Body size distributions

We calculated the average minimum and maximum terrestrial temperatures from across the ranges of species for which we had both data on mass and GIS shapefiles of geographic ranges (6714 birds and 2649 mammals). Mammal masses are from the PanTHERIA database (28) and bird masses are from Dunning, 2007 (29). Geographic range data for mammals are from the IUCN (30) while those for birds are from Birdlife International (31). For mammals and all non-migratory bird species minimum and maximum temperatures are the average of the minimum or maximum temperatures of the coldest or warmest months, respectively, from throughout the geographic range (32). For migratory bird species, we calculated temperatures based on when they are likely to occur in different portions of their range. For each species we calculated the following: the average minimum and maximum summer temperatures (from June and July for Northern hemisphere breeders, from December and January for Southern hemisphere breeders) from throughout the breeding portion of the range; the average minimum and maximum winter temperatures (December and January for Northern Hemisphere breeders, June and July for Southern hemisphere breeders) from throughout the winter portions of the species range; the average minimum and maximum temperatures from portions of the range where the species occurs as a year-round resident as explained above for non-migratory species. We used the minimum and maximum of these temperatures as the limits of the species' environmental temperature range. Using these values, we plotted frequency distributions of body sizes within each 10°C bin from -35°C to 45°C. A species was included in any temperature bin with which its range of environmental temperatures overlapped.

Thermal adaptation (A) and avenues of adaptation (I)

To calculate A and I, we used the residuals of $log(C_{MIN})$ and $log(BMR)$ from allometric relationships with body size for 211 birds and 178 mammals (see table S1 for data and sources). C_{MIN} was calculated as the slope of the line connecting T_{lc} at BMR to T_b when metabolic rate is zero (*32;* see Fig. S2). Using all species for which we had data on thermal physiology, we found the relationship between C_{MIN} to follow the form:

$$\log10\ (C_{MIN}) = 0.511*\log10\ (\text{Mass}) - 0.091$$

in birds and:

$$\log10\ (C_{MIN}) = 0.569*\log10\ (\text{Mass}) - 0.050$$

in mammals. Because more data is available on BMR than C_{MIN} we calculated residuals from known scaling relationships:

$$\log10\ (BMR) = 0.652*\log10\ (\text{Mass}) + 0.145$$

for birds (34) and:

$$\log10(BMR) = 0.725*\log10\ (\text{Mass}) + 0.540$$

for mammals (calculated from PanTHERIA data (28)).

Residuals of $log(C_{MIN})$ were plotted against the residuals of $log(BMR)$ following the model in figure 4. In addition to calculating I, each species was assigned to one of eight categories reflecting where it occurred within the thermal adaptation space: (i) hot adapted via increases to C_{MIN} only; (ii) hot adapted via increasing C_{MIN} to a greater extent than decreasing BMR; (iii) hot adapted via decreasing BMR to a greater extent than increasing C_{MIN}; (iv) hot adapted via decreases to BMR only; (v) cold adapted via increases to BMR only; (vi) cold adapted via increasing BMR to a greater extent than decreasing C_{MIN}; (vii) cold adapted via decreasing C_{MIN} to a greater extent than increasing BMR; or (viii) cold adapted via decreases to C_{MIN} only (Fig. 4b). To determine if any avenue of adaptation was more common than expected by random, we performed Chi-square tests separately for cold-tolerant mammals (i.e. $A < 0$), hot-tolerant mammals (i.e. $A > 0$), cold-tolerant birds, and hot-tolerant birds.

In order to determine if I is constrained by phylogeny, we used Blomberg's K which indicates the amount of phylogenetic relatedness in the tip data relative to expected (K = 1) for a trait under a Brownian mode of evolution. The significance of K was assessed by comparing the variance of independent contrast for 1000 randomized trees with that of the observed tree using the “phylosignal” function in R package picante (35).

We used OLS regression to test for a relationship between calculated values of *A* with maximum and minimum environmental temperatures. Species’ environmental temperatures were the same values calculated as outlined above for body size distributions. Because we used only terrestrial environments when calculating temperatures, we excluded species of birds whose ranges were primarily pelagic (orders Procellariiformes and Sphenisciformes as well as families Laridae and Alcidae). Bats (order Chiroptera), differing markedly from other mammals in lifestyle, and likely in how they experience the thermal environment, were also excluded from this analysis. A positive relationship between *A* and environmental temperature would indicate a match between mass-independent thermal adaptation and thermal environment. However, comparative analysis involving many species, are complicated due to the evolutionary relatedness and non-independence of species (36). To account for this, we used Phylogenetic General Least Squares (PGLS) to estimate the level of phylogenetic dependence in the regression residuals and weighing for this in generalized least squared regression calculations.

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TABLES

Mammals

	Environmental Temperature	Slope	R2	p	Lambda
OLS:	Minimum	0.0079	0.1444	<< 0.001	-
	Maximum	0.0179	0.1206	<< 0.001	-
PGLS:	Minimum	0.00026	0.0077	0.15	0.77
	Maximum	0.013	0.085	<< 0.001	0.69

Birds

	Environmental Temperature	Slope	R2	p	Lambda
OLS:	Minimum	0.0048	0.13	<< 0.001	-
	Maximum	0.012	0.18	<< 0.001	-
PGLS:	Minimum	0.0037	0.07	<< 0.001	0.45
	Maximum	0.01	0.16	<< 0.001	0.37

Table 1: Results for regression analyses comparing mass-independent thermal adaptation (*A*) and environmental temperatures in mammals and birds. In mammals, minimum temperatures explained more variation in *A* while the opposite was true for birds. When using PGLS to account for the relatedness of species, the relationship between *A* and minimum environmental temperature in mammals was no longer significant.

FIGURES

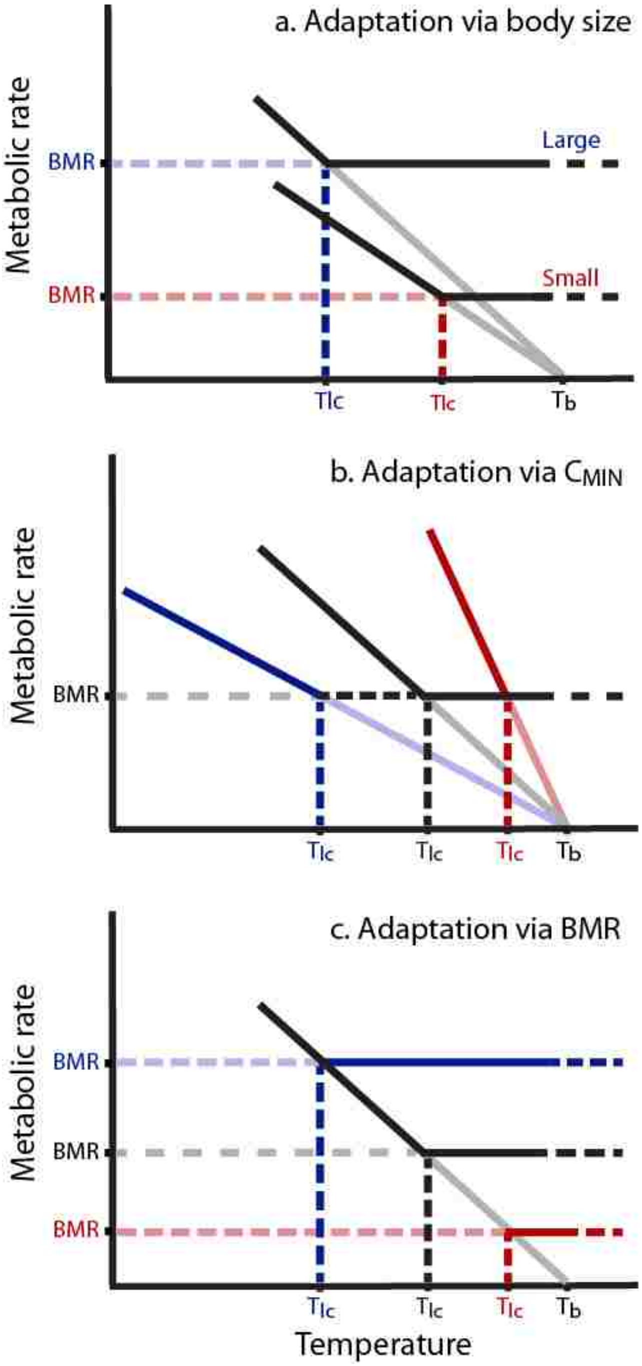


Figure 1: Conceptual diagram showing how body size (a), thermal conductance (C_{MIN}; b), and basal metabolic rate (*BMR*; c) effect the lower limit of the thermal neutral zone (T_{lc}). Blue indicates adaptations to cold and red indicates adaptations to hot temperatures. In panels b and c, black represents a species without mass-independent thermal adaptation.

Because heat production (*BMR*) increases more rapidly with body size than heat loss (C_{MIN}), larger species should be better able to tolerate colder temperatures than smaller species (a). T_{lc} can also be altered by body size-independent changes to *BMR* or C_{MIN}. Species with C_{MIN} lower than expected for their body size should be able to tolerate colder temperatures and *vice versa*. The opposite is true in the case of *BMR*: species with higher *BMR* will tolerate colder temperature and species with lower *BMR* will tolerate hotter temperatures.

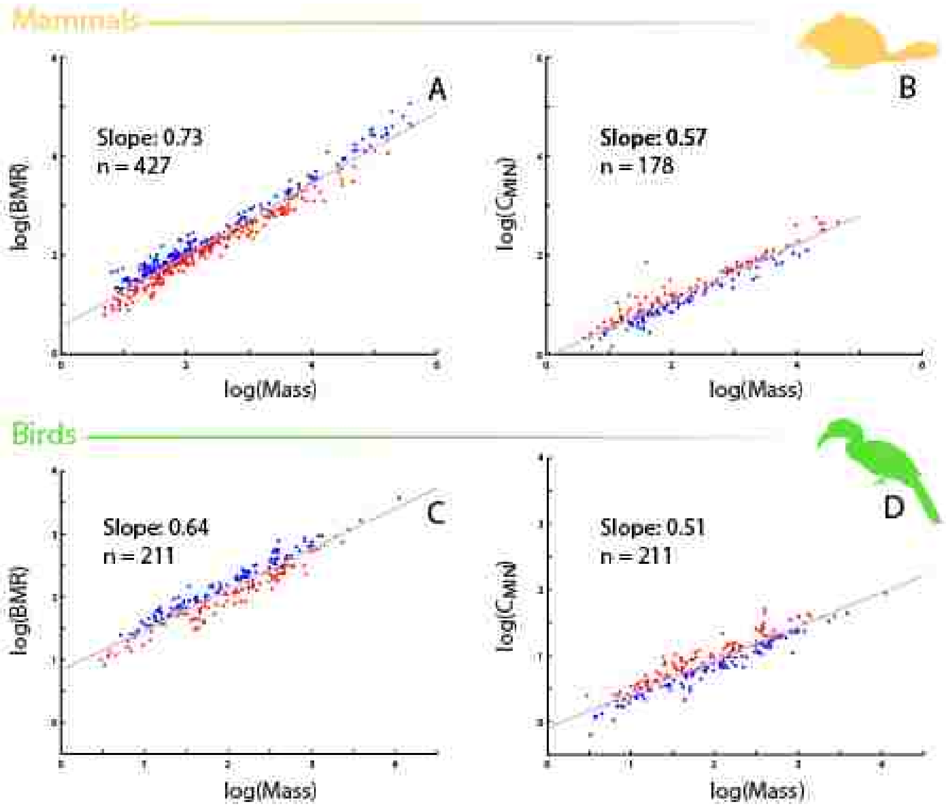


Figure 2: Allometric relationships of basal metabolic rate (*BMR*) and minimum thermal conductance (C_{MIN}) with body size in mammals and birds. In both groups, *BMR* (mammals (a) N = 427; birds (c) N = 211) and C_{MIN} (mammals (b); birds (d)) increase with body size. However, because *BMR* increases with mass more rapidly than C_{MIN} (mammals: *BMR* slope = 0.73, C_{MIN} slope = 0.57; birds: *BMR* slope = 0.64, C_{MIN} slope = 0.51), larger organisms have a higher ratio of BMR/C_{MIN} and therefore are able to tolerate colder temperatures compared to smaller organisms. Species plotted in red have a *BMR* or C_{MIN} that provides increased heat tolerance compared to similarly sized species while those in blue are more cold tolerant. *BMR* data for mammals are from the Pantheria dataset (28); C_{MIN} for mammals and data for birds are from the present study.

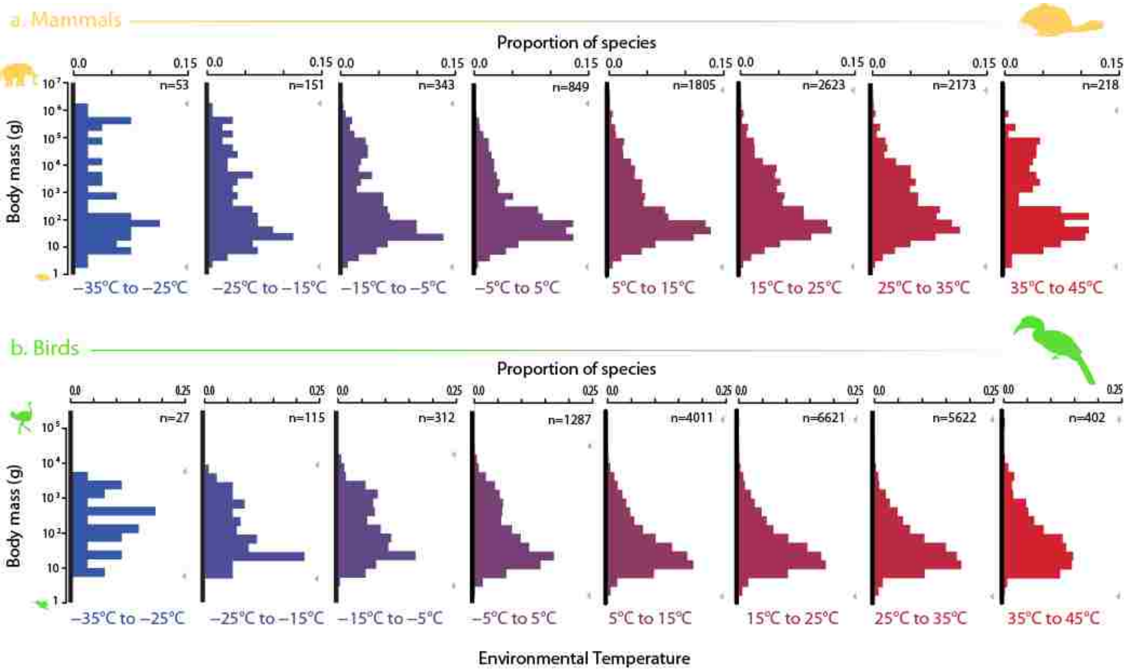
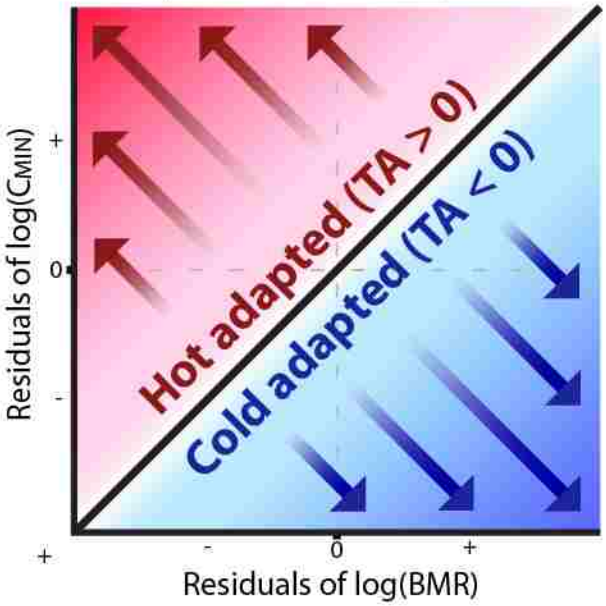
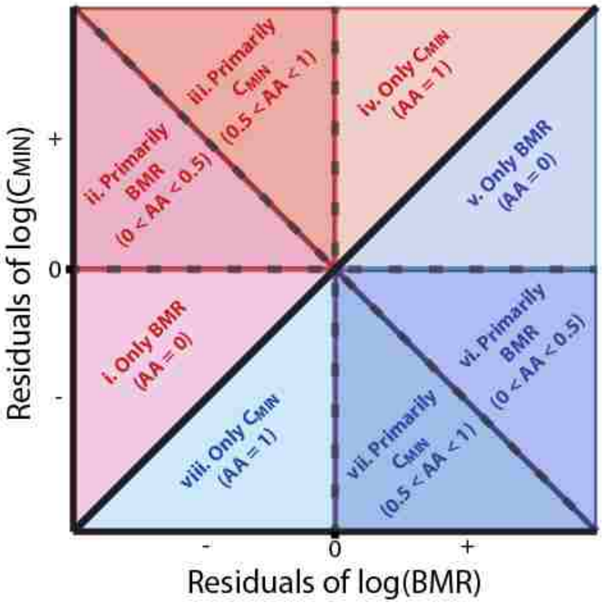


Figure 3: Body size distributions for mammals (a) and birds (b) across terrestrial environmental temperatures (coldest temperatures in blue; hottest temperatures in red). Maximum and minimum body sizes within each temperature bin are indicated by gray arrows. In mammals, the smallest species are present throughout temperature regimes, while the largest species occur only in relatively warm climates (5-35°C). The smallest birds do not occur in the coldest climates (-35-5°C); the largest species occur only in moderately warm or the hottest environments (5-45°C).



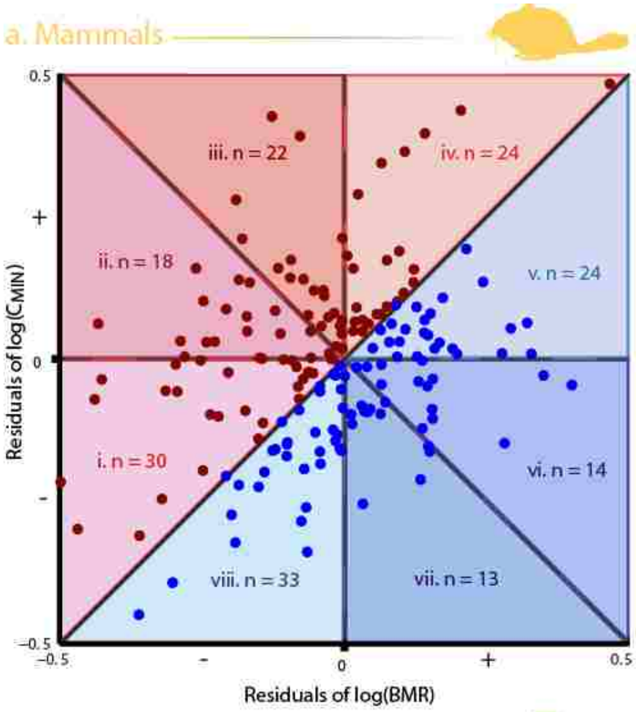
a. Mass-independant thermal adaptation (A)



b. Avenue of adaptation (I)

Figure 4: Conceptual diagrams outlining mass-independent thermal adaptation (*A*) and our index of avenue of adaptation (*I*). When comparing the residuals from the relationships of *log(BMR)* and $log(C_{MIN})$ with log(body size), any species falling on the one-to-one line (in black; *A* = 0) would have a thermal tolerance as expected for their body size (a). Species which fall below the line (area in blue; *A* < 0) should be cold

adapted for their body size and those above the line (area in red; $A > 0$) will be able to tolerate hotter temperatures (a). The relative importance of BMR compared to C_{MIN} in determining A is depicted by a species' position in (b) and corresponds to the value of I. A species can be (i) hot adapted via increases to C_{MIN} only ($I = 1$); (ii) hot adapted via increasing C_{MIN} to a greater extent than decreasing BMR ($0.5 < I < 1$); (iii) hot adapted via decreasing BMR to a greater extent than increasing C_{MIN} ($0 < I < 0.5$); (iv) hot adapted via decreases to BMR only ($I = 0$); (v) cold adapted via increases to BMR only ($I = 0$); (vi) cold adapted via increasing BMR to a greater extent than decreasing C_{MIN} ($0 < I < 0.5$); (vii) cold adapted via decreasing C_{MIN} to a greater extent than increasing BMR ($0.5 < I < 1$); or (viii) cold adapted via decreases to C_{MIN} only ($I = 1$).



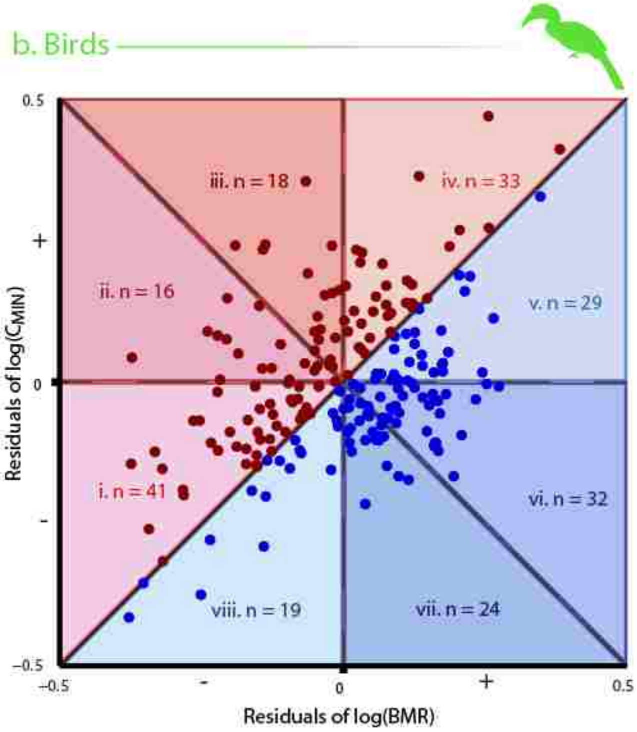


Figure 5: Plotting the residuals of the relationships between basal metabolic rate (*BMR*) and minimum thermal conductance (C_{MIN}) with body size, as outlined in figure 4b, reveals the mass-independent thermal adaptation (*A*) and avenues of adaptation (*I*) for

178 mammals (a) and 211 birds (b). Species that are cold tolerant for their body sizes ($A < 0$) are plotted in blue; those that are hot tolerant ($A > 0$) are plotted in red. In cold adapted mammals, changes to C_{MIN} only (area viii; $I = 1$) were the most common avenue of adaptation ($p = 0.005$). In hot adapted birds, changes to *BMR* alone (area iv; $I = 0$) were the most common avenue of adaptation ($p = 0.001$). In the remaining groups, the distribution of species across categories was not significantly different from random (hot adapted mammals: $p = 0.36$; cold adapted birds: $p = 0.29$). Naked mole-rat (*Heterocephalus glaber*; *BMR* residuals = -0.36; C_{MIN} residuals = 1.00) was excluded from (a) in order to maintain a similar scale and ease of comparison with (b).

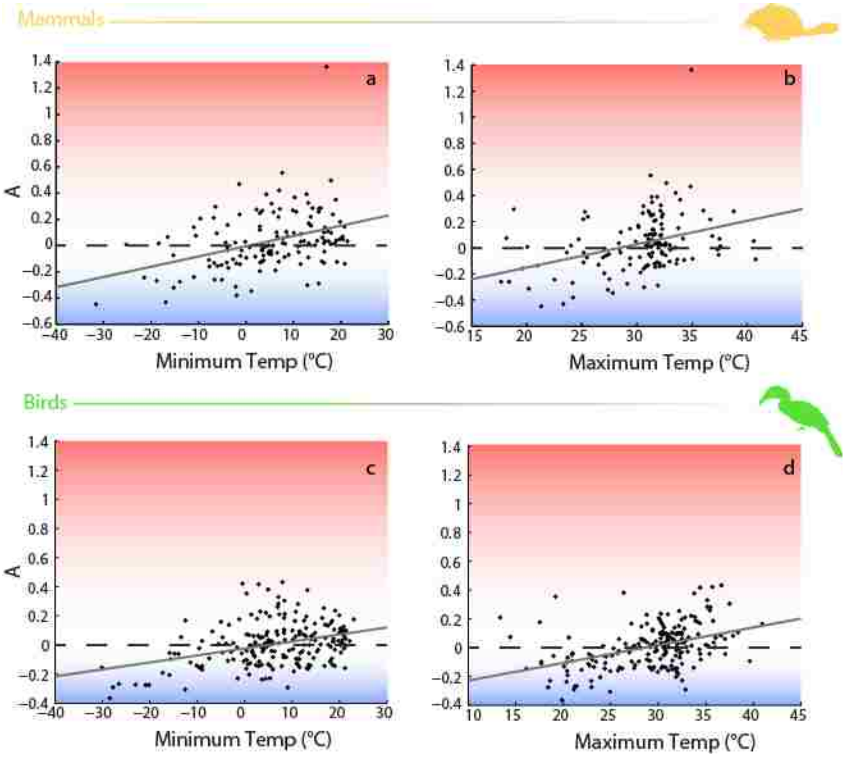


Figure 6: The relationship from OLS regression between mass-independent thermal adaptation (*A*) with environmental temperature in mammals (a and b; excluding Chiroptera, n = 139) and birds (c and d; n = 211). In mammals, minimum environmental temperatures explained more of the variation in *A* than maximum environmental temperature (min (a): $R^2 = 0.14$, $p << 0.001$; max (b): $R^2 = 0.12$, $p << 0.001$). In birds, the opposite was true (min (c): $R^2 = 0.13$, $p << 0.001$; max (d): $R^2 = 0.18$, $p << 0.001$).

SUPPLEMENTAL MATERIALS

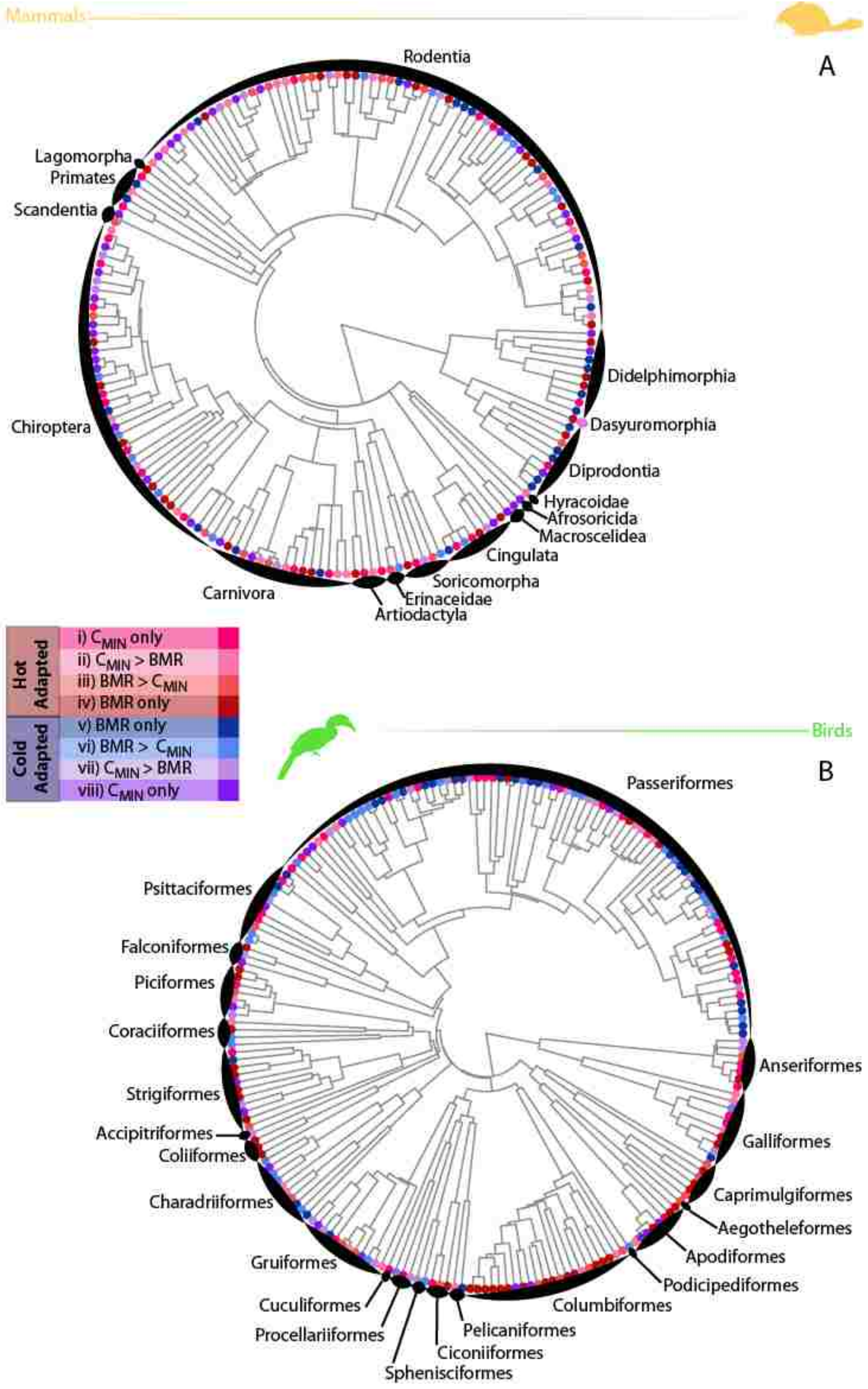


Figure S1: The phylogenetic distribution of various avenues to mass-independent thermal adaptation ((i) hot adapted via increases to C_{MIN} only; (ii) hot adapted via increasing thermal conductance ($C_{MIN)}$ to a greater extent than decreasing basal metabolic rate (BMR); (iii) hot adapted via decreasing BMR to a greater extent than increasing C_{MIN}; (iv) hot adapted via decreases to BMR only; (v) cold adapted via increases to BMR only; (vi) cold adapted via increasing BMR to a greater extent than decreasing C_{MIN}; (vii) cold adapted via decreasing C_{MIN} to a greater extent than increasing BMR; or (viii) cold adapted via decreases to C_{MIN} only) across mammals (A) and birds (B). The avenue of adaptation used by each species is reflected in its position in figure 5a or b. There was little evidence of an effect of phylogenetic relatedness on our index of avenue of adaptation (mammals: $K = 0.16$, $p = 0.28$; birds: $K = 0.01$, $p = 0.81$).

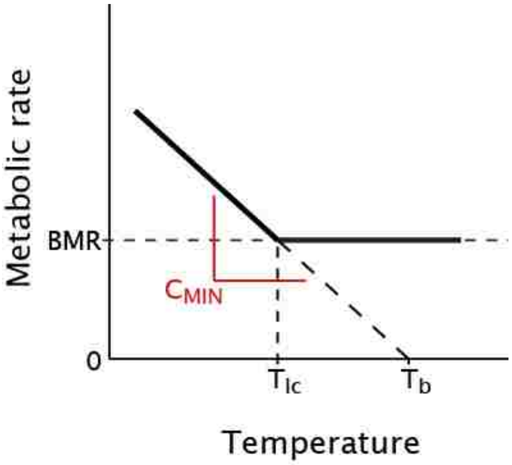


Figure S2: Conceptual diagram illustrating our calculation of minimal thermal conductance (C_{MIN}). For each species, we used the slope of the line connecting thermal lower critical temperature (T_{lc}) at basal metabolic rate (BMR) to body temperature (T_b) when metabolic rate is zero.

Table S1. Physiological data for mammal and bird species used. References are for body temperatures (T_b) and basal metabolic rates (BMR). Measures of mass-independent thermal adaptation (A) and index of avenues of adaptation (I) were calculated as outlined in the methods section.

Mammals

Species	Family	Order	Tb (°C)	BMR (mlO2/g *hour)	A	I	References
Setifer setosus	Tenrecidae	Afrosoricida	32.2	122.4	0.39	0.00	(1)
Philantomba monticola	Bovidae	Artiodactyla	39.1	1806.0	0.00	1.00	(2)
Raphicerus campestris	Bovidae	Artiodactyla	39	3696.0	0.25	1.00	(2)
Pecari tajacu	Tayassuidae	Artiodactyla	38	5800.0	0.26	1.00	(3)
Tragulus javanicus	Tragulidae	Artiodactyla	38.4	872.1	0.02	1.00	(4)
Canis latrans	Canidae	Carnivora	36	2700.0	0.07	0.88	(5)
Vulpes macrotis	Canidae	Carnivora	38	1143.2	-0.11	0.00	(5)
Vulpes zerda	Canidae	Carnivora	32	23.5	-0.09	1.00	(6)
Cerdocyon thous	Canidae	Carnivora	38.6	1497.1	0.04	0.00	(7)
Fossa fossana	Eupleridae	Carnivora	37.9	906.3	0.04	0.61	(8)
Suricata suricatta	Herpestidae	Carnivora	36.3	310.3	0.25	0.30	(9)
Galerella sanguinea	Herpestidae	Carnivora	38.7	410.4	-0.09	0.00	(10)
Spilogale putorius	Mephitidae	Carnivora	36.5	312.0	0.21	0.66	(11)
Eira barbara	Mustelidae	Carnivora	38.4	1221.3	0.04	1.00	(8)
Martes americana	Mustelidae	Carnivora	37	594.9	0.01	1.00	(12)
Ailurus fulgens	Ursidae	Carnivora	37.6	878.2	0.07	0.00	(13)
Genetta tigrina	Viverridae	Carnivora	38.5	747.1	0.00	1.00	(14)
Arctictis binturong	Viverridae	Carnivora	36	1128.1	0.28	0.00	(8)
Paradoxurus hermaphroditus	Viverridae	Carnivora	36.5	797.3	0.15	0.01	(8)
Arctogalidia trivirgata	Viverridae	Carnivora	36.2	552.8	-0.13	1.00	(8)
Nandinia binotata	Viverridae	Carnivora	37.4	862.5	0.14	0.00	(8)

Saccopteryx bilineata	Emballonuridae	Chiroptera	35.5	15.3	-0.01	1.00	(15)
Peropteryx macrotis	Emballonuridae	Chiroptera	35	11.8	0.05	1.00	(16)
Hipposideros galeritus	Hipposideridae	Chiroptera	31.9	9.4	0.27	0.11	(17)
Rhinonicteris aurantia	Hipposideridae	Chiroptera	36.1	16.2	0.18	1.00	(18)
Macroderma gigas	Megadermatidae	Chiroptera	35.6	94.2	0.16	0.76	(18, 19)
Molossus molossus	Molossidae	Chiroptera	36	22.5	0.17	0.69	(20)
Chrotopterus auritus	Mormoopidae	Chiroptera	37.2	141.3	-0.07	0.00	(20)
Mormoops blainvillei	Mormoopidae	Chiroptera	33	8.0	0.26	0.00	(21)
Pteronotus quadridens	Mormoopidae	Chiroptera	32.8	6.1	0.25	0.00	(21)
Diaemus youngi	Natalidae	Chiroptera	33	37.3	-0.07	1.00	(20)
Desmodus rotundus	Natalidae	Chiroptera	35	34.7	0.04	0.00	(20)
Natalus tumidirostris	Natalidae	Chiroptera	34	8.3	-0.07	1.00	(16)
Noctilio albiventris	Noctilionidae	Chiroptera	34.2	31.6	0.47	0.83	(20)
Noctilio leporinus	Noctilionidae	Chiroptera	33.3	70.8	0.14	1.00	(20)
Artibeus concolor	Phyllostomidae	Chiroptera	35	39.8	0.01	1.00	(20)
Phyllostomus elongatus	Phyllostomidae	Chiroptera	36	38.8	-0.21	1.00	(20)
Phyllostomus hastatus	Phyllostomidae	Chiroptera	35	100.2	-0.11	0.41	(20)
Rhinophylla pumilio	Phyllostomidae	Chiroptera	36	18.6	-0.04	0.41	(20)
Tonatia bidens	Phyllostomidae	Chiroptera	37	55.1	-0.14	0.00	(20)
Uroderma bilobatum	Phyllostomidae	Chiroptera	36.3	31.6	-0.02	0.00	(20)
Artibeus lituratus	Phyllostomidae	Chiroptera	36.7	108.0	-0.19	0.19	(20)
Phyllostomus discolor	Phyllostomidae	Chiroptera	34	47.9	-0.13	0.72	(20)
Artibeus jamaicensis	Phyllostomidae	Chiroptera	36	76.8	-0.19	0.25	(20)
Carollia	Phyllosto	Chiroptera	36.6	43.1	-0.11	0.00	(20)

perspicillata	midae						
Sturnira lilium	Phyllostomidae	Chiroptera	36.6	53.2	-0.02	0.00	(20)
Diphylla ecaudata	Phyllostomidae	Chiroptera	33	38.6	-0.03	0.99	(20)
Anoura caudifer	Phyllostomidae	Chiroptera	36.3	42.7	-0.26	0.00	(20)
Anoura latidens	Phyllostomidae	Chiroptera	38.12	36.9	0.23	1.00	(22)
Sturnira erythromos	Phyllostomidae	Chiroptera	34.4	39.9	-0.17	0.00	(22)
Glossophaga soricina	Phyllostomidae	Chiroptera	36.5	17.7	0.01	1.00	(23)
Glossophaga longirostris	Phyllostomidae	Chiroptera	37.5	26.5	-0.01	0.00	(24)
Leptonycteris curasoae	Phyllostomidae	Chiroptera	36	34.1	-0.15	1.00	(24)
Erophylla bombifrons	Phyllostomidae	Chiroptera	33	17.7	0.30	0.45	(21)
Monophyllus redmani	Phyllostomidae	Chiroptera	35.5	11.1	0.08	0.00	(21)
Nyctimene albiventer	Pteropodidae	Chiroptera	35.9	26.4	-0.08	1.00	(25)
Dobsonia praedatrix	Pteropodidae	Chiroptera	37.1	142.5	-0.11	1.00	(25)
Eonycteris spelaea	Pteropodidae	Chiroptera	34	48.0	-0.05	1.00	(17)
Cynopterus brachyotis	Pteropodidae	Chiroptera	36.5	47.5	0.02	0.84	(17)
Dobsonia anderseni	Pteropodidae	Chiroptera	36.4	174.0	0.04	0.27	(25)
Histiotus velatus	Vesperitilionidae	Chiroptera	32	10.0	-0.09	1.00	(20)
Miniopterus schreibersii	Vespertilionidae	Chiroptera	37.7	26.0	0.04	1.00	(18)
Chaetophractus vellerosus	Dasypodidae	Cingulata	34.4	306.4	0.42	0.38	(1)
Tolypeutes matacus	Dasypodidae	Cingulata	33	210.0	0.37	0.00	(1)
Zaedyus pichiy	Dasypodidae	Cingulata	35.2	393.2	0.24	0.00	(1)
Euphractus sexcinctus	Dasypodidae	Cingulata	34.2	1244.9	0.28	0.01	(1)
Chaetophractus nationi	Dasypodidae	Cingulata	35.5	559.0	0.30	0.30	(1)
Dasypus	Dasypodid	Cingulata	34.5	806.8	0.32	0.43	(1)

novemcinctus	ae						
Planigale maculata	Dasyuridae	Dasyuromorphia	34.2	13.2	0.26	0.12	(26)
Lutreolina crassicaudata	Didelphidae	Didelphimorphia	35.8	406.0	0.10	0.59	(27)
Chironectes minimus	Didelphidae	Didelphimorphia	35.3	548.7	0.02	1.00	(27)
Caluromys derbianus	Didelphidae	Didelphimorphia	34	203.5	0.03	0.00	(27)
Marmosa robinsoni	Didelphidae	Didelphimorphia	34	97.6	0.04	0.00	(27)
Philander opossum	Didelphidae	Didelphimorphia	35.8	338.0	0.24	0.60	(27)
Metachirus nudicaudatus	Didelphidae	Didelphimorphia	35	205.0	0.11	0.45	(27)
Monodelphis brevicaudata	Didelphidae	Didelphimorphia	33.8	75.5	0.14	0.00	(27)
Didelphis marsupialis	Didelphidae	Didelphimorphia	35	611.3	0.10	0.82	(27)
Didelphis virginiana	Didelphidae	Didelphimorphia	34.8	1074.8	0.03	0.00	(27)
Marmosa lepida	Didelphidae	Didelphimorphia	36.3	63.6	0.18	0.00	(28)
Macropus giganteus	Macropodidae	Diprotodontia	36.5	7074.0	-0.06	0.00	(29, 30)
Macropus rufus	Macropodidae	Diprotodontia	36.3	5032.8	0.22	0.98	(29, 30)
Lagorchestes conspicillatus	Macropodidae	Diprotodontia	35.8	851.2	0.09	0.00	(31)
Dendrolagus matschiei	Macropodidae	Diprotodontia	36.3	1426.8	0.22	0.22	(13)
Petaurus breviceps	Petauridae	Diprotodontia	36.3	93.6	-0.05	1.00	(29, 32)
Phascolarctos cinereus	Phascolarctidae	Diprotodontia	35.8	1048.3	-0.04	1.00	(33)
Cercartetus nanus	Pseudocheiridae	Diprotodontia	34.9	51.6	0.28	0.58	(34)
Cercopithecus mitis	Pseudocheiridae	Diprotodontia	37	3520.0	-0.30	0.51	(35)
Tarsipes rostratus	Tarsipedidae	Diprotodontia	36.6	29.0	-0.19	0.00	(36)
Lasiorhinus latifrons	Vombatidae	Diprotodontia	34	2750.0	0.32	0.10	(37)
Atelerix albiventris	Erinaceidae	Erinaceomorpha	35.2	146.7	0.29	0.00	(1)
Erinaceus concolor	Erinaceida	Erinaceo	35.2	347.2	0.16	0.28	(38)

	e	morpha					
Heterohyrax brucei	Procaviidae	Hyracoidae	36.4	669.2	0.02	1.00	(39)
Sylvilagus audubonii	Leporidae	Lagomorpha	38.25	456.4	0.02	1.00	(40)
Macroscelides proboscideus	Macroscelididae	Macroscelidae	36.23	52.0	0.27	1.00	(41)
Elephantulus edwardii	Macroscelididae	Macroscelidae	3.76E+01	54.3	0.15	0.76	(42)
Colobus guereza	Cercopithecidae	Primates	37	3132.0	-0.29	0.89	(35)
Eulemur fulvus	Lemuridae	Primates	38.8	324.8	0.17	0.00	(43)
Perodicticus potto	Lorisidae	Primates	36	347.6	0.01	0.00	(44)
Nycticebus coucang	Lorisidae	Primates	35.1	218.3	0.05	0.00	(45)
Aplodontia rufa	Aplodontidae	Rodentia	38	277.2	-0.04	1.00	(46)
Georychus capensis	Bathyergidae	Rodentia	36.4	113.6	-0.06	1.00	(47)
Cryptomys damarensis	Bathyergidae	Rodentia	35.2	70.7	0.00	0.00	(48)
Cryptomys hottentotus	Bathyergidae	Rodentia	33.8	48.5	0.12	0.00	(49)
Cryptomys bocagei	Bathyergidae	Rodentia	33.7	69.6	0.55	0.77	(49)
Cryptomys mechowi	Bathyergidae	Rodentia	34	160.2	0.27	0.65	(49)
Heterocephalus glaber	Bathyergidae	Rodentia	32.3	21.6	1.36	0.73	(50)
Dolichotis salinicola	Caviidae	Rodentia	38.4	725.9	0.07	0.94	(51)
Kerodon rupestris	Caviidae	Rodentia	38.2	282.9	-0.05	1.00	(51)
Hydrochoerus hydrochaeris	Caviidae	Rodentia	37.1	6600.0	0.10	1.00	(51)
Loxodontomys micropus	Cricetidae	Rodentia	37.2	97.8	-0.31	0.52	(52)
Phyllotis darwini	Cricetidae	Rodentia	37	71.4	-0.11	0.73	(52)
Isthmomys pirrensis	Cricetidae	Rodentia	37.5	123.6	0.05	0.91	(53)
Ochrotomys nuttalli	Cricetidae	Rodentia	38.08	27.1	-0.14	1.00	(54)
Peromyscus truei	Cricetidae	Rodentia	36.7	50.8	-0.16	0.61	(55)
Microtus ochrogaster	Cricetidae	Rodentia	37.8	40.3	-0.27	1.00	(56)
Peromyscus eremicus	Cricetidae	Rodentia	36.6	31.8	-0.08	1.00	(55)

Myodes gapperi	Cricetidae	Rodentia	37.6	48.5	-0.24	0.36	(57)
Peromyscus leucopus	Cricetidae	Rodentia	36	35.2	-0.13	0.66	(57)
Microtus longicaudus	Cricetidae	Rodentia	37.7	76.4	-0.43	0.35	(58)
Microtus montanus	Cricetidae	Rodentia	37.5	81.6	-0.24	0.00	(59)
Myopus schisticolor	Cricetidae	Rodentia	39	93.5	-0.45	0.10	(60)
Ctenomys talarum	Ctenomyidae	Rodentia	36.1	119.2	-0.13	0.89	(61)
Priodontes maximus	Dasypodidae	Rodentia	33.6	3027.7	0.49	0.12	(1)
Cabassous centralis	Dasypodidae	Rodentia	33.6	677.3	0.35	0.29	(1)
Dasyprocta azarae	Dasyproctidae	Rodentia	37.4	1886.0	-0.14	0.03	(51)
Myoprocta acouchy	Dasyproctidae	Rodentia	35.4	502.7	0.03	1.00	(51)
Dasyprocta leporina	Dasyproctidae	Rodentia	38.3	1558.5	-0.14	0.00	(51)
Jaculus jaculus	Dipodidae	Rodentia	37	91.6	0.28	1.00	(62)
Jaculus orientalis	Dipodidae	Rodentia	37	139.1	-0.03	0.00	(62)
Napaeozapus insignis	Dipodidae	Rodentia	37	92.0	0.02	1.00	(63)
Thrichomys apereoides	Echimyidae	Rodentia	37.6	206.7	-0.12	1.00	(51)
Geomys pinetis	Geomyidae	Rodentia	36.1	135.3	-0.01	1.00	(50)
Thomomys bottae	Geomyidae	Rodentia	36	120.1	0.02	0.00	(64)
Thomomys umbrinus	Geomyidae	Rodentia	34.6	72.3	0.01	0.00	(65)
Thomomys talpoides	Geomyidae	Rodentia	35.5	141.0	-0.07	0.00	(65)
Geomys bursarius	Geomyidae	Rodentia	36.4	137.9	0.14	0.55	(66)
Heteromys anomalus	Heteromyidae	Rodentia	36	100.5	-0.12	0.00	(46)
Liomys salvini	Heteromyidae	Rodentia	37.09	46.9	0.06	0.02	(67)
Liomys irroratus	Heteromyidae	Rodentia	36.63	53.9	0.10	0.72	(67)
Chaetodipus hispidus	Heteromyidae	Rodentia	37.5	44.8	-0.01	1.00	(68)
Chaetodipus intermedius	Heteromyidae	Rodentia	35	15.6	0.47	0.60	(66)

Dipodomys deserti	Heteromyidae	Rodentia	36.8	92.2	-0.01	1.00	(46)
Dipodomys microps	Heteromyidae	Rodentia	36.4	66.9	-0.11	0.89	(69)
Hystrix africaeaustralis	Hystricidae	Rodentia	37	2319.9	0.10	0.00	(70)
Abrothrix longipilis	Muridae	Rodentia	36.5	57.5	-0.14	0.70	(52)
Abrothrix andinus	Muridae	Rodentia	39.3	64.7	-0.26	0.40	(52)
Auliscomys boliviensis	Muridae	Rodentia	36.9	110.6	-0.26	0.47	(52)
Rattus fuscipes	Muridae	Rodentia	37.4	141.7	-0.05	0.00	(71)
Otomys irroratus	Muridae	Rodentia	36.5	84.9	-0.19	1.00	(72)
Mystromys albicaudatus	Muridae	Rodentia	37.5	126.8	-0.35	0.61	(73)
Notomys alexis	Muridae	Rodentia	37.7	45.2	0.07	1.00	(74)
Pseudomys hermannsburgensis	Muridae	Rodentia	37.5	23.3	-0.05	0.26	(75)
Gerbillurus paeba	Muridae	Rodentia	36	27.7	0.39	0.54	(76)
Rattus villosissimus	Muridae	Rodentia	38.9	220.5	0.01	1.00	(77)
Cannomys badius	Muridae	Rodentia	36	172.0	0.03	0.00	(46)
Baiomys taylori	Muridae	Rodentia	36	14.2	-0.12	1.00	(78)
Gerbillus andersoni	Muridae	Rodentia	37	39.4	-0.12	1.00	(79)
Gerbillus nanus	Muridae	Rodentia	38.8	22.0	0.05	0.00	(79)
Apodemus mystacinus	Muridae	Rodentia	38.3	70.6	-0.17	0.23	(80)
Akodon azarae	Muridae	Rodentia	37.7	51.0	-0.07	0.00	(81)
Saccostomus campestris	Nesomyidae	Rodentia	35.4	81.7	0.02	0.00	(2)
Octodontomys gliroides	Octodontidae	Rodentia	37.2	130.7	-0.16	1.00	(51)
Octodon degus	Octodontidae	Rodentia	37.6	191.6	-0.08	0.14	(51)
Spalacopus cyanus	Octodontidae	Rodentia	36	112.1	-0.04	1.00	(46, 82)
Pedetes capensis	Pedetidae	Rodentia	36	736.0	0.00	1.00	(83)
Spermophilus beecheyi	Sciuridae	Rodentia	37.6	317.8	-0.08	1.00	(84)
Ammospermophilus leucurus	Sciuridae	Rodentia	37.2	103.0	0.09	1.00	(85)
Tamias merriami	Sciuridae	Rodentia	37	91.2	-0.04	0.00	(86)
Cynomys ludovicianus	Sciuridae	Rodentia	37.2	422.7	0.21	0.41	(87)
Tachyoryctes	Spalacidae	Rodentia	36.2	163.5	-0.01	1.00	(50)

splendens							
Spalax leucodon	Spalacidae	Rodentia	37	159.9	-0.13	1.00	(50)
Tupaia glis	Tupaiidae	Scandentia	37	93.5	0.07	0.00	(88)
Tupaia belangeri	Tupaiidae	Scandentia	39.4	139.2	-0.07	0.00	(89)
Notiosorex crawfordi	Soricidae	Soricomorpha	38	13.1	-0.09	0.00	(90)
Blarina brevicauda	Soricidae	Soricomorpha	38	66.0	-0.32	0.00	(57, 91)
Scalopus aquaticus	Talpidae	Soricomorpha	36	67.7	-0.15	0.52	(46)
Condylura cristata	Talpidae	Soricomorpha	37.7	110.3	-0.27	0.00	(92)
Neurotrichus gibbsii	Talpidae	Soricomorpha	38.7	46.5	-0.38	0.08	(93)

Birds

Species	Family	Order	Tb (°C)	BMR (mlO2/ g*hour)	A	I	References
Buteo buteo	Accipitridae	Accipitriformes	39.8	646.3	-0.11	0.57	(94)
Anas aucklandica	Anatidae	Anseriformes	41.3	322.7	0.21	1.00	(95)
Anas castanea	Anatidae	Anseriformes	41.5	327.9	0.03	0.00	(95)
Anas gracilis	Anatidae	Anseriformes	41.3	572.7	0.21	1.00	(95)
Anas rhynchotis	Anatidae	Anseriformes	40.9	452.7	0.00	1.00	(95)
Aythya novaeseelandiae	Anatidae	Anseriformes	40	401.5	-0.10	0.57	(95)
Hymenolaimus malacorhynchos	Anatidae	Anseriformes	41	540.6	-0.16	0.60	(95)
Tadorna variegata	Anatidae	Anseriformes	40.2	575.5	0.07	0.28	(95)
Collocalia esculenta	Apodidae	Apodiformes	38.2	13.9	0.20	0.00	(96)
Collocalia vanikorensis	Apodidae	Apodiformes	38.9	20.6	0.11	0.00	(96)
Aegotheles cristatus	Aegothelidae	Caprimulgiformes	38.2	55.9	0.28	0.47	(97)
Caprimulgus macrurus	Caprimulgidae	Caprimulgiformes	38.1	53.5	0.08	0.00	(96)
Caprimulgus	Caprimulgi	Caprimulgi	37	55.9	0.06	0.00	(98)

vociferus	dae	formes					
Chordeiles minor	Caprimulgidae	Caprimulgiformes	40	76.0	0.17	0.14	(99, 100)
Eurostopodus mystacalis	Caprimulgidae	Caprimulgiformes	40.1	82.7	0.21	0.00	(96)
Phalaenoptilus nuttallii	Caprimulgidae	Caprimulgiformes	40.2	30.6	0.42	0.10	(101)
Podargus strigoides	Podargidae	Caprimulgiformes	38.6	177.8	0.33	0.27	(96)
Calidris alpina	Scolopacidae	Charadriiformes	37.6	83.2	0.18	0.89	(102)
Calidris minuta	Scolopacidae	Charadriiformes	39	53.1	0.07	0.38	(102)
Cepphus grylle	Alcidae	Charadriiformes	39.9	520.1	-0.26	0.02	(103)
Haematopus ostralegus	Haematopodidae	Charadriiformes	39.1	524.4	-0.04	0.00	(102)
Pluvialis apricaria	Charadriidae	Charadriiformes	38.9	213.7	-0.11	0.11	(104)
Rissa tridactyla	Laridae	Charadriiformes	40.2	569.8	-0.29	0.03	(103)
Sterna fuscata	Sternidae	Charadriiformes	39.3	137.7	-0.07	1.00	(105, 106)
Uria lomvia	Alcidae	Charadriiformes	39.6	872.4	-0.27	0.12	(103, 107, 108)
Bubulcus ibis	Ardeidae	Ciconiiformes	40	171.6	0.07	0.00	(109)
Egretta thula	Ardeidae	Ciconiiformes	40.2	233.7	0.10	0.32	(109)
Egretta tricolor	Ardeidae	Ciconiiformes	40.4	292.5	0.19	1.00	(109)
Colius colius	Coliidae	Coliiformes	37	30.6	0.23	0.00	(110)
Colius striatus	Coliidae	Coliiformes	39	40.6	0.00	0.00	(111)
Urocolius macrourus	Coliidae	Coliiformes	40.6	38.5	0.08	0.00	(112)
Caloenas nicobarica	Columbidae	Columbiformes	40.9	312.1	0.09	0.00	(113)
Columba livia	Columbidae	Columbiformes	41.6	247.6	0.01	0.00	(113)
Columba vitiensis	Columbidae	Columbiformes	39.9	248.3	0.02	0.00	(113)
Columbina inca	Columbidae	Columbiformes	40.2	44.9	0.22	0.02	(114)

Drepanoptila holosericea	Columbidae	Columbiformes	39	142.0	0.15	0.00	(115)
Ducula bicolor	Columbidae	Columbiformes	40.9	234.7	0.10	0.00	(113)
Ducula pacifica	Columbidae	Columbiformes	39.8	135.8	0.17	0.00	(113)
Ducula pinon	Columbidae	Columbiformes	39.7	306.4	0.07	0.00	(113)
Ducula pistrinaria	Columbidae	Columbiformes	40.8	184.5	0.13	0.00	(113)
Ducula rubricera	Columbidae	Columbiformes	40.8	234.7	0.04	0.00	(113)
Ducula rufigaster	Columbidae	Columbiformes	40.6	218.9	0.10	0.00	(113)
Ducula zoeae	Columbidae	Columbiformes	40.2	293.0	-0.05	1.00	(113)
Geopelia cuneata	Columbidae	Columbiformes	39	45.9	0.43	0.56	(116)
Geophaps plumifera	Columbidae	Columbiformes	40.5	72.7	0.30	0.27	(117, 118)
Goura cristata	Columbidae	Columbiformes	40.9	734.2	0.03	0.00	(113)
Gymnophaps albertisii	Columbidae	Columbiformes	39.2	162.5	0.00	0.00	(113)
Hemiphaga novaeseelandiae	Columbidae	Columbiformes	40.4	324.1	-0.04	1.00	(113)
Leucosarcia melanoleuca	Columbidae	Columbiformes	40.7	287.8	0.05	0.00	(113)
Oena capensis	Columbidae	Columbiformes	39	42.1	0.28	0.27	(115)
Ptilinopus melanospilus	Columbidae	Columbiformes	38.9	84.1	0.24	0.21	(113, 115)
Ptilinopus perlatus	Columbidae	Columbiformes	39.5	182.6	0.03	0.00	(113, 115)
Zenaida macroura	Columbidae	Columbiformes	40.5	111.4	0.16	0.72	(119)
Aceros plicatus	Bucerotidae	Coraciiformes	40.1	929.7	-0.02	0.20	(120)
Dacelo novaeguineae	Alcedinidae	Coraciiformes	37	192.2	0.03	0.00	(121)
Phoeniculus purpureus	Phoeniculidae	Coraciiformes	39.3	113.8	-0.04	0.27	(122, 123)
Todus mexicanus	Todidae	Coraciiformes	36.7	19.6	0.14	0.64	(124)
Guira guira	Cuculidae	Cuculiformes	40	185.9	0.09	1.00	(125)

Daptrius ater	Falconidae	Falconiformes	39.1	206.5	-0.03	1.00	(126)
Falco rupicoloides	Falconidae	Falconiformes	40	247.5	-0.17	0.62	(127)
Falco sparverius	Falconidae	Falconiformes	40.2	113.8	0.01	0.00	(127)
Alectoris chukar	Phasianidae	Galliformes	40.7	337.5	0.05	0.55	(128)
Callipepla gambelii	Odontophoridae	Galliformes	40	130.0	0.42	0.84	(129, 130)
Coturnix chinensis	Phasianidae	Galliformes	39	63.1	0.06	0.00	(131, 132)
Coturnix coturnix	Phasianidae	Galliformes	41.8	153.4	-0.23	0.66	(129, 133)
Coturnix japonica	Phasianidae	Galliformes	39.5	255.7	0.00	0.00	(134, 135)
Coturnix pectoralis	Phasianidae	Galliformes	41.6	109.5	0.02	0.00	(131)
Lagopus leucura	Phasianidae	Galliformes	39.9	406.3	-0.28	0.41	(136)
Leipoa ocellata	Megapodiidae	Galliformes	39.7	691.2	0.09	0.85	(137)
Syrmaticus humiae	Phasianidae	Galliformes	40.36	773.9	0.03	1.00	(138)
Aramides cajanea	Rallidae	Gruiformes	40.2	265.3	0.25	0.76	(139)
Fulica atra	Rallidae	Gruiformes	39.6	404.9	-0.03	0.00	(140)
Gallinula mortierii	Rallidae	Gruiformes	39.4	548.3	-0.07	1.00	(139)
Gallinula tenebrosa	Rallidae	Gruiformes	39.4	402.5	-0.07	0.55	(139)
Gallinula ventralis	Rallidae	Gruiformes	39.7	277.7	-0.04	0.74	(139)
Gallirallus australis	Rallidae	Gruiformes	39	314.5	0.35	0.42	(139)
Gallirallus owstoni	Rallidae	Gruiformes	40.2	157.7	0.18	0.37	(139)
Gallirallus philippensis	Rallidae	Gruiformes	40.6	167.8	0.12	0.63	(139)
Megacrex inepta	Rallidae	Gruiformes	38.6	230.9	0.00	1.00	(139)
Porphyrio hochstetteri	Rallidae	Gruiformes	39	1185.0	-0.10	0.71	(139)
Porphyrio porphyrio	Rallidae	Gruiformes	39.6	636.2	-0.09	0.29	(139)

Porzana cinerea	Rallidae	Gruiformes	38.9	85.1	0.11	1.00	(139)
Acridotheres cristatellus	Sturnidae	Passeriformes	41.4	119.5	-0.02	1.00	(141)
Actitis hypoleucos	Scolopacidae	Passeriformes	40.3	89.9	-0.08	0.00	(142, 143)
Aethopyga christinae	Nectariniidae	Passeriformes	39	24.9	-0.13	0.19	(144)
Aethopyga siparaja	Nectariniidae	Passeriformes	40.9	25.3	-0.14	0.72	(144, 145)
Amadina fasciata	Estrildidae	Passeriformes	43.1	36.8	0.00	0.00	(146)
Anthreptes collaris	Nectariniidae	Passeriformes	38.5	29.2	-0.09	0.49	(144)
Aphelocoma coerulescens	Corvidae	Passeriformes	41.5	165.4	-0.29	0.42	(147)
Astrapia stephaniae	Paradisaeidae	Passeriformes	41.4	277.2	-0.06	0.00	(148)
Bombycilla garrulus	Bombycillidae	Passeriformes	40.5	143.6	-0.19	0.15	(149)
Cardinalis cardinalis	Cardinalidae	Passeriformes	38.9	86.5	0.14	1.00	(150)
Cardinalis sinuatus	Cardinalidae	Passeriformes	38.7	67.4	0.18	1.00	(150)
Carduelis flammea	Fringillidae	Passeriformes	40.48	59.8	-0.36	0.46	(151, 152)
Carduelis pinus	Fringillidae	Passeriformes	38.8	59.3	-0.31	0.31	(153)
Carduelis tristis	Fringillidae	Passeriformes	39.3	52.1	-0.15	0.00	(153)
Carpodacus cassinii	Fringillidae	Passeriformes	39	58.3	-0.12	0.90	(154)
Carpodacus mexicanus	Fringillidae	Passeriformes	39	53.5	-0.05	0.00	(129, 155)
Carpodacus purpureus	Fringillidae	Passeriformes	39	146.3	-0.02	0.00	(156)
Carpodacus roseus	Fringillidae	Passeriformes	40.46	92.5	-0.15	0.00	(157)
Cicinnurus magnificus	Paradisaeidae	Passeriformes	40.4	135.8	-0.13	0.47	(148)
Cicinnurus regius	Paradisaeidae	Passeriformes	40.4	100.4	-0.16	0.64	(148)
Cnemophilus loriae	Cnemophilidae	Passeriformes	38.6	113.8	-0.10	0.91	(148)
Coccothraustes vespertinus	Fringillidae	Passeriformes	39	143.4	-0.21	0.11	(158)

Coereba flaveola	Coerebidae	Passeriformes	40.7	36.8	-0.14	0.35	(159)
Corvus corax	Corvidae	Passeriformes	41	946.5	-0.27	0.40	(160)
Cyanerpes cyaneus	Thraupidae	Passeriformes	40.22	46.8	-0.11	0.00	(161, 162)
Cyanocitta cristata	Corvidae	Passeriformes	40.3	143.4	-0.15	0.35	(163)
Emberiza chrysophrys	Emberizidae	Passeriformes	40.58	55.4	-0.11	0.00	(164)
Emberiza citrinella	Emberizidae	Passeriformes	39.8	75.0	-0.06	0.00	(165)
Emberiza hortulana	Emberizidae	Passeriformes	39.5	71.7	0.23	1.00	(165)
Emberiza pusilla	Emberizidae	Passeriformes	39.8	45.2	-0.24	0.37	(157)
Emberiza rutila	Emberizidae	Passeriformes	39.5	58.3	-0.08	0.00	(157)
Emberiza spodocephala	Emberizidae	Passeriformes	40.3	68.4	-0.23	0.00	(149)
Epimachus meyeri	Paradisaeidae	Passeriformes	41	316.9	-0.13	0.00	(148)
Eremalauda dunni	Alaudidae	Passeriformes	40	47.8	0.17	1.00	(166)
Eremiornis carteri	Megaluridae	Passeriformes	39.1	34.1	0.11	1.00	(167)
Eremophila alpestris	Alaudidae	Passeriformes	42	56.6	-0.10	0.86	(168)
Erythrura gouldiae	Estrildidae	Passeriformes	42.1	37.4	0.06	0.64	(169)
Estrilda melpoda	Estrildidae	Passeriformes	43	22.5	0.13	0.70	(146)
Fringilla montifringilla	Fringillidae	Passeriformes	40.4	66.0	-0.09	0.00	(170)
Hylophylax naevioides	Thamnophilidae	Passeriformes	40	41.1	0.08	1.00	(161, 171)
Icterus bullockii	Icteridae	Passeriformes	40	86.5	0.01	1.00	(172)
Icterus galbula	Icteridae	Passeriformes	39.8	86.5	0.02	1.00	(172)
Lanius collaris	Laniidae	Passeriformes	40	32.0	-0.04	1.00	(173)
Lanius excubitor	Laniidae	Passeriformes	39.73	92.7	0.17	0.96	(174, 175)
Lichenostomus virescens	Meliphagidae	Passeriformes	40	51.1	0.26	0.92	(176)

Lichmera indistincta	Meliphagidae	Passeriformes	40.4	36.3	0.04	1.00	(176, 177)
Lonchura fuscans	Estrildidae	Passeriformes	38.9	17.2	0.10	0.00	(178)
Lophorina superba	Paradisaeidae	Passeriformes	40.5	124.3	-0.16	0.63	(148)
Loxia curvirostra	Fringillidae	Passeriformes	39.5	87.0	-0.27	0.40	(179)
Loxia leucoptera	Fringillidae	Passeriformes	39.5	78.4	-0.29	0.60	(179)
Lullula arborea	Alaudidae	Passeriformes	40	98.5	0.01	1.00	(166)
Malurus cyaneus	Maluridae	Passeriformes	41	24.9	-0.13	1.00	(180, 181)
Manacus vitellinus	Maluridae	Passeriformes	37.9	40.2	0.00	1.00	(182)
Manucodia chalybatus	Paradisaeidae	Passeriformes	40.5	236.1	-0.09	0.00	(148)
Manucodia keraudrenii	Paradisaeidae	Passeriformes	40.4	206.0	0.03	1.00	(148)
Nectarinia bifasciata	Nectariniidae	Passeriformes	39	15.8	-0.15	1.00	(144, 183)
Nectarinia cuprea	Nectariniidae	Passeriformes	41	25.4	0.03	1.00	(183, 184)
Nectarinia kilimensis	Nectariniidae	Passeriformes	40	44.9	-0.10	0.52	(144)
Nectarinia senegalensis	Nectariniidae	Passeriformes	40	41.1	0.07	1.00	(183)
Nectarinia tacazze	Nectariniidae	Passeriformes	41.4	42.1	-0.14	0.53	(144, 183, 184)
Nectarinia venusta	Nectariniidae	Passeriformes	40	25.8	-0.14	0.89	(183, 184)
Onychognathus morio	Sturnidae	Passeriformes	39.1	221.3	-0.18	0.12	(185)
Onychognathus tristramii	Sturnidae	Passeriformes	40.6	196.0	-0.08	0.00	(186)
Padda oryzivora	Estrildidae	Passeriformes	42.5	51.1	0.04	0.58	(146)
Paradisaea raggiana	Paradisaeidae	Passeriformes	39.7	322.7	-0.14	0.00	(148)
Paradisaea rudolphi	Paradisaeidae	Passeriformes	40.5	262.0	-0.16	0.00	(148)
Parotia lawesii	Paradisaeidae	Passeriformes	39.1	206.0	-0.14	0.31	(148)
Parotia wahnesi	Paradisaei	Passerifor	39.7	221.8	-0.03	0.00	(148)

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Passer domesticus	Passeridae	Passeriformes	38.6	63.1	-0.17	0.44	(187)
Phytotoma rara	Cotingidae	Passeriformes	40.2	98.5	-0.12	0.02	(188)
Pica nuttalli	Corvidae	Passeriformes	39.4	252.4	-0.20	0.17	(189)
Pica pica	Corvidae	Passeriformes	39.5	206.0	-0.05	0.00	(189)
Pipra mentalis	Pipridae	Passeriformes	37.9	33.5	-0.01	1.00	(182)
Ptiloris magnificus	Paradisaeidae	Passeriformes	38.6	258.1	0.00	1.00	(148)
Pycnonotus sinensis	Pycnonotidae	Passeriformes	40.3	66.9	-0.08	0.00	(190)
Saltator coerulescens	Cardinalidae	Passeriformes	39.4	66.9	0.05	0.00	(191)
Saltator orenocensis	Cardinalidae	Passeriformes	38.8	54.0	0.01	0.00	(191)
Sporophila corvina	Thraupidae	Passeriformes	39.67	33.9	0.03	1.00	(192)
Sturnus sericeus	Sturnidae	Passeriformes	40.5	153.0	0.05	1.00	(190)
Syrmaticus ellioti	Phasianidae	Passeriformes	40.47	504.8	0.06	1.00	(138)
Taeniopygia guttata	Estrildidae	Passeriformes	39.8	35.4	0.07	1.00	(146, 193)
Thryothorus ludovicianus	Troglodytidae	Passeriformes	39.4	61.7	-0.02	0.00	(194)
Zonotrichia leucophrys	Emberizidae	Passeriformes	41	66.0	-0.14	0.63	(195)
Zosterops erythropleurus	Zosteropidae	Passeriformes	40.58	40.6	-0.14	0.00	(164)
Zosterops lateralis	Zosteropidae	Passeriformes	40.3	27.7	0.01	0.00	(181, 196)
Anhinga anhinga	Anhingidae	Pelecaniformes	39.7	549.2	0.19	0.83	(7)
Phalacrocorax auritus	Phalacrocoracidae	Pelecaniformes	39.5	945.0	-0.01	0.00	(7, 197)
Aulacorhynchus prasinus	Ramphastidae	Piciformes	38.1	142.9	0.04	0.00	(120)
Aulacorhynchus sulcatus	Ramphastidae	Piciformes	38.8	116.6	0.00	0.00	(120)
Pteroglossus aracari	Ramphastidae	Piciformes	40.9	153.0	0.15	0.16	(120)
Ramphastos	Ramphasti	Piciformes	39.2	217.5	-0.03	1.00	(120)

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Ramphastos toco	Ramphastidae	Piciformes	39.1	416.8	-0.06	0.81	(120)
Ramphastos tucanus	Ramphastidae	Piciformes	39.6	294.0	0.11	0.52	(120)
Selenidera maculirostris	Ramphastidae	Piciformes	38.6	186.4	0.04	1.00	(120)
Podiceps nigricollis	Podicipedidae	Podicipediformes	39.6	368.5	-0.14	0.08	(198)
Fulmarus glacialis	Procellariidae	Procellariiformes	39.9	622.4	-0.20	0.21	(103)
Oceanites oceanicus	Hydrobatidae	Procellariiformes	39.7	82.2	-0.26	0.84	(199)
Puffinus pacificus	Procellariidae	Procellariiformes	39.3	400.6	0.05	1.00	(200)
Amazona viridigenalis	Psittacidae	Psittaciformes	41.1	344.2	0.09	1.00	(201)
Bolborhynchus lineola	Psittacidae	Psittaciformes	40.4	107.1	0.06	1.00	(202)
Cacatua roseicapilla	Cacatuidae	Psittaciformes	39	240.9	0.01	0.00	(123, 203)
Cyanoramphus auriceps	Psittacidae	Psittaciformes	38.1	84.6	-0.06	1.00	(204)
Cyanoramphus novaezelandiae	Psittacidae	Psittaciformes	37.9	90.3	-0.05	0.98	(204)
Cyanoramphus unicolor	Psittacidae	Psittaciformes	40.2	185.9	-0.15	0.44	(204)
Neophema elegans	Psittacidae	Psittaciformes	40	100.4	-0.04	0.00	(205)
Neophema pulchella	Psittacidae	Psittaciformes	40	94.2	0.06	1.00	(205)
Neophema splendida	Psittacidae	Psittaciformes	40	90.8	-0.01	0.00	(205)
Nestor meridionalis	Nestoridae	Psittaciformes	39.7	368.5	-0.13	0.35	(204)
Nestor notabilis	Nestoridae	Psittaciformes	39.5	763.9	-0.23	0.25	(204)
Aptenodytes patagonicus	Spheniscidae	Sphenisciformes	37.5	3760.5	-0.17	0.16	(206)
Spheniscus humboldti	Spheniscidae	Sphenisciformes	39	1631.9	-0.17	0.57	(207)
Aegolius acadicus	Strigidae	Strigiformes	39	117.1	-0.06	1.00	(208)
Aegolius funereus	Strigidae	Strigiformes	39.4	194.6	-0.27	0.63	(209)
Athene cunicularia	Strigidae	Strigiform	38	133.8	0.09	0.00	(210)

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Bubo virginianus	Strigidae	Strigiformes	39.9	746.7	0.03	1.00	(211)
Glaucidium gnoma	Strigidae	Strigiformes	39	71.7	0.07	0.00	(212)
Megascops asio	Strigidae	Strigiformes	39	85.1	0.09	0.00	(212)
Megascops trichopsis	Strigidae	Strigiformes	37	79.3	0.20	0.00	(212)
Micrathene whitneyi	Strigidae	Strigiformes	39	43.5	0.19	0.00	(212)
Otus leucotis	Pycnonotidae	Strigiformes	38.9	126.7	-0.04	1.00	(213)
Strix occidentalis	Strigidae	Strigiformes	38.5	460.3	-0.05	0.00	(211)
Tyto alba	Tytonidae	Strigiformes	37.8	308.8	0.10	0.03	(214)
Archilochus alexandri	Trochilidae	Trochiliformes	40	8.1	-0.13	1.00	(215)
Calypte anna	Trochilidae	Trochiliformes	42	12.0	0.05	0.00	(215)
Patagona gigas	Trochilidae	Trochiliformes	39	49.2	0.01	1.00	(216)
Selasphorus rufus	Trochilidae	Trochiliformes	40	13.3	-0.04	1.00	(215)
Selasphorus sasin	Trochilidae	Trochiliformes	40	11.5	-0.01	1.00	(215)
Stellula calliope	Trochilidae	Trochiliformes	40	9.9	0.38	0.64	(215)
Turnix suscitator	Turnicidae	Turniciformes	39	66.4	0.38	0.62	(132)

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